United States
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727

April 2008

The Woody Plant Seed Manual

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Cover photo

The scientific names for the seeds shown on the cover are identified by the key and photo below. Seeds 2 and 7 have had their wings removed by cleaning.

1. Green ash (Fraxinus pennsylvanica Marsh.)
2. Ponderosa pine (Pinus ponderosa P. & C. Lawson)
3. Northern red oak (Quercus rubra L.)
4. Witch hazel (Hamame lis virginiana L.)
5. Service berry (Amelanchier arborea (Michx. F.) Fern.)
6. Persimmon (Diospyros virginiana L.)
7. White fir (Abies concolor (Gord. & Glend.) Lindl. Ex Hildebr.)
8. Tulip poplar (Liriodendron tulipifera L.)

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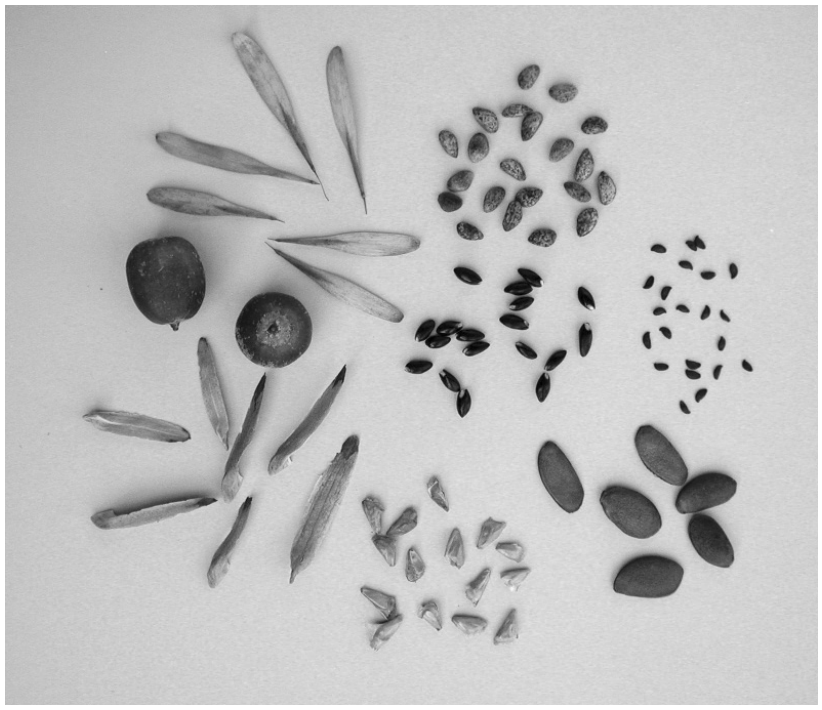

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This book is a revision of the USDA Forest Service's
1974 Agriculture Handbook 450, *Seeds of Woody Plants in the United States*
which was preceded by the USDA Forest Service's
1948 Miscellaneous Publication 654, *Woody-Plant Seed Manual*

Dedication

This handbook on the seeds of woody plants would not be possible if not for the pioneering work of many individuals in past years. They worked without the modern laboratory and information retrieval services that we now routinely use and take for granted. Their early efforts in the first half of the 20th century solved many seed problems and pointed the way for later research on numerous subjects. Without them, our body of knowledge about the seeds of woody plants would not be what it is today. Many contributed, but for their extensive work and leadership, we dedicate this book to the following pioneers:

George S. Allen *Canadian Forestry Service & University of British Columbia*
Henry I. Baldwin *New Hampshire Forestry Department*
Lela V. Barton *Boyce Thompson Institute*
Claude E. Heit *New York Agricultural Experiment Station*
Nikolas T. Mirov *USDA Forest Service*
Paul O. Rudolf *USDA Forest Service*
Charles F. Swingle *USDA Bureau of Plant Industry*
W. R. Van Dersal *USDA Soil Conservation Service*
Philip C. Wakeley *USDA Forest Service*

Acknowledgments

The development and publication of this book was supported by the USDA Forest Service's Research and Development (R&D) and State and Private Forestry (S&PF) National Offices as well as by R&D's Southern and Northeastern Research Stations, which supported Dr. Bonner and Ms. Nisley, respectively. We especially thank Drs. Jerry Sesco and Robert Lewis, Deputy Chiefs (retired) for Research and Development; Dr. Peter Roussopoulus, Director of the Southern Research Station; Dr. Michael T. Rains, Director of the Northeastern Research Station; and Debra Dietzman, Communications Director at the Northeastern Research Station, for their continued financial and personal support.

We also thank John K. Francis (retired after many years at the International Institute of Tropical Forestry), Robert P. Karrfalt (S&PF, Regeneration, Nurseries, and Genetics Resources National Team), Susan E. Meyer (Rocky Mountain Research Station), Peyton W. Owston (retired from the Pacific Northwest Research Station), and John C. Zasada (retired from the (North Central Research Station), the regional coordinators who solicited and organized the authors of the 236 genera.

We are grateful to Dr. Stanley R. Krugman for getting this effort going and sharing his experiences from the production of AH 450, *Seeds of Woody Plants in the United States* (1974). Sharon Friedman, Jacob L. Whitmore, Calvin Bey, Sam Foster, and Marilyn Buford served as our liaisons to the R&D National Office; Karl Dalla Rosa and Hal Brockman were the liaisons to S&PF; and Frank Burch to National Forest Systems. Becky Loth, at the National Seed Laboratory served admirably as the webmaster of our interim website, and Laura Cricco, Phyllis Grinberg, Jean B. Holland, Pamela Huntley, Barbara Johnson, and Kathy McManus, all of the Northeastern Research Station, provided much appreciated administrative and computer support.

Rebecca G. Nisley of the USDA Forest Service, Northeastern Research Station, Hamden, Connecticut, is acknowledged as principle editor for style and grammer.

Contents

Introduction

The first comprehensive handbook on the seeds of trees and shrubs produced by the USDA Forest Service was USDA Misc. Pub. 654, *Woody-Plant Seed Manual*. The manuscript was ready for publication in 1941, but World War II delayed publication until 1948. The boom in tree planting in the 1950s and 1960s created a large demand for seeds and exposed the gaps in our knowledge concerning production and quality of seeds of woody plants in general.

Realization of this condition led to the revision and considerable expansion of the manual, resulting in publication of USDA Agric. Handbk. 450, Seeds of *Woody Plants in the United States*, in 1974. Seed data were presented for about 800 species, varieties, and sub-species in 188 genera, considerable more than the 420 species and 140 genera in the 1948 edition. The 1974 Handbook proved to be very popular both in this country and abroad, leading to five printings and translations in several other languages. More than a quarter-century after its publication, however, numerous advances in tree seed technology have dictated that a new revision is needed; the result is the current volume.

The major audience for this book, as for its two predecessors, is those who are involved in the growing and planting of trees and shrubs. Their involvement can be collection and sale of seeds, production of nursery stock (both bare-root and container), or planting itself. Planting for commercial forest production is the traditional mainstay of tree planting, but planting for wildlife food, watershed protection, urban environmental improvement, ornamental enhancement, wetland mitigation, and carbon sequestration are all on the increase. Ecosystem management, now commonly used in the management of many federal and other governmental forest lands, has decreased the use of planting to regenerate the forests and has increased the role of natural regeneration. Those who apply these practices will find this book useful also in the data on flowering and seed production. Although the book is not intended to be a detailed textbook on seed ecology and physiology, there is sufficient scope and depth to the material included to make it useful to anyone who studies seeds. For additional information on these topics, readers should consult the recent works by Baskin and Baskin (2000) and Farmer (1997).

The organization of this book follows that of the earlier manuals. Part 1 comprises seven chapters that provide general principles on seed biology, genetic improvement, harvesting and conditioning, storage, testing, seed certification, and nursery practices. The chapter on genetic improvement combines two chapters from the 1974 Handbook but does not include the extensive technical information provided in 1974. Genetic improvement of tree and shrub species is now too common and widespread to be covered adequately in a chapter in a seed manual. For complete treatments on this subject, readers are referred to Zobel and Talbert (1984). In the same vein, pollen handling has been dropped; interested readers should refer to the handbook by Bramlett and others (1993). A chapter on nursery practices has been added to the current book, not to serve as a complete technical reference on the subject, but to point out the seed considerations in current nursery operations. Good technical manuals on nursery production of woody plants are those of Duryea and Dougherty (1991), Landis and others (1990–95), Liegel and Venator (1987), and Williams and Hanks (1976). Readers needing additional information on vegetative reproduction should consult Dirr and Heuser (1987).

Part 2 has been expanded to include almost 1,300 taxa in 236 genera. Most of the additions are either tropical species that are grown in Puerto Rico and the Virgin Islands, Hawaii, and the Pacific territories or native species that have increased in value for wildlife or environmental plantings in recent years. Many of these latter are shrubs from the western United States. Information is presented by genus in alphabetical sequence as before. Data have typically been grouped under the following headings: growth habit, occurrence, and use; flowering and fruiting; collection, extraction, and storage of seeds; pregermination treatments; germination tests; and nursery practices. For genera without much information, some of these headings have been combined. In general, the minimum standard for inclusion has been sufficient information to collect and germinate the seeds. Readers with wider interests in tropical species should consult Khullar and others (1991), Ng (1992), Schmidt (2000), Tompsett and Kemp (1996), and Vozzo (2002). An excellent reference on propagation of native plants of the Pacific Northwest is the work by Rose and others (1998).

If authors of the 1974 genus chapters were still working for the Forest Service, they were given the opportunity to write the updated version. Some did, and a number of retired authors also asked to be a part of the revision. If very little rewriting was done because of a dearth of new information about a genus since 1974 (and there were a few of these), names of the 1974 authors remain on the chapters. If new information required extensive rewriting, then the new authors got primary credit. In most cases, 1974 authors who are now deceased also got credit for their contributions. There were 95 authors engaged in the updating of this manual (page 1182), and they all deserve our thanks . Recruitment of authors and coordination of their activities were primarily carried out by a group of regional coordinators: Franklin T. Bonner, John K. Francis, Robert P. Karrfalt, Susan E. Meyer, Peyton Owston, and John C. Zasada.

One major change in the current book deals with nomenclature. A decision was made to use the nomenclature system under development by the USDA Natural Resources Conservation Service as part of a government-wide attempt to adopt standard nomenclature for plants, insects, etc. of North America. This on-line database (PLANTS 2004)

became the primary nomenclature resource. A second resource was needed for numerous non-native plants; for this purpose the USDA Agricultural Research Service Genetic Resources Program (GRIN 1999) was adopted. Other valuable data on plant nomenclature came from *Hortus third*, by the Liberty Hyde Bailey Hortorium at Cornell University (LHBH 1976). Use of these resources for nomenclature resulted in numerous name changes, which may be confusing in some cases. For example, *Libocedrus* (in the 1974 Handbook) is now *Calocedrus*; *Castanopsis* is now *Chrysolepis*. The Table of Contents for part 2 makes this transition easier by listing the old names where appropriate. Some genera have been divided or placed into different families also, and numerous species names have been changed. We have attempted to include all 1974 Handbook names that are now synonyms in the genus chapters. In addition, we have provided the scientific names and authorities for fungi from Farr and others (1989). Scientific names of insects, birds, and wild mammals have been taken from numerous accepted sources.

Another change in the current book is a shift from English to metric units. The metric system of measurements is now the "official" system of the United States, and it is commonly used in most USDA Forest Service publications. To assist users who are not yet comfortable with this, we have included both metric and English values for the most commonly used values in seedling production: number of seeds per unit weight (seeds per pound and seeds per kilogram), and number of seeds to sow per unit of bed area (seeds per square meter and seeds per square foot). A table of conversion factors is again included before the glossary (page 1193).

The vast majority of the line drawings and photographs used in the 1974 Handbook have been used again in this volume. For new species, efforts were made to collect specimens for new photographs that are similar in style and background to those of the 1974 Handbook. In most cases this was done, but samples were not available for every new species. As a result, line drawings from other publications were utilized.

The glossary has been expanded by several dozen terms; a few have been dropped. Others have been altered to reflect current usage. Most terms of seed biology and seed technology have been defined according to the glossary of the IUFRO Working Party S2.01.06 "Seed Problems" (Bonner 1984).

Those who use this book should realize that much new information on seeds of woody plants has appeared in print since the current chapters were finalized. Efforts to improve the utilization of our forest and range resources continue, and new information is constantly discovered and put to use. Like the seed manuals published before, this one will not be the last, although the next revision may be a digital data base. Until another revision takes place, however, genus chapters will be periodically updated with new information on the website that was established during the current revision: *www.nsl.fs.fed.us*.

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Using This Book

Many difficult editorial problems developed as we worked on the Manual; some of them have no one best answer. The first was the metric versus "English" units question. This we resolved as discussed in the Introduction. Ironically, the English don't use these units anymore, having made the switch to metric.

The next one was the problem of using common versus scientific names in the text. Switching back and forth from one to the other in the text (as was done in AH-450) can be very confusing, so we decided to use common names for the species and genera as consistently as possible in the text. All scientific names are provided in the text at first mention or in various tables listing the taxonomy of the genera; the preferred scientific name (according to PLANTS or GRIN 2004) are in listed in boldface.

We have also designated a preferred common name for a species in boldface. Please note that we have chosen these preferred common names with care. Although the other common names in use or found in various references are listed as well, we worked to provide preferred common names that are grammatically logical. Only those common names for a "true" genus stand alone as one word. Common names connected with hyphens or closed up as one word—such as Douglas-fir, mountain-laurel, mountain-ash, Cooke-pine, and Atlantic white-cedar, for example—indicate that these species are not members of the true fir, true laurel, true ash, true pine, or true cedar genera, respectively. The modifiers false mock, and pseudo, also indicate that the species is not a true member of the specified genus. Common names that include a person's name are not in the possessive case; for example, Nuttall horsebrush, Gambel oak, Gardner saltbush, or Joshua tree. However, vernacular names such as eastern virgin's-bower, traveler's-joy, and squaw waterweed seemed best left as they were. Wonderful names like rubber rabbitbrush, tingiringy-gum, messmate stringybark eucalyptus, mountain misery and hearts-a-bustin' provided some much needed humor during the editorial process.

Sometimes the correct or preferred word choice for a procedure or process is controversial or not in common use. For example, many of our authors used the traditional term "stratification"; others used the more current terms "chilling" or even "pre-germination chilling" (which is often shortened to "pre-chilling").

Standard abbreviations for metric and "English" units are used throughout the book. Other words and units are shortened or abbreviated in the tables in the interests of saving space. The following abbreviations were used extensively in the references and text:

United States Government Departments and Agencies: USDA = United States Department of Agriculture, USDC = United States Department of Commerce, USDI = United States Department of the Interior. USDOE = United States Department of Energy. ARS = Agricultural Research Service, CFSTI = Clearinghouse for Federal Scientific and Technical Information, FS = Forest Service, OECD = Organization for Economic Cooperation and Development, NPS = National Park Service, NRCS = National Resources Conservation Service (formerly the SCS), NTIS = National Technical Information Service, SCS = Soil Conservation Service.

Non-governmental agencies and publishers: AOSA = Association of Official Seed Analysts, FAO = Food and Agriculture Organization of the United Nations, FNAEC = Flora of North America Editorial Committee, ISTA = International Seed Testing Association, IUFRO = International Union of Forestry Research Organizations, LHBH = Liberty Hyde Bailey Hortorium, NBV = Nederlandische Boschbouw Vereeniging, WFTSC = Western Forest Tree Seed Council.

Other: avg = average, dbh = diameter at breast height, max = maxiumum, min = minimum, mon = month(s).

In addition to the book, this Manual is being made available as a CD-ROM and can be read, downloaded, and printed at our website, which can be accessed at: *www.nsl.fs.fed.us*. There we plan to set up a system to update and add to the 236 genera that are included in the Manual.

Invasives

We remind our readers that listing species in this book is not necessarily a recommendation to use them! Many species that earlier in the twentieth century were recommended and even planted by various federal and state agencies as erosion control and wildlife plants—multiflora rose, autumn-olive, and Russian-olive, for example—are now considered invasive non-natives and are targets of eradication campaigns! Other plants that have escaped from horticultural uses—broom, burning bush, oriental bittersweet, Japanese barberry, etc.—are also members of this infamous company. Finally, there are invasive plants such as ailanthus and royal paulownia that arrived here accidentally. We sincerely hope that the information contained in this new manual may be of help in efforts to control woody invasives.

Part I Principles and General Methods of Producing and Handling Seeds

Part 2 Specific Handling Methods and Data for 236 Genera

Part I

Principles and General Methods of
Producing and Handling Seeds

Chapter 1

Seed Biology

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Contents

Introduction

Seeds are the principal means of regeneration of most woody plants. They serve as the delivery system for the transfer of genetic materials from one generation to the next. The part of a tree's life cycle that involves seed formation, maturation, dissemination, and germination is a complex—yet fascinating—chain of events, many of which are still poorly understood. Yet some knowledge of these events is necessary for successful collection and utilization of seeds to produce the means for artificial regeneration. This chapter presents basic information on the biology of seeds and how this knowledge can be used in collecting, conditioning, storing, and sowing seeds.

Flowering Plants

The seed-producing organisms of the plant kingdom belong to the division Spermatophyta and are further classified into 2 sub-divisions—Gymnospermae (gymnosperms) and Angiospermae (angiosperms). Gymnosperms are further divided into orders. Only 2 are of interest here: Ginkgoales, which is represented by a single species, ginkgo (*Ginkgo biloba* L.), and Coniferales (conifers), by far the most important group of gymnosperms. The conifers contain 4 families in North America: Pinaceae, Taxodiaceae, Cupressaceae, and Taxaceae. These include economically important genera such as pine *(Pinus* L.), spruce (*Picea* A. Dietr.), sequoia (*Sequoia* Endl.), cypress (*Cupressus* L.), and yew (*Taxus* L.).

Angiosperms are divided into 2 classes—Monocotyledoneae and Dicotyledoneae. Monocotyledonous trees are not very common in North America, but they are represented in this book by the families Palmae (genera *Roystonea* O.F. Cook, *Sabal* Adans., and *Washingtonia* H. Wendl.) and Liliaceae (genus *Yucca* L.). Dicotyledonous species number over 30 families in North America and are by far the largest class of woody plants. This class includes such common genera as maple (*Acer* L.), acacia (*Acacia* Mill.), birch (*Betula* L.), ash (*Fraxinus* L.), holly (*Ilex* L.), oak (*Quercus* L.), and blueberry (*Vaccinium* L.).

Reproductive Cycles

The reproductive cycles of flowering plants begin with initiation of reproductive buds and end with maturation of the seeds. There are 3 types of reproductive cycles that have been recognized in trees of the temperate zone (Owens and Blake 1985).

The 2-year cycle is the most common type. Reproductive buds form late in the growing season of the first year; pollination occurs in the next spring, closely followed by fertilization. The embryo grows rapidly, and seeds are mature by summer or early fall of the second year. This is the cycle of most gymnosperms and angiosperms of North America. Detailed studies of individual species provide good descriptions of the cycle in birch (Macdonald and Mothersill 1987), larch (*Larix* Mill.) (Owens and Molder 1979), spruce (Owens and others 1987), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Owens and Smith 1964; Owens and others 1991a), thuja (*Thuja* L.) (Owens and Molder 1984a), and fir (*Abies* Mill.) (Owens and Molder 1977b).

The second type of reproductive cycle is the 3-year cycle that is common to most species of pines (Owens and Blake 1985). Buds form in late summer or early fall as before, followed by pollination the following spring. Pollen tube and ovule development then stop in mid- or late-summer and resume the following spring. Fertilization occurs that spring, and the seeds mature in the fall. Descriptive work on pines includes western white pine (*Pinus monticola* Dougl. ex D. Don) (Owens and Molder 1977a) and lodgepole pine (*P. contorta* Dougl. ex Loud.) (Owens and Molder 1984b). Other gymnosperms in this book that exhibit this type of reproductive cycle include araucaria (*Araucaria* Juss.) and sciadopitys (*Sciadopitys* Sieb. & Zucc.). Among angiosperms of North America, the 3-year reproductive cycle occurs only in the black oak group (Erythrobalanus) of oak (Mogensen 1965). Like that in pine, fertilization in black oak does not occur until 13 months after pollination.

The third type of reproductive cycle, found in members of the Cupressaceae family, is somewhat similar to the second type. The primary difference is that fertilization occurs within a few weeks of pollination during the second year, with embryo development going into a dormant phase in late summer or early fall (Owens and Blake 1985). This type of cycle has been described for Alaska-cedar *(Chamaecyparis nootkatensis* (D. Don) Spach) (Owens and Molder 1984a) and probably occurs in some juniper (*Juniperus* L.) species (Johnsen and Alexander 1974).

Flowering

Botanically speaking, angiosperms produce true flowers, but gymnosperms do not. Gymnosperm reproductive structures are actually strobili, but for this discussion, they will be considered flowers in the broad sense. All trees propagated from seeds pass through a period of juvenility before they acquire the capability of flowering and producing seeds of their own. The length of this juvenile period is extremely

varied among species, ranging from as little as 3 years for *Pinus gieggii Engelm*. (Lopez-Upton and Donahue 1995), to 40 years for sugar pine (*P. lambertiana* Dougl.) (Krugman and Jenkinson 1974). The majority of tree species in the temperate zone, however, begin flowering at the age of 10 to 15 and produce significant seedcrops by the age of 25 to 30 (Owens and others 1991b). Woody shrubs generally flower and fruit at earlier ages. Extensive data on seed-bearing ages are presented for all species in part 2 of this book.

Among species with unisexual flowers (flowers of one sex only, either staminate or pistillate), flowers of one sex may be produced long before flowers of the other sex. For example, Scots pine (*P. sylvestris* L.) may produce female strobili at age 5 to 7, but no male strobili until age 10 to 15 (Matthews 1970). Many other pines are the same. The extent of this phenomenon in angiosperms is not known, but it does occur in some species, for example, yellow birch (*Betula alleghaniensis* Britton) (Erdmann 1990).

The length of the juvenile period can be affected by many factors other than age. Physical size of the plant seems to be important in some cases (Hackett 1985; Schmidtling 1969). Genetic differences are often obvious in even-aged plantations where spacing and tree size are equal, and there is experimental evidence to confirm the genetic effect in a few species (Sedgley and Griffin 1989). Furthermore, tree improvement programs have demonstrated that selections for early flowering within species have the potential to produce clones with precocious flowering traits (Krugman and others 1974).

Initiation

In numerous woody plants, flower initiation and development is a lengthy process extending over several months. During this period, environmental factors and the internal physiological condition of the trees interact to produce the flower crops. The effects of some environmental factors have been observed through the years, and these relationships have been used to influence flowering and seed production in some species (see below). The internal factors involved are still poorly understood, as are their interactions with the environment.

Phenology. Flower buds on most trees and shrubs of the temperate regions are initiated late in the growing season of the year preceding flowering (table 1). In species with unisexual flowers, male flowers may start earlier and differentiate more rapidly as well. Flowers may bloom from late winter to fall, depending on the species and the location. In temperate trees, flowering is primarily seasonal, that is, production only occurs in certain times of the year. Most species bloom in the spring, but there are numerous exceptions to this rule. Witch-hazel (*Hamamelis virginiana* L.) flowers from September to mid-November; California-laurel (*Umbellularia californica* (Hook & Arn.) Nutt.) from December to May; September elm (*Ulmus serotina* Sarg.) *in* September; and deodar cedar (*Cedrus deodara* (Roxb.) Loud.) in September to October. The times reported in this book for flowering are typically expressed as a range of several months to allow for the latitudinal and elevational differences throughout the range of a given species. Local variations in weather may also affect the time of flowering from year to year on the same tree.

Table 1–Chapter 1, Seed Biology: times of flower initiation in selected species as determined from microscopic examination of buds

Species	Location	Time of initiation	
		Male	Female
Acer pseudoplatanus L.	Indiana	June	June
Betula papyrifera Marsh.	NW Ontario	Early May	Late June–early July
Carya illinoensis (Wangenh.) K. Koch	Georgia	May	Mar
Larix occidentalis Nutt.	British Columbia	June	June
Picea glauca (Moench) Voss	Ontario	Early Aug	Early Aug
Pinus elliottii Engelm.	Florida	Late June–July	Late Aug
P. monticola Dougl. ex D. Don	British Columbia	Late June–Aug	Mid-Aug
Populus tremuloides Michx.	Connecticut	Early July	Late June
Pseudotsuga menziesii (Mirb.) Franco	Oregon	Apr	Apr
Taxodium distichum (L.) Rich.	Florida	—	Aug
Thuja plicata Donn ex D. Don	British Columbia	Early June	July
Tsuga heterophylla (Raf.) Sarg.	British Columbia	June	July

Sources: Anderson and Guard (1964), Fraser (1962), Lester (1963), Macdonald and Mothersill (1987), Mergen and Koerting (1957), Owens and Molder (1974, 1977, 1979), Owens and Pharis (1971), Owens and Smith (1964), Takaso and Tomlinson (1990), Wetzstein and Sparks (1983, 1984).

In tropical species, the time period between initiation of floral buds and anthesis is relatively short, and flowering may occur once, twice, or several times a year or even continuously throughout the year (Kramer and Kozlowski 1979; Sedgley and Griffin 1989). Some species have 2 periods of flowering per year, 1 considerably heavier than the other. The irregularity of flowering is more evident in moist tropical forests, where seasonal changes are absent (or subtle), than in dry tropical forests (Willan 1985). Flowering patterns in dry tropical forests are usually related to rainfall patterns.

Influencing factors. The natural variations in flowering that are obvious to even casual observers are evidence that flowering must be affected by many factors. These factors can be either environmental or physiological (internal) in nature, and they all interact to influence the expression of flowering in woody plants.

Temperature. High temperatures during summer enhance formation of flower buds in many species of the temperate regions (Sedgley and Griffin 1989). Most flowering studies that show this effect have correlated weather records with records of fruit and seed production (Owens and Blake 1985), but the physiological reasons for this effect have not been elucidated. Most of the examples are of conifers: Norway spruce (*Picea abies* (L.) Karst.) (Lindgren and others 1977), Douglas-fir (Lowry 1966), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) (Maguire 1956), and red pine (*P. resinosa* Ait.) (Lester 1963). Among hardwoods, European beech (*Fagus sylvatica* L.) has shown similar responses (Matthews 1955). High summer temperatures usually accompany drought conditions, however, and it is difficult to say which is the most important (see below).

There are important low temperature effects also, but they occur in the spring following bud initiation. For some species in the warmer portion of the temperate regions and for subtropical species, there is a moderate cold requirement for flowering. Examples are pecan (*Carya illinoensis* (Wangenh.) K. Koch) (Amling and Amling 1983) and olive (*Olea europaea* L.) (Hackett and Hartmann 1967). Another low temperature effect that is familiar to most people is the killing of flowers by late frosts in the spring. Citrus and other fruit crops are well-known for this, especially in the South, but native trees and shrubs suffer the same fate. Complete seedcrop failures may only occur in local stands or microsites, however, as some trees may always be protected from the cold or exposed to winds that prevent frost formation on the flowers.

Light. Unlike flowering in annuals, flowering in most woody perennials does not appear to be under strict photoperiodic control (Sedgley and Griffin 1989). Mirov (1956) and Lanner (1963) concluded that flowering in pines was not affected by day length. Other studies suggest that photoperiod may have some control on the sex of reproductive buds (Owens and Blake 1985). Experimental evidence of some type of control does exist, however, so it may be that the effect is difficult to define in woody plants. In azaleas (*Rhododendron* L.), for example, flower initiation was accelerated by short days of 8 hours light (Criley 1969), whereas flowering in some varieties of apple (*Malus* Mill.) was better under long days (14 hours) than short days (8 hours) (Tromp 1984). In western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), pollen cone buds were favored by increasing daylengths, whereas seed cone buds were favored by decreasing daylengths (Owens and Molder 1974). In coniferous species where the photoperiod effect is different for male and female flower buds, there is a natural difference between the sexes in time of bud differentiation. In species without this difference, there may be an indirect effect of photoperiod through cessation of shoot elongation, which usually coincides with reproductive bud differentiation (Owens and Blake 1985). Clearly, photoperiodic effects on flower initiation for any species cannot be understood without knowledge of the timing of the reproductive cycle in that species.

Light intensity has a more demonstrable effect on flowering in trees than photoperiod. Open-grown trees with full crowns have more flowers than trees with shaded crowns, and this is not just an effect of more sites for bud formation on open-grown trees. Any collector of tree seeds can testify that, in northern latitudes, most of the crop will be found on the southern and western portions of open-grown crowns. Increased light intensity (or at least increased sunshine) is also reported to increase flowering in tropical trees (Nanda 1962; Ng 1977).

There are conflicting reports about the effects of light intensity on sexual differentiation. Higher light intensities of open stands were found to favor female flowers in walnuts (*Juglans* L.) (Ryugo and others 1980) and male flowers in striped maple *(Acer pensylvanicum* L.) (Hibbs and Fischer 1979).

Moisture. There have been many studies that showed increased flowering in trees subjected to moisture stress in late summer (Owens and Blake 1985; Sedgley and Griffin 1989). It is extremely difficult to separate the effects of temperature and light intensity from those of moisture stress, however, as the 3 conditions typically occur together. After careful examination of published data, Owens and Blake (1985) concluded that there was little evidence that moisture stress during the period of flower bud initiation led directly to increased flower production.

There are other effects of moisture besides drought, of course. A plentiful supply of moisture during peak growth periods will indirectly benefit flowering through increased shoot growth and crown development. Excess moisture during pollination, especially for wind-pollinated species, can be a problem, but this effect will be discussed later in this chapter.

Nutrition. In general, a favorable nutrient status is required for woody plants to produce good seedcrops. Many studies have shown increased seed production after the application of fertilizers, especially nitrogen and phosphorus, but the precise roles of these elements in flowering and seed production are not known (Owens and Blake 1985). Abundant flowering in fruit trees has long been associated with a high carbon to nitrogen ratio in the shoot tissues (Kramer and Kozlowski 1979). Although this condition may be explained in term of carbon partitioning within the plant, the controlling factors are still unknown. Fertilization to increase flowering and seed production may have 2 effects. There can be a short-term effect of direct impact on flower production and fruit/seed size, and there can be a long-term effect of more buds sites just by increasing crown size.

Physiology. The physiological status of woody plants is the most important factor of all in flower initiation, yet it is the factor that is most difficult to influence. Early plant physiologists searched for a single hormone that could turn flowering on or off (Kramer and Kozlowski 1979) but were not successful. Current knowledge suggests that the balance between gibberellins, cytokinins, and other natural bioregulators controls the change from juvenile to mature stage and also the amount of flowering in the mature stage. The weak link in this reasoning is that most of the evidence comes from results of experiments in which chemicals were applied to plants externally (Sedgley and Griffin 1989). The strong point of these experiments is that flowering really can be stimulated in a host of species (primarily gymnosperms) by chemical application. A considerable amount of research remains to be done before we can understand the internal controls on the flowering process in woody plants.

Manipulation of flowering. When speaking of manipulating the flowering process in trees, we must distinguish between forcing trees to flower while they are still in the juvenile phase, or treating trees that are already in the flowering phase to produce more flowers. In the first case, the interest is usually in speeding breeding programs. In the second, increased seed production for artificial regeneration programs is usually the goal.

Juvenile phase. Precocious flowering in conifers has been produced mainly with water-based foliar sprays of gibberellins (GA). A detailed review by Owens and Blake (1985) points out that GA_3 has been most successful with members of the Cupressaceae and Taxodiaceae, whereas non-polar $GA_{4/7}$ mixtures have provided successes with the Pineaceae. In Cupressaceae and Taxodiaceae, treatment with GA_3 alone is usually successful in stimulating flower bud production; this can be seen in the following genera: "cedar" (*Chamaecyparis* Spach.), cryptomeria (*Cryptomeria* D. Don), cypress, sequoia, baldcypress (*Taxodium* Rich.), and thuja (Owens and Blake 1985). Manipulation of other cultural treatments, such as drought, fertilization, or daylength, is not really necessary unless a change in the proportion of pollen to seed cones is the goal. For example, treatment of western redcedar (*Thuja plicata* Donn ex D. Don) seedlings with GA_3 under short days favored initiation of seed cone buds, whereas treatment under long days favored initiation pollen cone buds (Pharis and Morf 1972; Pharis and others 1969).

In Pineaceae, GA treatments are often combined with cultural treatments, because there is usually a strong synergistic effect. Precocious flowering has been induced in seedlings of jack pine (*Pinus banksiana* Lamb.) with a combination of moisture stress and $GA_{4/7}$ (Cecich 1981; Riemenschneider 1985) and in Douglas-fir seedlings with a combination of girdling and the same gibberellin treatment (Pharis and others 1980). Other Pineaceae genera for which success has been reported are larch, spruce, and hemlock (Owens and Blake 1985), although these results have generally not been as successful as those for Cupressaceae and Taxodiaceae. Other factors, such as timing of treatments, developmental stage of the plants, and method of application can also have significant effects. In loblolly pine, a combination of low temperatures and short photoperiods has been used to stimulate formation of strobili on potted stock as young as 3 years (Greenwood 1978). It should also be noted that the mechanisms for these treatment effects are still unknown, and much basic research is needed to fully understand them.

Mature phase. Stimulation of flower initiation in sexually mature trees is commonly practiced in seed orchards to increase seed production. Fertilization has been the most common and most successful treatment used. Owens and Blake (1985) summarized fertilizer tests on over 20 species of trees and found, that while many were successful, others produced variable results. Interactions with other factors, such as timing, method of application, rate, formulation, and moisture conditions following treatment have significant

effects (Schmidtling 1983). Most of the attention has been on nitrogen and phosphorus, but many trials used complete fertilizers. Current practice is to base fertilization levels on soil analyses of individual orchards. Typical fertilization prescriptions for seed orchards of southern pines have been annual application of about 400 kg/ha of nitrogen, 80 kg/ha of potassium, 40 kg/ha of phosphorus, and 50 kg/ha of magnesium (Zobel and Talbert 1984).

Another treatment widely used is manipulation of soil moisture levels. Irrigation of seed orchards in conjunction with fertilization is one practice, and in most cases the response is positive. Moisture stress has also been used, although this sort of treatment is difficult to apply in the field. In seed orchards, moisture stress has been created by root pruning the orchard trees to temporarily disrupt moisture uptake. The effect of moisture stress may be through its effect on carbon allocation in the tree, although other factors are sure to be involved. Ebell (1970) found that moisture stress increased the level of amino acids in Douglas-fir trees just as application of nitrate nitrogen did, and that both induced cone formation. When water was supplied to the trees, protein synthesis increased but cone formation did not.

Girdling and other wounding treatments have been popular as a means of increasing production in fruit trees. The theory behind these actions was that girdling prevented translocation of carbohydrates to the roots, thus raising the C to N ratio in the crown, which increased fruit production. Recent experimental evidence provides weak, if any, support for this theory, and a good explanation for the wounding effect is still lacking (Owens and Blake 1985). Despite the uncertainty, girdling is still used in seed orchards of Douglas-fir and other conifers.

Timing of wounding treatments seems to be important, at least in some species. Ebell (1971) girdled Douglas-fir trees at weekly intervals from April to mid-July. The optimal time of treatment was about 1 month before the vegetative buds burst. Many other studies of this nature have not controlled time of treatment as well, and timing effects cannot be determined (Owens and Blake 1985).

Thinning of seed stands is another commonly used practice to increase flowering. Thinning brings about increased light intensity to the crowns (see previous section) and less competition for moisture and nutrients. As one might expect, there is a delay before treatments are usually effective, ranging from 1 to 4 years (Allen 1953; Owens and Blake 1985). Flower and fruit production increases attributed to thinning have been documented for black walnut (*Juglans nigra* L.) (Ponder 1979), hoop-pine (*Araucaria cunninghamia* Sweet) (Florence and McWilliam 1956), loblolly pine (Bilan 1960; Allen and Trousdell 1961), longleaf pine *(Pinus palustri*s Mill.) (Allen 1953), and other conifers. Fertilization at the time of thinning enhanced cone production in Japanese larch (*Larix leptolepis* (Sieb. & Zucc.) Gord.) and Japanese red (*Pinus densiflora* Sieb. & Zucc.) (Asakawa and Fujita 1966) and ponderosa pines (Heidmann and others 1979).

Much less is known about stimulation of flowering in tropical and subtropical tree species. Many of the same treatments used on temperate species have been tested in the tropics also, and, as one would expect, results have not been consistent. Carbohydrate accumulation and an interruption of vegetative growth of the tree are the factors that have been most frequently associated with increased flower initiation (Dick 1995).

Structure and Development

Flower primordia are inconspicuous at first and rarely can be identified without careful microscopic examination of the tissues. Initially, there are no external features that serve to distinguish flower buds from vegetative buds. As flower buds grow and develop, they become distinguishable from vegetative buds by their general appearance and location. Variation among species is significant, but flower buds usually become wider and longer as they grow and may differ in color and shape from vegetative buds. In some species, such as flowering dogwood (*Cornus florida* L.), flower buds are distinctive in shape and large enough by late summer (July to August) for easy identification, thus providing a preliminary estimate of next year's flower crop.

Flower buds enlarge greatly as the flowering season nears and conditions become favorable for bud growth. Individual flowers of many species open rapidly once flowering begins. This is especially true if air temperatures are unseasonably high. Conversely, colder than normal temperatures will delay flower opening. Flower opening usually does not occur simultaneously over an entire inflorescence, over an entire tree, or even among plants of the same species in a stand, but it may be in progress for many days at any one location. The evolution of flowering in this way in wild populations is a distinct advantage in perpetuation of the species, as short-term events that destroy flowers or prevent pollination cannot destroy the entire crop.

Flowers of woody plants come in many different shapes, colors, odors, and sizes. They may be minute and inconspicuous, like the flowers of thuja, or they may be large, showy, and fragrant like the 1-foot wide, white, perfect flowers of bigleaf magnolia (*Magnolia macrophylla* Michx.) (Brown

and Kirkman 1990). The flowers of many species are sufficiently attractive to create a demand for their use in ornamental plantings. Well-known ornamental trees include serviceberries (*Amelanchier* Medic.), redbud (*Cercis canadensis* L.), dogwoods (*Cornus* L.), mountain-laurel (*Kalmia latifolia* L.), magnolias (*Magnolia* L.), and azaleas. Some woody vines included in this book are also used extensively for ornamental plantings because of their showy flowers: trumpet creeper (*Campsis radicans* (L.) Seem. ex Bureau), clematis *(Clematis* L.), and honeysuckle (*Lonicera* L.).

An angiosperm flower (figure 1) may have some or all of the following parts: a stalk or peduncle, a receptacle, a calyx composed of sepals, a corolla composed of petals, stamens with anthers and filaments, and 1 or more pistils, each with a stigma, style, and ovary. A flower is complete when it has a calyx, corolla, functional stamens, and 1 or more functional pistils. It may be considered incomplete when 1 or more of these parts is lacking or nonfunctional. Though lacking a calyx or corolla, a flower is perfect (or bisexual) when it has both stamens and pistil, and unisexual when only one or the other is present and functional. The calyx and corolla may be considered accessory parts, but stamens (which produce pollen) and the pistil or pistils (which contain the ovaries) are mandatory for normal seed production. The primary function of the calyx and corolla, both of which are modified leaves, is to enfold and protect the stamens and pistils while they mature. For entomophilous species, the color, odor, or nectar supply of the unfolded calyx and corolla play a role in attracting of the insects that are needed for pollination.

Many angiosperm trees and shrubs produce complete flowers, for example, cherry (*Prunus* L.), locust (*Robinia* L.), magnolia, and tuliptree (*Liriodendron tulipifera* L.). Other species bear incomplete flowers that lack a calyx as in some ashes, a corolla in silktassel (*Garrya* Dougl. ex Lindl.), or both calyx and corolla in willows (*Salix* L.) and hazels (*Corylus* L.). Some species bear separate male and female flowers on the same plant (monoecious); examples are alders (*Alnus* Mill.), birches, and oaks. Other species bear these separate flowers on different plants (dioecious); examples are maple and holly. In some species all floral parts are present but instead of being distinctly separate, some are more or less united, for example, sepals in viburnums (*Viburnum* L.), petals in catalpas (*Catalpa* Scop.), and pistils in azaleas (*Rhododendron*).

Some genera of angiosperms have polygamous floral habits. Bisexual as well as unisexual staminate and pistillate flowers may occur on the same tree, as in the hackberries (*Celtis* L.). This condition is defined as polygamo-monoecious, although the trees are functionally monoecious. If bisexual flowers occur with only staminate or pistillate flowers on separate trees, as in buckthorn (*Rhamnus* L.), the condition is defined as polygamo-dioecious, although the plant is functionally dioecious. In a few species, there are several flowering patterns. Silver maple (*Acer saccharinum* L.) and striped maple, for example, can be monoecious, dioecious, or sometimes polygamo-monoecious (Gabriel 1990; Hibbs and Fischer 1979).

Most coniferous gymnosperms are monoecious, but other genera—juniper and torreya (*Torreya* Arn.)—are dioecious. Coniferous gymnosperm flowers are strobili (small

Figure 1—Chapter 1, Seed Biology: structure of a complete angiosperm flower (from Krugman and others 1974).

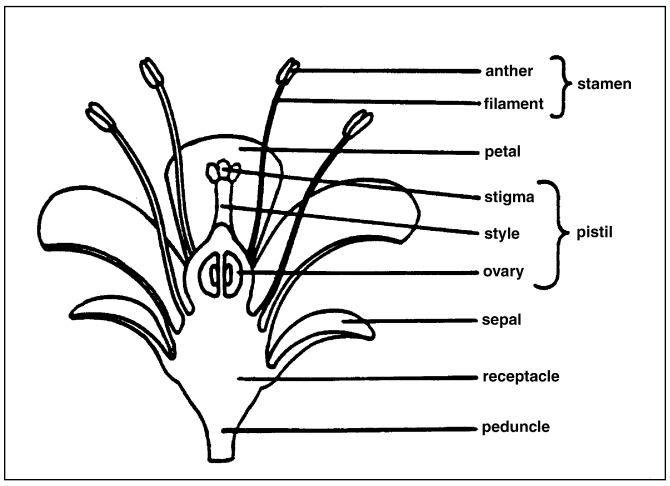
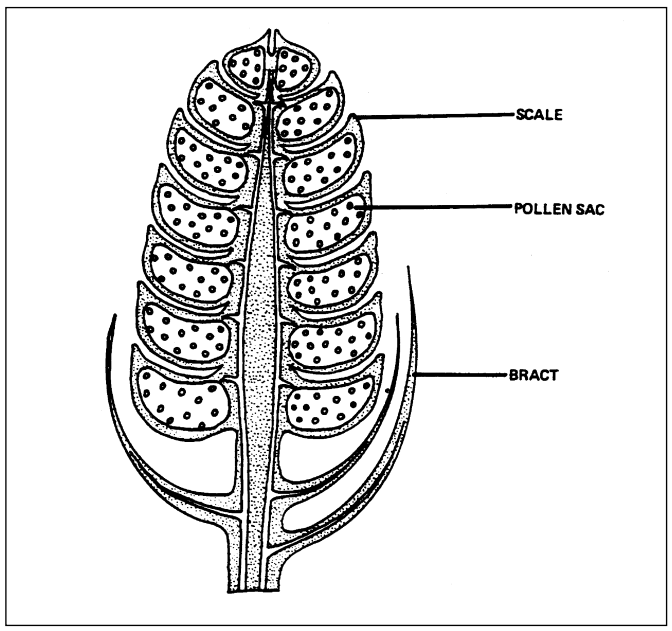


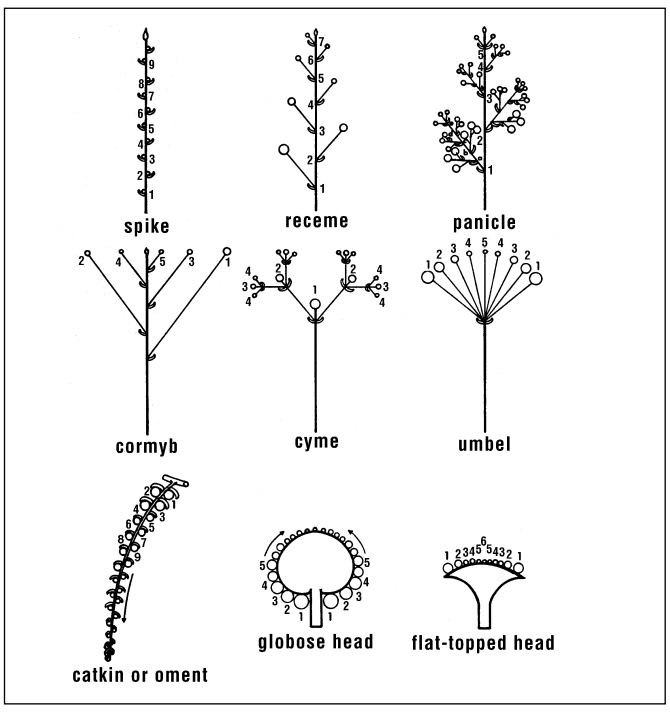
Figure 2—Chapter 1, Seed Biology: structure of a staminate flower typical of coniferous gymnosperms (Coniferales) (from Krugman and others 1974).



cones) without calyx, corolla, stamens, or pistils. These strobili characteristically have a central axis bearing a few to numerous distinctly shaped scales and bracts (figure 2). In staminate strobili, each scale (microsporophyll) bears 2 pollen sacs (microsporangia) on its lower surface. In ovulate strobili, 2 inverted ovules (megasporangia) form on the upper surface of each ovulate scale. Staminate strobili—often bright shades of yellow, red, or purple when fully developed—are numerous, short-lived, and highly productive of pollen. The less numerous, but infrequently colorful, ovulate strobili develop into woody, relatively durable structures (cones) that contain a varying number of seeds.

Coniferous strobili are similarly arranged around the central axes of cones (figure 2). Flowers of angiosperms, on the other hand, have varied and distinctive floral arrangements. Some species bear a single flower on each peduncle, for example, magnolia and tuliptree, but most others bear flowers in groups or clusters called inflorescences. The general structure of an inflorescence is a central stem, with or without branches, on which flowers, with or without pedicels, develop. Examples of the common forms of inflorescences of woody plants (figure 3) include catkin (ament), birch; raceme, serviceberry; spike, walnut (pistillate); head, sycamore (*Platanus* L.); cyme, viburnum; panicle, sumac (*Rhus* L.); and umbel, plum.

Figure 3—Chapter 1, Seed Biology: common forms of flower clusters, with individual flowers represented by circle and the order in which the flowers develop shown by numbers (#1 indicates the position of the oldest flower in the inflorescence) (from Krugman and others 1974).



On many woody plants, the flowers appear throughout the crown, but in some monoecious species, staminate or ovulate flowers tend to predominate or be restricted to certain parts of the crown. For example, in most pines, ovulate strobili are most numerous in the upper crown, whereas staminate strobili predominate in the lower crown. In true firs, ovulate strobili are found primarily on the tips of the uppermost branches, and staminate strobili are found below them, but still in the mid- to upper crown region.

In some species, flowering may occur on older branches or on the trunk itself. This phenomenon, called cauliflory, occurs frequently in tropical species, but rarely in temperate ones. Of the temperate woody plants in this book, redbud is the only genus for which cauliflory has been reported (Owens and Ewers 1991).

Pollination

Seed initiation by successful union of male and female reproductive elements is the culminating event in flowering. This union depends on 2 key steps: pollination and fertilization. Pollination is the transfer of male pollen grains from stamens in angiosperms, or staminate cones in gymnosperms, to pistils in angiosperms, or ovulate cones in gymnosperms. Fertilization occurs when subsequent pollen tube growth allows union of the sperm cell with the egg cell in the ovule. A detailed discussion of these processes is beyond the scope of this book, and the following sections will provide only brief descriptions. For additional information, readers should see the reviews by Owens and Blake (1985), Sedgley and Griffin (1989), and Marshall and Grace (1992).

Pollen grain development. Pollen grains are formed within structures called pollen sacs. In angiosperms, these sacs are found in the anthers at the tips of the stamens. Each pollen grain contains a tube cell and a generative cell, defined as the binucleate stage, and most angiosperm pollen is shed at this stage of development. The generative cell divides to form 2 male gametes, usually after shedding and germination, but before shedding in some species (Owens and Blake 1985). Pollen tube growth in most species occurs quickly after the trinucleate stage is reached. Detailed descriptions of this part of the sexual life cycle of angiosperm trees is very limited.

In gymnosperms, the pollen sacs are formed beneath each cone scale in the staminate cones. These sacs are initiated before winter in all conifers of the north temperate zone, but the rates of development after initiation vary greatly among species (Owens and Blake 1985). In the Pinaceae, the microspore division produces a large tube cell, a smaller generative cell, and 2 prothallial cells with no known function. In the Cupressaceae, Taxodiaceae, and Taxaceae, the pollen grains are binucleate, lacking prothallial cells (Owens and Blake 1985).

Pollen grains of trees are extremely varied in shape and size. Some examples of shape are spherical (hickory, *Carya* Nutt; and juniper), elongated (maple and Douglas-fir), triangular *(Eucalyptus* L'Herit.), and sac-like (pine and spruce). A few genera exhibit more than one shape: spherical or elongated (birch and mountain-ash, *Sorbus*) and triangular or tetrahedral (silk-oak, *Grevillea robusta* A. Cunn.). Pollen grains may range in size from 3 to 300 μm. Within a given genus, grain sizes are fairly uniform. Some reported ranges are 10 to 30 μm for birch and 70 to 103 μm for true firs (Sedgley and Griffin 1989). The outer walls of pollen grains (exines) are relatively thick and very resistent to degradation by external agents. The exine surfaces are furrowed and sculptured, which may play some role in pollination.

Pollen dispersal. Dispersal of tree pollen is primarily by wind (anemophily) and insects (entomophily), although birds (ornithophily) and animals (therophily) can also be dispersal agents, especially in tropical genera such as albizia, *Albizia* Durz.; bauhinia, *Bauhinia* L.; eucalyptus, and silk-oak (Sedgley and Griffin 1989). Pollen dispersal in conifers is mainly by wind, which is also the primary agent for angiosperms that lack floral parts (ash; casuarina, *Casuarina* L. ex Adans; sycamore; and elm, *Ulmus* L.), particularly if the flowers are catkins or aments (birch, hickory, walnut, oak, willow, and poplar, *Populus* L.). Species with brightly colored or scented flowers, such as dogwood, magnolia, apple, and tuliptree, often have heavy or sticky pollen grains. Their pollinating agents are almost always insects. Some species, notably maple, willow, and mulberry (*Morus* L.), are pollinated both by wind and by insects (Sedgley and Griffin 1989). Quite a few shrubs and understory plants depend on entomophilous pollination, as their positions within the stand preclude good wind movement. Some examples of this are azalea, mountain-laurel, and California-laurel.

Pollen dispersal must occur at the time of receptivity by the stigma of the pistil for pollination to be successful. This required synchronization occurs in many cases within and among perfect flowers or among monoecious flowers on a single plant. In other species, male and female organs mature at different times, creating a condition called dichogamy, in which pollen may be supplied by different perfect flowers on the same tree or by unisexual flowers from different trees. Dichogamy is strong in magnolia (Thien 1974). In southern magnolia (*Magnolia grandiflora* L.), stigmas are receptive in the morning before pollen is released (anthesis). The flowers close in the evening and reopen the following day. The stigmas are no longer receptive, but the anthers will now release pollen, which will only be "successful" in other flowers. Among dioecious species, dichogamy clearly will reduce self-pollination and encourage cross-pollination, thus promoting greater genetic diversity.

Weather conditions have a strong influence on pollination. Dry, warm weather will usually enhance pollen dispersal by wind. If winds are excessively dry, however, pollen of white oaks may be shed before maturity (Sharp and Chisman 1961). In contrast, rain or high humidity greatly hinders anemophilous pollination. Complete seedcrop failures can occur locally if heavy rains dominate the weather when anthesis is occurring. Late spring freezes can also kill staminate flowers and cones and prevent any dissemination of pollen in some species. Entomophilous pollination is not as greatly affected by the weather, but low temperatures and heavy rains will curtail the activities of insect pollinators.

Anemophilous pollen dispersal depends primarily on weather factors and stand structures. Under near-calm conditions, pollen of many pines and hardwoods can be expected to disperse only a few dozen meters (Sedgley and Griffin 1989), but in turbulent wind conditions, dispersal of pine pollen for 1 km and more is likely (Griffin 1980; Lanner 1966). Entomophilous pollen dispersal distances are not precisely known but probably are considerably less than anemophilous dispersals.

Pollen viability and flower receptivity. For pollination to be successful, the pollen grains must remain viable until they reach the stigma, and the female flowers or cones must be receptive when the pollen arrives. Not much is known about the length of viability of pollen in nature; some pollens survive for only hours and others for weeks. The pollen of many species, notably conifers, can be carefully dried to below 10% moisture content and stored below freezing for several years (Copes 1987; Wang and others 1993). Like pollen viability, flower receptivity varies greatly among species. For angiosperms, the receptive period for an individual flower may last for less than a day, as noted earlier for southern magnolia (Thien 1974), or it may continue for up to 10 days in some cherries (Stösser and Anvari 1982). Among gymnosperms, the receptive period ranges from less than a day in japanese larch, *Larix kaempferi* (Lam.) Carr. (Villar and others 1984) to 2 weeks or more in true firs, hemlocks, and pines (Owens and Blake 1985).

Pollination in angiosperms. When pollen grains reach the stigma of a receptive flower and germinate, the pollination process is set into motion. Pollen grains are captured on the stigmas due to their own sticky surface characteristics or the nature of the stigma surface. The stigma surface is naturally dry in some genera (maple; dogwood; sweetgum, *Liquidambar* L.; elderberry, *Sambucus* L.; and basswood, *Tilia* L.) and wet in others (hickory, eucalyptus, holly, plum, and serviceberry) (Sedgley and Griffin 1989), but there are no strong correlations between surface condition and other aspects of pollination and fertilization. Some have suggested that pollen germination rates are quicker on dry stigmas, but evidence for this is weak (Owens 1992). Germination is rapid, usually occurring within a few hours (Owens 1992), and is temperature-dependent. Luza and oth-

ers (1987) reported that pollen of English (*Juglans regia* L.) and black walnuts would not germinate at 40 °C or below 14 °C; maximum germination occurred at 28 to 32 °C.

Many of the pollen grains that reach stigmas may not germinate, and many that do will abort in the early stages of tube growth. Germinating grains form a microscopic tube that grows between the cell walls of the stigma and style toward an ovule. Usually only 1 pollen tube will penetrate an ovule; the others abort soon after germination.

Pollination in gymnosperms. In gymnosperms, the scales of the ovulate cones spread apart when the cones are receptive, and small drops of extracellular secretion (pollination drops) are formed. Pollen grains drift between the scales and are "captured" by the drops. Entry into the ovule through the micropyle is accomplished via these drops. The process differs among the gymnosperm families; Cupressaceae, Taxodiaceae, and Taxaceae have one mechanism, and Pinaceae another. These difference have been described in detail by Owens and Blake (1985) and Sedgley and Griffin (1989).

Fertilization

Fertilization occurs when the pollen tube enters the ovule and "delivers" the 2 sperm cells (gametes). In angiosperms, a typical ovule contains within its matured embryo sac 8 separate cells: an egg cell, 2 synergid cells, 2 polar cells, and 3 antipodal cells (figure 4). In the actual process of fertilization, 1 sperm (N) unites with the egg cell (N) to form a zygote that develops into the embryo (2N) of the seed. Generally, only 1 embryo develops, but multiple embryos are not uncommon in some species. The other sperm (N) unites with the 2 polar cells located near the center of the embryo sac, forming what will become the endosperm (3N). This process is commonly described as double fertilization. Endosperm tissue is triploid (3N) and functions as a source of nutrients available to the growing embryo and, in some species, to the young seedling that develops from the embryo at germination. As embryo and endosperm develop, the synergid and antipodal cells disintegrate.

Ovule and embryo sac formation in angiosperms may precede, occur synchronously with, or follow pollination. In tuliptree, the embryo sac is ready for fertilization by the time pollen is mature (Kaeiser and Boyce 1962). In sweetgum, sac development occurs 1 to 3 weeks after pollination (Schmitt 1966). Ovule development in oaks is extremely slow. It begins about 1 month after pollination in the white oak group, and 13 months afterwards in the black oak group (Stairs 1964). In all cases, development proceeds rapidly once it is underway. These time differences are also reflected in the elapsed times from pollination to fertilization. Most angiosperms require approximately 24 hours or less (Sedgley and Griffin 1989), but others require much longer: 60 hours in English walnut (Luza and others 1987), 8 to 9 days in *Rhododendron nuttallii* T.W. Booth (Palser and others 1989), 12 days in peach (*Prunus persica* Batsch) (Herrero and Arbeloa 1989), and 12 to 14 months in some species of oak (Kramer and Kozlowski 1979).

As the pollen tubes of gymnosperms elongate into the ovule, their generative cells divide into a stalk cell and a body cell. The body cell divides again to form 2 male gametes. One gamete fuses with the egg nucleus within an archegonium, a multicellular organ within the ovule, and the other usually disintegrates. Each gymnosperm ovule consists of an integument surrounding a multicellular body, the female gametophyte. The female gametophyte tissue is often incorrectly called "endosperm," a usage that should be discouraged. During later stages of ovule development, archegonia differentiate within the female gametophyte (figure 5). The number of archegonia varies by genus and by species. Florida torreya (*Torreya taxifolia* Arn) almost invariably has 1; the Pinaceae have 1 to 10; and sequoia may have up to 60 (Willson and Burley 1983). Occasionally more than 1 archegonium is fertilized, either by the second male gamete or by gametes from other pollen tubes, but normally only 1 embryo matures. Archegonia usually complete development less than 1 week before fertilization, but this interval is longer in some conifers. The elapsed time between pollination and fertilization in gymnosperms is generally much longer than that in angiosperms. These periods range from 3 weeks for Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) (Singh and Owens 1981) to 15 months for Monterey pine (*Pinus radiata* D. Don) (Lill 1976).

Reproductive Abnormalities

Occasionally the physiological processes associated with sexual reproduction break down and abnormalities result. In woody plants these abnormalities seldom have an impact on seed production or seed quality, but their general nature should be understood.

Polyembryony. Polyembryony is the occurrence of more than 1 embryo per ovule. It is unusual in angiosperms (Sedgley and Griffin 1989), but more common in gymnosperms with multiple archegonia, where pollination and fertilization produce multiple embryos, all differing in genetic composition. This type of polyembryony is found in araucaria, cypress, and all Pinaceae (Chowdhury 1962; Haines and Prakash 1980; Konar and Banerjee 1963). Another type of polyembryony can be produced through cleavage or division of a developing embryo. It has been noted in many coniferous genera of the northern temperate zone (Sedgley and Griffin 1989).

Parthenocarpy. Parthenocarpy is the formation of fruit without fertilization and is a desirable trait for selection in genetic improvement of fruit crops. Parthenocarpy is not

common in forest species but has been noted in apples and pears (*Pyrus* L.) when adverse environmental conditions induce ovule abortion (Sedgley and Griffin 1989).

Agamospermy. Agamospermy, sometimes called apomixis when it occurs in trees, is the development of seeds without fertilization. Some forms of this phenomenon seem to require pollination, while others do not. Agamospermy has been reported in sugar maple (*Acer saccharum* Marsh.) (Gabriel 1967), several species of serviceberries (Campbell and others 1987), and hawthorns (Crataegus L.) (Dickinson and Phipps 1986).

Figure 4—Chapter 1, Seed Biology: longitudinal section through a typical pistil just before fertilization (from Krugman and others 1974).

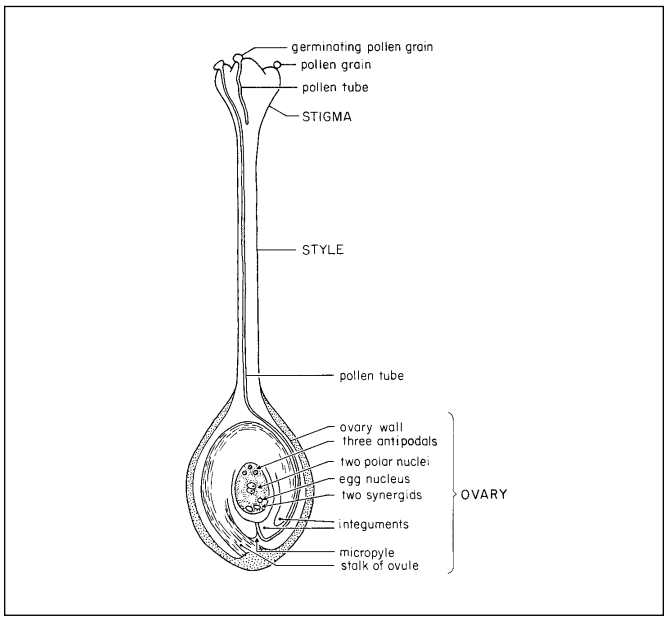
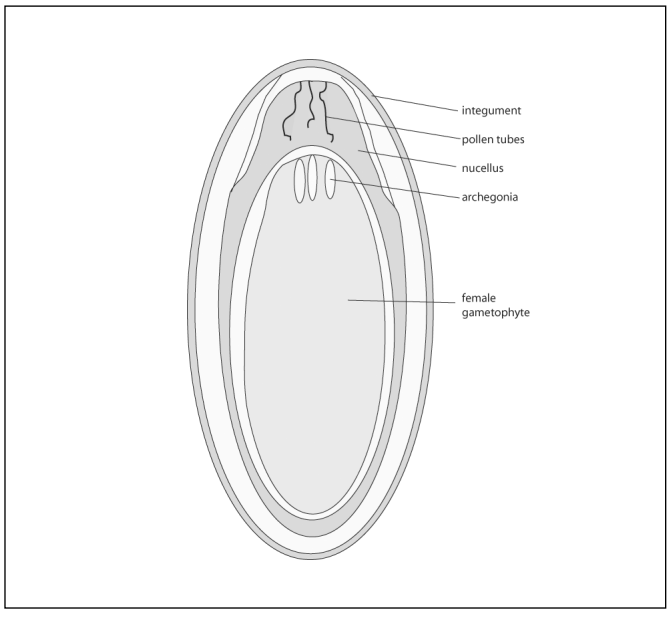


Figure 5—Chapter 1, Seed Biology: longitudinal section through an ovule of *Pinus ponderosa*. during the period of pollen tube development preceding fertilization.



Fruit and Seed Development

Morphological Development

The life history of a fruit generally includes 4 distinct phases of growth and development:

1 Pre-anthesis cell initiation and multiplication within the floral buds and enlarging flowers
2 Anthesis, pollination, pollen tube growth, and fertilization
3 Post-fertilization growth, mostly by cell enlargement in the fruit and cell multiplication in the seed
4 Maturation of the fruit through ripening and senescence (Nitsch 1965)

In most species, phase 3 does not proceed unless pollination and fertilization of some ovules has occurred. If it does proceed without fertilization, parthenocarpy or agamospermy is taking place. This section will briefly outline the events of phases 3 and 4. More complete discussions can be found in reviews on embryology, development, and maturation (Bewley and Black 1994; Chowdhury 1962; Johri 1984; Maheshwari 1950; Sedgley and Griffin 1989).

Angiosperms. Following fertilization, the first tissue to develop in the embryo sac is the endosperm, which follows 1 of 2 patterns. A nuclear endosperm, in which there is no early cell wall formation, is most common in woody plants. In the latter stages of growth, cell walls do form in this endosperm. Examples can be found in silk-oak and plum. Cellular endosperm, as found in ash and fringetree (*Chionanthus virginicus* L.), develops cell walls in the first and all subsequent divisions (Johri 1984). Endosperm tissue provides nutrition for the developing embryo, and in some genera, such as persimmon (*Diospyros* L.), magnolia, gooseberry (*Ribes* L.), and snowberry (*Symphoricarpos* Duham.), it persists as the primary food storage tissue in the mature seeds. Such seeds are described as endospermic. The monocotyledonous palms are also endospermic. In other genera, such as acacia, hickory, catalpa, and teak (*Tectona grandi*s L.f.), the endosperm is consumed during embryo development and is absent or exists only as a very thin layer of tissue in mature seeds. The cotyledons of the embryo become the site of food storage, and these species are designated as nonendospermic. Still other genera have significant food storage capacity in both endosperm and cotyledons; examples are barberry (*Berberis* L.), ash, wintergreen (*Gaultheria* L.), and basswood (*Tilia* L.).

In most species, the perisperm, comprised of the maternal nucellar tissue in the ovule, fails to develop and is absorbed by the developing embryo. In a few species, the perisperm develops into a food storage tissue that is outside of the embryo sac. In these cases there is no endosperm development, and the perisperm becomes the major food storage tissue. In this book, yucca is the only genus with a fully developed perisperm.

Embryos differentiate and attain their full size in most species by the time the fruits or seeds are shed. In fact, relative length of the embryo can be a good maturity index for decisions on when to collect seeds of many species. In a few species, however—for example, American holly (*Ilex opaca* Ait.), European ash (*Fraxinus excelsior* L.), and common snowberry (*Symphoricarpos albus* (L.) Blake—embryos are still immature when seeds are shed from the trees, and full size is only attained following a period of after-ripening. This condition causes the very slow germination that is a major problem in nursery production of these species.

As endosperm and embryo grow, the surrounding maternal tissues develop into the seed-covering structures, collectively called the seedcoat. Most seedcoats are composed of a firm outer layer, the testa, and a generally thin, membranous inner coat called the tegmen. There are many variations of seedcoat structure, however, and many species do not fit the model described above. In some genera, the testa is thin and permeable, as in poplar (*Populus* L.) and willow. In others, it may be thick and bony, as in hawthorn and apple. Some hard seedcoats have special cutinized layers, as in redbud and honeylocust (*Gleditsia triacanthos* L.). In some genera both covering structures are membranous, as in elm; the outer layer partially membranous and the inner one bony, as in chastetree (*Vitex* L.); or the outer layer soft and fleshy and the inner layer hard, as in magnolia.

Many species develop extended tissues on their seedcoats that play a role in dissemination of the seeds. These extensions may be wings, as in ailanthus, *Ailanthus altissima* (Mill.) Swingle, and tuliptree; tufts of short, bristly hairs, as in baccharis, *Baccharis* L., and sycamore; long soft hairs, as in poplar and willow; wings with hairs, as in catalpa and desertwillow, *Chilopsis linearis* (Cav.) Sweet; or various other appendages, such as small points on sourwood (*Oxydendron arboreum* (L.) DC.; and long, feathery styles on cercocarpus, *Cercocarpus* H.B.K. Actually, the appendages on baccharis, sycamore, and cercocarpus are on the fruits, which are single-seeded achenes, commonly called seeds.

It is useful to define and classify fruit types, although all authorities do not completely agree on the results. The classification presented here (table 2) is based on that of Krugman and others (1974) and Sedgley and Griffin (1989), but with modifications.

Premature fruit shedding may occur late in phases 3 or 4. Premature shedding can seriously reduce the size of the potential seedcrop, especially in tropical fruit crops, where over 99% of the fruits may drop (Chaplin and Westwood 1980). Three periods of premature shedding in angiosperm fruit trees are recognized (Sedgley and Griffin 1989). The first occurs within 2 weeks of anthesis and usually involves unfertilized flowers. The second period (the most serious) occurs within 2 months of anthesis when young fertilized fruits are shed. The third shedding period is when immature, but full-sized, fruits are shed. Premature shedding can result from a number of conditions, but an imbalance of growth regulators and competition for nutrients are probably the most important (Sedgley and Griffin 1989).

Gymnosperms. Postfertilization growth of most gymnosperm cones is actually the continued enlargement of an existing structure, the ovulate cone. In most genera, for example, true fir, spruce, and hemlock, the young conelet develops into the mature woody cone in just a few months. In pine, the conelet is already more than a year old at fertilization. In other genera, such as juniper, the cone scales fuse together to form a berrylike structure around the seeds. Other fleshy gymnosperm fruits are found on yew and torreya, where the seeds develop within fleshy arils.

The food storage tissue in gymnosperms, the female gametophyte, is already present when fertilization occurs, so development from that point centers on the embryo. The embryo grows and differentiates into a miniature plant with radicle (rudimentary root), hypocotyl (stem), plumule (bud), and cotyledons. The cotyledons are usually quite small and range in number from 2 in thuja and sequoia to 18 in some pine (Chowdhury 1962).

In most gymnosperms, the embryo is both morphologically and physiologically mature at the time of seed dispersal from the cones. Exceptions to this are ginkgo and certain pines that grow at high altitudes and/or extreme northern latitudes. Examples of the latter include Swiss stone (*Pinus cembra* L.), Korean (*P. koraiensis* Sieb. & Zucc.), Japanese white (*P. parviflora* Sieb. & Zucc.), and Siberian stone pines (*P. sibrica* Du Tour) (Krugman and Jenkinson 1974). Like the angiosperm seeds that are shed with immature embryos, these species require special treatments for prompt germination.

Seedcoats of gymnosperms may be relatively thin and soft, as in true fir; thin to thick and woody, as in pine; or very hard, as in juniper. Some genera have resin vesicles on

Table 2—Chapter 1, Seed Biology: classification of fruits of woody angiosperms

Fruit type	Description and examples
DERIVED FROM SINGLE FLOWERS	
Dry, dehiscent—pericarp dry and splitting open at maturity to release seeds	
Capsule	Two or more fused carpels, as in *Aesculus, Eucalyptus, Kalmia*
Legume (pod)	Splits along 2 sutures, as in *Acacia, Gleditsia, Lupinus*
Follicle	Splits along 1 suture, as in *Grevillea, Magnolia*
Dry, indehiscent—pericarp dry, but not splitting open at maturity	
Achene	Small, 1-seeded fruit with seed attached to ovary wall at only 1 point, as in *Cowania*, *Eriogonum*; or pericarp fused with calyx tube and embryo completely filling the ovarian cavity, as in *Artemisia, Chrysothamnus*
Nut	One-seeded fruit with woody or leathery pericarp, as in *Quercus*, or generally partially or wholly encased in an involucre (husk), as in *Carya, Corylus*
Samara	One-seeded pericarp modified with a wing-like appendage, as in *Fraxinus, Ulmus*; sometimes with 2 samaras fused together, as in *Acer*
Fleshy–part of the fruit wall comprised of fleshy or pulpy tissue with relatively high moisture content	
Berry	Pericarp has a skin that encloses a fleshy or pulpy mass that contains 1 or more seeds, as in *Berberis, Diospryros, Ribes*
Drupe	One-seeded fruit with pericarp usually in 3 distinct layers; the exocarp forms a skin, the mesocarp a fleshy layer, the endocarp a hard, stony layer, as in *Cornus, Nyssa, Prunus*; the seed, enclosed in endocarp only, is sometimes called a pyrene.
Pome	A many-sided fruit with the seeds enclosed in a papery inner wall, as in *Crataegus, Malus*
Hesperidium	Many-seeded fruit with leathery exocarp and mesocarp, and thick, fluid-filled endocarp, as in *Citrus*
DERIVED FROM INFLORESCENCES	
Dry, dehiscent—pericarp dry and splitting open at maturity to release seeds	
Strobile	A dry, conelike fruit developing from pistillate catkins, as in *Alnus, Betula*
Head	A multiple fruit that forms a compact cluster of simple fruits; the shape may be globose, as in *Liquidambar*, or conelike, as in *Casuarina;* the simple fruits can be different types, such as achenes in *Platanus* or capsules in *Liquidambar*
Fleshy—part of the fruit wall comprised of fleshy or pulpy tissue with relatively high moisture content	
Synconium	A type of pseudocarp in which achenes are actually borne on the inside of a hollow receptacle, as in *Ficus*
Sorosis	A fruit derived from the ovaries of several flowers, as in *Morus*
Coenocarp	A fruit incorporating ovaries, floral parts, and receptacles of many flowers, as in *Artocarpus*

or within their seedcoats: true fir, hemlock, and incense-cedar (*Calocedrus* Endl.). The resin makes seeds sticky and more difficult to handle in all phases of extraction and cleaning. Most gymnosperm seeds are winged, but there are exceptions: baldcypress, yew, torreya, and some pines. These pines are often called the "nut" pines: Swiss stone pine, piñyon (*Pinus edulis* Engelm.), chilgoza pine (*P. geradiana* Wall.), etc. Wings may be loosely adhering structures that are easily separated from the seeds, as in most pines, or they may be integral parts of the seedcoat, as in Douglas-fir, longleaf pine, and incense-cedar.

Cones of gymnosperms that require more than 1 year to mature generally remain small during the first year after flowering in the interval between pollination and fertilization. In a few species, such as western juniper (*Juniperus occidentalis* Hook) and Alaska-cedar, the fruit grows before fertilization occurs and attains almost full size during the first growing season, a full year or more before the seeds are physiologically mature. Seed collectors must be aware of this condition to avoid collecting cones with immature fruits. In Alaska-cedar, there are distinct color differences between immature and mature cones (Harris 1990), and position of cones on the branches is an indicator for both species. Gymnosperm fruit classification is much simpler than that of angiosperms (table 3) (modified from Krugman and others 1974).

Table 3—Chapter 1, Seed Biology: classification of fruits of woody gymnosperms

Fruit type	Description and examples
DRY STROBILI	
Cone	Woody structures that generally open on the trees and release seeds at maturity, as in *Abies, Picea,* and most *Pinus*; some *Pinus* cones remain closed at maturity and open only in fires or disintegrate over time
FLESHY STROBILI	
Drupelike	Enclosing a single seed, as in *Ginkgo, Taxus, Torreya,* and some *Juniperus*, or multiple seeds in other *Juniperus*, that are shed from trees intact

Sources: Modified from Kregman and others (1974).

Premature cone shedding can also be important in gymnosperms. It is most common several weeks after anthesis, when pollination has not occurred, but can also result from damage from frost, hail, drought, insects, or pathogens (Owens and Blake 1985; Sedgley and Griffin 1989; Sweet 1973). There are also losses from what Bramlett (1972) described as "physiological drop," when there were no visible signs of external injury. In general, the physiology of immature cone abscission is much less understood than premature fruit shedding in angiosperms (Sedgley and Griffin 1989).

Physiological Development

The growth of fruits that starts soon after fertilization (or prior to fertilization in a few species) involves a complex array of physiological processes and conditions. These processes are generally similar for fruits of most temperate trees, and they produce comparable trends in size, weight, and moisture content. A typical pattern of development for dry fruits is provided by the single-seeded samaras of green ash (*Fraxinus pennsylvanica* Marsh.) (figure 6). Fresh weight, dry weight, and moisture content increase slowly through early summer. By the end of August, the embryo is 2 to 3 mm long. Over the next 6 weeks there are sharp increases in dry weight and significant decreases in moisture as embryo length increases 5-fold (Bonner 1973). In drupes of the temperate zone, weight trends are similar, but moisture changes are somewhat different. In black cherry (*Prunus serotina* Ehrh.), for example, moisture contents decrease during spring to early summer, then increase again as maturity approaches (figure 7). In temperate recalcitrant seeds, such as acorns, the patterns are more like those of dry fruits (figure 8). Similar trends occur in the maturation of most tropical tree fruits also, but the changes are not always correlated with the seasons as they are in temperate species.

Moisture content. Any discussion of seed moisture must be based upon the 2 physiological classes of seeds in respect to moisture: orthodox and recalcitrant. Orthodox seeds are seeds that can be dried to low moisture levels (below 10% of fresh weight) without losing viability. Recalcitrant seeds cannot be dried below rather high levels (25 to 50%, depending on the species) without losing viability. This sensitivity to desiccation has important implications in the storage of seeds, and chapter 4 contains a broader discussion of this subject.

Among orthodox seeds, the dry types (tables 2 and 3) are generally shed from the trees at rather low moisture contents. Exact measurements of the moisture levels at which shedding occurs are hard to find, but some preliminary data suggest a range of about 10 to 15% for sweetgum, green ash, and boxelder (*Acer negundo* L.) (Bonner 1996). The fleshy fruits (tables 2 and 3) also contain orthodox seeds, but because they are still enclosed in the fleshy tissues of the fruits, they are shed at higher moisture contents. Black cherry fruits, for example, are shed at fruit moisture contents of 70 to 75% (Bonner 1975). Seed moisture contents are not quite as high, but they are much higher than those that are found in species with dry fruits. Some examples of seed moisture contents from fleshy fruits at shedding are 34% for flowering dogwood, a drupe, and 50% for persimmon (*Diospyros virginiana* L.), a berry (Bonner 1996).

Moisture contents of recalcitrant fruits are also high at the time of shedding. Some representative values for temperate species are 40% for acorns of black oaks, 50% for those of white oaks (Bonner and Vozzo 1987; Finch-Savage and others 1992), 50% for horsechestnut (*Aesculus hippocastanum* L.) (Tompsett and Pritchard 1993), and 58% for planetree maple (*Acer pseudoplatanus* L.) (Hong and Ellis 1990). Similar values have also been reported for tropical recalcitrant species (Tamari and Jacalne 1984).

In orthodox species with dry fruits, the maturation drying that occurs on the plants prior to shedding is the final stage of development as the seeds enter their quiescent period. This stage is apparently necessary for the synthesis of

Figure 6—Chapter 1, Seed Biology: seasonal changes in fresh weight, dry weight, and moisture content during maturation of a dry fruit, green ash (*Fraxinus pennsylvanica* Marsh.) (from Bonner and others 1994).

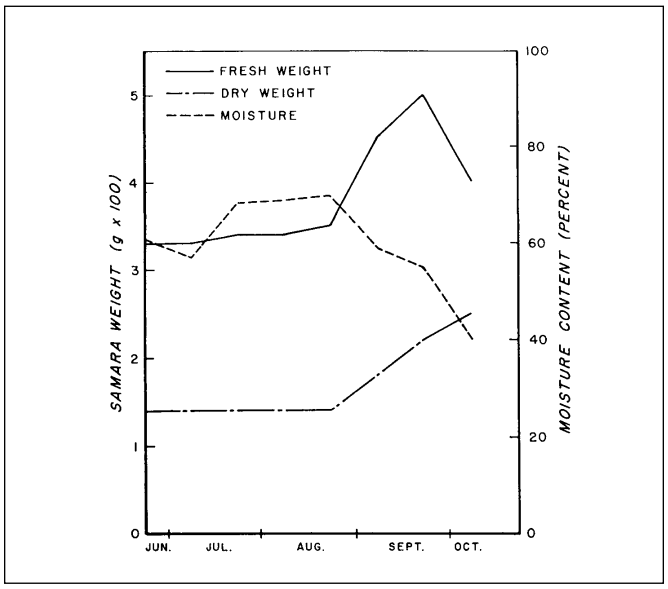
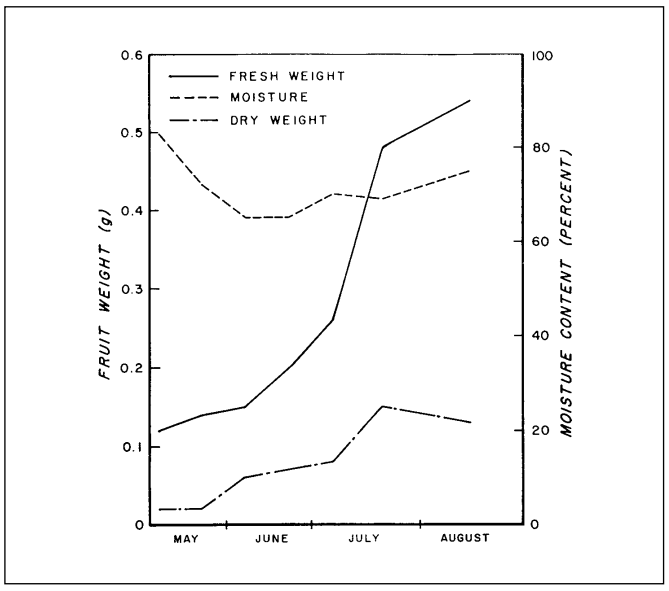
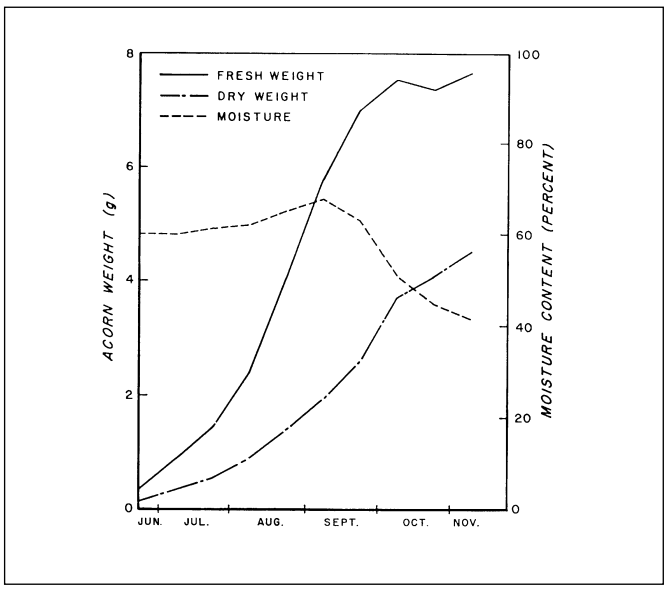


Figure 7—Chapter 1, Seed Biology: seasonal changes in fresh weight, dry weight, and moisture content during maturation of a fleshy drupe, black cherry (*Prunus serotina* Ehrh.) (adapted from Bonner and others 1994).



many enzyme systems, including those required for desiccation tolerance and germination when rehydration occurs (Bewley and Black 1994). There are some data for tree seeds (Finch-Savage and others 1994), but most of the work in this area has been done on castor bean (*Ricinis communis* L.) (Kermode and Bewley 1985) and cereal grains (Bewley and Black 1994). There is no reason to doubt, however, that the same physiological processes take place during maturation of orthodox seeds of woody plants. Conditions are different in orthodox seeds from fleshy fruits, however, as they are shed before complete desiccation. Desiccation occurs later after the fleshy covering has dried or been removed (eaten in many cases). Many of these species have complex dormancy periods, and it can be hypothesized that there are interactions between the dormancy and the delay in maturation drying of the seeds.

Figure 8—Chapter 1, Seed Biology: seasonal changes in fresh weight, dry weight, and moisture content during maturation of a recalcitrant fruit, Shumard oak (*Quercus shumardii* Buckl.) (from Bonner and others 1994).



In recalcitrant seeds, there is no pronounced maturation drying stage, because development never stops completely. There are slight decreases in moisture content that are apparently associated with shedding of fruits (figure 8), but there is no true quiescent period with recalcitrant seeds. Most species, especially tropical recalcitrant species, germinate soon after shedding, and some, including several *Quercus* species, will germinate while still on the tree, an event defined as vivipary.

Stored food reserves. As postfertilization growth proceeds, carbon fixed by photosynthesis is transferred to the seeds in the form of sucrose. In the seeds the sucrose is converted into many components, but most of it goes into stored food reserves of carbohydrate, lipid, or protein (Bewley and Black 1994). Many seeds have more than one type of food reserve, but one is usually predominant (table 4). The type of food reserve has implications for seed storage (see chapter 4), and it has been suggested that there are other important relationships. Korstian (1927), for example, suggested that dormancy in the black oak group was related to the high lipid content of these seeds, and that stratifica-

Table 4—Chapter 1, Seed Biology: some characteristic stored food reserves in tree seeds (expressed as % of dry weight)

Species	Tissue	Carbohydrate	Lipid	Protein*
Abies balsamea (L.) P. Mill.	Seed	—	37.6	13.9
Acer saccharinum L.	Samara	41.2	1.5	17.0
Aesculus pavia L.	Seed	42.9	1.9	8.2
Carya ovata (P. Mill.) K.Koch	Husked fruit	13.0	37.4	5.9
Cornus florida L.	Fruit	18.3	20.5	4.0
Euonymus americana L.	Seed	10.6	36.2	12.6
Juniperus virginiana L.	Cone	79.8	6.8	5.6
Liquidambar styraciflua L.	Seed	11.6	26.2	25.3
Picea glauca (Moench) Voss	Seed	—	44.2	23.8
Pinus palustris P. Mill.	Seed	3.1†	28.1	24.4‡
P. sylvestris L.	Seed	2.3	20.5	21.9
P. taeda L.	Seed	2.9†	18.5	13.8‡
Prunus serotina Ehrh.	Fruit	20.8	4.9	7.8
Pseudotsuga menziesii (Mirbel) Franco	Seed	5.1	37.2	—
Quercus alba L.	Acorn	46.6	2.9	4.6
Q. nigra L.	Acorn	25.8	20.3	3.8
Q. rubra L.	Acorn	67.1	20.8	6.6
Robinia pseudoacacia L.	Seed	12.3	9.0	38.7
Sassafras albidum (Nutt.) Nees	Fruit	13.6	46.6	17.1
Ulmus alata Michx.	Seed	8.9	15.3	27.4

Sources: Barnett (1976a), Bennett (1966), Bonner (1971, 1974a), Ching (1963), Pulliainen and Lajunen (1984), Waino and Forbes (1941).
* Most values obtained by multiplying total N by 6.25.
† Total sugars only.
‡ Insoluble N only multiplied by 6.25.

tion was needed to convert the lipid to soluble carbohydrates for germination. This conversion does take place during stratification of black oaks (Vozzo and Young 1975), but no direct connection to dormancy has been made. Also, some species with large lipid components, such as southern catalpa (*Catalpa bignonioides* Walt.) and winged elm (*Ulmus alata* Michx.), exhibit no dormancy, whereas some with high carbohydrate levels, such as sugarberry (*Celtis laevigata* Willd.) and eastern redcedar (*Juniperus virginiana* L.) are usually dormant.

Accumulation of food reserves follows similar patterns in most seeds. First there are slow increments of accumulation, then much more rapid accumulation as maturity and shedding are approached (figure 9). Soluble carbohydrates are converted to insoluble fractions in starchy seeds (figure 10), and the protein- nitrogen fraction increases at the expense of soluble forms (figure 11). During this period of development, seeds are strong sinks for current photosynthate, and vegetative growth is somewhat reduced (Bazzaz and Ackerly 1992; Owens and Blake 1985). The extent of growth lost in this trade-off in heavy seed years has not been accurately measured in woody plants, but estimates range from 30% in Norway spruce, *Picea abies* (L.) Karst, in Europe (Buyak 1975) to less than 5% in flowering dogwood in Mississippi (Bonner 1996). Rohmeder (1967) estimated that between the start of seed-bearing and the typical harvest age of forest trees, 10 to 30% of the potential volume yield may be used in seed production.

Some data on elemental concentrations in mature seeds are available (table 5). Such information is of great value to wildlife biologists in studies of the nutritive value of browse to wildlife.

Hormones. At the same time that the growing seeds are accumulating food reserves, there are certain hormonal changes that are taking place within the seeds. The major hormones in seeds are auxins, gibberellins, cytokinins, and abscisic acid (ABA) (Bewley and Black 1994). These hormones appear to play important roles in the growth and development of both fruits and seeds, but it is not always clear what these roles are. The major auxin in seeds, indoleacetic acid (IAA), is found in both free and bound forms. It has been extracted and identified from a number of tree seeds, for example, pecan (Lipe and others 1969), water oak (*Quercus nigra* L.) (Hopper and Vozzo 1982), English

Figure 9—Chapter 1, Seed Biology: changes in insoluble carbohydrate and crude lipid fractions in maturing acorns of white oak (*Quercus alba* L.) and water oak (*Q. nigra* L.) (from Bonner and others 1994).

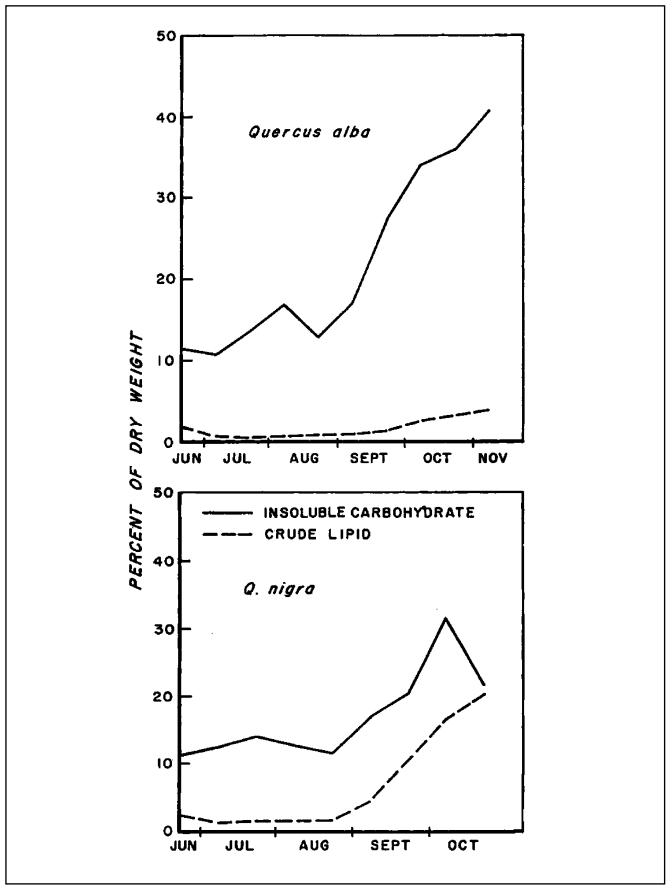


Figure 10—Chapter 1, Seed Biology: changes in soluble **(solid circles)** and insoluble **(open triangles)** carbohydrate contents of maturing acorns of whtie oak (*Quercus alba* L.) (adapted from Bonner 1976).

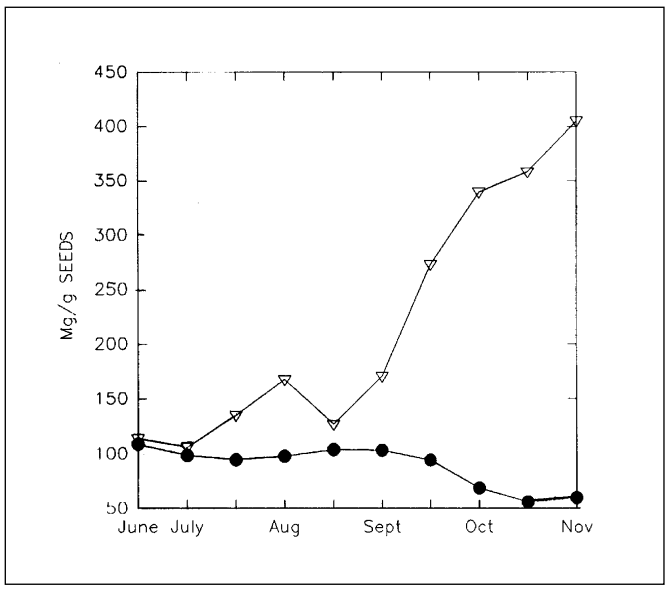
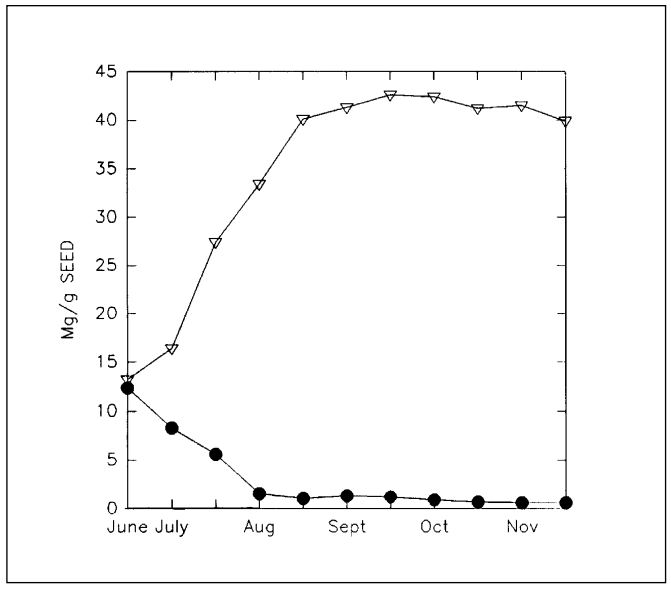


Figure 11—Chapter 1, Seed Biology: changes in soluble-nitrogen **(solid circles)** and protein-nitrogen **(open triangles)** contents of maturing seeds of sweetgum (*Liquidambar styraciflua* L.) (adapted from Bonner 1972).



oak (*Q. robur* L.) (Michalski 1969), apple, and plum (*Prunus cerasus* L.) (Bewley and Black 1994). Over 80 gibberellins are now known, and more than half of them have been identified in seeds (Bewley and Black 1994). Gibberellins or gibberellin-like substances have been identified in seeds of Jeffrey (*Pinus jefferyi* Grev. & Balf.), sugar, and ponderosa (Krugman 1967); and Monterey pine and Douglas-fir (Pharis and Kuo 1977); pear (*Pyrus communis* L.) (Martin and others 1977), water oak (Hopper and Vozzo 1982), and English oak (Michalski 1968).

Cytokinins have not been studied as much in seeds of woody plants, but they (or cytokinin-like compounds) have been found in English oak (Michalski 1974), apple, and sour cherry (Bewley and Black 1994). ABA has received much attention in seeds of woody plants, first for its possible role in dormancy, then for its possible role in tolerance of desiccation. ABA has been identified in developing seeds of English oak (Finch-Savage and others 1992), pear (Martin and others 1977), and peach (Piaggesi and others 1991).

The highest concentrations of gibberellins and cytokinins have been found in immature seeds during their most rapid phase of development, and both decline later as they apparently become bound up with other compounds. Immature seeds are also rich in auxins, and they are thought to be the source of this group of hormones needed for normal fruit growth. Removal of developing seeds will inhibit growth of the fruit (Bewley and Black 1994). In contrast to

Table 5—Chapter 1, Seed Biology: some characteristic seed elemental compositions (expressed as % of dry weight)

Species	Tissue	Ca	K	Mg	P
Acer rubrum L.	Samara	0.34	—	0.23	0.34
Callicarpa americana L.	Fruit	.26	1.34	—	.13
Corylus avellana L.	Seed	.10	.73	.19	.40
Ilex vomitoria Ait.	Fruit	.24	1.25	—	.11
Juglans regia L.	Nut	.08	.45	.17	.41
Picea abies (L.) Karst	Seed	.02	.79	.31	.66
Pinus sylvestris L.	Seed	.04	.63	.30	.73
Prunus serotina Ehrh.	Fruit	.14	—	.09	.14
Quercus pagoda Raf.	Acorn	.27	—	.06	.06
Q. stellata Wangenh.	Acorn	.25	—	.06	.08
Sassafras albidum (Nutt.) Nees	Fruit	.06	—	.11	.23
Ulmus alata Michx.	Seed	.51	—	.20	.52
Vaccinium arboreum Marsh.	Fruit	.33	—	.07	.06

Sources: Bonner (1971, 1974a), Hastings (1966), Lott and Buttrose (19780, Pulliainen and Lajunen (1984).

the other hormones, ABA concentration is low in developing seeds and highest at maturity. In conjunction with maturation drying, ABA may prevent embryos from germinating while still on the tree (Bewley and Black 1994). These correlations do not prove a causal relationship between seed maturity and dormancy, however, and much research remains to be done.

Factors That Influence Seed Production

There are many factors that can reduce the size of a seed crop on woody plants no matter how abundant flower production may be. Flower abortion and premature fruit drop have been discussed earlier. This section will briefly review factors that reduce seedcrops well after fertilization and early development of fruits or cones has occurred.

Physiological factors. Most of the fruit and cone losses that can be attributed to physiological factors occur early in the fruiting season. On some occasions, however, fruits or cones will abscise late in the growing season. The exact mechanisms are not understood, but they may be related to competition for a shrinking supply of nutrients late in the season between reproductive structures and vegetative shoots. Early abscision of acorns as maturation is completed may appear to be physiological in nature, but the primary cause is often insect damage that triggers a physiological reaction.

Weather. Weather can influence seedcrops in a variety of ways. Interference with flowering and pollination through late freezes, rain during pollination, etc., have been discussed previously. Severe drought can have a noticeable effect on the size of many angiosperm seeds. This effect is particularly noticeable for large single-seeded fruits such as oak acorns (Bonner 1996). Other damaging effects of weather can be more direct. Strong winds and hail can destroy flowers and fruits, sometimes to the point that most of the crop is lost. Hurricanes along the coastal areas of the Southeast are infrequent but very serious, and they can create problems locally for longleaf pine, a species with large, heavy cones that are fairly easy to knock to the ground.

Biotic factors. Flowers, fruits, and seeds are susceptible to damage by many insects, pathogens, and animals. Flower damage, particularly by insects, often goes unnoticed in branch terminals and in the tops of trees. Much more is known about damage to fruits and seeds, because they are handled and observed closely when collected.

Insects. Little is known about insects that destroy flowers, as the damage is often not seen. Both larvae and young adults of treehoppers (Membracidae) destroy pistillate flowers of oaks (Cecich 1993). Thrips, both Phlaeothripidae and Thripidae, destroy young strobili on several pines, true firs, and Douglas-fir (Hedlin and others 1980). The most serious economic damage is done by *Gnophothrips fuscus* (Morgan) on slash pine (*Pinus elliottii* Engelm.). Other insects that damage pine strobili in the Southeast include Nantucket pine tip moth, *Rhyacionia frustrana (*Comstock); pine conelet looper, *Nepytia semiclusaria* (Walker); the Virginia pine sawfly, *Neodiprion pratti pratti* (Dyar) and other sawflies, *Xyela* spp.; leaffooted pine seedbug, *Leptoglossus corculus* (Say); cone midges, *Cecidomyiidae*; and several coneworms, *Dioryctria* spp. (Ebel and others 1975). Strobili damage in other conifers has been reported for *Xyela* spp. on lodgepole, Coulter (*Pinus coulteri*

D. Don), ponderosa, digger (*P. sabiniana* Dougl.), and Monterey pine; western conifer seed bug (*Leptoglossus occidentalis* Heidemann) on Douglas-fir, grand fir, incense-cedar, and several pine species; and the European pine shoot moth (*Rhyacionia buoliana* (Schiffermuller)) on red, Scots, eastern white (*Pinus* strobus L.), pitch (*P. rigida* Mill.) and other pines (Hedlin and others 1980).

Insect damage to fruits and seeds is much more common than damage to flowers and strobili. Most damage is caused by larvae that hatch from eggs deposited in young, developing fruits and devour the embryo tissues. In angiosperms, major damage is caused by *Curculio* spp., *Conotrachelus* spp., and *Melissopus* spp. in oaks (Gibson 1972, 1982; Vozzo 1984); *Thysanocnemis* spp. in ash (Solomon and others 1993); several species of seed beetles (Bruchidae) in acacias (Southgate 1983); and the fruit borers *Pagyda salvalis* Walk. and *Dichocrosis punctiferalis* Guenee in teak (Neelay and others 1983). There are numerous insects that cause minor damage to fruit- and seed-crops of other angiosperms, but they do not seriously threaten to decimate seed supplies.

Because most major commercial forest species are conifers, insect damage to their cones and seeds is more economically important than damage to fruits and seeds of angiosperms. Cones of many species can be heavily damaged by cone worms (*Dioryctria* spp.) and cone beetles (*Conophthorus* spp.). Lesser damage to cones is also caused by the cone borers *(Eucosma* spp.) and cone midges (Cecidomyiidae) (Hedlin and others 1980). The southern pine coneworm, *D. amatella* (Hulst), is a major pest in seed orchards of the southern pines and many control programs are designed to reduce its impact (Ebel and others 1975). Significant damage to other conifers has been recorded for red pine cone beetle (*Conophthorus resinosae* Hopk.) (Hard 1964), sugar pine cone beetle (*C. lambertianae* Hopk.) (Bedard 1968), and *C. monticolae* on western white pine (Graham 1990). The major seed damage in conifers has been attributed to seedworms, *Laspeyresia* spp.; seed chalcids, *Metastigmu*s spp.; seedbugs, *Leptoglossus* spp.; and *Tetyra bipunctata* Herrich-Schaeffer (Ebel and others 1975; Hedlin and others 1980; Kinzer and others 1972; Krugman and Koerber 1969; Scurlock and others 1982).

Control of seed insects in natural stands is normally not economical. In seed orchards, where considerable resources have been invested to produce seedcrops and many other cultural practices are being carried out, control programs are feasible. In recent years, however, environmental concerns are forcing stringent limitations on chemical application programs in seed orchards. Insect populations can be reduced with light and chemical attractant traps, but these methods have a limited impact.

Pathogens. Flowers, fruits, and seeds of woody plants are exposed to great numbers of microorganisms in their natural environments; some of these are pathogenic and some are beneficial. Of the 3 types of pathogenic microorganisms causing damage to woody plants—viruses, bacteria, and fungi—only fungi have serious effects on seed production.

The most important group of fungi is the cone rusts. These fungi attack first- and second-year cones on a wide range of conifers throughout North America (table 6). Degree of infection varies, but losses are often significant. Losses from southern pine cone rust and inland spruce cone rust have been sufficient to warrant spraying orchards with fungicides (Sutherland and others 1987). Other fungi that can reduce seed production in conifers include sirococcus blight (*Sirococcus strobilinus* Preuss) and pitch canker (*Fusarium moniliforme* Sheld. var. *subglutinans* Wollenw. & Reink.). Sirococcus blight is primarily a problem in nurseries and young stands, but it can kill branches in older trees

Table 6—Chapter 1, Seed Biology: major cone rust diseases of conifers

Disease	Fungal pathogen	Species infected
inland spruce cone rust	*Chrysomyxa pirolata* Wint.	*Picea engelmannii, P. glauca, P. mariana, P. rubens, P. pungens, P. sitchensis, P. abies*
coastal spruce cone rust	*Chrysomyxa monesis* Ziller	*Picea sitchensis*
southern pine cone rust	*Cronartium strobilinum* (Arth.) Hedgc. & Hahn	*Pinus elliottii, P. elliottii* var. *densa, P. palustris*
southwestern pine cone rust	*Cronartium conigenum* Hedgc. & Hunt	Many *Pinus* species from S Arizona, S into Central America
western gall rust	*Endocronartium harknessii* (J.P. Moore) Y. Hirat.	*Pinus banksiana, P. contorta, P. ponderosa,* and to a lesser. degree, many others in W US, Canada, & NE US

Source: Sutherland and others (1987).

as well. It can be found on larch, spruce, pine, and Douglas-fir (Sutherland and others 1987). Pitch canker damages shoots, cones, and seeds of pines in the South and East. In a few short years, pitch canker has become a major disease problem in seed orchards of all southern pines (Barrows-Broaddus and Dwinell 1985; Blakeslee and others 1980).

With the exception of species that attack trees with edible nuts, such as scab disease—*Cladosporium caryigenum* (Ell. & Lang.) Gottwald—on pecan (Graves and others 1989), reduction of seedcrops in angiosperms by fungi is generally not serious. There are, however, numerous fungi that infect flowers and fruits and cause only incidental or local damage to the seedcrop (table 7). For additional information on seed pathogens and other microorganisms and the species on which they are found, readers are referred to Mittal and others (1990).

Birds. Birds feed on flowers, fruits, and seeds, especially the latter. Many small birds—such as finches, grosbeaks, and sparrows (Fringillidae), doves (Columbidae), and quail (Phasianidae)—feed on small seeds after they are shed, but these losses are incidental to the total seedcrop. Larger birds that feed on maturing fruits and seeds still on the trees can have serious, though usually local, impacts on seed yield. Acorns are a favorite of grackles (*Quiscalus* spp.), jays (Corvidae), and woodpeckers (Picidae). The California woodpecker *(Balanosphyra formicivora*) can devour enough acorns, its favorite food, to severely reduce the crop within its foraging range (Bent 1939). Pine seeds are a favorite of Clark's nutcracker (*Nucifraga columbiana*) and piñyon jays (*Cyanocephalus cyanocephalus*), which specialize in piñyon seeds and even young cones (Bent 1946). Berries of various juniper species are eaten in large numbers by jays, Clark's nutcracker, and robins *(Turdus migratorius*). Robins also are heavy feeders in the winter on Pacific madrone (*Arbutus menziesii* Pursh.) on the west coast (Bent 1949).

Losses of seeds are most serious when the birds feed in flocks. Heavy feeding of grackles on acorns has been mentioned previously in connection with seed dispersal. Flock depredation also occurs when robins or cedar waxwings (*Bombycilla cedrorum*) feast on cherries, eastern redcedar, hollies, and elms.

Not as many quantitative data or observational data have been collected for tropical and subtropical species, but it is certain that birds play a large role in the depredation and dispersal of tropical fruits and seeds (Terborgh 1990). A study of *Virola surinamensis* (Rol.) Warb. (Myristicaceae) in a moist, tropical forest in Panama by Howe (1990) found that more than 80% of the fruits were eaten or removed by birds.

Although less damaging to the total seedcrop, birds' feeding on flowers can have a local impact. Grouse (*Bonasa umbillas,* and *Dendragapus* spp.) are known to feed heavily on buds and flowers of alder and poplars and strobili of pines, spruces, firs, and larches (Bent 1932).

Mammals. Significant amounts of fruits and seeds are lost to mammal predation by many species. Squirrels (*Citellus* and *Sciurus* spp.) are heavy feeders on acorns of almost all species of oak throughout North America. Not only are many acorns eaten, but also many more are buried in the ground for winter retrieval. Squirrels are also heavy feeders on pines, usually dissecting or removing the green cones. Several western squirrel species cache the cones for winter retrieval, and these caches were once heavily utilized by cone collectors. Cone losses to squirrels can be very

Table 7—Chapter 1, Seed Biology: fungi that cause minor or locally severe decreases to fruit crops of angiosperms

Fungus	Tissue attacked	Species infected
Botrytis spp	Flowers	*Ilex opaca*
Ciboria acerina Whetz. & Buchew.	Flowers	*Acer rubrum, A. saccharinum*
Coniothyrium spp.	Seeds	*Betula alleghaniensis*
Cytospora spp.	Fruits	*Prunus serotina*
Gymnosporangium clavipes (Cooke & Peck) Cooke.& Peck	Fruits	*Amelanchier, Cotoneaster, Crataegus, Malus, Pyrus*
G. clavariiforme (Pers.) DC	Fruits	*Amelanchier, Cotoneaster, Crataegus, Malus, Pyrus*
Taphrina johansonii Sadeb.	Catkins	*Populus* spp.
T. occidentalis W.W. Ray	Catkins	*Alnus* spp.
T. amentorum (Sadeb.) Rostr.	Catkins	*Alnus* spp.

Sources: Hepting (1971), Ziller (1974).

significant. Fowells and Schubert (1956) reported that in 1 year in an area in California, the Douglas pine squirrel (*Tamiasciurus douglasii*) destroyed over 50% of the sugar pine and ponderosa pine cones. Squirrels may remove over 90% of the cone crops of white spruce (*Picea glauca* (Moench) Voss) in Alaska (Nienstaedt and Zasada 1990). Losses of cones of southern pines to squirrels in the Southeast are normally not nearly so severe.

Squirrels also reduce seedcrops by cutting and feeding on cambial tissues in branches in the spring, thus destroying buds, flowers, and strobili. There is evidence of this type of damage on ponderosa pine (Adams 1955), red pine (Roe 1948), sugar maple (Godman and others 1990), and American elm (*Ulmus americana* L.) (Bey 1990).

Minor fruit depredation also occurs from other animals, such as bears (*Ursus* spp.), raccoons *(Procyon lotor*), deer (*Odocoileus* spp.), and opossums (*Didelphis virginiana*). In tropical and subtropical forests, many more animals are fruit and seed predators than in temperate forests.

Maturity and Dispersal

As a general rule, fruits should be collected only after the seeds have reached full maturity. One problem with this rule is that full maturity is not easily defined. To some, dispersal from the tree of seeds with the ability to germinate and grow is a sign of full maturity, yet serotinous cones with germinable seeds remain on the some pine species for several years after others have dispersed and germinated. Other seeds are shed naturally but require an after-ripening period before they can germinate. These are examples of dispersal strategies that have been favorable for regeneration of these species but also seem to contradict the simple definition of maturity. Others propose that physical or chemical attributes of the seeds define maturity: minimum moisture content, maximum dry weight, maximum level of stored food reserves, or maximum germination performance. As in the previous definition, there are numerous apparent exceptions to all of the proposed criteria. Another problem with the general rule about collection at maturity is that, in actual practice, fruits and seeds must often be collected before full maturity, whatever that is, because of possible losses to predators, difficulties in collecting small wind-dispersed seeds, or time constraints in commercial collection operations. The solution to both of these problems is to develop practical indices of maturity for fruits and seeds so that collectors can tell when they can proceed without danger of gathering immature seeds that will not germinate properly and produce healthy seedlings.

Indices of maturity. In order to collect seeds at the optimum stage of their development, collectors need some sort of index of seed maturity to guide them in their choice of collection time. Indices of seed maturity should ideally be simple procedures that require little or no equipment and that can be administered in the field.

Physical. The most commonly used indices of fruit or seed maturity are those that are based on physical characteristics. Change of fruit color is widely used on both dry and fleshy fruits. The most common color changes are from a "vegetative green" to a shade of brown in dry fruits or to a bright or blue-black color in fleshy fruits. Common patterns are changes from green to yellow to brown (ash, maple, and white oak, *Quercus alba* L.); from green to red to purple or black (cherries and tupelos, *Nyssa* L.); from green to yellow to purple (for example, honeylocust); and from green to brown (conifers).

Embryo size is a simple maturity index. When embryo length reaches 75% of the length of the embryonic cavity, seeds of many species are considered mature enough to collect (Edwards 1979). The relative size of embryos can be easily seen on radiographs or determined from cross-sections of seeds.

Moisture content also is a simple indicator of maturity in some species, but overnight or 24 hours of drying of samples in ovens is required for accurate measurement. "Critical" samara moisture levels (percentage of fresh weight) were reported to be 16% for green ash (Cram and Lindquist 1982) and 59% for sugar maple (Carl and Snow 1971). Moisture content of cones is also a very good maturity index for many conifers, but instead of actually measuring it, most collectors estimate cone moisture content by measuring specific gravity of the cones. This can be accomplished easily in the field with a graduated cylinder of water

Table 8—Chapter 1, Seed Biology: cone specific-gravity values that indicate seed maturity in some conifers

Species	Specific gravity
Abies grandis (Dougl. ex D. Don) Lindl.	0.90
Cunninghamia lanceolata (Lamb.) Hook.	0.95
Pinus elliottii Engelm.	0.95
P. merkusii Junghuhn & Vriese ex Vriese	1.00
P. palustris P. Mill.	0.90
P. strobus (L.)	0.90
P. taeda (L.)	0.90
P. virginiana P. Mill.	1.00

Sources: Barnett (1976a), Bonner (1986), Daryano and others (1979), Fenton and Sucoff (1965), Jian and Peipei (1988), Pfister (1967).

(Barnett 1979). Cone weight is estimated by water displacement of the floating cone, and volume is estimated by water displacement of the submerged cone. Specific gravity is equal to weight divided by volume (examples of cone specific gravities used to judge maturity are listed in table 8).

Other physical indices of seed maturity are easy cup release from acorns of oak; a white, brittle embryo of some ash species that breaks when bent at a sharp angle; and white pine cone scales that flex open when cones are bent double. For details on maturity indices of individual genera or species, see part 2 of this book.

Chemical. Although chemical indices of maturity are biologically sound, they are seldom practical to use in collection. Most potential chemical indicators are based on the level of stored food reserves (table 9), but elemental phosphorus and IAA concentrations have been suggested as indices for green ash (Bonner 1973) and English oak (Michalski 1969), respectively.

Shedding and dispersal. The majority of temperate genera shed their fruits and seeds in the fall or winter, although many—for example, birch and poplar—shed theirs in the spring. In some genera—for example, maple, eucalyptus, willow, and elm—there are both spring-shedding and fall-shedding species. Other species have seeds that mature and are shed in mid-summer—for example, ceanothus (*Ceanothu*s L.).

The seeds of many species are shed or dispersed quickly (within a few days) after they mature, and collectors must be alert to the phenological characteristics of the species in order to collect what they need. Some species that shed fruits quickly when they mature are maples and elms. In others, the fruits are persistent on the tree but open to disperse the seeds quickly after maturity; examples include sweetgum, poplars, and willows. In still other species, fruit opening and seed dispersal are very dependent on the weather. Cones of loblolly pine, for example, open readily in warm, dry conditions and disperse their seeds. At night, they close back up again when humidity rises. If a weather front brings rain, the cones may close up completely and not reopen for dispersal for several days. The primary seed dispersal agent of all of the above species is wind.

Drupes, berries, and other fleshy fruits are not usually shed quickly, but they can be removed from the trees rapidly by birds and animals. This can be a major problem for seed collectors wishing to harvest the seeds of species such as pawpaws (*Asimina* Adans.), hollies, plums, and prickly-ash (*Zanthoxylum* L.). Seeds will usually have to be collected exactly at the time of maturity on the trees, or the entire crop may be lost. The same problem occurs for some fruits that are not fleshy, for example, hickories, walnuts, and oaks. These fruits are favorite foods of rodents, deer, and other animals, and they must be collected from the ground as soon as they are shed. Birds will also take many of these fruits before shedding; for example, a flock of grackles can completely strip a large willow oak (*Q. phellos* L.) of its acorn crop in several hours.

The cones of most conifers disperse their seeds soon after maturity. In true firs, dispersal occurs as the cone disintegrates on the trees, leaving the spike-like cone axis still upright on the branches. In some pines, cedars, and hemlocks, the cones are slow to give up their seeds, and dispersal may take 3 to 12 months. Serotinous cones of several species—such as jack (*Pinus banksiana* Lamb.), sand (*P. clausa* (Chapm. ex Engelm.) Vasey ex Sarg.), pitch (*P. rigida* Mill.), and lodgepole pines—do not normally open on the trees but open on the ground following fires that melt the resin seals on the cone scales. Other pines—Swiss stone and Siberian stone pines, etc.—shed their cones while still

Table 9—Chapter 1, Seed Biology: chemical levels that indicate seed maturity

Species	Chemical	Percent of dry weight fraction
Abies procera Rehd.	Crude fat	25
Fraxinus pennsylvanica Marsh.	Crude fat	10
Liquidambar styraciflua L.	Crude fat	25
Quercus (black oaks)	Crude fat	15–25
	Insoluble CHO	25
Quercus (white oaks)	Insoluble CHO	40
Pseudotsuga menziesii (Mirbel) Franco	Crude fat	23
	Reducing sugars	1.3

Sources: Bonner (1972, 1973, 1974b, 1976, Rediske (1961), Rediske and Nickolson (1965).
CHO=carbohydrates.

closed or only partly open, and seed dispersal occurs only as the cones disintegrate on the ground over several months (Krugman and others 1974).

The major dispersal agents for seeds of woody plants are wind, animals, and water. Wind-dispersed species are mostly small, and many have hairs or other appendages that help to prolong their flight. Other seeds, such as those of ailanthus, catalpas, or ashes, are somewhat larger but have wings that are large in relation to the size of the embryos. Food value and color aid in dispersal by animals, which is very local if by rodents or widespread if by birds. Dispersal by water is usually by flotation and can be very important for wetland species such as tupelos, willows, and the 1 oak species that has floating acorns–the overcup oak (*Quercus lyrata* Walt.). At least 2 genera in this book—ceanothus and witch-hazel disperse seeds with an explosive force when drying fruits split suddenly and expel the seeds. For more detailed treatments of seed dispersal, readers should see Bawa and Hadley (1990) and Fenner (1992).

Dormancy

Once seeds have matured and been dispersed, survival of the species requires that they germinate at a time and place favorable for growth and survival of the seedlings. Plants have evolved many mechanisms and processes that ensure survival. Some species produce prodigious numbers of seeds, so that even if only a tiny proportion germinate and grow, some seedlings will survive. In others, germination at unfavorable times is prevented by a mechanism that is commonly described as dormancy. Dormancy is defined as a physiological state in which a seed disposed to germinate does not, even in the presence of favorable environmental conditions (Bonner 1984). Seeds are able to overcome dormancy and germinate when "triggered" by certain internal processes that are usually induced by environmental changes. There is a tremendous range in the degree of dormancy among woody species. Some seeds lie in the soil for years before germinating, whereas other are delayed for only a few weeks. The latter condition is sometimes described as "delayed germination" to indicate something less than true dormancy. In fact, the distinction between dormancy and delayed germination is not at all clear, and among the majority of species, the interval between maturity and germination (in natural conditions) is a continuum with no distinct gradation.

Types of Dormancy

Many different classifications of dormancy have been devised by seed scientists and there is no universal agreement on the subject. Most tree seed workers accept the definitions of the Seed Problems Working Party of the IUFRO—International Union of Forest Research Organizations (Bonner 1984)—and these definitions will be used in this discussion.

Seedcoat (or external) dormancy. Seedcoat dormancy has 3 primary modes of action. In the most common mode, the seedcoats (or other covering structures) are impermeable to the entry of moisture or gases. Members of the Leguminoseae—for example, acacia, albizia (*Albizia* Durazz.), honeylocust, mesquite (*Prosopis* L.), black-locust, sophora (*Sophora* L.)—usually display this characteristic, which is commonly called hardseededness by those who work with seeds. Members of other families also have seedcoats that impose a similar dormancy, but seedcoat structures are different; some examples include American beautyberry (*Callicarpa americana* L.), hollies, sumacs, and basswood.

The second mode of dormancy action attributed to seedcoats is the mechanical resistance to swelling of the embryo as it absorbs moisture. This resistance delays full imbibition and emergence of the radicle from within the seed. Mechanical resistance frequently contributes to dormancy and has been documented in big sagebrush (*Artemesia tridentata* Nutt.) (McDonough and Harniss 1974), pecan (Van Staden and Dimalla 1976), loblolly pine (Barnett 1976b), Korean pine (Hatano and Asakawa 1964), and water oak (Peterson 1983). It does not appear to be the primary factor in tree seed dormancy, however.

A third possible mode of seedcoat dormancy is the presence of germination inhibitors in the seedcoats (Bewley and Black 1994; Nord and Van Atta 1960; Peterson 1983) that may or may not play a significant role in dormancy. Some of the phenolic substances in seedcoats that could possibly be germination inhibitors could actually be beneficial by inhibiting the growth of pathogenic microorganisms (Mohamed-Yasseen and others 1994). In some herbaceous species, there are inhibitors that must leach from the embryo before germination can take place, and seedcoats prevent this leaching (Bewley and Black 1994). There is no conclusive evidence of this condition in seeds of woody plants, but success in stratifying seeds by placing them in porous sacks in running water suggests that it may occur.

Embryo (or internal) dormancy. Embryo dormancy arises from a condition within the embryo itself. The most likely cause of embryo dormancy is the presence of germination inhibitors in the embryonic axis or in the food storage tissues of the seed. For germination to occur, these inhibitors must be metabolically inactivated, or their effect

must be overcome by germination-promoting substances. Germination inhibitors have been isolated and identified in a number of woody plant seeds, with ABA the most common inhibitor. Species with ABA functioning as an internal inhibitor include sugar (Enu-Kwesi and Dumbroff 1978), Norway (*Acer platanoides* L.) (Tilberg and Pinfield 1982), and planetree maples (Webb and Wareing 1972); European hazel (*Corylus avellana* L.) (Williams and others 1973); white ash (*Fraxinus americana* L.) (Sondheimer and others 1968); apple (*Malus pumila* Mill.) (Singh and Browning 1991); and northern red (*Quercus rubra* L.) and English oaks (Szczotka 1977). Correlations of changing ABA levels with degree of dormancy in mature seeds is not evidence of cause and effect, however, and more detailed research is needed in this field. ABA also seems to play a role in preventing precocious germination in English oak (Finch-Savage and others 1992) and shedding of silver maple samaras (Tomaszewska 1973). Other germination inhibitors have also been found in dormant seeds of woody plants, but there is no good evidence for their modes of action in the seed.

In another type of embryo dormancy, called physiological immaturity, a critical enzyme system or other biochemical factor is not in place at shedding and afterripening is required for complete physiological maturation. Evidence for the existence of this type of dormancy is weak, so it probably is the same as morphological dormancy.

Morphological dormancy. Morphological dormancy results from the embryo not being completely morphologically developed when seeds are shed. Additional growth of the embryo is required in an afterripening period. Morphological dormancy has been documented in black (*Fraxinus nigra* Marsh.) and European ashes (Vanstone and LaCroix 1975; Walle 1987), American holly (Ives 1923), and several pines that grow at high altitudes or latitudes (Krugman and Jenkinson 1974).

Combined dormancy. Combined dormancy is a condition in which 2 or more primary factors, such as seedcoat dormancy and embryo dormancy, are present to the extent that each requires treatment to overcome. Some examples of combined dormancy in North American species are seeds of Mexican redbud (*Cercis canadensis* var. *mexicana* (Rose) Hopkins) (Tipton 1992), skunkbush (*Rhus trilobata* Nutt.) (Heit 1967b), and American basswood (Barton 1934). For basswood, seedcoat scarification with acid for 10 to 40 minutes, followed by moist stratification for 90 days is the recommended treatment to overcome dormancy (Heit 1967b).

Double dormancy. Double dormancy is a condition in which there is dormancy in both the radicle and the epicotyl of the embryo, but each require different conditions to overcome it. This type of dormancy is difficult to demonstrate, but it has been reported for viburnums (Giersbach 1937). A similar condition is found in some oaks, in which radicles are not dormant, but epicotyls are.

Secondary dormancy. Secondary dormancy results from some action, treatment, or injury to seeds during collection, handling, or sowing. Pine seeds can incur secondary dormancy if exposed to high temperatures and moisture at crucial times (McLemore and Barnett 1966). When stratified seeds are redried to storage levels (below 10%), they are often said to have incurred secondary dormancy. Germination can certainly be delayed under these conditions, but this is not a true secondary dormancy.

Overcoming Dormancy

Dormancy is a great advantage when one wants to store seeds, but a disadvantage when prompt germination in desired. With the exception of hardseeded species, years of research have revealed little about how seed dormancy really functions and how it can be overcome. Applied research and practical experience, however, have combined to provide ways to hasten the germination of dormant seeds.

Seedcoat dormancy. Treatments are designed to breach the seedcoat, or other covering structures, and remove barriers to moisture uptake, gas exchange, swelling of the embryo, and radicle emergence. Methods used to overcome seedcoat dormancy are collectively known as scarification treatments, and there are risks to seed viability inherent in all of them. In selecting a scarification treatment, the most gentle method should be tested first; then increasingly severe treatments until the desired effect is obtained. The methods below are listed in order of increasing severity. Complete details on how to apply them can be found in chapter 5 for small samples, as in seed testing, and in chapter 7 for large quantities. Suggested methods for individual species may be found in part 2 of this book.

Cold water soak. In some hardseeded species, the seedcoats are not completely impermeable to water. Soaking such seeds in water at room temperature for 24 to 48 hours may be sufficient for full imbibition and subsequent germination.

Hot water soak. Similar to the cold water soak, except that seeds are put into very hot or boiling water and left there as the water cools. The hot water softens the seedcoats or causes them to crack, and imbibition occurs as the water cools. Numerous leguminous species can be treated in this manner—for example, acacia, albizia, and prosopis.

Hot wire. This technique requires a heated needle or an electric woodburning tool to burn small holes through

seedcoats (Sandif 1988; Stubsgaard 1986). A belt-driven burner that scarifies seeds electrically shows promise for treatment of larger lots (Danida Forest Seed Centre 1993). "Burned" seeds can be shipped or returned to storage after treatment (Lauridsen and Stubsgaard 1987), something that other scarification methods normally do not allow.

Acid treatment. Treatment with concentrated sulfuric acid (or other mineral acids such as hydrochloric or nitric acids) is the method of choice for many species. Seeds should be in contact with the acid for 15 to 60 minutes, depending on species or individual seedlot, and washed thoroughly in running water afterward to remove any acid that remains on the seedcoats. Acid has been used in North America to treat honeylocust and Kentucky coffeetree (*Gymnocladus dioicus* (L.) K. Koch) (Liu and others 1981), black locust (Heit 1967a), and snowbrush ceanothus (*Ceanothus velutinus* Dougl.) (Heit 1967b).

Mechanical treatments. Mechanical scarification is used extensively for large lots of seeds. There are various scarifiers in use, from small cement mixers filled with rough rocks or pieces of broken concrete, to the impact seed gun developed in Denmark (Stubsgaard 1986). A mechanical device has also been developed to crack peach seedcoats (Reid and others 1979). For small samples, seedcoats can be scarified by hand with knives, files, clippers, sandpaper, etc.

Internal dormancy. Treatments to overcome internal dormancy are expected to bring about physiological changes within the embryo that will enhance rapid germination. The most successful treatments have been those that simulate natural conditions in a crucial time period in the reproductive life cycle of the plant. For temperate species, this is usually a moist, chilling period, commonly called stratification, because it was formerly done by alternating layers of seeds and sand or peat in a pit in the ground. Stratification in pits is seldom used anymore, but the principles are the same.

Stratification (chilling). The usual procedure for stratification is to refrigerate fully imbibed seeds at 1 to 5 °C for 1 to 6 months. This procedure simulates the natural winter conditions of temperate seeds that are lying on the forest floor. During stratification (1) enzyme systems are activated (Eichholtz and others 1983; Li and Ross 1990a&b; Michalski 1982; Slater and Bryant 1987); (2) stored foods are changed to soluble forms (Dumbroff and De Silva 1972; Kao and Rowan 1970; Pukacka 1986; Tylkowski 1986; Vozzo and Young 1975); and (3) the inhibitor/promoter balances change (Enu-Kwesi and Dumbroff 1978; Tillberg and Pinfield 1982; Webb and others 1973; Williams and others 1973). For a more detailed review of the biochemical changes during this period, see Bewley and Black 1994.

The optimum length of the stratification period varies greatly among species and among different seedlots of the same species. There may be differences even within the same lot if some portions are handled differently. In southern pines, dormancy often appears to increase during storage, and stored seeds require longer stratification than the same lots when fresh (Bonner 1991). Details on stratification procedures can be found in chapters 5 and 7. Recommendations for particular genera or individual species are provided in part 2 of this book.

One tremendous benefit of stratification for nurseries is an increased uniformity of emergence. The low temperatures used in stratification inhibit germination of the seeds that are no longer dormant while the remaining seeds are undergoing the needed internal changes. When the seeds are finally sown in favorable temperatures, there is a flush of uniform germination and emergence, which is crucial to even seedling development. This condition also explains why some non-dormant species appear to respond favorably to short periods (1 to 2 weeks) of stratification with faster and more complete germination.

There is a growing body of evidence that suggests that full imbibition is not the optimum moisture content for stratification. Careful regulation of seed moisture content at levels below full imbibition has produced improved seed performance and sowing options for both conifers (Edwards 1986; Poulsen 1996) and hardwoods (Muller 1993).

Incubation and stratification. A number of species that exhibit complex embryo dormancy or morphological dormancy will germinate quicker if given a warm, moist incubation period prior to cold stratification. The incubation period promotes embryo growth and other internal processes and is usually shorter than the stratification period. Species for which this treatment has been effective include cherry plum (*Prunus cerasifera* Ehrh.) (Tylkowski 1986), black ash (Vanstone and LaCroix 1975), and several species of juniper (Rietveld 1989; Van Haverbeke and Comer 1985).

Chemical treatment. Various studies have shown that some species will germinate quicker following treatment with exogenous chemical agents, such as hydrogen peroxide, citric acid, and gibberellins. Although these benefits can be demonstrated in the laboratory with small samples, they are rarely, if ever, used in production nurseries.

Combined treatments. Some species—such as American basswood—have seeds with combined dormancy charateristics that seem to require 2 types of treatment for good germination. Impermeable seedcoats must first be scarified before seeds are stratified (Brinkman 1974).

Variation in Dormancy

As noted earlier, there is widespread variation in the degree of dormancy, both among species, and within a species. For some species, there are patterns of dormancy that have been documented and that can have practical application. For example, degree of dormancy appears to increase with increasing elevation of seed source for black cherry and red maple (*Acer rubrum* L.) in Tennessee (Farmer and Barnett 1972; Farmer and Cunningham 1981). Seeds from more northern sources generally require longer stratification periods than seeds from southern sources. This relationship has been reported for sugar maple (Kriebel and Gabriel 1969), red maple (Farmer and Goelz 1984; Tremblay and others 1996), sweetgum (Wilcox 1968), and sycamore (Webb and Farmer 1968). In contrast, eastern white pine showed just the reverse in a range-wide study (Fowler and Dwight 1964): seeds from the southern sources are more dormant, but this phenomenon may be related to the higher altitudes of the natural stands of white pine at the southern extremities of its range. Warmer climates during seed maturation typically produce heavier and larger embryos in seeds (Durzan and Chalupa 1968), presumably because the growing seasons are longer. This conditions suggests that degree of dormancy (or delayed germination) is related to degree of physiological maturity in temperate seeds, but the evidence for this is lacking.

Variation in dormancy among individual trees at the same site has been documented for loblolly pine (McLemore and Barnett 1966) and sweetgum (Rink and others 1979), and can probably be assumed to occur in all woody plants. Partial genetic control of dormancy is also obvious, because most seed dormancy is related in some way to seedcoats or other covering structures, all maternal tissues. The best way to understand dormancy is to quantify it in mathematical terms. A number of studies have attempted this for temperate trees (Bonner and Harrington 1993; Donald 1987; Richter and Switzer 1982; Rink and others 1979; Sorensen 1983) and all of the proposed methods have application under certain conditions.

Germination

Germination is defined as "the resumption of active growth in an embryo which results in its emergence from the seed and development of those structures essential to plant development" (Bonner 1984). In another sense, it is the culminating event of seed maturation, the establishment of the seedling. It is useful to think of germination as occurring in overlapping events (Kramer and Kozlowski 1979):

1. Absorption of water
2. Increased respiration, enzymatic activity, and assimilation of stored foods
3. Increased adenosine phosphate and nucleic acids
4. Cell growth and division
5. Differentiation of tissues

All of these events are influenced by environmental conditions and events within the seeds themselves.

Environmental Factors

The most important environmental factors that influence germination are moisture, temperature, light, and aeration.

Moisture. The typical pattern of moisture uptake by seeds has 3 phases (Vertucci 1989): a rapid initial uptake, a short lag period of extremely slow uptake, and another rapid period of uptake just before germination. The first phase is primarily imbibitional in nature and occurs in dead seeds as well as live ones. It is a physical process of moisture moving from a substance with high water potential (soil) to one with a low water potential (dry seed). This uptake displaces gases from dry seeds (Simon 1984) and is visually evident in the bubbles that slowly escape from dry seeds when they are submerged in water. The length of the second phase is related to the degree of dormancy or delayed germination in the seeds. It can be practically absent in the rapidly germinating seeds of oak (Bonner 1968) or extended in the case of very dormant seeds. The third phase occurs when metabolism becomes very active, and the seedcoats split, leading to greater oxygen uptake.

There are minimum amounts of moisture required for germination to proceed, and several studies have sought to measure the moisture stresses that will retard or halt germination (table 10). Significant decreases in germination occurred, in general, from – 0.8 MPa and below, and germination was effectively stopped at stresses of – 0.3 to – 2.0 MPa. All of these studies used osmotic solutions to impose stress, and there are concerns that this method may hinder germination by inhibiting gas exchange. McDonough (1979) used thermocouple psychrometer chambers to impose moisture stress on seeds of quaking aspen (*Populus tremuloides* Michx.), however, and his results agree quite well with those reported with osmotic solutions. Comparisons among species should be made with caution, as methodology and equipment varied widely in these studies. There were also significant interactions with seed source, seed treatment, and temperature for some species (Bonner and Farmer 1966; Farmer and Bonner 1967; Moore and Kidd 1982).

Table 10—Chapter 1, Seed Biology: critical levels of water potential (MPa) for germination within a 20 to 30 °C range of temperatures as determined with osmotic solutions*

Species	Water potential (MPa)	
	Strongly decreased germination	Effectively stopped germination
Artemisia tridentata Nutt.	–0.1	–1.6
Acacia tortillis (Forsskal) Hayne	–0.29	–0.51
Cercocarpus montanus (Raf.)	–0.4	–1.3
Chrysothamnus nauseosus (Pallas ex Pursh) Britt.	–0.4	–1.6
Liquidambar styraciflua L.	–0.5	–1.52
Pinus contorta Dougl. ex Loud	–0.8	—
P. eldarica Medw.	–0.6	–1.2
P. elliottii Engelm.	–0.81	–1.82
P. palustris P. Mill.	–0.81	–1.82
P. ponderosa P. & C. Lawson	–0.4	–0.8
Picea engelmannii Parry ex Royle	–0.8	—
Populus ciliata Wall. ex Royle	–0.1	–0.3
P. deltoides Bartr. ex Marsh.	–1.01	–1.52
Quercus palustris Muenchh.	–0.5	–2.0

Sources: Barnett (1969), Bonner (1968), Bonner & Farmer (1966), Choinski and Tuohy (1991), Djavanshir and Reid (1975), Farmer and Bonner (1967), Kaufman and Eckard (1977), Moore and Kidd (1982), Sabo and others (1979), Singh and Singh 1983

* Some data were converted from atmospheres and bars to MPa as follows: 1 bar = 0.1 MPa; 1 atm = 0.1013 MPa.

Temperature. Seeds of temperate woody plants can germinate over a wide range of temperatures, from a minimum of 2 or 3 °C, to a maximum of about 45 °C (Bonner and others 1994). Radicle emergence will occur in most species at 45 °C, but few will produce normal seedlings at this temperature. Low temperatures, on the other hand, are favored by some species. Northern red oak from Wisconsin, for example, germinated best at 1 °C in a trial reported by Godman and Mattson (1980). Some true firs and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) will germinate in snowbanks in Oregon and Washington (Franklin and Krueger 1968). Many dormant temperate species will sometimes germinate in stratification bags at 3 to 5 °C if left for long periods. The major effect of temperature on germination, however, is on rate rather than total germination.

Natural seedbeds do not remain at constant temperatures, but experience diurnal fluctuations from lows at night to highs in the daytime. Most temperate woody plants have adapted to these conditions and germinate most rapidly at alternating temperatures of approximately 20 °C at night and 30 °C in the daytime. Other species germinate faster at lower temperatures regimes, for example, 15 to 25 °C or 10 to 20 °C, or at constant temperatures of 5 to 22 °C (Sabo and others 1979; Wang and Pitel 1991). Official seed testing prescriptions are based on the known optimum temperatures for each genus or species (ISTA 1993). Experiments with 2-way thermogradient plates suggest that germination of many temperate species will occur at a wide range of temperature regimes, and that an amplitude of change between day and night of 10 to 12 °C may be more important than the cardinal points (Bonner 1983; Mayer and Poljakoff-Mayber 1963; Sabo and others 1979).

In the tropics, pioneer species that invade forest gaps also respond to alternating temperatures with increased germination (Vázquez-Yanes and Orozco-Segovia 1982). Temperatures are more constant underneath canopies, and light becomes more of an important factor in germination in these conditions (Clark 1990; Vázquez-Yanes and others 1990.).

Light. Light plays a complex role in the germination of woody plants, in that it stimulates the germination of most species but is absolutely necessary for only a few. It is often difficult to separate the effects of light and the effects of temperature. Dry, dormant seeds normally do not germinate in the dark, but stratification at low temperatures or treatment with high temperatures can overcome the dark inhibition in some species.

The key to seed response to light is thought to be the phytochrome system. Phytochrome is a pigment that exists in 2 forms within the embryonic axes of seeds (Bewley and Black 1994). One form (Pr) has a maximum absorption at 660 nm, whereas the other form (Pfr) has a maximum absorption at 730 nm. Red light converts Pr to Pfr in imbibed seeds, which is associated with overcoming dormancy. Far-red light drives the process in the other direction, accompanied by a partial return of dormancy. The red/far-red reaction has been demonstrated in seeds of numerous temperate species: Virginia (*Pinus virginiana* Mill.) (Toole and others 1961), longleaf (McLemore and Hansbrough 1970), and Scots pines (Nyman 1963); red alder (*Alnus rubra* Bong.) (Bormann 1983); paper (*Betula papyrifera* Marsh.) (Bevington and Hoyle 1981), hairy (*B. pubescens* Ehrh.), and European white birches (*B. verrucosa* Ehrh.) (Junttila 1976); and northern catalpa (*Catalpa speciosa* Warder ex Engelm.) (Fosket and Briggs 1970). There is also evidence that the red/far-red system is operative in seeds of many tropical rainforest species (Vázquez-Yanes and Orozco-Segovia 1990). For a detailed discussion of phytochrome and its reactions, readers should see Bewley and Black (1994).

Phytochrome reactions require only a short exposure to the proper wavelength to take effect (Bewley and Black 1994). Other light responses that are related to daylength have been noted in seeds of woody plants. In terms of germination, eastern hemlock appears to have long-day light requirements of 16 hours at 27 °C, but shorter requirements of 8 to 12 hours at 17 °C (Stearns and Olson 1958). In many temperate species—for example, Fraser fir (*Abies fraseri* (Pursh.) Poir). (Adkins and others 1984); sweetgum (Bonner 1967), and ponderosa pine (Harrington 1977)—stratification decreases the light requirement for prompt germination. These responses may or may not be related in some way to phytochrome, but they demonstrate the complex nature of the relationship of light to seeds.

Aeration. Respiration supplies energy to germinating seeds, and oxygen is a primary electron acceptor in the process (Kramer and Kozlowski 1979). Insufficient oxygen is not usually a major barrier to germination, except when seeds are buried too deeply in the soil or are submerged in water. A few small seeds can germinate as they float on the surface of water—for example, willows, cottonwood (*Populus deltoides* Bartr. ex Marsh.), and sycamore—but oxygen is usually too limiting for germination when seeds are submerged. Poor oxygen supply is often a problem in seed testing when blotters are kept too moist. Moisture will actually form a film around seeds and inhibit the entry of oxygen (Gordon and Edwards 1991).

As seeds begin to germinate, the pattern of oxygen uptake is practically identical to that of water uptake (Kozlowski and Gentile 1959): (1) a short period of rapid uptake; (2) a period of very slow uptake; and (3) a second period of rapid uptake. Measurements of seedcoat permeability to oxygen in some herbaceous species suggest that the coats are much more permeable to water than to oxygen. Part of this may be due to the consumption of oxygen by the seedcoat itself in oxidative reactions (Bewley and Black 1994). There are lots of phenolic compounds in seedcoats, for example, and their oxidation could consume a considerable amount of oxygen.

Biochemical Changes

When non-dormant seeds are placed in environments that are conducive to germination, internal processes that drive the growth of the embryo start to take place. These processes are dominated by the conversion of storage foods into soluble forms and their translocation into the embryonic axis. In stratified seeds, these processes have already been initiated during the treatment period. In the past 25 years, there has been an enormous amount of research that has greatly advanced our knowledge of the biochemical mechanisms of seed germination. Although most of this research has been centered on seeds of agricultural crops, the basic processes are similar in most seeds and the conclusions drawn from this research can be readily extrapolated to include the seeds of woody plants. A detailed discussion of biochemical changes in seed germination is beyond the scope of this book. For additional information, readers should see Bewley and Black (1994), Murray (1984), and Pehap (1983).

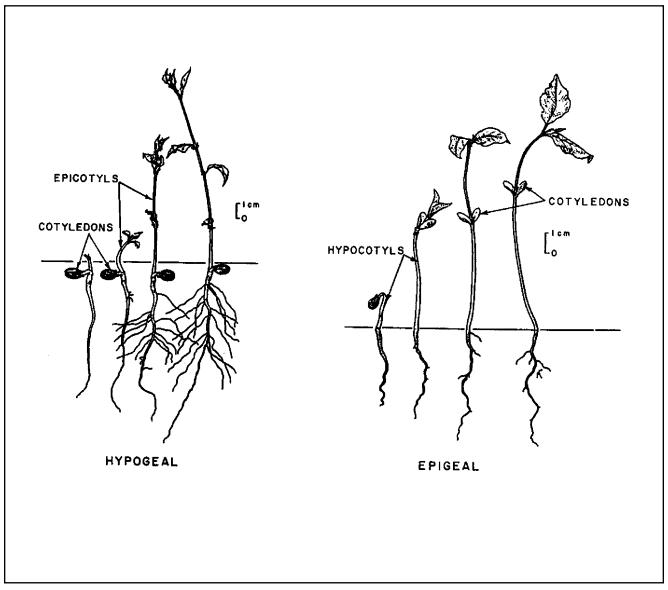
Most recent work on seeds of woody plants has been on oily seeds. In these seeds, lipid reserves are converted to starch, which is then hydrolyzed into soluble carbohydrates (mainly glucose) for embryo growth. Much of this change takes place within the storage tissues (endosperm, cotyledon, female gametophyte, or haustoria) before axis elongation signals the start of germination, so it is difficult to say if this change is part of dormancy removal or part of the germination process (Arce and others 1983; Li and Ross 1990a&b; Murphy and Hammer 1993;). Recent studies on gene expression and enzyme formation in several pine species should help in this regard (Gifford and others 1991; Murphy and Hammer 1993; Pitel and Cheliak 1988; Pitel and others 1984; Salmia 1981).

Other changes within germinating embryos include the hydrolysis of storage proteins to form amino acids and other soluble nitrogenous compounds for enzyme synthesis

(Bouvier-Durand and others 1984; Salmia 1981) and a large increase in soluble phosphorus compounds (Ching 1966).

The transfer of reserve foods from storage tissue to the axis is usually direct. In endospermic Leguminosae (which include honeylocust), however, the reserves are transferred from the endosperm to the cotyledons, then to the growing axis (Bewley and Black 1994). A similar transfer process may exist in other species that have both endosperm and cotyledons, but there is no evidence for it. In oil palm (*Elaeis guineensis* Jacq.), a slow-germinating monocot, the haustoria form at one end of the embryo and absorb the food reserves from the endosperm as they are broken down and pass the nutrients on to the developing plumule and radicle (Oo and Stumpf 1983).

Figure 12—Chapter 1, Seed Biology: the common forms of seed germination in temperate trees. These are hypogeal germination **(left)**, here that of American plum (*Prunus americana* Marsh.), with seedlings at 1, 3, 5, and 9 days after germination, and epigeal germination **(right)**, here that of common chokecherry (*P. virginiana* L.) seedlings at 1, 3, 7, and 11 days after.



Physical Development

Physical changes in germinating seeds are practically the same for all species. The first sign is usually swelling of the seed from water uptake. Embryo elongation occurs second, but unseen within the seed's covering structures. Then the seedcoat splits, and the emerging radicle elongates. At this point, germination in temperate species takes one of two forms. One form is epigeal germination, in which the hypocotyl elongates, arches upward, then straightens, pushing the cotyledons upward through the soil (figure 12). In many species the seedcoats are still attached to the cotyledons after emergence and are not shed until the cotyledons start growing. Genera that exhibit epigeal germination include pine, cedar, eucalyptus, juniper, magnolia, and mountain-ash.

In the second form, hypogeal germination, it is the epicotyl that elongates, pushing the young plumule through the soil while the cotyledons remain below ground (figure 12). There they remain attached to the seedling and supply reserve foods for weeks or more. Genera that exhibit hypogeal germination include buckeye, oak, walnut, chestnut (*Castanea* Mill.), and torreya.

Germination form is normally the same for all species in a genus, but like most things in seed biology of woody plants, there is an exception. In cherries and plums, both forms occur; common chokecherry (*P. virginiana* L.) is epigeal, but the remaining species of the genus are hypogeal (figure 12).

Some authorities recognize other forms of germination in tropical species. Bunya-pine (*Araucaria bidwillii* Hooker) and Parana-pine (*A. angustifolia* (Bert.) O. Kuntze) seeds germinate on the surface of the soil, then the cotyledonary stalks elongate and push the hypocotyl, plumule, and radicle into the soil. The hypocotyl subsequently develops into a tuber that serves to transfer the food reserves from the female megagametophyte to the growing seedling. This type of germination has been defined as cryptogeal (Burrows and Stockey 1994), and these araucarias are the only species in this book that exhibit this form of germination. Ng (1991) also has defined durian germination in which the hypocotyl elongates but the cotyledons remain within the seed. This form of germination occurs in common durian (*Durio zibethinus* Murr.), a popular, edible fruit of Southeast Asia that is cauliferous.

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Chapter 2

Genetic Improvement of Forest Trees

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Contents

2

Introduction

In this chapter, readers can gain a basic understanding of why certain procedures are used to improve forest trees. The references listed can be used as a source for obtaining more detailed information, both historical background and technical details. Examples are frequently cited from operational tree improvement programs to focus the chapter on an applied level. Although many of the examples are taken from the author's professional focus of over 40 years in the southern United States, the principles they exemplify can be used world-wide.

Terminology

Many of the terms used in this chapter are listed in the Glossary; a more detailed glossary may be found in Snyder (1972) and Wright (1976). Comprehensive references on forest genetics include Dorman (1976), Wright (1976) and Zobel and Talbert (1984).

"Forest genetics" is the general term often used for the study of inheritance in forest trees, whereas "forest tree improvement" usually refers to the applied use of forest genetics to actually improve the quality of the trees. "Tree breeding" is often used as a synonym for tree improvement, but it also may be found referring to specific activities such as controlled pollination. Zobel and Talbert (1984) define forest tree breeding as "activities geared to solve some specific problem or to produce a specifically desired product." Tree improvement will be the term used most frequently in this chapter.

It is important to understand that tree improvement is an integral part of silviculture. Tree improvement provides the raw material for artificial regeneration, which is one of the most important weapons in the arsenal of the silviculturist. Tree improvement provides a direct avenue to introduce genetically improved seedlings (or cuttings) into the reforestation system with no additional "handling fees." It costs no more to plant a genetically improved seedling than a "woods-run" seedling. (Note that although the costs of producing genetically improved planting stock are not insignificant, they can be viewed as an investment in future increased productivity. Dividends accrue in terms of increased growth, better form and wood quality, and improved insect and disease resistance).

Allocation of Resources

One of the key elements of land management is allocation of resources. An ever-expanding world population demands an ever-increasing supply of wood products. These must be produced on both private and public lands. The most productive sites should be devoted to maximum timber production. Maximum wood production on these acres relieves the pressure on other acres, which can be devoted to native vegetation, wildlife production, aesthetic considerations, and other uses not compatible with maximum timber production.

Even those acres devoted to maximum wood production via artificial regeneration with genetically improved planting stock are not lost to most aspects of good forest management practices. These acres will support strong wildlife populations, preserve watersheds, and provide many recreational opportunities. All these are fully compatible with timber production.

Monoculture

Critics of plantation forestry programs often cite the dangers of monoculture as reasons to reject these programs. The reasons quoted range from disease outbreaks to site deterioration, but usually focus on lack of biodiversity. In point of fact, there are few documented cases of severe problems, even in clonal plantations. Where there have been losses from pathogens, the increased productivity of the plantations usually greatly overbalances the losses. [It should be noted that most Forest Service restoration plantings after fire and logging are not monocultures. Seedlings of the various species that are planted are grown from seeds collected from areas near the new site.]

There can be interactions between intensive culture and diseases, as in the case of fusiform rust—*Cronartium quercum* (Berk.) Miyabe ex *Shirai* f. sp. *fusiforme* (Hedgc. & Hunt) Burdsall & Snow—which may be increased by site preparation procedures and fertilization (Miller 1972). Some clonal plantations such as those of cottonwood and eucalyptus have encountered disease problems, but these are often due to "off-site planting" (that is, growing a species on a site for which it is poorly adapted) rather than the lack of genetic diversity. Even the fabled case of "Saxony spruce" in which pure stands of Norway spruce—*Picea abies* L.—were blamed for "site deterioration" was actually due to off-site planting. This, in conjunction with poor management and poor seed source selection, led to drastically decreased productivity of the plantations (Lutz and Chandler 1946).

Gene Conservation

The fundamental concepts of gene conservation are an integral part of the tree improvement process. In the preservation of selected trees in seed orchards, clonal banks and progeny tests, valuable germplasm is not only preserved but

also replicated on different sites where it may enrich local tree populations via wind pollination. The planting of genetically improved seedlings on new sites likewise enriches the local gene pool of that species. Future populations of these trees can be expected to be more heterogeneous than the local stands as well as more productive (Namkoong 1974).

During the selection and breeding of forest trees, a tremendous volume of data is generated regarding species—site interactions, growth and tree quality information, and other physiological relationships. These data serve to increase our understanding of the importance of high-quality seedlings that are well-adapted to the planting site. Good forest stewardship requires vigorous, fast-growing trees as well as a diversity of flora and fauna.

The use of isozyme analysis has been adopted by many forest geneticists as a tool for estimating diversity in natural populations. For example, Shimizu and Adams (1993) used isozyme analysis in natural stands of Douglas-fir—*Pseudotsuga menziesii* (Mirbel) Franco—and found no evidence that planting nursery-grown seedlings contributed any less genetic diversity than natural regeneration.

Tree Improvement Versus Crop Improvement

The genetic improvement of forest trees has many similarities to the breeding of field crops. Most of the concepts are the same, namely the selection of above-average individuals from large populations, and subsequently breeding these individuals using a specified mating design. Following the breeding phase, the progeny must be tested on a variety of sites and under differing climatic conditions. Progeny tests are specially designed genetic tests that expose hereditary differences among trees, by bringing different genotypes together under a common set of environmental conditions.

When the progeny have developed sufficiently for a reliable assessment of their value, improved individuals or groups can be released for operational use and/or the breeding cycle can be repeated.

There are two major differences between working with field crops and forest trees. The first is time. Field crops such as corn and wheat reach reproductive maturity in a few months, while most trees require many years. Crop rotations with corn and wheat are also only a matter of a few months whereas trees may not produce a marketable crop for 25 to 100 years! Even in the tropics, it is rare to harvest a timber crop in less than 8 or 10 years. In practical terms, this means that a corn or wheat breeder can complete a breeding cycle in 2 or 3 years compared to the tree breeder's 8 to 10 years, at the very least (table 1).

Table 1—Chapter 2, Genetic Improvement of Forest Trees: the time factor

	Field crops	Trees
Reproductive maturity	1–2 months	5–20 years
Rotation length	4–6 months	10–100 years
Breeding cycle	1–2 years	8–20 years

The second major difference is that most field crop breeding is done with domesticated varieties that have been manipulated by humans for centuries and are often genetically homogeneous. Forest tree breeding, in contrast, usually starts with wild stands of trees that have been little-changed by humans. An exception here is "high-grading," the common logging practice of cutting the best quality trees and leaving the worst to regenerate the next generation. Unfortunately, tree improvement foresters are often forced to work with the results of one or more cycles of high-grading, namely trees of poor form and marginal value for breeding material. On the other hand, working with wild, unselected stands of trees does provide an opportunity to produce large gains in quality in the first few generations of breeding.

Field-crop breeding, therefore, usually involves working with well-known varieties that are often pure lines (genetically pure). With corn, for example, pure lines are crossed to produce heterozygous (genetically different) progeny that exhibit hybrid vigor (improved performance due to the interaction of different genotypes). Site considerations are also important here, as the corn will be planted on uniform, well-prepared sites while the trees may be planted on rough, cut-over sites with little or no site preparation. Adaptation is also a consideration as the corn is bred for a very narrow spectrum of soils, sites, and climatic zones. The trees, on the other hand, may be planted over a much wider range of soils, sites, and climatic zones.

The Biology of the Species

The genetic improvement of any crop will be effective only after a careful analysis of the biology of the species and how this influences the breeder's approach to the problem. For example, insect-pollinated species require special considerations from tree breeders. Genera such as maple (*Acer* L.), tuliptree (*Liriodendron* L.), magnolia (*Magnolia* L.), some species of willow (*Salix* L.), basswood (*Tilia* L.), and many tropical species are all insect-pollinated and, therefore, cannot be managed with the same techniques as

wind-pollinated species. The majority of commercial timber species are both wind-pollinated and monoecious, producing both male and female "flowers" (cones or stroboli) on the same tree. The location of these stroboli usually favors cross-pollination. For example, most conifers bear female cones in the upper areas of the crown with the male cones below, usually favoring cross-pollination rather than self-pollination.

Cross-pollination, in most plants, is an adaptation designed to increase heterozygosity, which is usually linked to vigorous growth, high fertility, and strong resistance to attack by pathogens. Conversely, self-pollination often leads to poor growth, weakness, and reduced fertility. Most breeding programs are designed to favor cross-pollination for these reasons.

Some tree species are dioecious, with the sexes separated on different trees. Members of the following genera are dioecious: ash (*Fraxinus* L.); holly (*Ilex* L.); juniper (*Juniperus* L.); poplar, cottonwood, and aspen (*Populus* L.); willow (*Salix* L.); and yew (*Taxus* L.). Fortunately, many of these genera can be propagated vegetatively. Also, in the case of the poplars, cross-pollination can be accomplished very quickly on a greenhouse bench by simply brushing pollen onto the receptive female flowers (Miller 1970).

Precocious (early flowering) species are adaptable to seedling seed orchards because they produce flowers at a young age and their seed production is abundant. Examples include Virginia pine (*Pinus virginiana* P. Mill.), sand pine (*P. clausa* (Chapman ex Engelm.) Vasey ex Sarg.), lodgepole pine (*P. contorta* Dougl. ex Loud.), and European black alder *(Alnus glutinosa* (L.) Gaertn.). Species that can be vegetatively propagated present unique opportunities because sexual reproduction is not necessary, and, therefore, the recombination of parental characteristics can be avoided. Species such as eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) can be produced vegetatively with unrooted stem cuttings planted directly in the field (figure 1). Other species require rooting under special conditions before they can survive field planting. These include Monterey pine (*Pinus radiata* D. Don), Norway spruce (*Picea abies* (L.) Karst.), tsugi (*Cryptomeria japonica* (L.f.) D. Don), Alaska-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach), sweetgum (*Liquidambar styraciflua* L.), and sycamore (*Platanus occidentalis* L).

Figure 1—Chapter 2, Genetic Improvement of Forest Trees: hybrid poplar plantation in Oregon planted from unrooted cuttings.

Concepts of Genetic Improvement

Phenotype and Genotype

When we look at an individual Sitka spruce (*Picea sitchensis* (Bong.) Carr.), a cherrybark oak (*Quercus pagodafolia* Raf.), a Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), or even an Angus bull, for example, we see a phenotype, a living organism with its own unique genetic constitution, as modified by its environment. In contrast, the genotype of the organism is encoded in its DNA. Each tree, therefore, has its own individual set of genetic blueprints. These are the instructions that will determine the genetic potential of its progeny.

The formula that "phenotype is the product of the genotype as affected by its environment" is often written as P = G + E. The phenotype is the organism that we see, measure, and with which we work. Life would be much simpler if the genotype was as obvious! Geneticists spend a great deal of their time and energy working to ascertain the actual genotype of their target organism. A major reason for progeny testing is to gain a better understanding of the genotypes of the selections that we are breeding. Recent advances in gene mapping with loblolly pine (*Pinus taeda* L.) (Sewell and Neale 1995) indicate that real progress is being made with the description of the loblolly genome. Some day we will understand the genomes of important commercial conifers as well as we understand common research bacteria and the common fruit fly.

The Genetic Code

The physical basis of genetic information is the DNA molecule, a long double helix of base pairs. This molecule is sufficiently stable to provide for the continuity of the species, yet flexible enough to allow for periodic changes. DNA therefore serves as both the blueprint for cell structure and metabolism and also the template for replication of many exact duplicates. These unique properties enable evolution to proceed in a remarkably stable universe. The evolutionary forces of mutation, migration, hybridization, and natural selection are responsible for the great variety of life that exists today.

New genotypes that result from mutations may move about (migration) and interbreed with other genotypes (hybridization). The new gene combinations that result are then sorted out by the process of natural selection. If these new genotypes are able to survive, reproduce, and leave more progeny than their competitors, they are "well-adapted." Therefore the tree species, races, and stands with which we are working are well-adapted to a specific site by virtue of their survival and reproduction in that environment.

Chromosome numbers. Chromosome numbers can change as a result of mutations. Polyploidy has been an important evolutionary factor in the plant kingdom. In most of the commercially important conifers, chromosome numbers range from n = 11 to 23 (Saylor 1972)(table 2). A notable exception is redwood—*Sequoia sempervirens* (Lamb. ex D. Don) Endl.—which is hexaploid (6n = 66). In contrast, chromosome numbers in the commercially important broadleaved trees vary widely, from n = 7 to 19, with a number of polyploids, including the genus alder (*Alnus* P. Mill.), birch (*Betula* L.), several *Prunus* species, and magnolias. A comprehensive table of chromosome numbers is found in Wright (1976).

Selection. Almost every process of genetic improvement starts with selection. This is true regardless if we are working with dairy cattle, winter wheat, or forest trees. The concept of selection involves the selection of a very small proportion of a population for one or more desirable characteristics. The difference between the proportion selected and the population mean (average) is called the selection differential.

Genetic gain or progress is measured by the product of the selection differential and the heritability (degree of genetic control) of the trait in question (for example height, straightness, and volume). Therefore by selecting individuals that are well above average in height, and assuming that the heritability (h^2) of height growth is sufficiently high to show progress, some gain in height should be expressed in the next generation. On the other hand, if the population in question is extremely uniform in height, and/or the heritability of height growth is low, selection may not be an effective approach. In some species, for example red pine—*Pinus resinosa* Soland.—the population is so uniform that selection for many traits is not cost-effective (Fowler and Morris 1977).

Hybridization

When populations are uniform and selection is not likely to be effective, one possible technique of genetic improvement is hybridization. Most of the successful hybrids in forestry have been interspecific (between species) hybrids. Examples include hybrid larch (*Larix leptolepis* x *decidua*), hybrid poplars (*Populus* spp. widely hybridized with many cultivars), the *Pinus rigida* x *taeda* cross in Korea (Hyun (1976), and the eucalyptus hybrids (Campinos 1980).

Heterosis (hybrid vigor) is a controversial topic among tree breeders. Many interspecific hybrids grow better than their parental species when planted in transitional environments. The actual quantitative documentation of heterosis is seldom published however.

A great deal of effort has been expended to produce a hybrid chestnut resistant to the chestnut blight—*Cryphonectria parasitica* (Murr.) Barr. Unfortunately, the American chestnut—*Castanea dentata* (Marsh.) Borkh.—which was devastated by the disease in the early 1900's, has little resistance to the disease. It is possible to cross American chestnut with Chinese chestnut—*C. mollissima* Blume—which is resistant to the blight. The hybrids produced are resistant, but unfortunately their form is so poor

Table 2—Chapter 2, Genetic Improvement of Forest Trees: chromosome numbers for some commercially important genera

# chromosomes	Genus
11	*Juniperus, Nyssa, Sequoia, Thuja*
12	*Abies, Larix, Picea, Pinus, Quercus, Tsuga*
13	*Acer*
14	*Betula*
15	*Liquidambar*
16	*Carya, Juglans*
19	*Liriodendron, Populus, Salix*
21	*Platanus*
23	*Fraxinus*

that they have little value as timber trees. There are two possible approaches to this problem. One is genetic engineering; the other is back-crossing to pure American chestnut. The American Chestnut Foundation has produced many successful back-crosses with the potential of restoring this grand tree to its former dominance in the eastern hardwood forest.

Many tree species that coexist on the same sites maintain their status as separate species primarily by a separation of flowering time. On transitional sites (ecotones) when one species is accelerated or retarded in flowering time, hybrids often result as in the case of the Coulter pine (*Pinus coulteri* D. Don) x Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) hybrids in California (Zobel 1951) and the pond pine (*Pinus serotina* Michx.) x loblolly pine (*P. taeda* L.) mixtures in North Carolina (Saylor and Kang 1973). Hybridization often occurs near the edge of the range where the species is losing its adaptive advantage. In southeastern Oklahoma and northeastern Texas, shortleaf (*P. echinata* P. Mill.) and loblolly pines occupy many sites together and hybrids are not uncommon (Abbott 1974).

Natural hybridization is a common phenomenon among the oaks (*Quercus* L.) (Muller 1952), some birches (Barnes and others 1974), and aspens (Pauley 1956).

Testing for Breeding Value

After the elite, select, or superior individuals have been selected, some system of testing their genetic value must be used. We have identified these trees as good phenotypes but we do not know their genotypes and therefore we are uncertain as to their value as breeding stock. Sometimes the outstanding trees in a stand may be taller than their neighbors due to an environmental advantage such as better soil or more moisture. It is important to use only trees with better than average genetic characteristics, as the environmental differences will not be passed on to future generations. In natural stands, it is critical to determine the age of individual trees. Trees growing together may have a similar size, yet be quite different in age. Obviously we would prefer that our select trees not be outstanding merely based on the fact that they are older than their neighbors.

The usual way to test vegetatively propagated trees is to plant them in blocks and compare performance with a standard population. This may be a clone of known performance, or in some cases seedlings from a standard seedlot may be used. Tests that are designed to evaluate the relative performance of a specific clone are called clonal tests.

Trees propagated from seed are usually progeny tested with one or more test designs modified from crop breeding. Early work with trees involved open-pollinated tests in which cones or seeds were collected from select trees and the half-sib progeny (female parent known, males unknown) were evaluated in plantations. As technology evolved, control-pollinated tests were developed that provided much better estimates of breeding values.

Most progeny tests are designed with row plots in field plantations, although single-tree plots have some advantages over row plots. A technique developed by the Western Gulf Forest Tree Improvement Cooperative uses greenhouse testing (Lowe and van Buijtenen 1989). This technique culls the poorest 17 to 20% of the progeny at about 5 months, based on shoot dry weight. This system reduces both the time and the cost of testing greatly.

Screening for Fusiform Rust Resistance

Due to the economic importance of fusiform rust with the southern pines, the USDA Forest Service established the Rust Testing Center at Bent Creek, North Carolina, in 1976. Forest Service pathologists developed a standardized inoculation system to screen loblolly and slash pine seedlings for susceptibility to fusiform rust (Knighten 1988). The Resistance Screening Center inoculates an average of 40,000 seedlings annually (figure 2). The southern tree improvement cooperatives routinely screen all new selections by sending seeds to the Rust Testing Center for evaluation. This is an essential part of the progeny testing procedure.

Screening for White Pine Blister Rust Resistance

Cooperative programs designed to develop resistance to white pine blister rust—*Cronartium ribicola* J.C. Fisch.—

Figure 2—Chapter 2, Genetic Improvement of Forest Trees: fusiform rust inoculation chamber at USDA Forest Service, Southern Station, Resistance Screening Center in North Carolina.

have been operating for a number of years in California and Idaho. For example, the USDA Forest Service, Pacific Southwest Region's program has identified 985 rust-resistant sugar pines—*Pinus lambertiana* Dougl.—for future tree improvement use. Family selection has been used as a breeding strategy.

Advanced Generation Breeding

Advanced generation breeding is usually designed with a combination of selections from first generation progeny test plantations in conjunction with new selections from operational plantations or other sources. A major advantage of selection in plantations is that the environment is usually more uniform than in natural stands. Tree age, spacing, and soils are often relatively uniform, with the result that the phenotype more closely approaches the genotype. In this case, selection is more efficient and gain can be increased. In most advanced generation breeding plans the best individuals are selected from the best families. It is important, however, to separate the production population from the breeding population to minimize the effects of inbreeding (Lowe and van Buijtenen 1986).

Starting a Tree Improvement Program

Establishing Objectives

Before a tree improvement program is begun, the situation needs comprehensive analysis. Tree improvement is long-term work, and a great deal of time and energy can be saved with some careful planning. The following factors should be considered.

1. **Desired products**
   - Wood properties necessary to produce the desired products
   - Required volume of wood
2. **Possible species**
   - Native or exotic (long-term consequences of using exotic species?)
   - Rotation length (shorter rotations give major improvements in gain per unit time)
3. **Chosen reforestation system**
   - Seed propagation or vegetative?
   - Bareroot or container seedlings?
   - Storage and distribution methods
   - Planting techniques and cultural procedures
4. **Plantation evaluation/survival system**
   - Required personnel
   - Numbers and skill levels
   - Required facilities and equipment
   - Required long-term budgets

Identifying the Raw Material To Be Used

Native versus exotic species. Are there native species available that are well-adapted to the planting sites to be used or would exotic species be more productive? The temptation to introduce an exotic species may be strong but there are a number of advantages of native species.

- They have evolved in harmony with their environment and usually have developed a mutual tolerance with competitors and pathogens. Exotics, on the other hand, may not perform well in a new environment—they have not been exposed to the stresses of this new environment and often have not had sufficient time to adapt to local conditions.
- Native species have well-defined management regimes that have been tested over time. Reforestation personnel have learned how to grow, ship, store and plant the seedlings or cuttings.

An exotic species introduced into a new environment does not necessarily produce wood with the same characteristics as in its place of origin. Excessive amounts of juvenile wood are common, as are wide bands of earlywood and narrow bands of latewood. These growth patterns lead to low-density wood and drying defects (Zobel 1981). There are notable exceptions, such as Monterey pines grown in New Zealand, but in general the wood quality of native species is more desirable than that of exotics.

Public opinion is running strongly in favor of native species both in the United States and overseas. Plantation forestry with exotic species has encountered strong public resistance in a number of locations.

Successful introductions of exotics. There have been many successful introductions of exotic species world-wide (table 3). Native U.S. species have been introduced into other countries, especially Monterey pine, a minor species in coastal California that has become the backbone of the forest products industry in New Zealand, a country with few conifers of economic importance. Monterey pine has also done well in Australia, Chile, and South Africa. Douglas-fir and Sitka spruce, both native to the Pacific Northwest, have been widely planted in Great Britain and northern Europe. Several of the southern pines have been widely planted in Australia, South America, and South Africa.

Land races. When the decision has been made to use a given exotic species, the question arises as to the source of material to be used. Often it is more efficient to select within a land race of the species rather than the original population in its native environment. A land race has become adapted to

its new environment by virtue of its survival there for a number of years. For example, Monterey pine has been growing in New Zealand for over 100 years. During that period, this species has weathered many storms and fought off many pathogens. Thus, natural selection has altered the population by gradually eliminating individuals not well adapted to their new environment. Selection of individual trees within this land race will be more cost-effective therefore than returning to the native populations in California.

Geographic variation. Philip Wakeley of the USDA Forest Service established one of the first definitive studies of geographic variation in the United States in 1926 and 1927. Wakeley collected loblolly pine seed from Arkansas, Georgia, Texas, and locally (Louisiana), grew the seedlings and planted them on a site near Bogalusa, Louisiana (table 4). This study was the first solid evidence that the source of seeds was important in the growth and rust resistance of loblolly pine. The trees grown from seeds collected locally produced almost twice the volume of wood as the other sources after 22 years. In addition, this was the first evidence that loblolly pine from Livingston Parish, Louisiana, had special merit as a rust-resistant source.

Following this test at Bogalusa, the Southwide Pine Seed Source Study was designed by Wakeley as a cooperative project involving 17 different agencies, with field plots established from Texas to the Atlantic coast. This study demonstrated that loblolly pines grown from sources west of the Mississippi River usually had better planting survival and greater rust resistance than those from eastern sources. On the other hand, seedlings grown from sources along the southern Atlantic coast had faster growth rates than those from western sources (Wells 1969; Wells and Wakeley 1966; Wells 1983).

The results of this study have led to widespread planting of Livingston Parish loblolly seedlings throughout the southeastern coastal plain, leading to major reductions in fusiform rust infection (Wells 1985). Likewise, forest industry has planted seeds from Atlantic coast sources of loblolly in Arkansas and Oklahoma with impressive gains in volume growth on the better sites (Lambeth and others 1984) (figure 3).

On the Pacific coast, the Eddy Tree Breeding Station was established in California in 1925. This later became the Western Institute of Forest Genetics and played a major role in the development of forest genetics in the West.

The 2 varieties of Douglas-fir (coastal and interior) (figure 4). have been studied extensively (Kung and Wright 1972). The coastal variety has been widely planted in Great Britain and northern Europe. Other western species with pronounced racial differentiation are ponderosa pine, and grand (*Abies grandis* (Dougl. ex D. Don) Lindl.) and white firs (*A. concolor* (Gord. & Glend.) Lindl. ex Hildebr.). In the Northern United States, white spruce (*Picea glauca* (Moench.) Voss) occupies an extensive east–west range with considerable racial variation (Nienstaedt 1968).

Table 3—Chapter 2, Genetic Improvement of Forest Trees: examples of exotic species used in plantation forestry

Origin	Location of planting					
	North America	Central America	South America	Europe	Africa	Australia & New Zealand
North America						
Picea sitchensis (Bong.) Carr.				X		
Pinus elliotti var. *elliotti* Engelm.		X	X		X	X
Pinus radiata D. Don			X			X
Pinus taeda L.		X	X		X	X
Populus L. spp.				X		
Pseudotsuga menziesii (Mirb.) Franco				X		X
Central America						
Pinus caribea Morelet			X			X
Pinus oocarpa Schiede ex. Schltdl.		X			X	
Europe						
Picea abies L.	X					
Populus L. spp.	X					
Asia						
Gmelina arborea Roxb.			X		X	
Tectona grandis L. f.		X	X		X	
Australia/New Zealand						
Eucalyptus L.Her. spp.	X	X	X		X	

Figure 3—Chapter 2, Genetic Improvement of Forest Trees: areas of major commercial use of non-local loblolly pine seedlings. Coastal North Carolina seeds were used in Arkasas and Oklahoma **(A)** for increased growth rate and Livingston Parish, Louisiana, seeds were used from Mississsippi to South Carolina **(B)** for improved rust resistance.

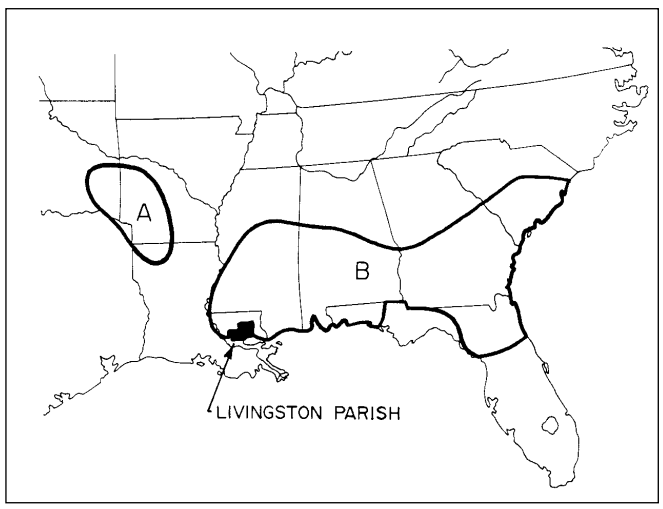
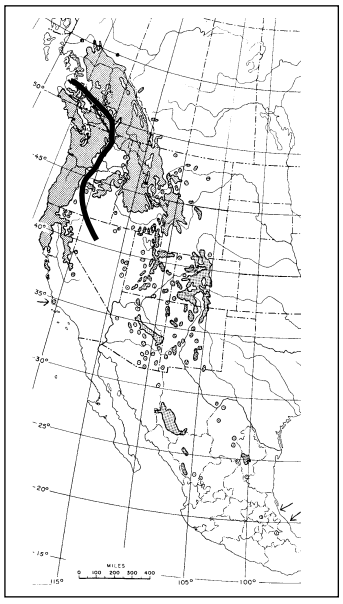


Figure 4—Chapter 2, Genetic Improvement of Forest Trees: the range of Douglas-fir, with the 2 varieties separated by a black line.



Utilizing the Raw Material

Seed production areas. Time is a critical factor in determining the route to follow in a tree improvement program. A useful expedient is the seed production area (seed stand). This is a high-quality stand that can be thinned to remove the lower quality individuals and then managed for seed production (Cole 1963; Rudolf 1959). Although the gain from these stands is not high, (Easley 1963), the time saved can be more important than the degree of improvement. These stands can be managed by prescribed burning, fertilized, and sprayed for insect control. Seeds can be collected by climbing, shaking, tarping, or felling trees. An efficient seed collection system can be designed where the felling of trees is planned to coincide with good seedcrops.

Although natural stands are preferred sources for seed production areas (figure 5), plantations are often used where the seed source can be verified. In these cases, the plantation is treated like a land race, and good performance over a

Figure 5—Chapter 2, Genetic Improvement of Forest Trees: longleaf pine seed production area in Georgia.

Table 4—Chapter 2, Genetic Improvement of Forest Trees: loblolly pine (*Pinus taeda* L.) plantation* performance illustrates the importance of geographic sources of seed

Source	Survival (%)	Height		dbh		Volume		Rust infection (%)
		m	ft	cm	in	m^2/ha	cords/ac	
Louisiana (Livingston Co.)	82	14	46	12	6.7	265	42	4
Texas (Montgomery Co.)	83	12	41	13	5.2	145	23	6
Georgia (Clarke Co.)	77	11.5	38	13	5.2	113	18	37
Arkansas (Howard Co.)	84	11	36	12	4.7	94	15	5

Source: Wakeley (1954).

* Located in Bogalusa, Louisiana.

given time is evidence that this plantation has adaptive value on this site.

Clonal seed orchards. The most common tree improvement system is the clonal seed orchard (figure 6). These have been established for many outcrossing species worldwide. The procedures used involve selection of individual trees, progeny testing to determine their breeding value, and replication of the ortets (selections) in an orchard environment. In actual practice, the orchard is usually established by grafting and the progeny testing is done by controlled pollinations within the orchard or in clonal banks.

Seed production usually begins before progeny testing is completed, resulting in the production of improved seeds that cannot be certified as genetically superior (seed certification is covered in chapter 6) until progeny testing is completed and the orchard can be rogued (that is, trees with low breeding value are removed).

Selecting Plus Trees

Selection of plus trees from wild stands that are pure (single species) and relatively even-aged usually involves grading candidate trees in comparison with the best adjacent crop trees (of similar age) in the stand. Characteristics compared with southern pine (for timber) are straightness, height, DBH, volume, form class, crown size, branch diameter, branch angle, natural pruning and wood quality. Any evidence of insect or disease susceptibility usually calls for rejection of the candidate. Acceptance of the candidate tree depends on the numerical rating of the tree, its wood quality, age class, geographic location, and any special attributes.

Figure 6—Chapter 2, Genetic Improvement of Forest Trees: loblolly pine clonal seed orchard in Arkansas.

Selecting Orchard Sites

All seed orchards require good access, level topography, and well-drained soils. Because vehicular traffic is essential in the management and harvesting of orchards, a coarse-textured soil is mandatory. Subsoiling is practiced in many seed orchards to fracture any hardpans formed from compaction by vehicles. Even in sandy soils, compaction can seriously reduce root growth of the trees. Establishment of a year-round ground cover is important to stabilize the soil and prevent or reduce erosion (Jett 1986).

Establishment

Most clonal orchards are established by grafting, although at least one slash pine orchard has been planted with cuttings (Bengston 1969). Rootstock planted in the field can be grafted in-place (field-grafting) or potted stock grown in a greenhouse, lath-house, or nursery bed can be grafted. Grafting on potted stock is more cost-effective, but field-grafting is preferred by some orchard managers because of the often shorter time to reach commercial cone production.

Graft incompatibility occurs in many species, including most conifers. This is a problem in roughly 22% of southern pine clones (Lantz 1973) and it is particularly serious in Douglas-fir, where up to 67% of the clones may be affected (Wheat 1967). There is some evidence that clonal root stocks from related material may reduce incompatibility rates (Bower and McKinley 1987) but the data are not conclusive. Copes (1967) has developed a tissue sampling technique that can be used to predict incompatibility in Douglas-fir.

Management

Most seed orchards are fertilized to promote flowering and some are irrigated to reduce the impact of moisture stress. Insect control is essential for maximum seed production. In the absence of cone and seed insect control, Belcher and DeBarr (1975) have estimated that 11% of the loblolly cones were attacked by cone worms (*Dioryctria* spp.). In their report on 26 seed orchards surveyed over 3 years, an average of 9.9% of the collected seeds were damaged by insects. There was a large amount of clonal variation, as the range of cone worm attack was from 0 to 67%, depending on clonal susceptibility.

More recently, Jett and Hatcher (1987) reported that cone worms can cause losses exceeding 90% of loblolly cones when pesticides are not used.

Pollen Contamination

Most seed orchards are located with some consideration for pollen contamination. Unfortunately economics often

dictates locations that cause a major problem with pollen contamination. Early seed orchard establishment in the South carried a recommendation of at least 122-m (400-ft) isolation zones surrounding the orchard (Squillace 1967). Later studies indicated that vegetation formed a more effective barrier than either soil or sod.

Pollen contamination in seed orchards was estimated by Adams and Birkes (1989) using isozyme analysis. In seed orchards of Douglas-fir, loblolly pine, and Scots pine (*Pinus sylvestris* L.), they estimated that as much as 50% of the pollination within the orchards was due to outside pollen. The amount of self-fertilization within the orchards was estimated as less than 10%, with considerable variation by clone.

An additional study by Smith and Adams (1983) also indicated that pollen contamination was in the 40 to 52% range for 2 Douglas-fir seed orchards in Oregon. Suggestions for reducing contamination included more complete geographic isolation, water spraying to retard flower development, and supplemental mass pollination.

Supplemental Mass Pollination

Supplemental mass pollination (SMP) has been used effectively in southern pines, Douglas-fir, and Scots pine (Bridgwater and others 1993). The authors have summarized their recommendations for success with SMP:

1. The goals of SMP must be clear.
2. Orchard phenology must be monitored in order to apply SMP prior to maximum pollen flight in the orchard.
3. Fresh pollen or high viability stored pollen must be used.
4. The pollen application system must be effective.
5. The success of the SMP can be monitored with isozymes or other procedures.

Harvesting

Cones, seeds, and fruits may be harvested by climbing or with bucket trucks, aerial lifts (figure 7), tree shakers, or seed collection nets. Seed collection nets as developed by the Georgia Forestry Commission are effective when bulk collections are harvested from the orchard (figure 8). When individual tree (or clonal) collections are needed, the other systems must be used. The USDA Forest Service Missoula Technology Development Center refined the net retrieval system concept (McConnell and Edwards 1984), which has been widely copied and modified. This system is an effective method of harvesting southern pine seeds on nets when orchard mix collections can be used.

Figure 7—Chapter 2, Genetic Improvement of Forest Trees: cone collection with JLG lift in South Carolina.

Genetic Gains

Realized genetic gains in volume growth from first generation southern pine clonal seed orchards have ranged from 6% with un-rogued loblolly and slash pine orchards to 17% for rogued orchards of these species (Squillace 1989). The gains from advanced generation loblolly orchards have been predicted at 25% greater volume than unimproved material for the second generation, 35% for the third generation, and 45% for the fourth generation (Zobel and Talbert 1984).

Advanced-Generation Breeding

Advanced-generation breeding often is designed to combine the best individuals from the best families in the first generation with unrelated individuals from a separate breeding population. The Western Gulf Forest Tree Improvement Program has developed a sub-line system separating the breeding population into breeding groups that are crossed to produce seeds only when a production orchard is established (Lowe and van Buijtenen 1986). With this system, inbreeding is restricted to the breeding populations and the production populations are not affected.

A similar system has been used with northern red oak—*Quercus rubra* L.—in Indiana. Coggeshall and Beineke (1986) have designed 6 sub-lines with 30 clones in each for a total of 180 clones. These sub-lines will be crossed only when the production seed orchard is established.

Figure 8—Chapter 2, Genetic Improvement of Forest Trees: seed collection nets deployed on floor of Georgia Forestry Commission seed orchard.

Figure 9—Chapter 2, Genetic Improvement of Forest Trees: accelerratedd breeding orchard in North Carolina.

Seedling Seed Orchards

When working with precocious species, considerable time can be saved by collecting open-pollinated seed from select trees, growing the half-sib progeny in a nursery, and establishing a progeny test/seed orchard with the seedlings. A major problem with this system is designing a plantation that is effective for progeny testing and will also permit effective seed production after the poor performers are removed. Effective designs have been developed by Wright (1976) and Hodge and others (1995).

A recent report by Hodge and others (1995) indicated a gain of 10.7% in volume for a seedling seed orchard of longleaf pine (*Pinus palustris* Mill.) at 8 years. In this case the heritability of volume growth was calculated at 0.21 and there was a moderate genotype × environment interaction related to geographic regions.

Accelerated Breeding

Accelerated breeding techniques developed in recent years can substantially reduce the breeding cycle. One of the most direct methods is selection at younger ages. A pilot-scale accelerated breeding study was developed by van Buijtenen and others (1986). This study used a 3-phase procedure with half of the loblolly pine families eliminated in each test. The tests measured dry weight, root growth potential, and resistance to heat stress. The survivors of these tests were then subjected to flower-induction techniques.

Potted seed orchards growing in greenhouses can reduce the length of the breeding cycle by at least 20% (Zobel and Talbert 1984) (figure 9). In this case, a 20-year cycle can be reduced to 16 years by accelerating flowering in the greenhouse as compared to a conventional outdoor seed orchard. The trees can be maintained in 20- to 40-gallon tubs with a drip irrigation system. McKeand and Weir (1983) calculated that a reduction of 6 years in the breeding cycle with a 30,000 seedlings per year regeneration program would amount to a savings of $2 million. A similar system has been reported for western hemlock (Bower and others 1986). In this case, potted ramets produced about 10 times the amount of seeds as field-grown trees.

With a potted orchard, several techniques can be utilized to increase both male and female flowers. Water stress and applications of gibberelic acid ($GA_{4/7}$) will promote early female flowers (Todhunter 1988), whereas out-of-phase dormancy (Greenwood 1981) will speed up the development of male flowers. Wire girdling is also an effective way to promote male flowering.

Top-working grafted loblolly ramets has also accelerated flower production (Bramlett and Burris 1995). In this case, both male and female flowers were produced in the year following grafting.

Deployment of Genetically Improved Material

Seed Zones

Seed zones have been established for most of the major commercial forest species. These are areas that are environmentally similar and within which a given source can be expected to perform uniformly. When reforestation is needed within the zone, seeds should be collected from that zone. In some cases, when seeds are not available from that zone, seeds from an adjacent zone may be substituted.

In the Western United States, seed zones can be quite narrow, depending on the topography. For example, seed zones for Douglas-fir in Oregon are delineated on 152-m (500-ft) elevation intervals (Ching 1978). Restricted zones have also been recommended in the northern Rocky Mountains for western white—*Pinus monticola* Dougl. ex D. Don—and ponderosa pines (Rehfeldt and Hoff 1976).

In the South, seed zones for most species are much broader, reflecting the larger geographic provinces and more uniform topography (Lantz and Kraus 1987)(figure 10). The Western Gulf Forest Tree Improvement Program has defined specific seed deployment zones for areas west of the Mississippi River (Byram and others, 1988), and the North Carolina State University—Industry Cooperative Tree Improvement Program has adopted a more flexible approach for areas to the east (McKeand and others 1992)

Genotype x Environment Interactions

Progeny tests of the first and second generation select trees have highlighted some outstanding families in the southern pines. Some of these families perform well on dry sites, some on wet sites, and some do well across-the-board. The famous International Paper clone 7-56, for example, seems to be a top performer wherever it is planted.

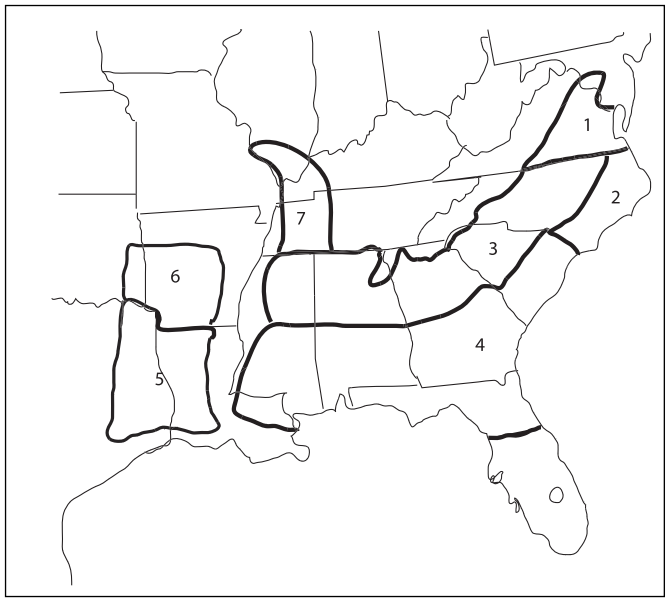
In general the genotype × environment interaction (change in relative rank among tested families) of most improved material has been unimportant. However, the University of Florida Cooperative Forest Genetics Research Program has reported a strong genotype x environment interaction for growth with some recent loblolly pine tests (Hodge and others 1995).

Single-Family Block Plantations

Many forest industries in the South routinely establish single-family block plantations and often record a growth advantage compared to mixed family blocks (Williams and others 1983). Using block plantings rather than progeny tests, Gladstone and others (1987) recorded 16% greater stand volumes for single-family plantings than for woods-run material. Mixed family blocks had only 11% greater volume than the checks.

Although single-family blocks may perform well on company land for short rotations, few non-industrial private forest landowners understand the risks involved. When a single family is planted on private land where long rotations are used and where natural regeneration may be employed, genetic diversity can be reduced to a low level. In only 1 or 2 cycles of natural regeneration, inbreeding could seriously reduce growth and productivity.

Figure 10—Chapter 2, Genetic Improvement of Forest Trees: seed zones for loplolly pine.



Molecular Biology

Isozymes

Brewbaker (1967) was one of the first scientists to propose the study and use of isozymes in forestry. Since then, isozymes have been widely used for taxonomic work, pollen contamination estimates, heterozygosity estimates, and a number of other uses. In isozyme analysis, a single gene codes for production of a single protein that can be visually distinguished as one band on an electrophoretic gel. The band pattern on a stained gel may be interpreted as a direct reflection of the genotype of the tree. Cotyledons, needles, or embryos (all diploid tissues) may be used or pollen grains and female gametophytes (haploid tissues) may be used.

Isozymes have been used to compare the rates of heterozygosity and outcrossing (El-Kassaby and others 1986) with Douglas-fir. These authors found no significant differences between clonal and seedling seed orchards in outcrossing rates. There were, however, significantly greater proportions of homozygous progeny from the seedling orchard.

Although isozyme analysis has been an effective tool for many forest genetics studies, Libby and others (1997), summarizing a southern meeting on genetic diversity, found that isozyme data have a number of limitations when used to estimate the genetic variation within a single species. However, isozyme analysis has been widely used to estimate the amount of pollen contamination in seed orchards (Adams and Birkes 1989).

The USDA Forest Service has established a National Forest Genetics Electrophoresis Laboratory in Camino, California, where genetic variation studies, taxonomic determinations, "DNA fingerprinting," and the effect of silvicultural and management procedures can be evaluated. This laboratory served an important role after Hurricane Hugo demolished the longleaf pine seed orchard on the Francis Marion National Forest in coastal South Carolina. Isozyme and DNA analyses were used to identify the surviving ramets in the orchard and facilitate reconstruction of the orchard.

Gene Mapping

New techniques such as RFLPs (restriction fragment length polymorphisms) (Nance and Nelson 1989) and RAPDs (random amplification of polymorphic DNA) (Sewell and Neale 1995) have paved the way for significant advances in gene mapping of QTLs (quantitative trait loci). Conkle (1981) produced linkage maps for several *Pinaceae* species and Sewell and Neale (1995) constructed a "consensus" map for loblolly pine. Another technique for mapping genes using PCR (polymerase chain reaction) markers has been developed for pines by Harry and Neale (1993). Other mapping work has been done with *Eucalyptus* spp. and *Populus* spp. These mapping techniques are resulting in a great deal of data on the genome of loblolly pine. This information will allow more efficient selection procedures (marker-assisted selection) to be employed in the future.

In addition to the work done on pollen contamination and heterozygosity using isozymes, RAPD markers have been used to assess genetic variation in aspen following the 1988 Yellowstone fires (Tuskan 1995).

Fingerprinting

Electrophoresis has been used for a number of years to "fingerprint" clonal material in seed orchards. Now PCR techniques have been used to identify Douglas-fir seedlots produced in a seed orchard in British Columbia and RAPD markers have been used to identify Norway spruce clones in Austria (Neale 1995).

Genetic Engineering

Genetic engineering has received a considerable amount of attention from the media, but few examples of forest tree applications are available. There has been a case of gene transfer in hybrid poplar that conferred resistance to glyphosate (herbicide). There is also interest in transfer of DNA with resistance to chestnut blight (Carraway and others 1993). In this case, somatic embryogenesis could be used to establish ovules and zygotic embryos on culture media. Transfer of this material would be accomplished by bombardment with plasmid DNA containing the resistant gene or genes.

Tree Improvement Cooperatives

Tree improvement cooperatives have been established in the major timber-growing regions of the United States and Canada, including California, the Pacific Northwest, the Inland Empire (also known as the intermountain region or the Great Basin), the Great Lakes region, and the South. Advantages of these cooperatives include a long-term breeding plan, often developed by forest geneticists at a land grant university, statistical support for progeny test design and analysis, laboratory facilities for wood-quality determinations and soil tests, and pollen and seed processing facilities. Technology transfer of new developments in the field of tree improvement and training is also an important function of these cooperatives.

Often select trees, pollen, seed, and grafting material are shared among members of the cooperative. Some cooperatives share orchards and even nursery sites. Duplication of effort is minimized and cooperative members gain significant economies of scale as they share breeding and testing workloads. Separate staffs are not needed by the individual organizations as the scientists and support personnel employed by the cooperatives are shared by all member organizations.

The South

Bruce Zobel started tree improvement cooperatives in the United States in 1951 at Texas A&M University. A few years later, Tom Perry began the University of Florida Cooperative Forest Genetics Research Program. Zobel later moved to the North Carolina State University and organized the NC State University Industry Cooperative Tree Improvement Program. J.P. van Buijtnen reorganized the Texas A&M Cooperative as the Western Gulf Forest Tree Improvement Coop in 1969. In the Spring 1988 Society of American Foresters Tree Genetics and Improvement Working Group newsletter, Tim White reported that in 1987 these 3 cooperatives involved 28 forest industries, 12 State forestry agencies, and 3 seed companies. Average annual seed production over all members at that time ranged from 60,000 to 90,000 kg (70 to 100 tons) of pine seed and the average annual hectares planted with seedlings was 728,000 (1.8 million acres). Recent divestitures of industrial forest land dramatically decreased cooperative membership. This may seriously and negatively impact future seed production.

The Pacific Northwest

Tree improvement activities began in the Pacific Northwest in the 1950's when the Industrial Forestry Association coordinated the establishment of clonal seed orchards for coastal Douglas-fir. In the 1960's, forest industry started hiring forest geneticists and individual programs were started by several companies. About this time, the USDA Forest Service started a tree improvement program for Douglas-fir; western hemlock (*Tsuga occidentalis* (Raf.) Sarg.); and ponderosa, western white, and sugar pines on national forest lands in Oregon and Washington (Daniels 1994). The Forest Service program was followed in the 1970's by the USDI Bureau of Land Management's tree improvement program for Douglas-fir in western Oregon.

From 1967 to 1985, Roy Silen at the USDA Forest Service's Pacific Northwest Forest and Range Experiment Station and Joe Wheat of the Industrial Forestry Association developed 20 cooperatives for Douglas-fir and 2 for western hemlock. These "progressive tree improvement programs" featured low-intensity selection of large numbers of roadside trees followed by open-pollinated progeny tests (in contrast to the high-intensity selection practiced in most of the southern pine programs). In 1986, the Industrial Forestry Association's Pacific Northwest Program was reorganized and named the Northwest Tree Improvement Cooperative of the Western Forestry and Conservation Association. This organization currently has 37 members, with a land base of 2.8 million hectares (6.9 million acres) and more than 80 breeding zones (Daniels 1994).

The overall Pacific Northwest region had a total of 282 seed orchards with a total of 1,389 ha (3,473 ac) in western Washington, western Oregon, and northern California in 1994 (Daniels 1994). Federal agencies manage 64% of this area; industry, 30%; and States and other cooperative groups, 6%.

The Inland Empire

The Inland Empire Tree Improvement Cooperative membership has 20 separate organizations, including forest industry, State forestry agencies, tribal councils, Federal agencies, universities, and other private organizations. Lauren Fins established the cooperative in 1978 at the University of Idaho to serve Idaho, western Montana, and eastern Washington. The cooperative has established 16.8 ha (42 ac) of western white pine and ponderosa pine orchards which have produced an average of 322 kg (710 lb) of seed annually. In addition to these cooperative orchards, many member organizations have established their own orchards.

California

The California Tree Improvement Association, organized in 1978 with 26 members, manages over 9 million acres of forestland. Ponderosa pine was the first species selected, followed by Douglas-fir and sugar pine. Members include forest industry, the State of California, and the USDA Forest Service. Local tree improvement associations were formed to focus on one or more of the California tree seed zones. The main objectives of the association are the selection of superior trees, the establishment of clone banks, the establishment of progeny test sites, and the establishment of a ponderosa pine seed orchard.

The Great Lakes Region

The Minnesota Tree Improvement Cooperative was established in 1980 and currently has 18 full members and 7 supporting members. The cooperative is working with black (*Picea mariana* (Mill.) B.S.P) and white spruces, and jack, red, and white pines. There are 35 seed orchards occupying about 50 ha (125 ac). In 1995, about 30 hl (84 bu) of cones were collected from 3 of these orchards. Six orchards were approved for production of certified seed in 1995. Gains in height growth have ranged from 3 to 9%.

The Future

The demand for wood products will continue to increase worldwide. Computer and printing paper will be in great demand, particularly in Southeast Asia where population growth is expanding exponentially (Kellison 1997).

In the United States, timber harvesting on the forest land base is being progressively restricted, which dictates that wood production be concentrated on less land area each year. This requires management for maximum wood growth on our most productive sites. Fortunately this will result in reduced pressure on average and marginal sites which often have high value for recreation and aesthetic pursuits.

Tree improvement programs, combined with intensive management, have dramatically increased wood yields. In the Southeastern United States, genetically improved loblolly pine on good sites, under maximum cultural care, can be expected to yield 10.8 to 14.4 m^3 (3 to 4 cords) per 0.4 ha (1 ac) per year. On the Pacific Coast, vegetatively propagated hybrid cottonwood grown under maximum culture on 6- to 7-year rotations is producing 25.2 m^3 (7 cords) per 0.4 ha (1 ac) per year (Kellison 1997). In South America, southeast Asia, and South Africa, plantations of acacia, eucalyptus, and Gmelina from genetically improved sources are expected to yield about 25.2 m^3 (7 cords) per 0.4 ha (1 ac) per year. Many of these plantations can be managed with coppice rotations to further increase their economic value.

Tree breeding techniques must be fine-tuned in order to provide these increased yields of wood. Vegetative propagation procedures can be improved to provide more propagules at lower cost. Accelerated breeding will shorten generation intervals. Marker-assisted selection using molecular biology technology will result in both more efficient selection and shorter breeding cycles.

Continued research is needed to identify those parameters that predict the performance of specific genotypes on specific sites and work is needed to quantify genotype × environment interactions over a wide range of sites.

Public education will assume even greater importance in the future as competition for land increases. Engagement with many diverse groups will be required for making progress based on sound scientific principles. Many different approaches and mixes of objectives are possible and the consequences, both positive and negative, will have to be weighed in the balance of public opinion. Topics such as the long-term effects of using biotechnology in the forest, planting selected families on large land areas, and preservation of non-commercial species must be openly discussed.

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Chapter 3

Seed Harvesting and Conditioning

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Introduction

Most forest trees and shrubs grown for artificial regeneration purposes, and some grown horticulturally, are reproduced from seeds. Seed quality is, therefore, of critical importance in determining the many options and outcomes in producing a crop of seedlings. Only high-quality seeds that can be planted by machinery permit bareroot seedlings to be grown at the uniform and controlled bed densities needed to produce the desired seedlings at the most economical cost. Uniform and controlled bed densities facilitate more efficient and mechanized methods of weed control, root-pruning, and lifting of seedlings. Adverse consequences occur in both labor costs and the genetic makeup of the seedlings unless high-quality seeds are used and properly managed. Therefore, a poor job of seed handling at harvest and conditioning can have serious negative impacts on the quality and availability of seedlings. However, a good job at this point will have positive impacts on seedling status. It also makes sense economically to focus effort at this point in the process, because more efficiencies can then be realized at later stages.

This chapter begins with what to consider in planning a seed harvest, how to harvest, how to temporarily store seeds, and how to extract, clean, and upgrade the finished seeds. A discussion of quality control concludes the chapter.

Harvesting

Seed harvest is the first step in producing a high-quality seedlot. This statement assumes that genetic considerations have been properly addressed in planning the seed harvest (see chapter 2). Quantities of seeds to collect, initial seed quality, and the timing of collections are the key quality factors in seed harvest. Timing is important because maximum seed viability and vigor occur at physiological maturity (figure 1). Collecting too early results in lower seed quality due to seed immaturity and reduced yield. Collecting too late can also be detrimental, because seeds may be lost to seed shed, predation by animals or insects, or seed deterioration. However, some species mature after natural seedfall; these include various ash species (*Fraxinus* spp.) and ginkgo (*Ginkgo biloba* L.). The initial seed quality must be assessed to avoid collecting seeds that are empty, malformed, or damaged. Quantity of seeds to collect influences quality because the seeds must be processed before deterioration becomes measurable.

Planning and preparation

Quantities to collect. The quantity of seeds to collect can be computed from nursery records and seed-plant production records of past harvests (table 1). If this information is not available, then general averages can be taken from the tables in the generic chapters of this handbook. Determining the number of cones or fruits needed to give this desired amount of seed can be predicted by cutting open a sample of cones or fruits. Because of variation from crop to crop, location to location, and even tree to tree, it is wise to always cut a few fruits to be sure of the quality and not waste collection effort on poor crops. Figure 2 shows a cutting method for assessing the number of filled seeds in a conifer cone; table 2 lists a good average seed count for 4 western conifers. When the desirable number of seeds per cone is found on the cut face, then collections are made. Usually a minimum number of good seeds must be found when cutting before the crop is accepted. This minimum number will vary with the need for the seeds, the cost of collection, and the quality of alternative collection sites. Douglas (1969) suggests that 50% of the seeds exposed on the cut face of true fir (*Abies* spp.) cones should be full, and Schubert and Adams (1971) set this percentage of good seeds at 75% for pines (*Pinus* spp.).

How the number of seeds on the cut face of a cone corresponds to the total number of seeds in the cone is shown in table 3. Such a table is constructed by making longitudinal cuts on the cones, counting the number of seeds on the cut face, and then opening the cone by drying or dissection to determine the total number of good seeds in the cone. For example, the authors of the data in table 3 found in their samples that when 8 good seeds appeared on the cut face of longleaf pine (*Pinus palustris* P. Mill.) cones, there would be, on the average, 59 seeds per cone. In figure 3, cutting ash seeds to determine the percentage of filled seeds is an example of a way to examine the quality of a hardwood fruit. Such cutting procedures provide an estimate of the amount of good seed that can be expected from a given quantity of fruits or cones.

Positive species identification. Another vital step is making a positive identification of the species. Sometimes this is relatively easy. For example, there may be no close relatives to the species in the area. Douglas-fir—*Pseudotsuga menziesii* (Mirbel) Franco—is the only species in its genus in the coastal western United States and has a unique cone. It thus presents little problem in species identification. Oaks (*Quercus* spp.), on the other hand, overlap in their range in many parts of the country and often hybridize, making positive identification more challenging. An addi-

Figure 1—Chapter 3, Seed Harvesting and Conditioning: seed quality changes over time.

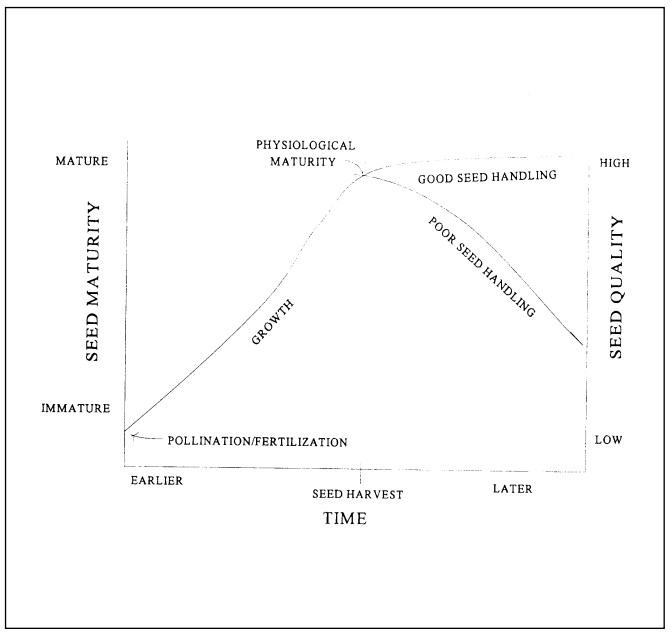


Figure 2—Chapter 3, Seed Harvesting and Conditioning: cutting a pine cone longitudinally helps estimate when and where to collect cones

Table 1—Chapter 3, Seed Harvesting and Conditioning: the questions to answer in computing the amount of seeds to collect

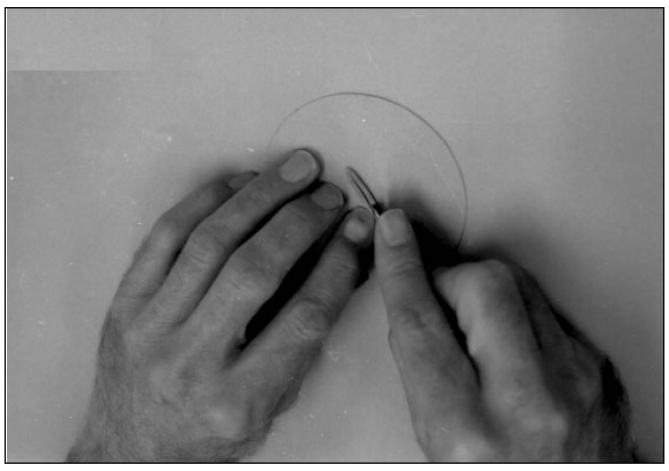
Question	Value	Calculated quantity of seeds needed	Example
How many plants are to be produced?	200,000	—	—
How many years of production is this?	3	200,000 x 3	600,000
What is the ratio of seedlings to viable seeds?	80%	600,000 ÷ 0.8	750,000
What is the viability of the seeds?	80%	750,000 ÷ 0.8	937,500
How many seeds are there per unit weight*?	99,000	937,500 ÷ 99,000	9.5 kg
What is the purity?	95%	9.5 ÷ 0.95	10 kg
What volume of the "raw collection unit" (that is, seeds, fruits, or cones) must be collected to obtain the desired weight* of pure seeds?	0.8 kg/hl	10 kg x 0.8 kg/hl	12.5 hl
Is there sufficient capacity for post-harvest storage & timely conditioning for the desired volume of seeds?			

* Weight in kilograms (kg) or pounds (lb).

tional challenge is presented when the scientific names are debated by taxonomists. Genera such as locust (*Robinia* L.) and blueberry (*Vaccinium* L.) have gone through extensive reclassifications. Therefore, careful attention to nomenclature and good record keeping are very important in maintaining control over regeneration work. This is especially true when many diverse species are involved. The finished seeds of many related species are impossible to identify and separate. Without good collection records, the true identity of a seedlot can easily be lost. Collecting and preserving leaf, bud, and twig samples along with a seedlot can serve as an excellent check on species identity. Collecting these vegetative parts is important for seed collectors who lack knowledge of botany. Later, knowledgeable persons can verify the identity of a seedlot from the vegetative parts.

Careful seed-source identification is also vital. Not properly documenting the source of a seedlot can be as disastrous as misidentifying the species, perhaps even more so,

Figure 3—Chapter 3, seed Harvesting and Conditioning: cutting ash samaras open will tell if the fruits are filled and if the embryos are mature.



because the mistake might not be known until an outplanted crop fails because of poor adaptation. Seed certification procedures are a good way to track seed-source identity.

Seed structures. Accurate and complete knowledge of seed and fruit structures is essential for making accurate estimates of initial seed quality. When beginning work with an unfamiliar species, workers should dissect some fruits and seeds in order to become familiar with the normal seed structures. The condition of the embryo cannot be evaluated if its location and shape are not known. Workers also need to recognize the outside appearance of seeds. Seeds, especially small ones, can be confused with trash or other floral parts if their true shape is not known. Chapter 1 provides a general discussion of flowering and seed formation. Detailed descriptions and drawings showing the seed structure and maturity indices are presented for each genus in part 2 of this manual.

Seed maturity. Fruits and cones should be collected only when seeds are sufficiently mature. Properly timing the collection of seed depends on correctly estimating seed maturity, which is often difficult because it is influenced by weather, genotype, site quality, site aspect, and location on the plant. Seasonal events and location cause wide variability in timing and length of the collection period. For example, if snow is deep and melts late at a high-elevation site, trees may flower so late that seedcrops do not even mature. Conversely, an early spring and dry summer can cause seeds to ripen and disperse very early. When drying winds occur in the autumn, most seeds of several western conifers and eastern white pine (*Pinus strobus* L.) will disperse in a few days. Conversely, rainy conditions may result in cones retaining most of their seeds for weeks or months. A high wind or a rainstorm may rapidly disperse an entire crop of mature seeds of some shrubs. Cones generally ripen first at lower elevations and south and west slopes, later at higher elevations and north and east slopes (Schubert and Adams 1971). Maturity may be reached several weeks earlier on hilltops than in nearby bottoms (Cobb 1959). The write-ups for the individual genera in part 2 should be consulted for maturity indices. Judging maturity, however, requires experience; in lieu of experience, careful observation and experimentation are essential to properly apply maturity indices or to develop them. Fortunately, for many species, there is a week or more between seed maturity and seed shed or fruit

Table 2—Chapter 3, Seed Harvesting and Conditioning: minimum average number of good seeds on cut face of cones needed to justify collection of cones of some western conifers

Species	Seed count
Pseudotsuga menziesii (Mirb.) Franco	6
Tsuga heterophylla (Raf.) Sarg.	8
Pinus ponderosa P.&C. Lawson	10
Picea sitchensis (Bong.) Carr.	14

Table 3—Chapter 3, Seed Harvesting and Conditioning: sound seed yield per cone for 4 pine species as estimated from the number of sound seeds exposed when cones are bisected longitudinally

Sound seeds exposed	*Pinus palustris* (Louisiana)	*Pinus taeda* (Louisiana)	*Pinus elliottii* (Louisiana)	*Pinus elliottii* (Georgia-Florida)	*Pinus echinata* (Virginia)
2	23	31	20	31	12
4	35	44	35	50	22
6	47	57	50	69	31
8	59	70	65	87	41
10	71	83	80	106	51
12	83	96	95	124	60
14	95	109	110	143	70

Sources: Derr and Mann (1971).

drop. This delay provides some margin for error in estimating maturity. Prompt action is, however, necessary once maturity has been reached.

Immature fruits may be collected by mistake from species having fruits that require 2 or 3 years for development. Alaska-cedar (*Chamaecyparis nootkatensi*s (D. Don) Spach) and western juniper (*Juniperus occidentali*s Hook.) are examples of species that bear immature seed structures that are nearly equal to mature ones in color and size. Collecting intermingled mature and immature fruits should be avoided, because these fruits are difficult to separate (Stoeckeler and Slabaugh 1965). At the other extreme is the possibility of collecting empty conifer cones. Cones that have recently shed their seeds will close during rainy weather (Allen and Owens 1972), and workers must be careful not to collect these closed empty cones by mistake.

Maturity for collection is most often judged subjectively from the appearance of the cones, fruits, or seeds. Green color changes to yellow-green, yellow, brown, reddish, or purple. Fruits begin to soften. Scales or bracts begin to crack or flex. A few early-maturing individuals begin to drop their seeds. Such subjective indicators have a variety of shortcomings (Schubert and Adams 1971). The color changes may not be the same with every individual or population of plants. Weather can accelerate or modify the appearance of the indicator. On the whole, however, these indicators have proven to be reasonably practical. Their chief drawback is their dependence on the experience and judgment of collectors. When in doubt, it is generally better to shorten the collection period than to collect immature seeds that will have low viability and the tendency to produce low-vigor, deformed seedlings (Heit 1961, Schubert 1956).

Some attempts have been made to develop more-objective maturity indices. Chemical constituents have been analyzed and related to maturity for Douglas-fir and noble fir (*Abies procera* Rehd.) (Rediske 1968). This type of approach has not been widely used, mostly because of the difficulty of getting samples to a laboratory and then returning the information on a timely basis to the field.

Measuring specific gravity is used to evaluate the maturity of conifer cones. As a cone matures, it loses water and its specific gravity decreases. The flotation procedure to measure specific gravity can be done in the field by collectors. Cones placed in a liquid with the appropriate specific gravity will sink if immature and float if mature. The specific gravity values for ripe pine and fir cones are listed in tables in part 2 of this manual. Although simple in application, this version of the flotation procedure requires finding a fluid with the correct specific gravity and carrying supplies of it into the woods. Many of these fluids are potentially polluting substances such as ethanol, kerosene, motor oil, or linseed oil and they and the tested cones, which have become contaminated, must be carried out of the woods. Thus, this version of the flotation method is rarely used today.

Instead, specific gravity values of cones can be calculated from values obtained by using water in a graduated metric cylinder with increments marked at 1-ml intervals. The cylinder should be the smallest size that the cone will fit into and made of lightweight plastic. Water obtained in the field can be used, thus minimizing the amount of material to transport.

Specific gravity estimates must be made immediately after the cone is removed from the tree. A few minutes delay, even in a moisture-proof container, will allow the cone to dry slightly, causing the specific gravity to be estimate below (lower s.g.) than it actually was on the tree.

Early collection, that is, before natural maturity date, is possible with the following species:

- sweetgum *(Liquidamber styraciflua L.)* (Bonner 1970a; Wilcox 1966)
- loblolly pine (*Pinus taeda L.*) (Cobb and others 1984; Waldrip 1970)
- Douglas-fir (*Pseudotsuga* menziesii (Mirbel) Franco) (Silen 1958)
- eastern white pine (*Pinus strobus* L.) (Bonner 1986)
- grand fir (*Abies grandis* Dougl. ex D. Don Lindl.) (Pfister 1966)
- white spruce (*Picea glauca* (Moench) Vozz) (Winston and Haddon 1981)
- red pine (*Pinus resinosa* Ait) (Winston and Haddon 1981)
- blue spruce (*Picea pungens* Engelm.) (Fechner 1974)

For these species, the cone or fruit is dried in a strictly controlled manner to allow for proper maturation of seeds, fruits, or cones. Those who wish to attempt to collect cones or fruits early and after-ripen them should consult the literature and do some test runs of the procedure. For further references on after-ripening and other seed maturation topics, check the review by Edwards (1980) on maturity and quality of tree seeds.

FLOTATION PROCEDURE

The flotation procedure to measure specific gravity begins with partially filling an appropriately sized graduated cylinder with water, leaving enough room so that the entire cone can be submerged in the water without raising the water level above the graduations. The volume of water placed in the cylinder should be recorded, and the cone then placed in the water. If it sinks, the specific gravity is greater than 1, and the cone is immature.

If it floats, the new water level should also be recorded. The increase in water level is caused by the cone pushing the water up. Because the specific gravity of water is 1 (1 ml of water weighs 1 g), the volume of water displaced (usually measured in milliliters) is approximately equal to the weight of the cone (usually measured in milligrams). Therefore, subtracting the original volume of water from the second volume of water gives the weight of the cone.

Next, the cone should be pushed down until the water just fully covers it. A worker's finger or stick can help push the cone down, but only the cone should be pushed below the water. Only the cone should be measured, not the finger or the stick! This last measurement is the weight of the volume of water displaced by the cone. Dividing the weight of the cone by the weight of the displaced water yields the specific gravity of the cone.

A large cylinder is needed for larger cones. As the graduations of larger cylinders will represent 10 or 20 ml each, water levels will often fall between marks. Estimating the exact water displacement is then required, resulting in greater error in the readings. To control this error, a 2-cylinder system can be used. One cylinder, large enough to hold the cone and water, is equipped with a side spout that can direct any displaced water into a smaller cylinder (figure 4). The second cylinder should be a 100-ml graduated cylinder, which eliminates any need to estimate the exact displacement. To operate this system, the larger cylinder is filled with water until water freely spills out the spout into the smaller cylinder. The water is allowed to drain to its natural level. The small cylinder is then emptied and returned to the spout. The cone is placed into the water, and the overflow collected in the smaller container. Once the dripping stops, which may take a while, the weight of the cone is read directly from the water level in the smaller cylinder. For example, the displaced water volume might be 40 ml. Next, the cone is pushed completely below the water surface. This is best done with a wire, perhaps with a small cradle bent into the end to hold the cone and keep it from rolling. The wire should be kept in the larger container during initial water fill to avoid any bias from its volume. The final amount of displaced water is read after dripping stops. Continuing the example, assume this water volume is 41 ml. This final displacement equals the total volume of the cone. The first displacement divided by the second displacement is equal to the specific gravity. Finishing the example, we divide 40 by 41, which results in a specific gravity of 0.976.

Figure 4—Chapter 3, Seed Harvesting and Conditioning: two-cylinder system for measuring specific gravity of pine cones.

Seed Acquisition

Seed harvesting can begin once a seedcrop of appropriate genetic make-up, adequate quality, adequate quantity, and proper maturity has been identified. However, seed quality must be monitored at the time of collection, for the situation may have changed since first determinations were made. Unexpected seed dispersal, insect-feeding, or other animal predation may have occurred. Certain seeds, such as acorns, can dry out or germinate shortly after they are shed (Bonner and Vozzo 1987; McDonald 1969; Olson 1957). Cones, fruits, and seeds should be cut open and examined again. Sometimes a 10 x hand lens is useful in making a quick evaluation. Prompt collection reduces losses to fungi, insects, and larger animals and birds. Some caution is advised in collecting the first fruits or seeds to be shed from the plant, which may be of poor quality and dropping because of death rather than maturation (Aldhous 1972; Stoeckler and Jones 1957).

Collection. The actual gathering of the seed or fruit from the plant takes many forms depending on the botanical characteristics of the mother plant. The first characteristic important to seed conditioning is the seed-bearing structure. In gymnosperms (for example, pines, spruces, firs, and ginkgo), this is the female strobilus or cone; in angiosperms (for example, all the hardwood trees), it is the fruit. If this structure is not easily removed from the plant or shed naturally, it is classified as persistent. Persistent cones and fruits require more effort to remove them from the plant. Either hard twisting and pulling, or a sharp cutting tool such as pruning shears is needed to sever the connection (figure 5). Alternatively, the seeds are allowed to shed naturally and caught on netting (figure 6). When not persistent, the cones or fruits can be quickly picked by hand or pulled off with rakes, hooks, or vacuum. Another method is to gather cones or fruits from the ground after shaking them from the plant or after natural drop (figures 7 and 8). Yard tools such as rakes, leaf blowers/vacuums, forks, and shovels can be useful in gathering seeds from the ground or off of low plants (figure 8).

In some loblolly, shortleaf (*Pinus echinata* P. Mill.), and eastern white pine seed orchards an extensive system of nets is used to collect seeds. Loblolly cones are very persistent, and much labor and equipment expense is saved by gathering seeds that shed naturally rather than using lift trucks or other devices to pick cones. Problems related to seed maturity are almost totally avoided by relying on natural shedding of the seeds. Avoiding such problems is the strongest attraction of the system in white pine orchards, because the window of time to collect is quite narrow for white pine. The system has several disadvantages, however. There must be enough dry weather during the collection period for natural seed shed to finish by the desired collection date. Predation from insects and larger animals can occasionally be too great, and weed seeds can enter the seedlot from ground plants and vines in the orchard and from droppings of birds that roost in the orchard. Also, family identities are lost in the bulk collection of seeds. This system can be used only for seeds with at least moderate levels of dormancy; non-dormant seeds germinate on the netting, resulting in great loss of quality and quantity.

The netting is carpet backing with UV light inhibitors. It is used in widths equal to the distance between rows of trees in the orchard. The individual strips are then drawn together at the edges and fastened with standard wire staples commonly used for paper (figure 9). If the ground is soft, tree shakers are used to shake the seeds from the open cones of loblolly pine, which has a hard seedcoat. As the trees are shaken twice, the shaker actually drives over some seeds that fell on the netting during the first shake. For this reason, shakers cannot be used for eastern white pine, for their seedcoats are too fragile and can be mechanically damaged when the seeds are driven over. Totally natural seed shed must be used in this case. Alternatively, overflights with helicopters can be used, although these are usually too expensive.

Figure 5—Chapter 3, Seed Harvesting and Conditioning: persistent cones or fruit can be cut from the branch with pruning shears.

Figure 6—Chapter 3, Seed Harvesting and Conditioning: seeds from persistent cones or fruits can be caught on netting after natural seed shed as an alternative to cutting the fruit from the branch.

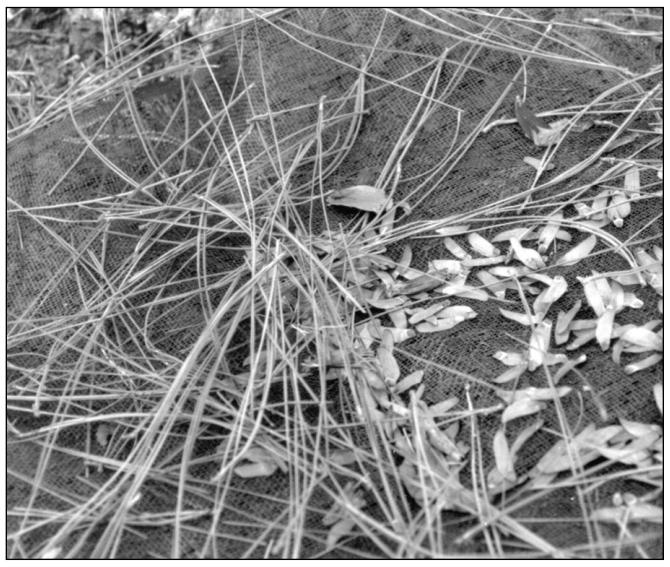


Figure 7—Chapter 3, Seed Harvesting and Conditioning: non-persistent fruits and cones can be shaken from the plant using tree shakers.

Once the seeds are shed from the trees, the netting is rolled up. This is done by a net retrieval machine or simply by drawing the net over itself and piling the seeds in a windrow. The windrow is then combined with a peanut combine to separate the seeds from the bulk of the needles

Figure 8— Chapter 3, Seed Harvesting and Conditioning: fruits such as acorns can be gathered from the ground after natural drop.

(figure 10). Large quantities of needles are gathered with the seeds, because needle drop occurs at the same time as seeds are shed. The staples holding the netting together pull free easily when the netting is rolled up.

Location on the plant is another factor determining the method of collection. Cones or fruits near to the ground are generally easily accessible to pickers. Those high in the air require some other means of reaching them. Using cone rakes carried by helicopters (Baron 1986; Haddon 1981) and shooting branches out of trees with a high-powered rifle are methods that are generally safer, faster, and more economical than climbing. Helicopter or rifle harvesting is restricted to species were the cones are clustered on a branch or at the top of a relatively narrow crown such as with spruce or true firs. Shooting the top out of a tree will of course deform the tree; both the rifle and cone rake techniques reduce cone production for a year or 2 at least, because the branch tips that would bear the next crop are removed with the cones. Therefore, climbing is still sometimes the best choice for collecting from tall-growing species. On relatively level land that is accessible by trucks, or in seed orchards, bucket trucks are widely used to lift workers into the crown quickly and with a minimum of personal danger. Another method for obtaining seeds from tall trees is collect them from the tops of trees felled for harvest or fallen over from storm damage (Bonner 1970b). It is important, however, to make certain that the seeds are sufficiently mature when falling occurred. The cones or fruits may appear mature, but the

appearance could be due to the general drying of the whole treetop rather than a true maturation. Collection may be necessary promptly after felling to forestall cone opening from high temperatures or losses to birds or mammals. Collecting from felled trees does not always prove cost effective. In some instances fruits or cones shatter or become deeply covered by limbs, tops, and foliage.

Squirrel caches have in the past been used as major sources of cones. This method is now generally avoided because the squirrels cut the cones before they mature, and the cones become heavily infected with fungi in the cache. Both these factors frequently lower seed quality more than is usually considered acceptable.

Purchase. Purchasing cones or fruits from independent collectors is an alternative to collecting the material directly. Independent collectors can range from the general public to professionally trained consultants. The relationship between collector and buyer may be totally informal, with people walking in off the street on the day of purchase, or it may involve a formal written contract that describes specifics of the harvest. The explicit formal arrangement provides the greatest guarantee of correct genetic source, species identity, and seed quality. However, successful collections have been made by buying from the general public. Whatever system is used to acquire cones and fruit, the important point is that there must be reasonable assurance that the correct species, genetic source, and quality are acquired. If any doubt exists about these factors, it is absolutely essential to modify the procedures to provide reasonable assurance.

Cones or fruits, especially those purchases from the general public, who may not be as knowledgeable or committed to quality as might be desired, must be inspected thoroughly. Containers of fruits or seeds need to be emptied for inspection. A rough cleaning can be done at this point to remove leaves, sticks, stones and other tramp items to obtain a truer volume or weight. A grading table is useful for making this inspection and for quick repackaging. A table for cones and larger fruits can be made from wooden slats measuring 2.5 by 5 cm (1 by 2 in) placed 2.5 cm (1 in) or less apart (Lott and Stoleson 1967). Litter can fall through the slats and the fruits can roll down the table to be repackaged (figure 11). Larger pieces of trash can be hand picked. Cutting or x-raying fruits and seeds is also necessary at this time to verify proper development and maturity.

No matter how the seeds, cones, or fruits were collected, it is best to minimize the amount of trash that is brought in with them. Needles, leaves, grass and other debris that are collected with the fruits will fragment during drying and handling and generally increase the difficulty of cleaning the seed. Such debris should be separated during collection if feasible, or, when not feasible at collection, upon arrival at the seed plant. Tumblers and large flat screens have been successfully used to do this mechanically.

Figure 9—Chapter 3, Seed Harvesting and Conditioning: edges of seed collection netting are stapled together at center of rows of trees in a seed orchard.

Figure 10—Chapter 3, Seed Harvesting and Conditioning: a windrow of needles and seed in one method of gathering loblolly pine seed from netting.

Lot identity. Maintaining the identity of the seedlot is critical. All the work of collection can come to nothing if the identity of the seedlot is lost. Therefore, all containers need to be precisely and carefully labeled. A unique seedlot (identification) number needs to be written on tags placed both inside and outside of the containers. The outside tag is usually enough and is accessible for easy inspection. The inside tag is easy insurance in case the outside tag is removed. Identification numbers should be simple; a long complicated number increases the chance that error will occur as the number is transcribed. The species name or initials, the year, and an accession number should be sufficient. Additional information should be kept in a record book, rather than incorporated into a complicated code. One aid to maintaining seedlot integrity is the use of official seed certification. This system (see chapter 6) and Karrfalt 1996) is most useful if seedlots are being bought and sold among many parties. It is particularly useful when seed buyers do not have first-hand knowledge of the collections or the seed company.

Transportation. A variety of rigid and nonrigid containers are available to transport fruits. Cones are shipped in bulk, in sacks, or in wire-bound boxes. New containers or ones that can be thoroughly cleaned should be used to prevent physical or pathological contaminants from getting into the seed. Bags may be completely filled when cones are to be in them for only a short time; however, for any temporary storage, bags should be filled only half-way. One bushel of cones goes well in a 2-bushel sack. Space is thus left for expansion of scales as cones dry. Otherwise, scales may dry in the closed position or partially closed position, severely impairing seed extraction. This condition can sometimes be overcome by wetting or soaking the cones and redrying. However, allowing scales to dry in a closed position results, at best, in extra work and time delays that can be completely avoided by leaving more space in the bags. Bags made of material having a tighter weave than burlap may be needed for small dry fruits or seeds. Never use an unventilated bag, such as one made of plastic, for cones or fruits that need to dry. Unventilated bags lead to loss of seed quality, because of molding and heating. Wire-bound boxes make good transport containers. Their main advantage is that they can be handled mechanically. They also hold a relatively large amount of seeds but not so much that aeration is inadequate for maintaining seed quality. These boxes are widely used for southern pines.

Figure 11—Chapter 3, Seed Harvesting and Conditioning: a grading table for quick inspection and cleaning of cones or fruits (Lott and Stoleson 1967).

Seed Cleaning and Conditioning

Post-Harvest Storage

Post-harvest storage is the period between collection and the preparation of the seed for planting and long-term storage. (For a discussion of long-term storage, see chapter 4.) At this stage, seeds are grouped according to their ability to be dried and whether the fruit is fleshy or not fleshy. Seeds that cannot be dried are called recalcitrant. These include the seeds of oaks, chestnuts (*Castanea* spp.), buckeyes (*Aesculus* spp.), many tropical hardwoods, and some maples (*Acer* spp.). These seeds cannot be allowed to dry. Premature germination or deterioration can occur as a consequence of the high moisture. Therefore, these species require cool storage or, if the species is injured by chilling, immediate planting. Storage near freezing is often best with temperate species, as long as ice does not form, which would cause cell damage and death. If controlled near-freezing storage is not available, seeds may be hold in a cellar, air-conditioned room, or shaded spot. To maintain the high moisture content of recalcitrant species, it is helpful to seal them in moistureproof containers, usually plastic sacks, or to add moisture to compensate for drying losses (Bonner 1973; Bonner and Vozzo 1987; Tylkowski 1984).

Those seeds that can be dried are referred to as orthodox. Orthodox seeds are broken into 2 groups:

- fleshy fruits—for example, those of dogwoods (*Cornus* spp.), cherries (*Prunus* spp., and junipers (*Juniperus* spp.)
- non-fleshy fruits—for example, those of ash, elm (*Ulmus* spp. L.), and pine

Fleshy fruits must be prevented from drying until the pulp is removed, otherwise the pulp hardens and is then not easily or adequately removed. Pulp is generally removed to make handling easier and to control fungi or bacteria that can grow in the pulp. As with recalcitrant species, the fleshy-fruited orthodox seeds must be kept cool and ventilated to prevent the buildup of heat and subsequent deterioration. They may be treated basically the same as the recalcitrants; however, fleshy-fruited orthodox seeds might require more ventilation because of higher moisture content.

The dry-fruited (also referred to as non-fleshy) orthodox species should be allowed to dry to prevent deterioration. High moisture in these fruits usually leads to heating, molding, and subsequently, loss of viability. Spreading the seeds on screen racks is an economical way to dry these fruits. Minimal drying is necessary during post-harvest storage when the seeds are collected dry. Post-harvest storage conditions usually need to allow for the loss of moisture at a gradual rate and to protect the seeds from the weather. If the fruit expands upon drying (for example, a pine cone), sufficient space must be allowed for expansion. Otherwise the fruit will become case-hardened and the seed locked inside the fruit as discussed previously. Figure 12 shows wire-bottom racks for air-drying cones under shelter. Alternatively, moisture must be maintained at a high level to prevent the expansion of cones. Because high moisture can lead to seed deterioration, it is important to evaluate a system that keeps orthodox seeds moist to be sure there is no loss of seed quality. Cones in full sacks or in bulk must be re-bagged into half-full sacks or placed in ventilated storage. Drying racks with cones spread out about two cones deep are very good. Cones have also been successfully stored in temporary cribs of snow fencing 8 to 10 feet in diameter. Storing cones in this type of crib or in 35-liter (20-bushel) wire-bound boxes ventilates the cones but also keeps them from drying and loosing their seed. Both cribs and boxes are used out of doors. Cones should never be stored in a large pile as this will result in heating. Smaller piles will cause many surface cones to open and the seeds will be lost. Also, piling cones on the ground invariably leads to stones in the seedlot.

Fruiting structures (that is, cones) that are serotinous require additional consideration; such cones require a brief period of very high temperature to melt resin seals that prevent cones from opening. In nature, this happens after forest fires. In North America, lodgepole pine, jack pine, sand pine, and black spruce have serotinous seeds. Black spruce seeds require a high initial kiln temperature only. The pines generally need a hot water dip or a steam treatment. This operation must often be done immediately after harvest, because not all trees will produce serotinous cones or the same degree of serotinony. Therefore, some cones will begin to open without the heat treatment, exposing some of the seeds to lethal temperatures when the treatment is done. The heat treatment can be delayed if it is absolutely certain that all cones will remain closed. The treatment cannot be done on seedlots with some open cones without losing seeds. The treatment must be hot enough and long enough to release all cones, otherwise, the undesirable situation of some cones open and some completely closed will be created artificially. Generally, the treatment is for 30 seconds or less, with boiling water or live steam. As the seal is broken, the cones often crackle. When the crackling has stopped, the cones are adequately treated. If the operator lacks experience in this procedure or faces new conditions, it is best to run a small trial batch to be sure the procedure is properly timed. Germination of the seeds should be tested to evaluate the procedure. The discussion on quality control later in this chapter explains how to do this.

Figure 12—Chapter 3, Seed Harvesting and Conditioning: screen bottom trays under shelter for air-drying dry fruits.

Species vary considerably in tolerance to high moisture and the length of time that they can be at high moisture. This tolerance is related to the degree of dormancy to germination. Some species—such as cottonwoods and aspens *(Populus* spp. L.) and red maple (*Acer rubrum* L.)—are all orthodox but require rapid drying and processing to maintain highest viability. Species with dormancy to germination—such as white pine, white ash (*Fraxinus* americana L.), and tuliptree (*Liriodendron tulipifera* L.)—can be held for relatively longer periods without loss of viability. How long a species can remain in post-harvest storage is the critical factor in determining the work schedule. Those without dormancy must be dealt with first and dealt with rapidly enough to preserve their viability.

Seed Extraction

Extraction is the first step after post-harvest storage. In terms of extraction, fruits are classified as being single or in clusters, fleshy or non-fleshy, dehiscent or indehiscent. Seeds in clusters (for example, those of ash and maple) must be singularized so they will flow easily through cleaning and planting machines. Fleshy fruits—for example, those of cherry and dogwood—are usually de-pulped for ease of handling and to control pathological problems. Indehiscent or unopened fruits—for example, those of black locust (*Robinia pseudo-acacia* L.) and manzanita (*Arctostaphylos* spp.—can be hulled to remove the seed from the fruit. The dehiscent dry fruits—for example, those of sweetgum and spruce—can be tumbled or shaken to separate the seeds from the fruit following drying.

Fleshy fruits. De-pulping fleshy fruits, such as those of magnolia and chinaberry, is done using a macerator, grinder, or mill that is carefully adjusted to avoid seed damage. It does not matter if the fruits are in clusters or single– de-pulping also singularizes the seeds. Macerators are most often used to depulp fruits (figure 13). The most common design uses a flat spinning plate on the bottom of a roughly 26-liter (7-gallon) can. The plate has 4 bars arranged in a 90-degree cross on the bottom. These bars strike the fruits and burst them. The abrasion of fruit against fruit also breaks up the fruits. Water is run into the can while macerating to wash away the separated pulp. Some machines have an angled baffle just above the spinner plate to force the fruit against the plate, creating a squeezing motion. Another refinement involves lining the can with hardware cloth or striking the outside of the can with a punch to create bumps on the inside. A 3.8-liter (1-gallon) can is then bolted to the spinner plate with the retainer nut for the spinner plate. This can is also wrapped with hardware cloth (figure 14). The addition of these rough surfaces decreases maceration time by 50 to 75%. The flow of water into the can is also improved by installing a ball valve directly to the side of the can. Water is then added to the seed simply by attaching a water hose to the valve and turning the valve (figure 15). This feature saves time and prevents pulp from being splashed on the operator.

A food blender can be used as a small-scale version of a macerator. Cover the blades with rubber or plastic tubing to prevent the seeds from being cut. About 240 ml (1 cup) of fruit at a time can be cleaned with this small macerator. The pulp must be rinsed and floated away in a separate operation.

A grinder (figure 16) can also be used to de-pulp fleshy fruits such as those of dogwood, blackberry, and cranberry. This grinding step is followed by a separate washing operation to rinse the pulp away. The grinder must be adjusted carefully to avoid crushing or cracking the seeds.

The pulp is easiest to remove if softened first. The flesh is ideally ready when it can be smashed between thumb and fingers. A 3- to 10-day running water soak will usually soften the fruit to the desired condition. Changing the soak water daily is an acceptable alternative to having running water. Some fruits—such as crabapple (*Malus pumila* P. Mill.)—are very hard and require more severe treatment. Crushing under vehicle tires or a fruit crusher or freezing followed by a storage period for fruit deterioration are needed for these hard fruits. However, it is vital to avoid any

Figure 13—Chapter 3, Seed Harvesting and Conditioning: a common type of macerator for de-pulping fleshy fruited seeds.

Figure 14—Chapter 3, Seed Harvesting and Conditioning: maceration time is reduced by adding to the macerator a hardware cloth liner and a can wrapped with hardware cloth.

Figure 15—Chapter 3, Seed Harvesting and Conditioning: a water Chapter 3, valve installed on the side of the macerator improves ease of operation.

heating or fermentation during these steps to soften the fruit, for any buildup of high temperatures or alcohols from fermentation can be lethal to the seeds. However, regular exchange of soak water will easily prevent this problem.

Dry fruits. Non-fleshy, or dry, orthodox fruits or seed-bearing structures—for example, those of pine, larch, and sycamore—usually require drying as a first step for both dehiscent and indehiscent types. The most common way to achieve this is to heat ambient air to temperatures that result in the relative humidity dropping to about 30%. Some locations have air that is naturally dry and require little or no heat to achieve the necessary drying conditions. Other locations may have high ambient relative humidities, which must be measured to be certain an adequate drying temperature is used. In many locations the ambient conditions can fluctuate, and the drying temperature should be adjusted to meet the current conditions for best economy and efficiency of drying. Always using the same drying temperature could result in using a temperature higher than necessary, wasting fuel, or a temperature that might not dry the air enough.

Figure 16—Chapter 3, Seed Harvesting and Conditioning: a grinder can also be used to crush fleshy fruits for seed extraction.

Table 4 shows what the maximum ambient relative humidity can be for a given drier temperature and ambient air temperature combination, while maintaining relative humidities of 30% or less in the drier. The numbers in the body of the table are the maximum ambient relative humidities. For example, at 20 °C and 65% RH, a drier temperature of 30 °C is too low, because the maximum permissible ambient RH is shown as 58. In this case, it would be necessary to use a drier temperature of 35 °C , for which the maximum permissible ambient RH is 71%, as shown in the table. The maximum drier temperature that should be used is 43 °C. If this temperature must be exceeded to obtain dry air, first dry

the air by cooling with an air conditioner. When treating serotinous or semiserotinus cones (for example, lodgepole pine or black spruce), it might be necessary to use temperatures in excess of 43 °C.

A well-constructed pressurized drier is needed to effectively use the dry air produced by heating. A laboratory model of a pressurized drier is shown in figure 17. The fan on this drier forces air into the box or plenum and the screen that holds the seeds is laid on top of the box. The drier becomes pressurized once the screen is covered evenly with seeds, causing the air to be uniformly forced through the seeds. The box containing the seeds must fit on the plenum with an airtight seal to provide the pressurized condition. If the drier were not pressurized, the air would take the path of least resistance and go around the seeds, drying only the surface layer of seeds. Inner layers would dry much more slowly. Pressurizing ensures that the seeds inside the seed mass are drying as well as seeds on the surface and that all the air is used for drying rather than simply passing by.
Pressurizing the drier, therefore, gives more uniform, rapid, and efficient drying. Without pressurizing, the seeds, cones, or fruits need to be spread loosely so that air can easily pass over and among the material. Alternatively, the material can be stirred several times an hour, but this is not practical during the night or with large quantities.

After drying, dehiscent fruits and cones such as sweetgum or pine can be tumbled or shaken to remove the seed from the fruit (figure 18). Indehiscent fruits can be hulled to remove fruit walls or wings or to singularize. Removal of fruit or wings and singularization are done usually in a single step. Some fragile fruits (for example, those of red maple) can only be singularized and not de-winged. Hammer mills or scarifiers have been used for hulling but

Figure 17—Chapter 3, Seed Harvesting and Conditioning: laboratory model of a pressurized seed drier.

might be too destructive (Young and others 1983). Tough legumes—for example, those of honey-locust (*Gleditsia triacanthos* L.)—have also been successfully broken up in a concrete mixer by adding small pieces of broken-up concrete. Debearders are also used. One that has been found to be very versatile and safe for the seed is the brush machine (figure 19) (Karrfalt 1992). In this machine, the fruit is rubbed against a slightly ovoid wire sleeve by rotating brushes. This sleeve is called a shell and can be made of coarse wire for much abrasion or fine wire for less abrasion. The brushes can be of varying degrees of stiffness ranging from very fine hair brushes to stiff nylon. Adjustments can also be made for the speed at which the brushes turn, how

Table 4—Chapter 3, Seed Harvesting and Conditioning: maximum recommended ambient relative humidity values for drying seeds, cones, and fruits with heated air at various drier temperatures from 24 to 43 °C

Ambient air temp (°C)	Relative humidity (%)							
	24 °C	27 °C	29 °C	32 °C	35 °C	38 °C	41 °C	43 °C
4	100	100	100	100	100	100	100	100
7	78		100	100	100	100	100	100
8	57	75	94	100	100	100	100	100
9	66	86	100	100	100	100	100	100
11	50	65	77	88	100	100	100	100
16	44	58	68	78	94	100	100	100
18	39	51	60	65	84	95	100	100
20	31	42	50	58	71	81	95	100
22	30	38	45	49	65	69	82	100
24	30	31	38	45	55	63	74	87
27	30	30	35	38	47	54	64	75

tightly they press against the shell, and how long the seeds are retained in the machine. The fruits need to be dry for the hulling operation to work well. The effect of hulling with a brush machine can be seen in figure 20. A partial list of genera and species that can be successfully de-winged or hulled with the brush machine includes ash, maple, tuliptree (*Liriodendron tulipifera* L.), southern catalpa (*Catalpa bignonioides* Walt.), black locust, sycamore, big sagebrush (*Artemisia tridentata* Nutt.), mountain-mahogany (*Cercocarpus montanus* Raf.), and winterfat (*Krascheninnikovia lanata* (Pursh) A.D.J. Meeuse & Smit)

Conifer seeds. Conifer seeds are usually de-winged after tumbling from the cone. De-winging can be done either wet or dry. Some species, white pines, for example, separate easily when tumbled in a drum such as a concrete mixer. Others—for example, hard pines and spruces—require adding a small amount of water to the seeds as they are tumbled to release the wings. In other machines, pressure can be applied with brushes or paddles to remove wings from dry seeds. A mortar mixer is an example of a machine commonly adapted to the dry de-winging of conifer seeds with a modest amount of pressure. However, using pressure increases the chance of mechanical damage. To minimize the amount of mechanical injury, the paddles should be slowed by changing gears on the mixer and de-winging the seeds for only a limited time. A timer switch can be used to easily control de-winging time. The Missoula small-lot pine seed de-winger (figure 21) is another commonly used machine that rubs wings off. It has been particularly widely used in the West and has de-winged millions of pounds of seed. However, if liners are improperly installed, liners or flaps selected improperly, or flaps turned too fast, serious seed damage can result. As always, proper use of equipment is essential.

Figure 18—Chapter 3, Seed Harvesting and Conditioning: a tumbler can be used to extract seed from dehiscent cones or fruits.

Figure 19—Chapter 3, Seed Harvesting and Conditioning: brush machine used for hulling indehiscent fruits, de-winging, and singularizing seeds.

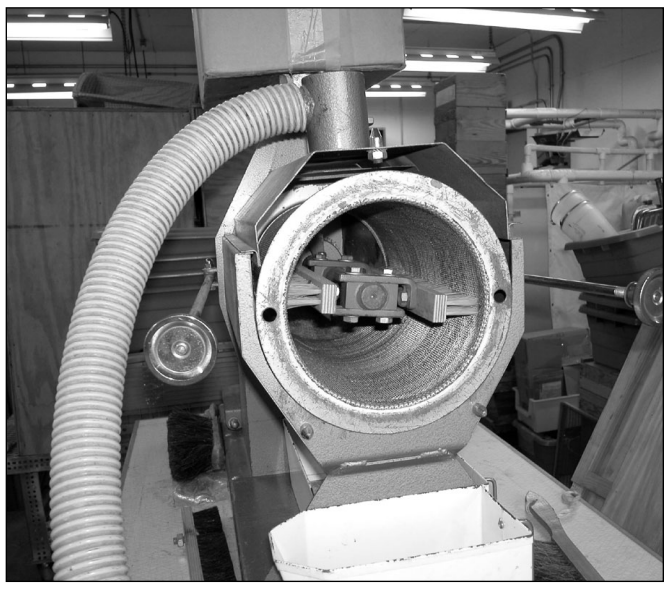


Figure 20—Chapter 3, Seed Harvesting and Conditioning: tuliptree and green ash seeds after treatment with the brush machine.

Because wet de-winging presents minimal chance of mechanical damage, it is the preferred procedure when appropriate. Wet de-winging is accomplished generally by tumbling the seeds in a rotating drum in the presence of an intermittent fine water mist. The drum can be simply a small concrete mixer (figure 22) or it can be a special-order machine (figure 23). The water can be added by computer-controlled valves or sprayed on with a hand sprayer. Intermittent compressed-air spray can be used to partially dry the seeds and blow the wings out of the drum. The compressed air and the water are alternated with each other until the de-winging is finished. Without the compressed air in the drum, the seeds need a quick pass through an air cleaner to blow out the wings. Wet de-winging requires immediate drying after de-winging to prevent deterioration. The drying is brief, because the moisture is near the surface of the seeds. The pressurized drier described previously is also best for this drying.

Some conifer seeds (longleaf pine and true firs, for example) have a wing that is one structure with the seedcoat. These wings must be removed with care; for some particularly fragile species such as true firs, the seed plant operators sometimes opt not to de-wing.

If the wings need to be rubbed from the seeds it might be necessary to remove large or abrasive trash from the seedlot first. This is called scalping and is done with a screen machine.

Another factor to keep in mind before de-winging is the separation of particles from the seedlot that are of equal size and weight to the finished seeds. These are sometimes all but impossible to remove from the finished product.

Figure 21—Chapter 3, Seed Harvesting and Conditioning: small-lot pine-seed de-winger developed by the USDA Forest Service's Missoula Technology and Development Center, Missoula, Montana.

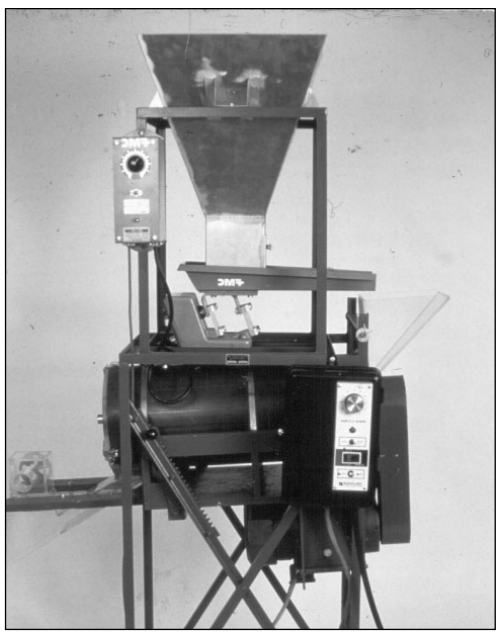


Figure 22—Chapter 3, Seed Harvesting and Conditioning: small mixer for tumbling seeds for wet and dry de-winging; the spray bottle is used to apply water for wet de-winging.

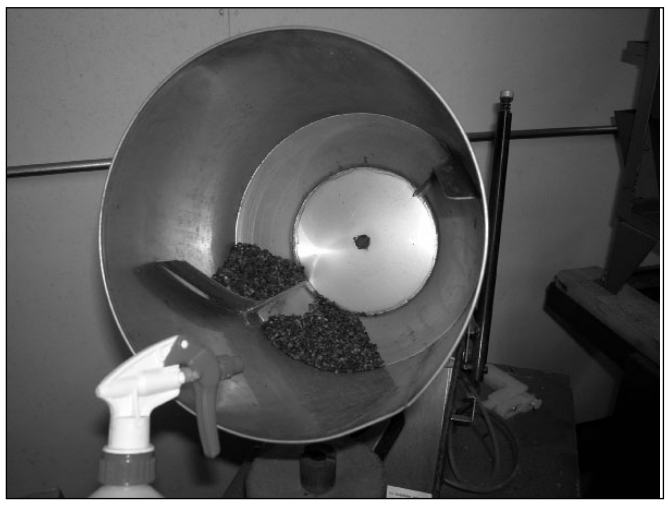
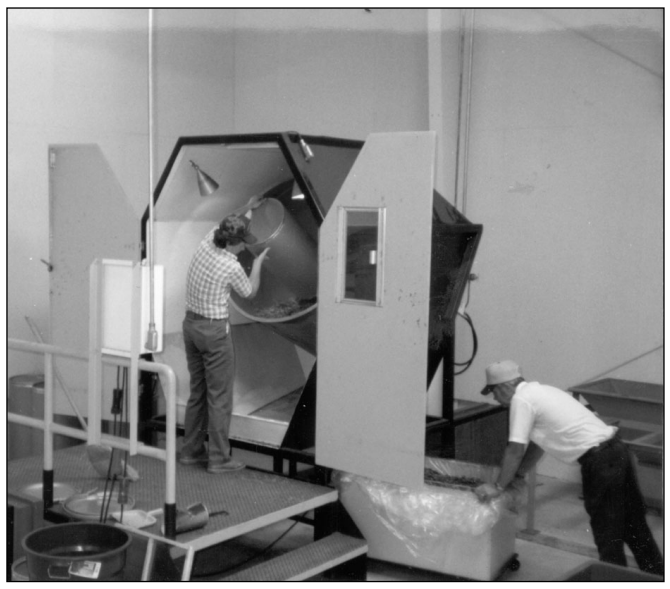


Figure 23—Chapter 3, Seed Harvesting and Conditioning: commercially made wet pine-seed de-winger.



However, before the wing is removed, the seeds will be very much lighter than the trash in an air column. This is the case with species that have a great deal of pitch in them such as western larch. A sensitive air column can blow the seeds up and let the pitch or other trash fall, giving a perfect separation.

Cleaning and Upgrading

Basic cleaning and upgrading steps for orthodox hardwoods, shrubs, and conifers become similar once the seeds are extracted, de-winged, and dried. Basic cleaning is accomplished with air-screen machines, screens, aspirators, and blowers (figures 24–27). These devices have historically been the workhorses of seed cleaning.

Removing trash with air. Air can be used to remove particles that are either lighter or heavier than the seeds. Dust, small pieces of pine needles, leaves, and wings are examples of lighter materials that can be taken out of seeds using air. The removal of pitch from conifer seeds is an example of using air to remove seeds from heavier particles. Aspirators use negative pressure by having the fan placed above the seeds. Blowers, on the other hand, use positive pressure by placing the fan below the seeds. Either approach works well if the air can be applied uniformly, constantly, with enough force, and varied precisely so that a high level of control over the force of the air is acheived. Without precise control, only the coarsest separation would be possible. The more refined the air control, the more refined the separation. Air-screen machines, blowers, and aspirators can all accomplish good air separations, but not all models of machines have the same degree of control over the air and, therefore, different quality of work can result.

Removing trash with screens. While air is used to clean seeds by weight, screens separate seeds from trash according to width and thickness. Screens are made either by punching holes in sheet metal to make perforated metal screens or by weaving wire together to make screens that resemble those used for home windows. The perforated metal screens are most common, the woven wire (figure 28) less common, being used generally for very fine seeds such as those of eucalyptus (*Eucalyptus* spp.) and grass. The perforations are mostly made in round or oblong hole sizes (figure 28). Screens made in the United States are measured in 64ths of an inch; screens made in other countries are measured in millimeters. As an example, the holes in a U.S.-made number 8 round-hole screen are 8/64 of an inch in diameter. [Note: Some authors have described using soil screens, which have an entirely different size description system, for extracting seeds from fleshy fruits.]

Figure 24—Chapter 3, Seed Harvesting and Conditioning: air-screen machines come in many sizes and are used for basic seed cleaning; a small-seedlot cleaner is in front of a very large capacity cleaner.

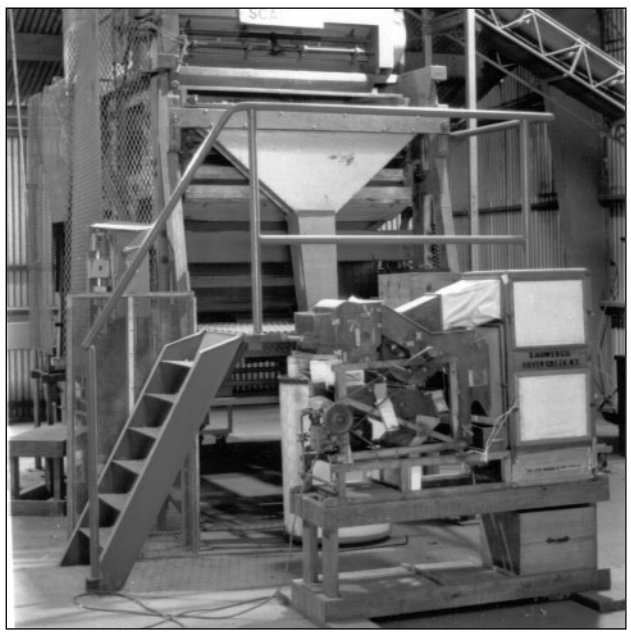


Figure 25—Chapter 3, Seed Harvesting and Conditioning: cleaner–sizer machine has 5 screens to give 6 separations at once.

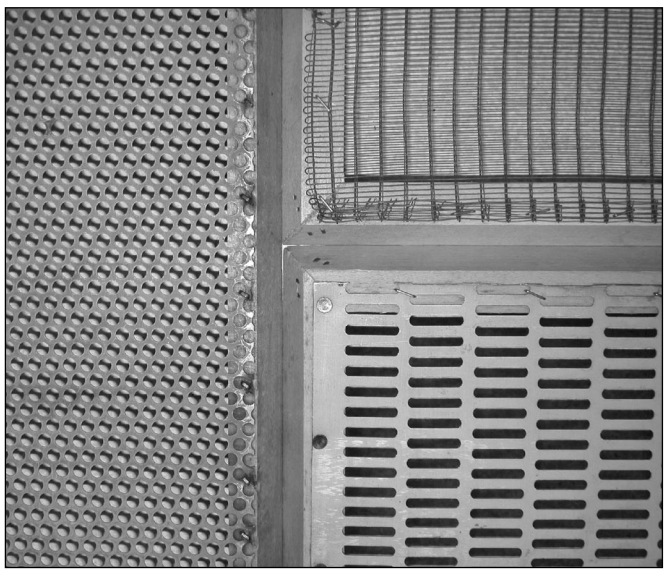
A proper selection of screens is necessary to get the desired separations. First, it must be determined if seeds need to be separated by their width or thickness. In cross-sections of seeds or trash particles, the dimension that is greater is the width and the lesser dimension is the thickness. Round-hole screens sort for difference in width,

Figure 26—Chapter 3, Seed Harvesting and Conditioning: a laboratory aspirator removes trash with vacuum.

Figure 27—Chapter 3, Seed Harvesting and Conditioning: a laboratory blower removes trash with positive pressure.

oblong-hole screens for difference in thickness. An example of a thickness separation is the sieving of flattened immature seeds out of redbud (*Cercis canadensis* L.). Slotted screens easily remove the wire staples that get into pine seeds when net collection systems are used. The separation of cone scales from pine seeds is another example of separation by width.

Figure 28—Chapter 3, Seed Harvesting and Conditioning: hand screens showing the 3 main types of screens used to clean seedlots (**counter-clockwise from left**): perforated metal round hole, perforated metal oblong holes, and woven wire.



After the correct type of hole has been determined, the proper size of hole is selected. Several screens are stacked on top of each other with the largest size screen on top and each successive screen the next size smaller. As an example, screens could be stacked from top to bottom in this order: 12, 11, 10, 9. The next step is to pour a sample of seeds on the stack of screens and shake the stack back and forth. Disassembling the stack reveals which sizes made the best separation. Typically, one size will hold both seeds and trash. A decision must be made whether to keep some trash in the seeds, discard some seeds with the trash, or take the mixed fraction and separate it in some other manner. When trash is left in the seeds, we are saying that we can live with that level of contamination. When some seeds are discarded with the trash, we are saying that we can afford to loose some seeds because the higher level of purity is worth the cost of the lost seeds. When the mixed fraction is cleaned, we are saying we need all the seeds but cannot afford the lower purity and are willing to pay for extra cleaning.

Once the screens have been selected, the air-screen or screen machine should be set up. In a 2-screen machine, the top screen would be the one that held the most trash and the bottom screen the one that passed the desired amount of small trash. Remember that there might be a few seeds in the large trash or the small trash so that purity is higher, or some trash may be left in the seeds to keep every seed possible. For machines with 3 or more screens, additional fractions can be created. The effectiveness of the screen in the

machine is determined by the speed of the shake of the screen, how well the screens are kept from blinding, and the feed rate; in some machines the slope of the screen is also adjustable.

Blinding occurs when the seeds or trash particles drop into a hole and can neither fall through nor bounce out (figure 29). This of course reduces the effective area of the screen. There are 3 types of devices to clear the holes: tappers, brushes, and ball decks. A tapper hits the screen to jar out any particles. Brushes are pressed against the bottom of the screen and pulled back and forth by ropes or cables. The brushes directly push the seeds out of the blinded holes. Ball decks consist of a cage attached to the bottom of the screen that contains small rubber balls. These balls bounce against the bottom of the screen and jar the seeds out of the blinded holes. Ball decks are now generally used on new machines, because they are easier to maintain than other devices and increase the capacity of the screen. They can also be put on many older machines to replace brushes and tappers.

Air and screens can be used to separate by particle width, thickness, and weight. However, they are generally unable to separate by particle length. Only the riddler screen (figure 30) can separate by length; this screen is used with a pulsing shake instead of the more steady shake of the standard air-screen machine. The holes in this screen have a right-angle bend in them. The long particles are unable to turn the corner and are walked up the screen by the shake. Short particles make the turn and pass through. The riddler screen is used principally in making dockage tests (a type of purity test) on grain, but has been used on a limited basis to clean trashy lots of tree and shrub seeds. Needle fragments can be removed from loblolly pine seeds with this type of screen.

Removing sticks and needles. Removal of sticks, stems, or needles from seeds is an example of length separation. Length separations are usually done using indent discs or indent cylinders (figure 31). An indent cylinder can remove stems from hardwood seeds that are not removed by basic cleaning. Seeds in an indent separator settle into the indents of the cylinder and are lifted as the cylinder is rotated. The stem piece also fits into the indent, but because it is longer its center of gravity is outside of the indent and subsequently it falls out of the indent before the seeds will (figure 32). The stem falls back to the bottom of the cylinder while the seeds are carried up and dropped into a collection trough. The indents need to be large enough to let the seeds seat completely. The speed of cylinder rotation and the angle of the collection trough are also adjusted to obtain the separation.

There are a few ways to perform length separation when an indent cylinder is not available. These techniques usually do not work as effectively but can be helpful. The first is to use flat screens with the upper portion of the screen covered with a sheet of paper (figure 33). The paper allows the seeds and long trash to travel parallel to the screen before encoun-

Figure 29—Chapter 3, Seed Harvesting and Conditioning: the seeds caught in the screen holes are said to have "blinded" the screen.

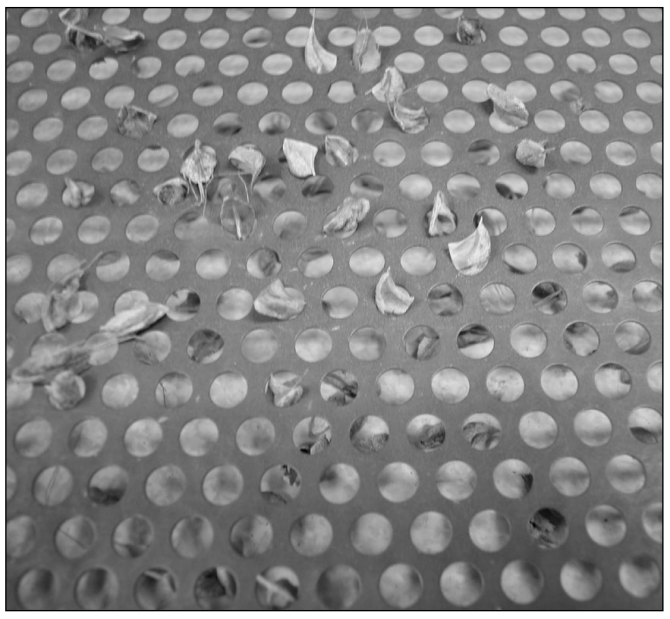
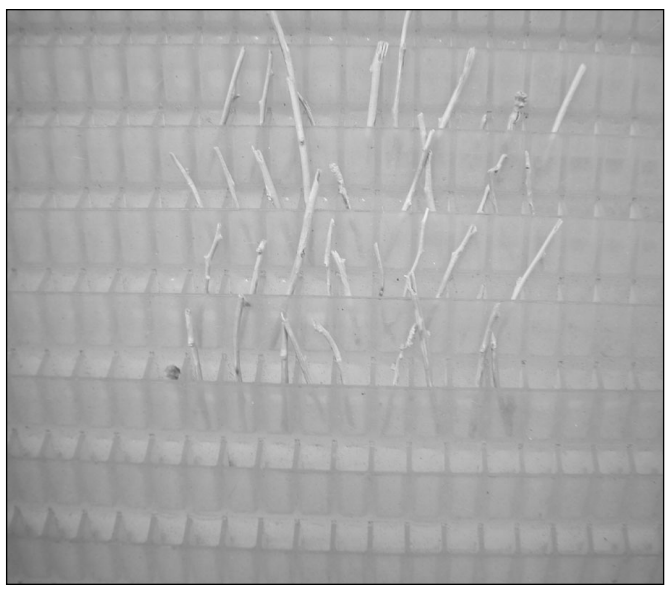


Figure 30—Chapter 3, Seed Harvesting and Conditioning: pine needles separated from seeds using a riddler screen.



tering a hole. As a result, the long particles, the sticks, tend to ride over the hole while the short seeds fall through. Without the paper, the sticks come endways towards the hole and, having a small dimension, their diameter, in line with the hole, drop straight through. Several passes will usually be required for this procedure to remove most of the sticks.

Sometimes the sticks will be removable with air because of their aerodynamic properties. Even though they may be heavier than the seeds, they catch the air well and can be lifted away. Similarly, the sticks may float to the bottom of the specific-gravity table by the process described below.

Removing trash with static electricity. Electrostatic separators also separate by weight using the force of an electrostatic field instead of air to make the separation. Charges on the particles cause them to be drawn to a negatively charged plate. Picking up small pieces of paper with a piece of plastic that has been vigorously rubbed with a dry cloth is a simple example of using an electrostatic force to pick up a light particle. One type of electrostatic separator is shown in figure 34. Electrostatic separation has had little application with trees and shrubs and only with light-seeded species (Karrfalt and Helmuth 1983). A glass beaker rubbed on the inside with a nylon or other synthetic cloth makes a simple type of electrostatic cleaner for very small seedlots. Uncleaned seeds are poured into the rubbed beaker and rolled against the sides of the beaker. After the trash has clung to the sides of the beaker, the clean seeds can be poured out. Plastic cups can substitute for the glass beaker.

Removing trash by rolling and sliding. Another characteristic that can be used to separate seeds and trash is surface texture, or the ability to slide or roll down a slope. Conifer seeds, especially larch or white pines, can contain a

Figure 31—Chapter 3, Seed Harvesting and Conditioning: indent cylinder machine for removing needles, sticks, and stems from seeds.

Figure 32—Chapter 3, Seed Harvesting and Conditioning: seeds are caught in indent cylinder while pine needles slide away

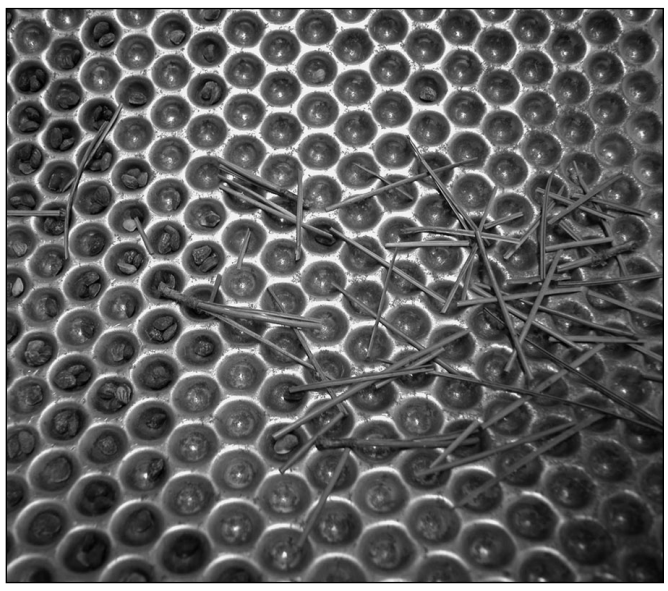
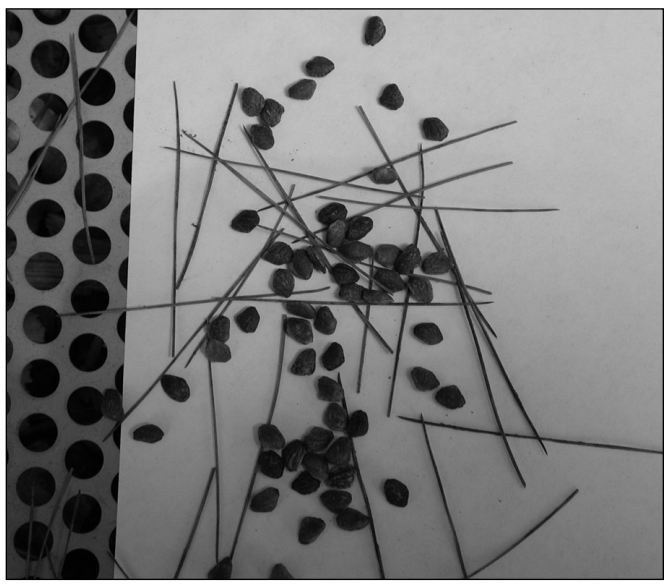


Figure 33—Chapter 3, Seed Harvesting and Conditioning: paper on screen aids in screening-out needles and sticks.



large amount of pitch. The pitch particles have a sticky surface whereas the seeds are relatively smooth. The vibratory separator (figure 35) is often able to use this difference to remove the pitch. This separator consists of a 22.9-cm-square (9-inch-square) deck mounted on a variable-speed vibrator. The deck has adjustable side and end tilt. The vibration causes the pitch, which grips the deck surface because it is tacky, to walk up the slope while the seeds, which are smoother, slide down the slope. The rate at which seeds are fed onto the deck, the speed of deck vibration, the roughness of the deck, the degree of side and end tilts, and the arrangement of the cut gates are all important. Trial and error determine what adjustments are necessary to get a separation.

Not all pitch will separate on the vibratory separator. Some may be too dry and, therefore, too smooth to stick to the deck well enough. Other pieces of pitch may be too round. Screening will sometimes work in these cases.

Another approach to surface texture is to modify it. Sometimes pitch can be removed with a gravity table (see section below on gravity tables), but only after it has been very well dried or stiffened by placing the seedlot in a cooler or freezer (Zensen 1980). This drying or cooling keeps the seeds from balling up around the pitch particles.

Another type of machine that separates by particles' ability to roll is the inclined draper (figure 36). This machine is a variable speed belt that can be set at different slopes. Particles that are round, or able to slide more easily, go down the slope while the flatter particles with greater friction ride up the hill on the moving belt and are placed in the upper collection box. Separating juniper berries from juniper leaves is an example of a separation that can be done with the draper. A board with a piece of cloth over it makes a simple draper for a small quantity of seeds. A handful of seeds can be cleaned at one time with this board. The seeds are allowed to roll down the board and then the needles are manually dumped off.

Spiral separators also use rollability. These are made of two concentric metal spirals. Seeds are poured into the top of the inner spiral. As they slide down the spiral, the round particles roll and gain momentum, causing them to fly out of the inner spiral into the outer spiral. Trash can be removed from dogwood and juniper berries in this manner (Delany 1998).

Improving quality with specific gravity tables. Specific gravity tables are another class of machine that separates by weight (figure 37). Gravity tables can be used on almost any species of seed that flows freely. They have been very successful in cleaning true firs, longleaf pine, tuliptree, and sycamore when other methods have not provided the desired results. The separations are made in the following manner. Seeds are fed onto a wire or cloth deck that has air blowing through it from below. This air is just enough to cause the seed mass to fluidize, with the lighter material floating to the top. Only enough air is applied to slightly lift

Figure 34—Chapter 3, Seed Harvesting and Conditioning: diagram of one type of electrostatic separator.

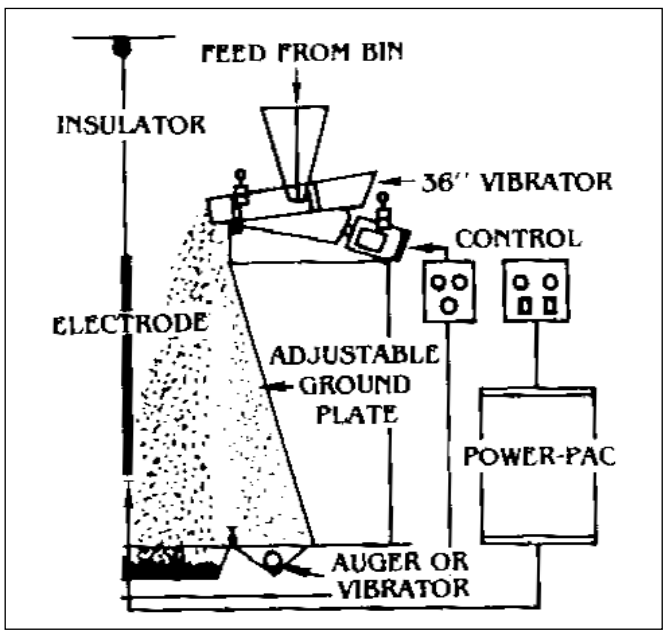


Figure 35—Chapter 3, Seed Harvesting and Conditioning: the vibratory separator removes trash from seeds by differences in surface texture.

Figure 36—Chapter 3, Seed Harvesting and Conditioning: the inclined draper separates particles on their ability to roll or slide down the inclined belt.

Figure 37—Chapter 3, Seed Harvesting and Conditioning: a specific gravity table for separating seeds and trash by weight.

the lighter material, not toss it into the air. This more gentle air flow results in a finer stratification of particles by weight than is possible in the air columns of blowers and aspirators. To pull the light and heavy particles apart, the deck shakes back and forth and is tilted sideways to oppose the direction of the shake. The shake of the deck pushes the heavy particles up the hill while the light particles drift down the slope, floating on top of the heavier seeds and pulled down the slope by gravity. This stratification of particles by weight and separation by the use of the shake and slope continues as the seed mass works its way across the deck, giving a continuous gradation of particle weights until the heaviest are at the top, intermediate weights are in the middle, and the lightest are at the bottom. When seedlots are upgraded on gravity table, the lightest particles can be empty seeds, cone particles, straw, partially filled seeds, or even good-quality seeds that are lower in weight. The heavier particles are usually the heaviest good-quality seeds but might also be pitch, stones, dirt balls, or tramp metal that has fallen into the seeds.

Dimensional grading of seedlots before using the gravity table improves the effectiveness of the table and may even be essential. Grading should be done both by width, thickness, and, if possible, length. The more dimensional grading is done, the better the table will work. The table sorts by density or dimension but never effectively for both at the same time. For example, partially filled large-diameter seeds and same-weight seeds that are completely filled but smaller in diameter sort to the same location on the gravity table.

A final point on gravity table operation is the need for seedlots need to be clean of light trash. Otherwise a great deal of dust will be blown into the operator‘s face and create an unhealthy, unpleasant, and difficult working situation.

Upgrading quality with liquids. Fluid separations based on difference in specific gravity are another way to upgrade seeds. The separation sorts lighter seeds from heavier, but because differences in specific gravity are used, the problems of dimensional sorting are avoided. Fluid separations can be very precise separations based on weight. Water flotation, the simplest version of this, for example, can be used to remove insect-damaged acorns. The good seeds, being high in moisture content, will have specific gravities greater than 1.0 and will sink. Seeds that have been damaged significantly by insects will contain air and therefore will float (figure 38). Water can also float empty stony-coated seeds such as loblolly pine or cherries; the full seeds of these species will sink. Mixtures of hexane and chloroform have been used to separate lighter seeds from empty or partially filled seeds (Taylor and others 1982). However, phytotoxicity needs to be tested before broadly adopting fluid separation using organic solvents (Barnett 1970).

In Sweden, the fluid separation of Scots pine (*Pinus sylvestris* L.) and lodgepole pine has reached a highly sophisticated level in the processes called PREVAC (“prevacuum”) and IDS (incubate, dry, separate) (Simak 1984; Bergsten 1993). The PREVAC system removes seeds with

damaged seedcoats. The seeds are placed in water in a vacuum chamber and a vacuum is then drawn on the chamber to break the surface tension and allow the water to wet the surface of the seeds. Water will enter seeds with damaged seedcoats rapidly, increasing their weight and causing them to sink. These sinkers are discarded, for they have damaged seedcoats and will be dead. The seeds that float are drawn off the top and kept. Conducting the PREVAC procedure before IDS prevents the mechanically damaged seeds from sorting out with the good seeds in the IDS procedure.

The IDS procedure uses the fact that dead or weak seeds lose water faster than living or more vigorous seeds. In the first step, all seeds are allowed to imbibe water. With Scots pine, this is done at 15 °C for 8 to 12 days. Then the seeds are dried in super-dry air with a relative humidity ranging from 5 to 15%. The extremely rapid drying resulting from the super-dry air maximizes the difference in drying rates between viable and nonviable seeds. The living tissue in the viable seeds holds water more tightly than the nonliving tissue in the nonviable seeds. Eventually, however, the viable and nonviable seeds will both dry to the same moisture content. Meanwhile, though, samples of seeds are drawn at set intervals through the drying period and placed in water to determine the best length of time to dry. When the number of seeds floating equals the number to remove, all the seeds are placed into the water. The floaters are nonviable and are discarded; the sinkers are viable and are kept (figure 39). Unless sown immediately, the sinking seeds must be dried thoroughly to a proper storage moisture content. The process has been completely automated in Sweden using sophisticated machines. However, the basic principle can be followed using pans of water and a kitchen sieve. The key is proper incubation and very rapid rate of drying. In extremely cold climates, it is possible to simply heat ambient air to near 40 °C to achieve the desired relative humidity. However, it may be necessary to dehumidify the air further by cooling it with an air-conditioner before heating. The IDS process is protected by patent in Canada and the United States, and royalties must be paid to use the process commercially (Downie and Bergsten 1991). Successful upgrades have been reported for seedlots of Douglas-fir (Sweeney and others 1991) and *Pinus roxburghii* Sarg. (Singh and Vozzo 1990). Attempts at upgrading seedlots of white spruce, sitka spruce (*Picea sitkensis* (Bong.) Carr.), and ponderosa pine (*Pinus ponderosa* P. & C. Lawson) gave mixed results (Downie and Bergsten 1991; Downie and Wang 1992; Karrfalt 1996).

Figure 38—Chapter 3, Seed Harvesting and Conditioning: water flotation of acorns for separating good seeds from damaged seeds and trash.

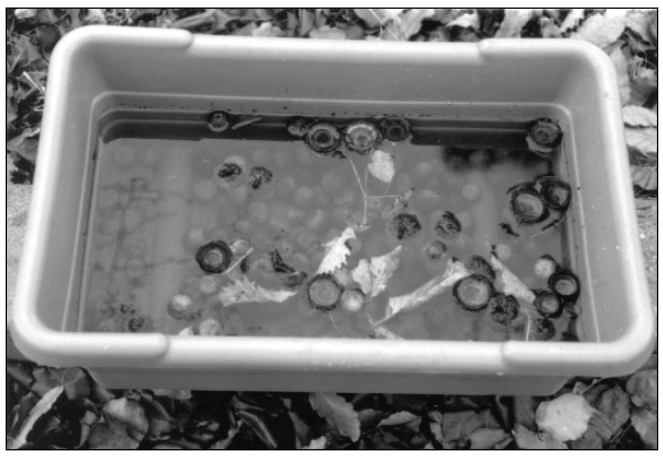


Figure 39—Chapter 3, Seed Harvesting and Conditioning: incubate-dry-separate (IDS) separation chamber; the floating seeds are discarded because of low viability and vigor, and the sinking seeds are kept because they have higher viability and vigor.

The final stage of conditioning seeds is preparation for storage, which is discussed in chapter 4. Those wishing to study further the mechanical methods and principles of seed cleaning are referred to Brandenburg (1977) and Brandenburg and Park (1977).

Conveying seeds. Moving seeds in forest seed processing plants is usually best accomplished by batch movement. In most cases, this means that a 4.5-liter (5-gallon) pail must be lifted and emptied into a hopper that feeds a conditioning machine about every 15 to 20 minutes. Larger amounts are sometimes moved with a hopper and forklift. The advantages of batch movement are greater control and flexibility of seed flow, easier clean-out, and a simpler, less expensive design. Greater control is provided because the seeds can be seen more easily for continual inspection. If the desired result is not obtained on one pass, the seeds can be immediately rerun. In continuous flow systems the seeds must flow to the next machine. Batch processing also provides greater flexibility, because the order of conditioning can be altered to match the lot and kind of seeds. In continuous flow the order of processing is relatively fixed. Bucket elevators have been used frequently in the past to move seeds, but these can be difficult to clean out. With many elevator designs, as much as 0.45 to 2.3 kg (1 to 5 lb) of seeds remain in the bottom or boot of the elevator and must be cleaned out by hand. This is much work and highly impractical with lots of less than 23.7 kg (50 lb). Because of this clean-out problem, the bucket elevator might present a major threat to lot integrity. A continuous bucket elevator (figure 40) eliminates the clean-out problem but can add to the cost of the plant. Vacuum elevators also eliminate clean-out problems but can seriously damage seeds; they move seeds very fast and sometimes stop them too quickly against hard surfaces, causing mechanical damage. Bucket elevators have also been found to damage seeds when not properly installed. The damage may not be immediately visible to the naked eye or even in a radiograph (see chapter 5). The softer the seedcoat, the easier damage can occur. Seeds of true firs would be most easily damaged; those of longleaf pine and red maple would be slightly more resistant; whereas those of ponderosa pine, loblolly pine, and dogwoods would be most resistant but still easily damaged if too much force is applied in conveying the seed. Not having elevators in the seed processing plant results in lower equipment cost, more available floor space, less noise, and lower maintenance cost.

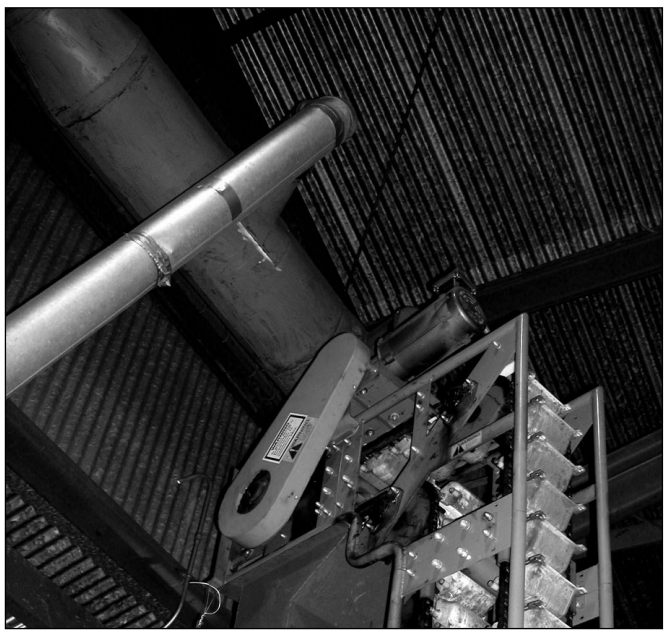
Scooping seeds by hand must also be done with proper consideration. Even a hand scoop if thrust into the seeds too hard or rapidly will cause damage and lower viability. Seed

Table 5—Chapter 3, Seed Harvesting and Conditioning: the application and interpretation of various seed tests to seed conditioning

Test	Observation	Interpretation/action
Moisture content (MC)	Orthodox seeds	
	Above 10% MC	Dry seeds immediately to prevent deterioration
	Below 10% MC	Safe for storage; seal seeds in moisture-proof container
	Recalcitrant seeds	
	Above 25%	MC high enough to preserve viability usually
	Below 25%	Seeds likely are non-germinable
Purity	Low (trash present will clog a seeder)	Seedlot needs to be re-cleaned
Germination, tetrazolium staining, or Excised embryo	95% or better	Best quality for container seedlings & precision sowing for bareroot seedlings
	90% or better	Good quality for container & bareroot seedlings
	80%	Minimum quality for bareroot seedlings
	Below 80%	Generally more difficult to achieve good seedling densities in the nursery; to improve results, determine if empty, insect-damaged, or filled nonviable (see x-ray test below) seeds are cause for low germination
Seed weight*	High number/weight	Smaller seeds
	Low number/weight	Larger seeds
X-radiography	Cracked seedcoat	Modify handling to eliminate damage
Standard	Broken embryo	Water soak or use PREVAC to remove damaged seeds
	Empty seeds	Remove with air separators, fluid separation, &/or gravity table
	Partially filled, insect-or fungus-damaged	IDS, Dimensional grading in conjunction with specific-gravity table separation
Contrast agent	No darker (more radio-opaque) spots on image	No damage to seeds from handling
	Darker spots on image	Seeds bruised in handling; reduce number, severity, & length of drops; remove damaged seeds with IDS

* Measured in either kilograms or pounds.

Figure 40—Chapter 3, Seed Harvesting and Conditioning: continuous bucket elevator for gentle handling of seeds.



should be gently gathered onto the scoop. If time does not permit gentle scooping, then another means of conveying should be arranged.

Quality Control

Quality control is very important in conditioning seeds. Seed conditioning can be a highly complex operation, usually involving many steps and many different persons. A procedures manual is crucial, so that the role of everyone involved can be clearly identified and thought out. Writing out the steps in detail, from preparing for collection through storage and planting, provides an opportunity for a careful examination of all steps to identify potential problems and inefficiencies. Also, when procedures are fully documented, the same steps can be followed if there is a change in personnel. Many good techniques and small nuances gained through years of seed conditioning can be lost if not documented in permanent form. Typically, plant managers are not expected to publish their techniques, and knowledge is lost at retirement or job transfer. It is therefore imperative that the manager document all procedures used, in detail, either on the manager's own initiative or with the manager's supervisor. Sometimes an interview with someone who has good writing ability will help a manager get thoughts on paper.

The procedure manual should indicate all the types of records to be kept and what to do when an error occurs. Sooner or later a mistake inevitably will occur, and procedures need to be in place to handle these errors. Quality control involves more than preventing mistakes; mistakes will occur despite the best precautions. Quality control also consists of making sure that mistakes do not go undetected and that reasonable effort is made to rectify the mistake. To aid in this, records should be kept in detail showing time spent, inputs, outputs, conditions during the work, and who did the work. Who did the work is often an important factor when trying to unravel a mistake. The people who did the work will be the ones who know the most about it and have the best chance to explain what happened. A third-party review of procedures can also be of great help. Preparing to explain a process to someone else encourages a more thorough review of the work. A properly administered seed certification or seed plant accreditation program can provide this type of review.

Constantly monitoring seed quality is necessary for a high-quality conditioning operation. The specifics of testing are discussed in more detail in chapter 5. The application of the tests (table 5) is discussed here. Testing begins before harvest with cutting and x-ray tests to judge the maturity and quality of seeds. Unless it is determined that good seeds are present, a crop of totally empty or damaged seeds can be collected.

Moisture testing is critical to monitor how well we are maintaining seed moisture in all types of storage. The electronic moisture tester (figure 41) is adequate for most orthodox seeds but needs to be periodically (annually, for example) verified by a laboratory oven test. The electronic meters also must have conversion charts developed; they do not give direct readings for tree and shrub seeds. These conversion charts are made by regressing (comparing) meter readings with oven moisture tests over a range of seed moisture values. Recalcitrant seeds do not test well in electronic meters, but the procedures used to handle them should be checked at least initially to be sure moisture is kept at sufficiently high levels. This is done by drawing samples and having them tested for moisture. Otherwise, the problem might not be discovered until the seed is bought, sold, tested for germination, or, worst of all, planted in the nursery and a poor germination occurs. Following wet de-winging of conifer seeds, de-pulping of fleshy fruits, or water separation of seeds, it is necessary to dry and then test the moisture content before moving to the next step. Seeds held at high moisture even overnight could begin to respire too rapidly and begin heating. Some seeds (for example, those of longleaf pine) are shed from the cone or fruit at a high moisture content, and moisture needs to be checked and reduced if too high for safe storage.

Figure 41—Chapter 3, Seed Harvesting and Conditioning: electronic moisture testers are used to monitor seed moisture content.

Figure 42—Chapter 3, Seed Harvesting and Conditioning: radiography of pine seedlots quickly and accurately shows how many bad seeds to remove.

Visual inspection, cutting tests, and, ideally, x-radiography is used to monitor the conditioning operation. Visual inspection leads us in improving purity. Cutting tests and x-radiography reveal how many bad seeds still need to be removed. X-radiography is the better method, for it can easily show mechanical damage to the seeds, is very fast, and is more accurate than cutting tests in differentiating between good and bad seeds. If an x-ray shows that 20% of the seeds are bad and must be removed, the cleaning equipment should then be adjusted to remove 20% of the seeds by number or volume (figure 42). A second check can then be made of the seeds after the machine has been adjusted to ensure the adjustment has removed all the bad seeds it should without removing too many good seeds. The separation may not be able to be completed with one setting.

In addition to daily monitoring, the conditioning procedures need to be verified as correct by full laboratory tests, to be sure no harm is coming to the seeds and that the desired quality is achieved. Purity tests tell how much of the seed by weight is pure seed and how much is trash. A low purity value means that a better job of cleaning needs to be done. Periodically, and after any modifications of procedures, it is critical to test each step in the process for its effect on viability. Samples should be taken before and after every step in the process. X-radiography and germination tests need to be run on these samples. The x-ray will help detect mechanical damage that causes cracks in the seeds, and, if used with a contrast agent, smaller bruises on the seeds. Germination tests detect any step that stresses the seeds. Two germination tests need to be run on each sample, one on the fresh sample and one on a sample after storage. The first test will pick up the immediate problem areas. The test after storage will be more effective in detecting latent damage. Some damage is not immediately obvious in the germination test but requires time for deterioration to develop to the point at which a drop in germination can be measured.

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Chapter 4

Storage of Seeds

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Contents

Introduction

In the simplest form of seed storage, mature seeds are held for a short period until weather or other factors permit sowing or planting. In the more comprehensive view, there are at least 3 objectives for storing seeds, and each of them dictates different strategies and procedures. These objectives may be described as storage for the following periods:

1. Very short periods (overwinter) between collection and sowing
2. Several years (10 or less) to ensure a reliable supply of seeds in the absence of annual crops
3. Long periods (10 to 50+ years) for germplasm conservation

The strategies employed will depend on all of the factors that influence seed longevity. Some of these factors have been discussed in chapter 1, but now they will be explored in the context of seed storage only. Following this, recommendations will be made for storage procedures to achieve the objectives listed here.

Factors Affecting Longevity of Seeds

Seed Characteristics

Basic seed physiology. In his classic paper, Dr. E. H. Roberts (1973) divided seeds into 2 groups based on their storage characteristics: orthodox and recalcitrant. Orthodox seeds are those that can be dried to moisture contents of 10% or less; in this condition they can be successfully stored at subfreezing temperatures. Recalcitrant seeds, on the other hand, are those that cannot be dried below relatively high moisture levels (25 to 45%) and therefore cannot be stored below freezing. Current knowledge of seed physiology can allow additional classification of tree seeds into the following groups (Bonner 1990): (1) true orthodox, (2) sub-orthodox, (3) temperate-recalcitrant, and (4) tropical-recalcitrant. In addition, Ellis and others (1990) have proposed an intermediate storage class that falls between orthodox and recalcitrant.

True orthodox seeds can be stored for relatively long periods at subfreezing temperatures—if their moisture contents are reduced to about 5 to 10% (wet weight basis). [Throughout this chapter, seed moisture will be expressed as a percentage of wet weight in keeping with the international protocol (ISTA 1993).] Most species of the economically valuable tree genera of the Northern Temperate Zone are classified as having true orthodox seeds: fir (*Abies* P. Mill.), alder (*Alnus* P. Mill.), birch (*Betula* L.), ash (*Fraxinus* L.), larch (*Larix* P. Mill.), spruce (*Picea* A. Dietr.), pine (*Pinus* L.), sycamore (*Platanus* L.), cherry and plum (*Prunus* L.), Douglas-fir (*Pseudotsuga* Carr.), hemlock (*Tsuga* Carr.), etc. Many valuable genera of the tropics and subtropics are also true orthodox: *Acacia* L., *Albizia* Durz., many other Fabaceae, *Casuarina* Rumph. ex L., *Eucalyptus* L' Her., mesquite (*Prosopis* L.), and teak *(Tectona* L.f.). The time limits for storage of true orthodox seeds under optimum conditions is not really known. Eliason and Heit (1973) reported 86% germination in red pine (*Pinus resinosa* Soland.) samples stored for 42 years. Martin (1948) found that herbarium samples of velvet mesquite (*Prosopis velutina* Woot.) germinated quite well after 44 years. Barnett and Vozzo (1985) found that slash pine (*P. elliottii* var. *elliottii* Engelm.) still germinated at a rate of 66% after 50 years of storage at 4 °C. Other examples of storage data for true orthodox tree seeds are found in table 1.

Sub-orthodox seeds can be stored under the same conditions as true orthodox seeds, but for much shorter periods. The reasons for their decreased longevity are not completely known. However, indirect evidence suggests that some causes are high lipid contents—as in hickory (*Carya* Nutt.), beech (*Fagus* L.), walnut (*Juglans* L.), and some pines (*Pinus* L.) and thin fruits or seedcoats, including some maples (*Acer* L.), poplars (*Populus* L.), and willows (*Salix* L.) (Bonner 1990). Retention of viability for more than 10 years would be rare for sub-orthodox species with current storage technology (table 2).

Temperate-recalcitrant seeds cannot be desiccated but can be stored at or slightly below freezing. Genera with temperate-recalcitrant seeds include buckeye (*Aesculus* L.), chestnut (*Castanea* P. Mill.), oak (*Quercus* L.), and redbay (*Persea* P. Mill.). Some, but not all, of these species can be stored for 3 to 5 years at near-maximum moisture contents (30 to 50%) and low temperatures (–3 to +4 °C) (table 3).

Tropical-recalcitrant seeds have the same desiccation sensitivity of temperate-recalcitrant seeds and are also sensitive to low temperatures. Even short periods of exposure to temperatures below 10 to 15 °C can cause loss of viability (Berjak and Pammenter 1996; Chin and Roberts 1980). Included in this group of species are *Araucaria* Juss., *Hopea* Roxb., *Shorea* Roxb., ex C.F. Gaertn., and *Theobroma* L. Longevity of these seeds is usually measured in months, not years (table 4).

Intermediate seeds can be dried to moisture levels almost low enough to meet orthodox conditions (12 to 15%) but are sensitive to the low temperatures typically employed for storage of orthodox seeds. Viability is retained usually only for a few years. The research that led to the concept of

Table 1—Chapter 4, Storage of Seeds: storage test results for some true orthodox species

Species	Test conditions		Test results	
	Temp (˚C)	Seed moisture (%)	Period (years)	Viability loss (%)
Abies procera Rehd.	0	9	7	11
Acacia mangium Willd.	4–8	—	1.2	6
Acer saccharum Marsh.	–10	10	5.5	5
Alnus rubra Bong.	2–4	5–8	4	0–13
Araucaria cunninghamii Aiton ex D. Don	–15	16–23	8	Little
Atriplex canescens (Pursh) Nutt.	[??]	—	4	Little
Betula alleghaniensis Britt.	3	—	8	2
Casuarina equisetifolia L.	–3	6–16	2	0–5
Cercocarpus montanus Raf.	5	8	6	7
Cowania mexicana D. Don	5	8	6	1
Eucalyptus spp.	3–5	4–8	5–20	—
Grevillea robusta A. Cunningham ex R. Br.	–6	6	2	<5
Krascheninnikovia lanata (Pursh)	5	—	2.5	<10
Larix decidua P. Mill.	2–4	7.5	14	27
Liquidambar styraciflua L.	3	5–10	9	3
Paraserianthus falcataria (L.) I. Nielsen	4–8	—	1.5	10
Picea sitchensis (Bong.) Carr.	2–4	7–9.5	13–24	0–11
Pinus banksiana Lamb.	2–4	11	17–18	0–8
P. merkusii Junghuhn & Vriese ex Vriese	4-5	<8	4	None
P. ponderosa P. & C. Lawson	0	8	7	None
Tectona grandis L. f.	0–4	ca.12	7	None
Tsuga heterophylla (Raf.) Sarg.	5, –18	8	2	None
Ulmus laevis Pall.	–3	10	5	None

Sources: Bonner (1990), Clausen (1967), Jones (1987), Springfield (1968, 1973, 1974), Tylkowski (1987), Wang and others (1993).

Table 2—Chapter 4, Storage of Seeds: storage test results for some sub-orthodox species

Species	Test conditions		Test results	
	Temp (°C)	Seed moisture (%)	Period (years)	Viability loss (%)
Citrus limon (L.) Burm. F.	–20	5	0.9	± 5
Fagus silvatica L.	–10	10	5	34
Gmelina arborea Roxb.	–5	6–10	2	10
Populus deltoides Bartr. ex Marsh.	–20	6–10	6	21
P. grandidentata Michx.	–18	11–15	12	14–29
P. tremuloides Michx.	–18	6–8	2	1
Salix glauca L.	–10	6–10	1.2	0

Sources: Bonner (1990), Fechner and others (1981), Wang and others (1982).

intermediate seed behavior was done with coffee (*Coffea arabica* L.) (Ellis and others 1990), and although no forest tree species have been identified as intermediate as yet, there is a very good chance that some will fit this classification.

There are several genera that contain both orthodox and recalcitrant species. In the Northern Temperate Zone, maple (*Acer*) is such a genus. Silver maple (*Acer saccharinum* L.) is clearly temperate-recalcitrant in nature (Tylkowski 1984), but red maple (*A. rubrum* L.) can be dried to 10% seed moisture content and is either true orthodox or sub-orthodox. Among tropical species, the genus *Araucaria* Juss. has a similar distinction. *Araucaria cunninghamii* Aiton ex D. Don is orthodox in nature, and *A. hunsteinii* K. Schum. &

Table 3—Chapter 4, Storage of Seeds: storage test results for some temperate recalcitrant species

Species	Test conditions		Test results	
	Temp (°C)	Seed moisture	Period (months)	Viability loss (%)
Acer saccharinum L.	–3	50	18	8
Quercus macrocarpa Michx.	1	44	6	None
Q. pagoda Raf.	3	35	30	6
Q. robur L.	–1	40–45	29	31–61
Q. rubra L.	–1 to –3	38–45	17	18–46
Q. virginiana P. Mill.	2	—	12	35

Sources: Bonner (1990), Schroeder and Walker (1987).

Table 4—Chapter 4, Storage of Seeds: storage test results for tropical recalcitrant species

Species	Test conditions		Test results	
	Temp (°C)	Seed moisture (%)	Period (days)	Viability loss (%)
Araucaria hunsteinii K. Schum. & Hullrung	19	25–30	54	±30
Azadirachta indica Adr. Juss	26	10–18	56	65
Dipterocarpus turbinatus C. F. Gaertn.	16	41–44	161	47
Hopea helferi (Dyer) Brandis	15	47	37	2
Shorea robusta C. F. Gaertn.	13.5	40–50	30	60
S. roxburghii G. Don	16	40	270	±30
S. talura Roxb.	23.5	47	105	50
Symphonia globulifera L. f.	15	—	270	None

Sources: Bonner (1990), Bras and Maury-Lechon (1986), Purohit and others (1982), Tompsett (1987).

Hollrung is tropical-recalcitrant (Tompsett 1982). There are undoubtedly other genera, still unidentified, with these characteristics.

Placing seeds into these precisely defined groups of storage behavior is often tenuous, however, because recalcitrance is not an all-or-nothing characteristic (Berjak and Pammenter 1996). There is a great deal of natural variation, and species should be viewed as lying somewhere along a spectrum that stretches from extreme orthodoxy to extreme recalcitrance. Furthermore, as technology improves, a species may not be what it was once thought to be. *Fagus* L. was once thought to be recalcitrant, but with carefully controlled drying, seeds of this genus can attain low moisture contents and an extended storage life at subfreezing temperatures (Bonnet-Masimbert and Muller 1975; Suszka 1975) and should now be considered as sub-orthodox in storage behavior.

Seed morphology. Seed morphology is important to the storage life of seeds in the context of protection for the embryo. The hard seedcoats of species of the Leguminosae help maintain the low level of metabolism in these dry orthodox seeds by excluding moisture and oxygen. Hard, thick seedcoats, such as those of *Carya* Nutt., *Cornus* L., and *Nyssa* L., help protect the embryos from mechanical damage during collection and conditioning. The thinner or softer a seedcoat may be, the more likely that the seed has a shorter storage life because of rapid moisture uptake or bruising of internal seed tissues. Thin seedcoats may be a significant factor in storage difficulties of *Acer rubrum* L., *Pinus palustris* P. Mill., and *Populus* L. spp., but there is no direct evidence of this.

Chemical composition. General observations of seed behavior in storage has suggested that chemical composition is an important factor in longevity; for example, oily seeds do not store as well as starchy seeds. One can find support for this concept with the relatively poor performance in storage of *Carya* Nutt. spp., *Juglans* L. spp., and *Sassafras albidum* (Nutt.) Nees, all oily seeds, and the relatively good performance of *Celtis laevigata* Willd., *Fraxinus* L. spp., and *Platanus occidentalis* L., all starchy seeds (Bonner 1971). Exceptions to this rule abound, however. Oily seeds of *Liquidambar styraciflua* L. as well as *Pinus taeda* L., and many other conifers keep very well in proper storage. Within *Quercus* L., acorns of the black oaks, which are somewhat oily with very little carbohydrate, store longer than acorns of the white oaks, which are full of carbohy-

drates and very little lipid. Even among the black oaks, species with the highest lipid contents seem to store better, even though there is no evidence of cause and effect. One must conclude that among a wide range of species there is no compelling argument for gross chemical composition as the critical factor in seed longevity under proper storage conditions. There is some evidence, however, that suggests that the relative concentrations of particular carbohydrates play key roles in desiccation tolerance, a critical property in determining storage behavior of seeds (Lin and Huang 1994). This topic is obviously one that deserves more research.

Seed maturity. Seeds of many orthodox species that are immature when collected (or extracted from fruits) are likely to fare poorly in storage (Stein and others 1974). Experimental evidence has demonstrated this fact for Scots (*Pinus silvestris* L.) (Kardell 1973), loblolly (*P. taed*a L.), longleaf *(P. palustris* P. Mill.), and eastern white *(P. strobus* L.) pines (Bonner 1991). The physiological basis for this effect is not known, but it seems logical that immature seeds have not been able to complete the normal accumulation of storage food reserves, develop all needed enzymes and/or growth regulators, or complete their full morphological development and cell organization. For species with seeds that are naturally dispersed while still physiologically immature, such as *Fraxinus excelsior* L., there is no apparent damage to storage longevity (Willan 1985). The ability to complete maturation naturally after separation from the mother tree has apparently evolved with these species. For conifers like the pines noted above, storage of immature cones for several weeks prior to extraction of the seeds appears to enhance seed maturity and viability retention during storage (Bonner 1991).

Seed Handling Prior to Storage

Poor fruit or seed handling that damages seeds will often lead to reduced viability in storage, especially in orthodox seeds. The most common example of this is impact damage to seeds during extraction and conditioning. Seeds can be bruised by excessive tumbling of cones, running dry dewingers too fast or too full, or poor transport systems (Kamra 1967). During kiln drying of conifers, excessive heat while seed moisture is still high can easily lead to damage that will show up later as reduced vigor and viability in stored seeds (see chapter 3).

Another factor to consider in damage to seeds during extraction and conditioning is cracks or other breaches of the seedcoats that will allow microorganisms to enter. Cracks in seedcoats that occur during seed conditioning are usually not visible to the naked eye but can be detected on radiographs (see chapter 5). This is one reason why hard-seeded legumes are usually not returned to storage after mechanical scarification. An exception to this is when seed burners are used for scarification (Lauridsen and Stubsgaard 1987). Seed burners tend to cauterize the breach in the seedcoat and kill surface contaminants.

Recalcitrant seeds, with their high moisture contents, are potentially very susceptible to damage during handling, but they seldom are subjected to rigorous cleaning or conditioning procedures. Furthermore, the most important group of recalcitrant species in North America—the oaks (*Quercus* L.)—have single-seeded fruits with rather strong outer covering structures and rather well-protected embryonic axes. Silver maple *(Acer saccharinum* L.), on the other hand, has recalcitrant seeds with a large embryo that is protected by a soft and pliable pericarp and is very susceptible to bruising during seed handling.

Storage Environment

Storage environment is obviously very important in extending the life of seeds. The general objective is to reduce the metabolism of the seeds as much as possible without damaging them and to prevent attack by microorganisms. The ideal metabolic rate in storage will conserve as much of the stored food reserves in the seeds as possible, yet operate at a level that maintains the integrity of the embryos.

Moisture. Seed moisture is the most important factor in maintaining viability during storage; it is the primary control of all activities (table 5). Metabolic rates can be minimized by keeping seeds in a dry state. For true orthodox and sub-orthodox seeds, optimum moisture contents for storage are 5 to 10%. The normal practice with all orthodox tree seeds is to dry them to these levels and store them in moisture-proof containers that maintain them at these levels. Moisture in seeds (or any objects) will come to an equilibrium with the moisture in the storage atmosphere based on the differences in the vapor pressures and the chemical nature of the seeds (table 6). Proteins are the most hygroscopic, followed by carbohydrates, then lipids. These differences are reflected in the equilibrium moisture contents (the seed moisture content when equilibrium is reached) of various seeds (figure 1). Starchy seeds have higher equilibrium moisture contents than fatty seeds. For this reason, seed managers should know the dominant chemical constituents of the seeds they are storing.

Recalcitrant seeds equilibrate in a similar fashion, but their naturally high moisture contents and rapid metabolism

make it difficult for a true equilibrium to be reached with the atmospheric moisture. The large differences in chemical makeup of various species of oak lead to large differences in their equilibrium values (figure 2). Because all recalcitrant seeds are stored at high moisture contents, their equilibrium moisture contents are not as important in seed storage management as they are for orthodox seeds.

Temperature. Metabolic rates can also be minimized with low temperatures, both for orthodox and for recalcitrant seeds. The storage moisture content determines just how low temperatures can be set for seed storage. From freezing to –15 °C, 20% is the approximate upper moisture limit. Below –15 °C, the limit is about 15%; and in cryogenic storage in liquid nitrogen (–196 °C), 13% is the limit. Therefore, true orthodox seeds maintained at moisture levels of 5 to 10% can be safely stored at just about any temperature. The longevity of orthodox tree seeds in liquid nitrogen is really not known, but short tests with several species suggest that they can survive for long periods just like orthodox agricultural seeds (table 7). It is not known if sub-orthodox seeds have this same tolerance of low temperatures, but it is known that they can be stored for a few years at temperatures as low as –20 °C (table 2).

Table 5—Chapter 4, Storage of Seeds: potential moisture damage thresholds

Moisture content (%)	Potential effect
> 30	Germination can occur
10–18	Active fungal growth
< 8–9	Insect activity reduced
5–8	Best range for sealed storage
< 5	Desiccation injury possible in some species

Figure 1—Chapter 4, Storage of Seeds: equilibrium moisture contents at 25 °C for 3 orthodox species: American sycamore (*Platanus occidentalis* L.) has the lowest lipid content; sweetgum (*Liquidambar styraciflua* L.) the highest (from Bonner and others 1994; Bonner 1981).

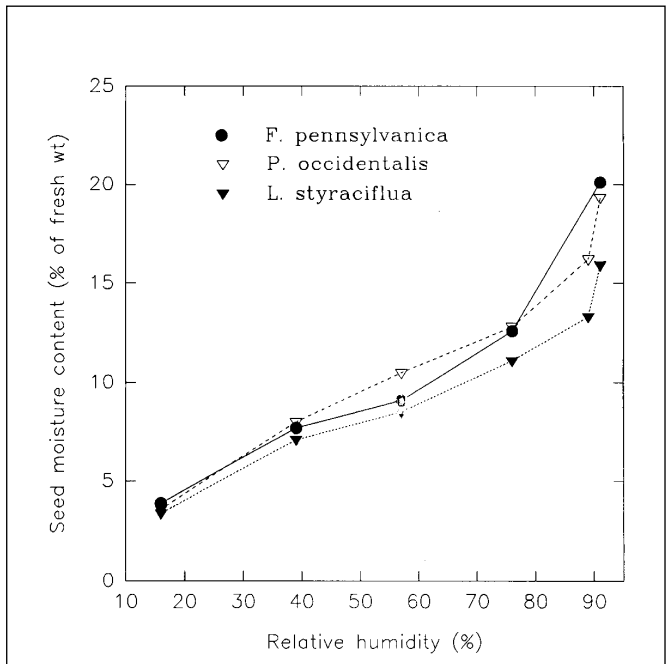


Table 6—Chapter 4, Storage of Seeds: equilibrium moisture content at 4 to 5 °C and 3 relative humidities for some seeds

Species	20% RH	45% RH	95% RH
Trees with orthodox seeds			
Carya ovata (P. Mill.) K. Koch	—	10	15
Juglans nigra L.	—	11	20
Liquidambar styraciflua L.	—	8	20
Liriodendron tulipifera L.	—	10	19
Picea abies (L.) Karst.	6	8	—
Pinus sylvestris L.	6	8	—
P. taeda L.	—	10	17
Prunus serotina Ehrh.	—	9	17
Crops with orthodox seeds			
Glycine max (L.) Merr.	6	8	19
Zea mays L.	8	12	20
Trees with recalcitrant seeds			
Quercus alba L.	—	37	50
Q. nigra L.	—	17	29
Shorea robusta Gaertner f.	—	—	35

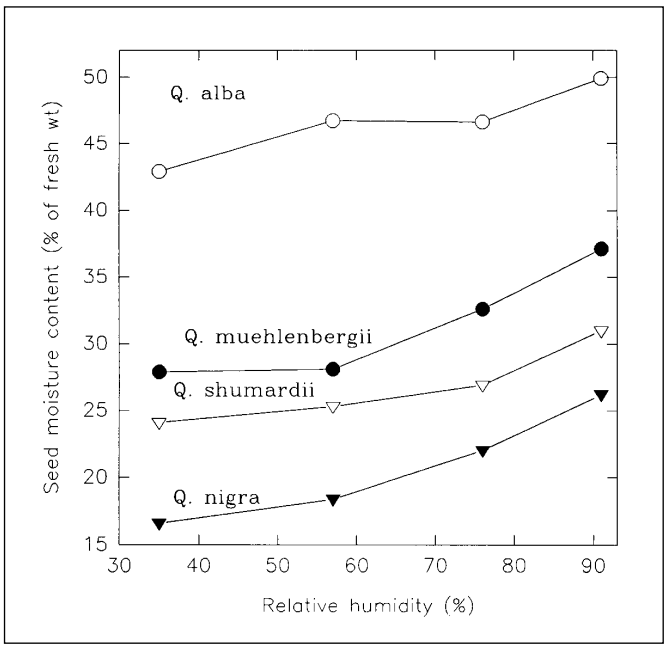
Sources: Bonner (1981), Bass (1978).

Table 7—Chapter 4, Storage of Seeds: cryogenic storage test results for some forest tree seeds

Species	Seed moisture (%)	Period (days)	Viability loss (%)
Abies alba P. Mill.	—	6	5
Fagus silvatica L.	—	6	total
Larix decidua P. Mill.	—	6	5
Picea abies (L.) Karst.	—	6	1
Pinus sylvestris L.	—	6	0
Populus tremula H *P. tremuloides*	—	6	1
Pinus echinata P. Mill.	—	112	0
Ulmus pumila L.	—	112	0
Abies concolor (Gard. & Glend.) Lindl. ex Hildebr.	<13	180	0
Pinus ponderosa P. & C. Lawson	<13	180	0

Source: Bonner (1990).

Figure 2 —Chapter 4, Storage of Seeds: equilibrium moisture contents at 25 °C for 4 recalcitrant oak (*Quercus* L.) species. White oak (*Q. alba* L.) has the lowest lipid content; water oak (*Q. nigra* L.) the highest (adapted from Bonner and others 1994).



If seeds have impermeable seedcoats that will inhibit the uptake of moisture and oxygen from the surrounding atmosphere, they can be stored for a number of years at room temperature. The primary examples of such storage come from seeds of the *Leguminosae* (Bonner 1990).

Recalcitrant seeds require different conditions. Temperate recalcitrant seeds can be stored at or just below freezing (–3 °C) (table 3), but lower temperatures for just a few months will kill them (Bonner 1973), apparently due to intracellular ice formation. The lethal exposures for temperate-recalcitrant seeds are poorly defined and appear to be a function of both temperature and length of exposure. On at least one occasion, sub-freezing temperatures for a week killed all *Quercus* acorns that were on the ground or still on the trees in central Louisiana. On the other hand, exposure to sub-freezing temperatures for 3 days on the ground, with a minimum of around –10 °C at night, did not kill acorns of *Quercus pagoda* Raf. in Mississippi (Bonner 1992). This question will require research to provide a satisfactory answer.

Tropical-recalcitrant seeds have a much higher lethal minimum temperature than temperate species. Chilling damage and death will occur below 12 to 20 °C, depending on the species. Among the species included in this book, only certain *Araucaria* Juss. can be considered as tropical-recalcitrant species. Because there are no ice crystals formed at these temperatures, the chilling damage in these seeds must have a different physiological basis than damage in temperate-recalcitrant seeds.

A number of conifer species can be partially redried after stratification and returned to storage when planting is delayed. Seed moisture contents may be over 20% in such cases, so subfreezing temperatures cannot be used. Good results have been obtained by storing stratified seeds of ponderosa pine and Douglas-fir with seed moisture contents of around 26% at 2 °C for 9 months (Danielson and Tanaka 1978).

Atmosphere. Reduction of oxygen levels will slow metabolism and increase longevity of seeds, but it is not practical to regulate this factor precisely in operational storage situations. In past years, seeds of *Populus* L. species were often stored in vacuum desiccators to extend storage life; the beneficial effect in this case was reduction of oxygen for metabolism. (Proper drying and refrigeration have replaced vacuum storage for *Populus* now.) Recalcitrant

seeds, with their active metabolisms, require oxygen to such a degree that it is quickly depleted in airtight storage containers, and the seeds die. Any recalcitrant seeds must be stored in containers that afford free access to the surrounding atmosphere.

There have been extensive trials with storage of seeds in inert gases (Justice and Bass 1978), primarily crop species, but these procedures show no long-term advantage over good standard temperature and moisture conditions. One advantage of gas manipulation may be for transport of seeds in tropical regions where refrigeration may not be available. Success of this nature has been reported for shipment of Monterey pine (*Pinus radiata* D. Don) seeds sealed in atmospheres of nitrogen or carbon dioxide (Shrestha and others 1985).

Carbon dioxide can also be used to kill insect larvae in storage. Dry orthodox seeds can be placed in atmospheres that are 60 to 80% CO_2 for 4 weeks at room temperature to kill larvae. If seed moisture is below 8%, there should be no damage to the seeds for at least several years (Stubsgaard 1992). If there is enough moisture in the seeds to stimulate metabolism, the seeds will absorb the CO_2. In small sample bags, the absorption will collapse the bag around the seeds as if a "heat-shrink" packaging process were in use. This same condition is often observed in plastic bags of seeds in moist stratification.

Storage Facilities

Cold Storage

Facilities for seed storage will vary by the amount of seeds to be stored and the projected length of storage. Small seedlots—a liter (quart) or less—can be stored in household refrigerators and freezers. Larger seedlots and quantities will require a walk-in refrigerator or freezer (figure 3). These units are usually assembled from prefabricated insulated panels and can be made almost any size to fit the owner's needs. A suggested size for a nursery operation is one large enough to hold a 5-years' supply of seeds. The cold storage at the USDA Forest Service's W. W. Ashe Nursery in Brooklyn, Mississippi (figure 3) has a capacity of 1,584 m^3 (52,800 ft^3). One cubic meter will hold from 125 to 140 kg (275 to 310 lb) of seeds. Many orthodox and sub-orthodox seeds show declining germination and vigor after a few years in storage at temperatures just above freezing (Bonner 1991; Zasada and Densmore 1977), so freezers maintained at about –18 to –20 °C are preferred for any storage of sensitive species longer than 3 or 4 months. Because it would be inconvenient to have separate facilities, most users just place all orthodox species in freezers. For reasons discussed earlier, recalcitrant species must be stored at temperatures no lower than –3 °C. It is usually convenient to store recalcitrant seeds in the same facility used for stratification and seedling storage. Short-term storage of any redried stratified seeds as noted earlier should be done here also. All of these facilities should have backup generators and safety alarms in case of power failure.

For cryogenic storage, special tanks must be employed to hold the liquid nitrogen, and special equipment is needed to maintain its level. The tanks (figure 4) in place at the USDA National Seed Storage Laboratory in Fort Collins, CO, each have a capacity of 2,600 to 5,500 samples, depending on the size of the sample container. Samples are stored in sealed glass tubes and suspended above the liquid nitrogen in its vapor (temperature approximately –150 °C).

Containers

Orthodox seeds should be dried to safe moisture contents (5 to 10%) and stored in sealed containers that prohibit absorption of moisture from the atmosphere. The containers used most commonly for tree seeds are fiberboard drums with a thin plastic coating on the inside (figure 5). These drums are available in sizes of about 0.5 and 1.0 hl (1.5 and 3 bu); they hold approximately 25 and 50 kg (55 and 110 lb) of loblolly pine seeds. Any large, rigid container can be used, as long as it can be sealed. The best practice is to insert a polyethylene bag liner for this purpose. It is also a good idea to do this with fiberboard drums, as repeated use of the drums over a number of years will cause breaks in their interior plastic lining. Glass containers, very popular in pre-plastic days, should not be used because of the danger of breakage. If they are used, plastic bags should be inserted to hold the seeds in case the glass is broken.

Figure 3—Chapter 4, Storage of Seeds: a large walk-in refrigerator for seed storage.

Figure 4—Chapter 4, Storage of Seeds: liquid nitrogen tanks for long-term storage of seeds for germplasm conservation at the USDA National Seed Storage Laboratory, Fort Collins, Colorado.

Figure 5—Chapter 4, Storage of Seeds: fiberboard drums that are commonly used for storage of tree seeds.

Small seedlots can be stored in polyethylene bags or bottles (figure 6). All plastic is not the same, however; low-density polyethylene with water vapor transmission rates of 4 g/m^2/day or lower at 25 °C is good for seeds (Lauridsen and others 1992). This requirement is met by polyethylene bags with a wall thickness of 0.075 to 0.1 mm (3 to 4 mils). As temperature is lowered, permeability of these materials decreases (Stubsgaard 1992). The common household freezer bags in the United States meet this thickness requirement, but most sandwich bags do not. Bags thinner than 0.075 mm should not be used, because they are too permeable to moisture vapor. For recalcitrant seeds, maximum bag wall thickness is 0.25 mm (10 mils); thicker plastics can limit gas exchange because they are impermeable to oxygen and carbon dioxide. There is no maximum thickness for orthodox seeds. Seeds with sharp points or appendages, such as *Fraxinus* L., *Taxodium* L.C. Rich, or *Carya* Nutt., can cause problems by piercing the bag walls and allowing moisture to enter. When storing these types of seeds, double bags can be used to reduce the problem. The same steps can be taken when emerging insect larvae from oak acorns eat holes in the bags. Information on vapor transmission rates of other packaging materials can be found in Lauridsen and others (1992).

Figure 6—Chapter 4: Storage of Seeds, polyethylene bags and bottles that are commonly used for storage of small samples of tree seeds.

Moisture Control

Refrigerated storage units can be made with controlled humidity so that orthodox seeds can be stored in unsealed containers without danger of moisture absorption. At the low temperatures usually employed for tree seeds, however, this feature would be very expensive. It is much cheaper to dry the seeds and store them in sealed containers. If recalcitrant seeds are stored in the same facility as orthodox seeds, dehumidification could not be used because of desiccation damage to the recalcitrant seeds. Dehumidification is also a factor when seeds are stored in household refrigerators. Most currently manufactured refrigerators are frost-free, which means that the moisture has been removed from the inside atmosphere. In such units recalcitrant seeds will quickly become desiccated if care is not taken.

Storage Recommendations

Orthodox Seeds

All orthodox seeds should be stored in moisture-proof, sealed containers with seed moisture contents of 5 to 10%.

If the period of storage will be 3 years or less for true orthodox species, or 2 years or less for sub-orthodox species, temperatures of 0 to 5 °C are sufficient. For longer periods of storage for both types of orthodox species, freezers (–18 to –20 °C) should be used.

Temperate-Recalcitrant Seeds

Temperate recalcitrant seeds should be stored with moisture contents at least as high as that present when the mature seeds were shed from the tree. (Refer to genus chapters in this manual for information on individual species.) This moisture level must be maintained throughout storage, which may require occasional rewetting of the seeds. Temperatures should range from 0 to 5 °C, although 1 or 2 degrees below freezing will not harm most species. Containers should be basically impermeable to moisture loss, but must allow some gas exchange with the atmosphere. Polyethylene bags with a wall thickness of 0.075 to 1.0 mm (3 to 7 mils) are suitable. Some oak acorns can be stored for 3 years in this fashion (table 3), but some viability will be lost. For other recalcitrant species, few data are available.

Tropical-Recalcitrant Seeds

Storage of tropical recalcitrant seeds is done in the same manner as storage of temperate species, except that temperatures must be kept at a high level. There are differences among species but the lower limits are generally 12 to 20 °C. Successful storage for more than 1 year should not be expected.

Cryogenic Storage

For long-term germplasm conservation programs, true orthodox and sub-orthodox seeds can be dried to moisture contents of 5 to 10% and stored in liquid nitrogen. Such programs require special equipment and procedures and are beyond the scope of this book.

Other Management Considerations

The first step in planning for seed storage facilities or programs is to consider the objectives of storage. If storage is only needed for periods of 6 to 30 months, freezers may not be needed. If storage will be for longer periods, then at least some freezer capacity will be needed. If recalcitrant seeds will make up the bulk of the stored materials, then freezers will not be needed. If seeds and seedlings will be stored in the same facility, then space requirements will be very large. Overestimating storage needs can be a problem, but underestimating them is an even bigger one.

Germination should be retested on seedlots that will be stored for more than 5 years. After the initial test, tests should be carried out after 3 years and every fifth year thereafter. Seed vigor will decline before germination percentage (Hampton and TeKrony 1995), so tests on stored seedlots should include some measure of vigor or germination rate (see chapter 5). When total germination has declined 15% from its original level, plans should be made to use the seeds as soon as possible.

In long-term storage for germplasm conservation, genetic damage or shifts are always a consideration. A few studies have demonstrated some chromosome damage during storage of tree seeds of the following species: *Fraxinus americana* L. (Villiers 1974), *Pinus echinata* P. Mill (Barnett and Vozzo 1985), and *P. sylvestris* L. (Simak 1966). There is no evidence yet, however, that these aberrations cause damage that is transmitted to the next generation. While more research should be done on this question, especially in seeds stored cryogenically, there seems to be no cause for alarm.

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Chapter 5

Seed Testing

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Contents

5

Introduction

Seed testing is the cornerstone of all other seed technologies. It is the means by which we measure the viability and all the physical factors that regulate the use and maintenance of seeds. Everything that is done with seeds should have some test information to guide the work and ensure high quality. Seed tests tell if a crop of seeds is worth collecting, if handling procedures are correct, and how many potential seedlings are available for regeneration.

The earliest form of seed analysis, the cut test, is still often used today. Before seeds are collected in the field, some seeds are cut open with a knife or razor blade to see if their internal tissues are fully developed and undamaged. This analysis is made more accurate in some cases by the use of a hand lens. It is also used for simple analysis during extraction and cleaning, or after germination to determine if the ungerminated seeds have deteriorated or remained dormant. Although the cut test is often very good at producing some information quickly, it is limited in the amount of information it can supply and it lacks accuracy compared to more sophisticated procedures. Therefore, it should never be taken as a substitute for a formal laboratory analysis.

Sampling

Formal seed analysis begins with the sampling of the seedlot. The Rules for Testing Seeds (AOSA 1996) and the International Seed Testing Rules (ISTA 1996) both give instructions on how to draw samples from a seedlot so that the sample is representative of the entire seedlot. Representative means that any tests conducted on this sample will accurately estimate the mean value of the lot quality.

Sampling can be done with the hand or with a seed probe, also known as a trier (figure 1). If a probe is used, it must be long enough to reach to the farthest edge of the container. A probe has gates that prevent seeds from entering until the probe is inserted the full dimension of the container. The probe should be inserted into the seed container with these gates closed. Otherwise, seeds from the upper layers will fill the probe as it is inserted and the bottom layers will not be sampled. Once the tip reaches the bottom or far side of the container, the gates should be opened and the probe gently turned back and forth to help the seeds fall in. Then the gates should be closed gently, not forced, so that any seeds that are caught in the opening and are preventing the gates from closing fully (figure 2) are not crushed. (Mechanically damaged seeds would bias the sample.) After the probe has been withdrawn from the seed container, it should be held horizontally, with the gates facing upward. Then the gates should be opened gently and the probe shaken gently back and forth, so that seeds caught in the gates will slip down into the probe and the gates can be safely closed. Finally, the probe should be emptied by pouring the seeds out the top of the probe and into a second container (figure 3). This sample is the first primary sample.

If there is only 1 container, primary samples should be taken until there are 5 of them. When more than 1 container holds the seedlot, at least some of the other containers must be sampled. When there are between 1 and 5 containers, all containers should be sampled, at least 1 probe from each container. When there are more than 5 containers, 5 of the containers plus 10% of the remaining ones should be sampled. It is never necessary to sample more than 30 containers. (It would be rare that a forest seedlot would need 30 containers or more, or possibly even 20.) All of the primary samples are then placed together to make up the composite sample.

Sampling by hand is sometimes necessary when the seeds will not flow into the probe because of their size, shape, or surface texture. Sampling by hand can be done by inserting the open hand (figure 4) into the seeds, closing it once the point of sampling is reached, and then withdrawing it closed. The seeds are then placed in a second container to form the composite sample, just as in sampling with the probe. At least 5 handfuls must be taken, and all levels must be sampled. When the hand cannot be inserted into the seedlot, the seeds can be poured from one container into a second. The tester then should stop at a minimum of 5 evenly spaced intervals and remove a handful of the seeds for the composite sample.

The composite sample, whether taken with a probe or by hand, is usually too large to submit to a seed laboratory for analysis. The composite sample is, therefore, mixed and divided to obtain a submitted sample. This procedure is very important and must be done correctly for the results to be accurate.

The composite sample can be mixed either mechanically or by hand with rulers. Hand-mixing the composite sample is done by pouring the seeds into a cone on a flat, clean surface. An open file folder makes a good work surface that can be picked up to return the seeds to a container. With one ruler held stationary against the seeds, the second ruler is used to pull the outer edge of the pile up to the top of the pile, allowing the seeds to roll down the sides and over the top of the stationary ruler (figure 5). The full pile is thoroughly turned over and all layers mixed together. This procedure should be repeated for 1 full minute. Then the pile should be divided by cutting the cone in half and then into

Figure 1—Chapter 5, Seed Testing: seed probes are used to sample free-flowing seeds.

Figure 2—Chapter 5, Seed Testing: seeds caught in the gates of the seed probe must not be cut when the gates are closed.

Figure 3—Chapter 5, Seed Testing: the seed probe is emptied by pouring the seeds out the top.

Figure 4—Chapter 5, Seed Testing: an open hand is inserted into a seedlot to take a sample for testing.

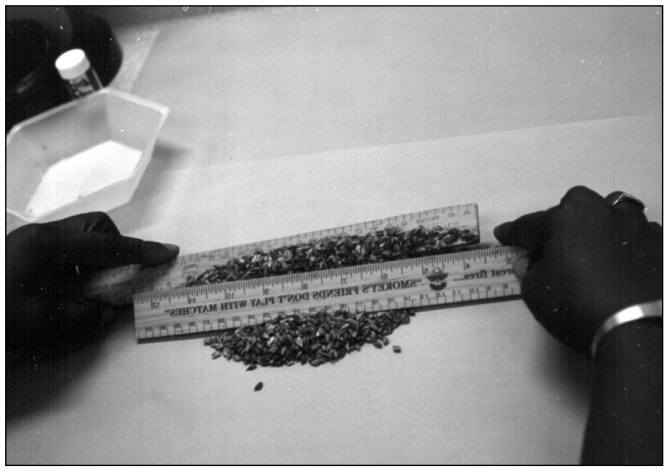
quarters. The quarter is then weighed to see if it is enough for the sample. If not, then another quarter, an eighth, or a smaller fraction is taken until the minimum weight is obtained (figure 6).

Hand-mixing can be replaced by mixing with either a soil divider or a gamet divider (figure 7). These devices can save a substantial amount of time and also, by reducing the tedious nature of the work, increase the likelihood of doing a quality job. The seedlot needs to be poured through the divider 3 times. When the gamet divider is used, the motor must not be turned on until the seeds have been poured completely into the hopper. Once the seeds are cleared out of the machine, the motor must be turned off before the seeds are poured back into the hopper for the next pass. The seedlot is then divided in half, then quarters, eighths, and so forth, to obtain the correct weight for the submitted sample, just as in the hand mixing and dividing.

The size of the submitted sample for some species is stated in the Rules for Testing Seeds (AOSA 1996) and is twice as large as the minimum amount for the purity test.

This amount is different for each species and the rules need to be consulted to be sure the correct amount is submitted for purity tests that are to be done according to the rules. A smaller sample of seeds can be submitted, but the test will not be according to the rules and the accuracy cannot be assured to the same degree as a test that is done according to the rules. If a species is not listed in the rules, an amount that contains 2,500 seeds should be taken. This amount can be estimated by counting out 100 seeds and multiplying their weight by 25. Under the AOSA rules, samples can be as small as 600 seeds when only germination is tested. It is important to work quickly when drawing the sample, if the submitted sample is to be tested for moisture content. This will prevent the gain or loss of moisture from the air. Once obtained, the submitted sample should be put in a moisture-proof container to maintain its true moisture content until it is sampled and tested at the laboratory. Plastic bottles with tight-fitting lids or tightly closed plastic bags of at least 0.1 mm (4 mil) thickness are adequate. Metal containers can be used but are harder to find. Glass containers should not be used; they easily break in transport, allowing the samples to be exposed to the air or, worse, mixed together.

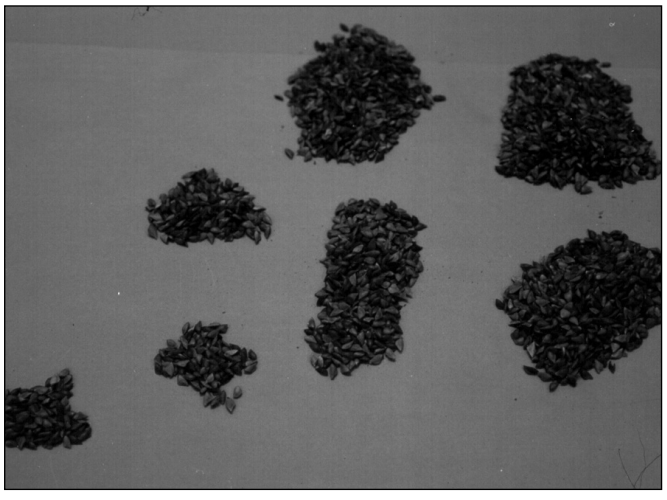
Figure 5—Chapter 5, Seed Testing: seed can be hand-mixed before withdrawing a submitted sample from a composite sample.



Sample Identification

Assignment of a test number is the first step in handling every seedlot that is received in the laboratory. This number allows for the orderly tracking of the test sample among the other samples in the laboratory. A typical test number indicates the test year and an accession number. For example, the 300th test conducted in 2005 would have a number such as 05-300.

Figure 6—Chapter 5, Seed Testing: the composite sample is divided systematically into quarters, eighths, sixteenths, and smaller fractions to obtain the submitted sample at the seed storage plant or the working sample in the laboratory.



Moisture Tests

Moisture tests must be the first tests conducted on samples when they arrive at the seed laboratory. Once a sample container is opened and work begun, the seeds will likely

Figure 7—Chapter 5, Seed Testing: a soil divider (**left**) and a gamet divider (**right**), devices that systematically mix and divide seed samples.

gain or lose moisture in exchange with the ambient air. The standardized laboratory test for moisture content is the oven method (ISTA 1996). This procedure was determined, after many years of research, to be a best estimate of moisture for general testing work (Bonner 1972, 1981, 1984, 1992; Buszewicz 1962; Hart and Golumbic 1966). This test is made on 2 subsamples containing 3 to 5 g of whole seeds. These 2 samples are placed in containers with lids and weighed to determine the wet weight (figure 8). Then they are placed in a forced-draft drying oven (figure 9) for 16 to 18 hours at 105 ± 2 °C. The lids are removed during drying but are also placed in the oven. The samples are then placed in a desiccator to cool for about 20 minutes before being weighed a second time to determine their dry weight. The lids are placed on the cans while cooling and weighing. The loss of weight represents the weight of water in the undried sample. This water weight is divided by the wet weight to obtain the percentage moisture content on a wet-weight basis. The percentage moisture is expressed on a wet-weight basis because this value most accurately represents how much of the seedlot is water. Therefore, the buyer knows the weight of seeds and the weight of water that are purchased. For example, when the price per weight is the same, a pound of seeds at 7% moisture content is a better value than a pound of seeds at 9% moisture content. For example, a 100-kg seedlot (or a 100-lb seedlot) at 7% moisture contains 93 kg of seeds, whereas the lot at 9% moisture contains 91 kg of totally dry seeds, 2 kg less.

Figure 8—Chapter 5, Seed Testing: 2 seed samples are tested to measure the moisture content of a seedlot.

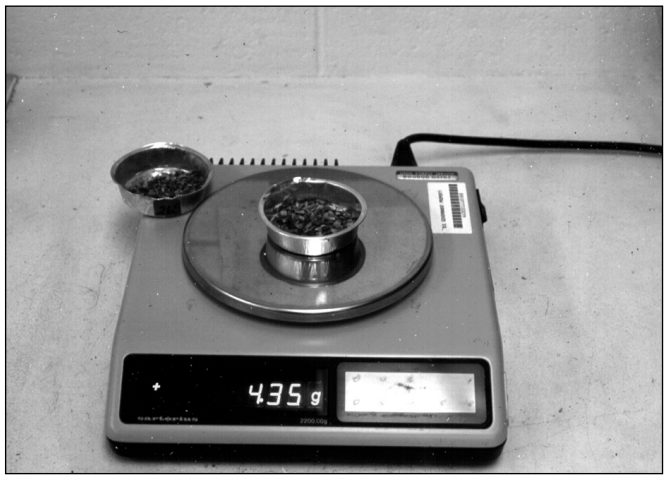


Figure 9—Chapter 5, Seed Testing: a convection oven and desiccator are used to conduct a seed moisture test.

Some larger seeds and seeds with impermeable seedcoats need to be cut to make an accurate test (Bonner 1974, 1981, 1992). If the seed is not cut open, the moisture is not freely released, and the moisture content is underestimated (figure 10).

The oven method is not a direct measure of the content of water. It measures weight loss that is assumed to be due to the loss of water. A basic analytical procedure is required to verify the temperatures and length of drying. The currently accepted procedure is the Karl Fisher procedure (figure 11) (Hart and Golumbic 1962). The moisture committee of the ISTA uses this procedure in its work to standardize and validate the oven procedures.

Another widely used method to measure seed moisture is the electronic moisture meter. Although there are numerous brands of electronic moisture meters on the market, not all of them will work for tree and shrub seeds (figure 12), and those that do will not have calibrations for tree seeds. Therefore, conversion charts must be developed for them by testing samples with high to low moisture contents with both the meter and the oven. A linear regression between the oven and meter readings is calculated, and the conversion chart predicted from this regression (Bonner 1981; Hart and Golumbic 1966; Jones 1960; Karrfalt 1987; Lanquist 1965). These meters provide quick results, are nondestructive to the seed, and are usually accurate to within ±1% of the moisture estimated by the oven method.

Figure 10—Chapter 5, Seed Testing: cutting large seeds open before drying them in the moisture test is necessary to release all the moisture.

Figure 11—Chapter 5, Seed Testing: the Karl Fisher apparatus is used as the analytical standard for determining seed moisture content.

Purity, Noxious Weed Content, and Seed Weight Tests

Purity, noxious weed content, and seed weight tests are sometimes called physical tests because they do not relate to viability. These tests are described individually as follows.

Purity Analysis

After samples for the moisture-content test are withdrawn, the remainder of the submitted sample should be mixed and divided to obtain the working sample, which

Figure 12—Chapter 5, Seed Testing: electronic moisture testers can give a quick and reasonably accurate estimate of seed moisture.

contains the minimum weight for conducting a purity analysis. Each species has its own specified minimum weight, which has been determined to contain 2,500 seeds. The mixing and dividing should be done in the same way as described in the sampling section for drawing the submitted sample from the composite sample. However, at this point it is necessary to be very close to the minimum weight for 2 reasons. First, the analyst does not want to examine more seeds than necessary, and second, the accuracy of the test is evaluated using tolerance tables that were developed using these minimum weights. Using substantially more seeds than the minimum will invalidate the use of these tables.

Purity is determined differently by each of the 2 major testing organizations. The ISTA rules specify a 3-part purity and the AOSA rules specify a 4-part purity. The ISTA purity values report percentages of pure seeds, other seeds, and inert materials. The AOSA purity values report percentages of pure seeds, weed seeds, other crop seeds, and inert materials. The pure-seed fraction consists of all those seeds that are of the kind specified on the seedlot's label. Specific descriptions in the rules define "pure seeds," but basically the pure-seed fraction comprises whole seeds and seeds that are not more than half broken away. "Other seeds" in the ISTA rule are all kinds of seeds other than those listed on the label. The AOSA rule makes a distinction between "crop seeds" and "weed seeds" and uses a detailed list (AOSA 1995) to specify when a species is a weed and when it is a crop. Weed seeds are mainly a problem in lots collected from nets or directly from the ground. Contaminated cleaning equipment can also result in weed seeds entering a seed-

lot. “Inert matter” is all other material that is not classified as crop seeds or other seeds. It could include soil particles, stones, wire, small pieces of broken seeds, or other plant parts. Purity is calculated by dividing the weight of the of pure seeds by the total weight of all the fractions in the sample (figure 13) and is expressed as a percentage.

Purity work can often be tedious and very technical. Devices such as the mechanical purity board (figure 14) can speed up the procedure. The analyst must understand important taxonomy principles and accurately use the seed herbarium (figure 15) to identify all the kinds of seeds in the sample.

Noxious Weed Examination

The noxious weed exam is a specialized purity examination. It is not a test traditionally associated with forest seeds but may become more common as the commercial exchange of native plants increases. A noxious weed is a highly aggressive competitor or a plant with other highly objectionable characteristics, such as being poisonous. It is so offensive it has been put on a noxious weed list compiled by an individual state or the federal government. A noxious weed exam is made solely to identify the number of noxious weed seeds found in the sample. Nothing else is noted in this exam. The presence of any noxious weed seeds makes it illegal to sell the seeds until the noxious weeds have been removed. The sample size for a noxious weed examination is 25,000 seeds.

Seed Weight Determination

The number of seeds per unit weight (kilogram and gram or pound and ounce) is determined on the pure-seed fraction from the purity test. This test is called the seed weight determination in the ISTA rules. It is made by counting out 8 replicates of 100 seeds and weighing them to the same precision as the weights for the purity test. The coefficient of variation for these 8 values is computed. This coefficient cannot be greater than 6 for chaffy seeds or greater than 4 for all other seeds. Otherwise, an additional 8 replications need to be counted and weighed and combined with the first 8 weights. All 16 weights are then used to compute the mean. Any weight diverging from the mean by more than 2 standard deviations is discarded; only the remaining weights are used to compute the number of seeds per unit weight.

Seeds can be counted by hand, with a counting tray, a shutter box, or a vacuum counter (figure 16). When seeds are counted by hand, it is usually best to count out the appropriate number of piles of 10, 20, or 50 seeds, in order not to lose one’s place. A counting tray is simply a block of wood

Figure 13—Chapter 5, Seed Testing: a purity sample is divided into its component parts.

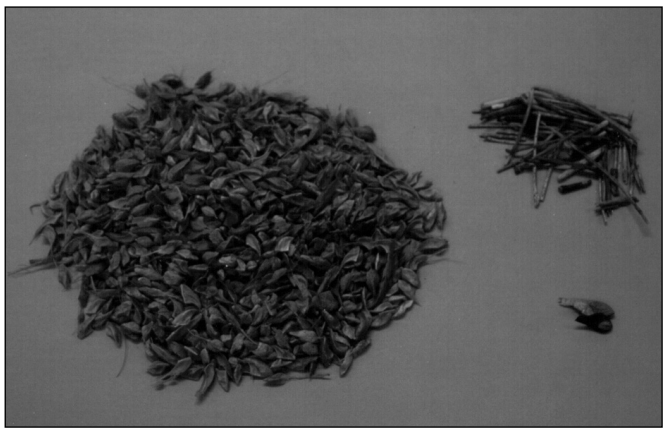


Figure 14—Chapter 5, Seed Testing: a mechanical purity board can reduce the time required to conduct a purity analysis.

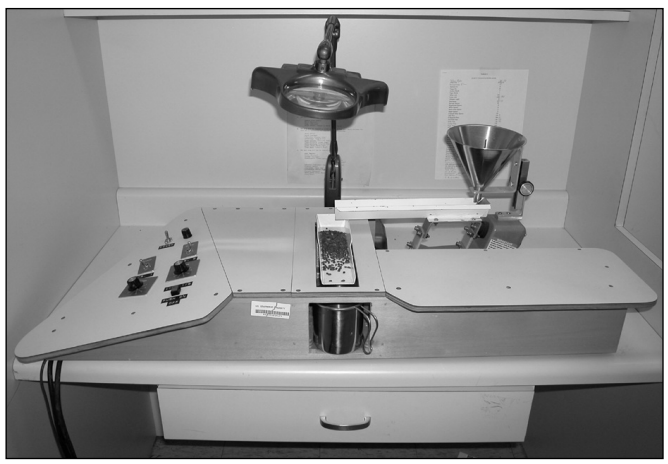


Figure 15—Chapter 5, Seed Testing: seed herbaria are used to make positive identification of the species of seed tested.

or plastic with impressions drilled into it to hold the seeds as they are poured across the plate. The counting tray may or may not be faster than counting by hand, depending on the seeds' size and shape, which determine how many double- or triple-seeded holes must be thinned by hand. Using the shutter tray is similar to using the counting tray, but the shutter tray is emptied by sliding the bottom tray rather than turning it over. For uniformly sized seeds, using either the counting tray or the shutter tray can speed up counting considerably.

The vacuum counter is probably the fastest and one of the most common ways to count seeds in the laboratory. The vacuum counter is made of an acrylic (or sometimes metal) plate that is drilled with 25, 50, or 100 holes and attached to a hollowed-out second plate. A vacuum line is attached to the head and a shut-off valve controls the application of the vacuum. To use the vacuum counter, the seeds are spread out loosely in a 1-seed-deep layer, the counter is placed on top of the seeds, and the vacuum is then turned on. Moving the counting head back and forth for about the diameter of a seed will bring the seeds into contact with a vacant hole. With the vacuum still on, the seeds can be transferred to a dish for weighing or to a germination container (figure 17). Some users of vacuum counters report a tendency for lighter seeds, such as empty or partially filled seeds, to be picked up in preference to heavier seeds. To eliminate this problem, this device must be used according to the procedure described above.

Seed weights are sometimes determined with an electronic counter (figure 18). The ISTA rule calls for counting all pure seeds in the working sample when this is done. No error-check is then made. A recent internal report made by the Seed Count Committee of the Association of Official Seed Analysts, augmented by the author's personal observations, suggests caution in the use of electronic counters for seed weight determinations. A high potential for error in counts exists. If carefully calibrated, these machines can count quite accurately, but the machines need to be adjusted and used correctly. A thorough evaluation of the degree of desired accuracy and the amount of time required to achieve it needs to be made before deciding to use the electronic counter.

Germination Testing

Germination testing is designed to estimate the maximum number of seeds that will produce a normal seedling and to give results that are as repeatable as possible. Without uniform procedures, there would be no standard on which to base the value of seedlots for commercial transactions and the seed trade would be chaotic and filled with dispute. Germination also tells a grower about a seedlot's potential. A seedlot with 80% germination cannot produce more than 80 seedlings per 100 seeds. Therefore, if 100 seedlings are needed, a minimum of 125 seeds must be planted (100/0.80 = 125). How to use test data to compute sowing rates is presented in detail in chapter 7 (Nursery Practices) and later in this chapter in the section on the use of test data.

Figure 16—Chapter 5, Seed Testing: seeds can be counted sometimes more quickly using a counting tray, a shutter box, or a vacuum counter.

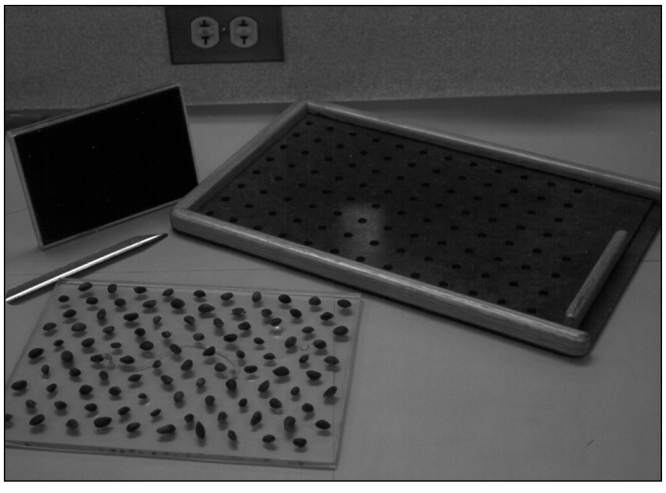


Figure 17—Chapter 5, Seed Testing: a vacuum counter is often used to count out seeds for weight determinations and for planting germination tests

The germination test is conducted on the pure-seed fraction from the purity test. Both the AOSA and ISTA prescribe the use of 4 replications of 100 seeds. These replications can either be planted 1 to a container (figure 19), 2 to a container, or all on 1 tray. Alternatively, the 4 replications can be further divided into smaller replications, but the total number of seeds tested must remain 400 to remain in compliance with the rules. If fewer than 400 seeds are available, then the number of seeds per replication should be reduced so that an equal number of seeds is present in each of the 4 replications. Using fewer than 100 seeds in a replication is not according to the rules, and the test would thus be unofficial. However, it is better statistically to have 4 replications of 50 seeds each rather than 2 replications of 100 seeds each. The 4 replications are then placed under optimal germination conditions for the period specified in the rules. Germination is the number of normal seedlings produced from 100 pure seeds expressed as a percentage. A normal seedling has all the essential plant structures necessary for the plant to continue to grow normally under favorable conditions (AOSA 1996; ISTA 1996).

Seeds can be planted in a number of ways. They can be scattered or placed one at a time with forceps, although more generally a vacuum counter or other type of planting plate is used for speed and to ensure even spacing of the seeds. The vacuum counter is the most expedient technique, because it can handle a variety of seed sizes (figure 17). Counting devices are described in the seed weight discussion above. Seeds should be hand-planted only when counting devices cannot be used in order to save time.

Seeds can be germinated on various media. Sand, sand and perlite mixtures, potting mixtures, soil, and various papers—blue blotters, white blotters, or crepe-cellulose papers (such as Kimpak®)—can be used (figure 20). Testing rules, however, specify what is an acceptable medium for the kinds of seeds tested. Specifying the medium helps assure uniformity in test results. The blotters resist penetration by the roots of the plants, whereas the crepe-cellulose paper allows for root penetration. Blotters offer the advantage of keeping the roots where the analyst can actually see them for evaluation, but if a seedling is very large it will fall over and tangle with other seedlings, making counts difficult. The media also differ in their water-holding ability. Blotters usually need to be watered several times during the test, whereas crepe-cellulose paper, sand, sand mixtures, potting soils, and soil are absorbent enough to hold all the water the seeds need for up to 3 months, if kept in a moisture-proof container. Watering the medium can be done by hand or by machine. Watering by hand is usually done using a squeeze bottle or a small hose from the tap and requires subjectivity on the analyst's part to estimate that the correct amount of water has been applied. Too much or too little is harmful, but in most cases there is wide latitude in the amount that will give optimal results (Belcher 1975).

Figure 18—Chapter 5, Seed Testing: an electronic seed counter is sometimes used to estimate the number of seeds per weight (in either kilograms or pounds).

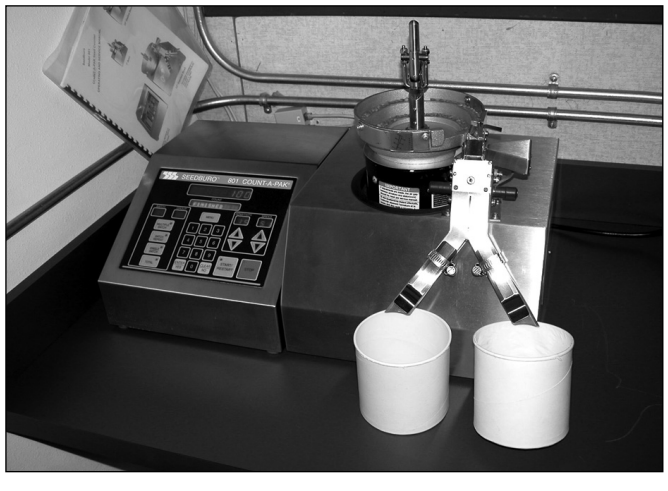


Figure 19—Chapter 5, Seed Testing: 2 germination tests, each composed of 4 dishes containing 100 seeds each, the dishes are stacked for transport and prechilling.

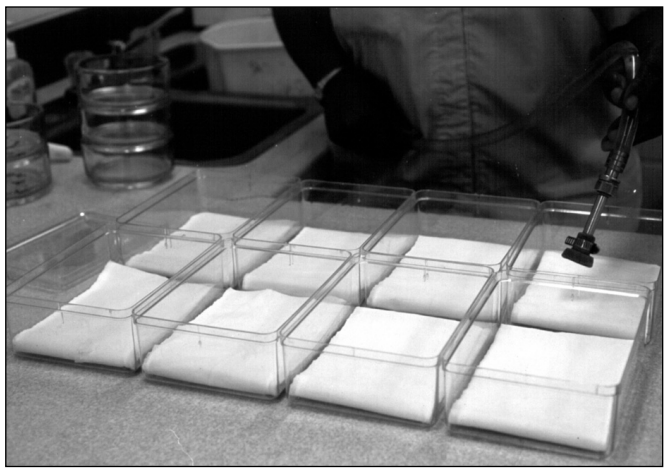
Machines for watering include automatic pipetting machines (figure 21) or small traveling spray booms. Both save a great amount of time if many tests are conducted and, once adjusted, take all the guesswork out of applying the correct amount. These machines should be checked periodically, however, to verify that they are in fact applying the desired amount of water.

Germination tests should be run in cabinets or rooms that meet exacting requirements for temperature and light control in order to make accurate and repeatable estimates. Temperatures should be carefully checked throughout the chamber at the level of the substrate to be sure there are no places that deviate from the desired temperature by more than 1 °C. Poor air circulation and hot spots from lights or light ballasts are the most common causes of temperatures that are too high or too low. The temperature at which the germination chamber is set depends on the species being tested. Many species do well at an alternating 20 and 30 °C. For this regime, the chamber is held for 16 hours at 20 °C and for the remaining 8 hours of the day at 30 °C. Other possibilities are constant temperatures of 15, 20, or 22 °C, with light usually supplied for either 8 or 16 hours. When temperatures alternate, the light is provided during the higher temperature to follow a natural cycle of light and temperature. Sources of light need to contain abundant amounts of blue and/or red light but not far-red light because far-red light is known to inhibit germination. Cool white flourescent lamps are most commonly used. The temperature/light regime used for a germination test is determined by experiments that germinate the same seedlot at different temperature/light combinations. The combination that supports the highest percentage of germination in the most reasonable time is the one that is then adopted in the rules for testing.

Dormancy is the condition of a seed that prevents it from germinating when it is placed in conditions that are favorable for germination. (For a discussion of dormancy, see chapter 1.) Dormancy must be overcome in order to conduct the germination test, just as when trying to grow seedlings. Pre-germination chilling (commonly called "prechilling" and traditionally called "stratification") is the procedure most used for breaking dormancy in forest seeds. The seeds are held in moist conditions at temperatures between 0 and 3 °C. Pre-germination chilling can be accomplished in 1 of 3 basic ways. In the first, the seeds can be planted on moistened germination medium in sealed containers and then put in the cold. In the second, the seeds can be placed in a moist medium, placed in the cold, and then at the end of the prechilling period, planted on the germination medium. In the third method (similar to the second), the seeds are soaked for 16 to 48 hours in water to become fully imbibed, placed in a moisture-proof container, held in the cold for the specified period, and then planted on the germination medium. This last procedure is sometimes called naked stratification, because no moisture-holding medium is used (figure 22). How long seeds are held in prechill varies widely by species and genetic source of the seedlot. The period can range from 10 days to many months. For some species, a warm period preceding the cold period is required. This is called "warm stratification" or "warm incubation." Western white pine (*Pinus monticola* Dougl. ex D. Don) (Anderson and Wilson 1966) and European ash (*Fraxinus excelsior* L.) (Piotto 1994) have been reported as requiring this warm-cold stratification .

Figure 20—Chapter 5, Seed Testing: seeds are germinated on various media, from right to left: crepe-cellulose paper (such as Kimpak®), blue blotters, sand–perlite mixtures, and potting soil.

Figure 21—Chapter 5, Seed Testing: an automatic pipetting machine can help to uniformly and rapidly water germination dishes.



A species that does not require prechilling is called nondormant. If 10 to 14 days of prechilling are needed, the dormancy would be considered light. If 30 to 60 days of prechilling are required to break the dormancy, it would be considered moderate. More than 60 days of prechilling classifies the seedlot as highly or strongly dormant. The degree of dormancy varies within the seedlot of even lightly dormant species; some seeds germinate without prechilling, whereas other seeds in the same lot will not germinate until they are prechilled. However, the term variable dormancy is usually reserved for seedlots in which some seeds germinate during prechilling, whereas other seeds in the same lot will not germinate even after being placed in favorable germination conditions. Species that fit the deep and variable dormancy category are Rocky Mountain juniper (*Juniperius scopulorum* Sarg.) and basswood (*Tilia americana* L.).

Because of the above-mentioned variation in dormancy, seedlots will often be tested with and without prechilling or with varying lengths of prechilling. Such tests are referred to as paired or double tests; usually only 2 tests are done. More tests, of course, can be and are done with some seedlots. This type of testing can determine the presence of dormancy, the strength of dormancy, or a weakness in the seeds (Belcher 1995). When the seedlot has the same germination with and without prechilling, it is said to be nondormant. When the germination is increased with prechilling, the seedlot is classified as dormant; the longer the prechilling period needed, the stronger the dormancy is said to be. A decrease in germination with prechilling is an indication of weakness in the seeds. This last condition is similar to the situation of the type of vigor test known as the cold test, which is described in the following section.

Prechilling is not the only treatment to break dormancy. Light is useful to break dormancy and can reduce the need for prechilling. Birches (*Betula* L.) and loblolly pine (*Pinus taeda* L.) are prime examples where light helps break dormancy. Seedcoat dormancy is treated by scarifying the seedcoat with either acid, bleach or mechanical means. Chemical stimulates such as gibberellins or potassium nitrate have been little used with forest tree seeds.

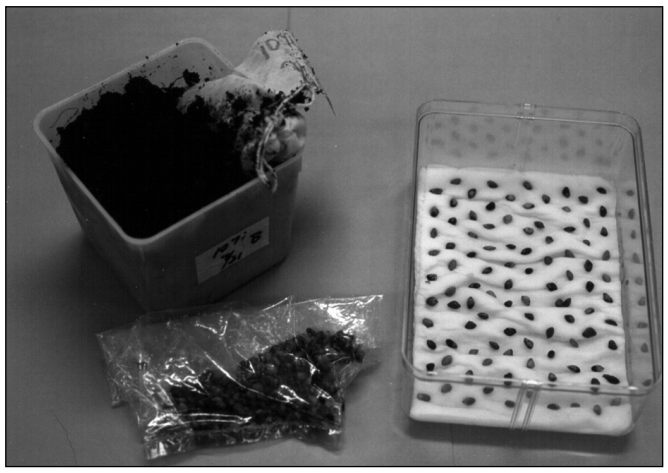
Vigor Testing

Sometimes standardized laboratory germination procedures are criticized as not predicting field performance very well (Moreno 1985; Stein 1967). These critics suggest using a variety of test conditions to find an optimum for each seedlot. The problem in predicting field germination is that it is impossible to predict the weather with the necessary precision. Vigor testing is one possible solution. The vigor test does not predict performance for a particular set of fluctuations; rather, it predicts the general ability of a seedlot to germinate normally over a range of adverse conditions. Its purpose is to differentiate seedlots, with essentially equal germination, according to their ability to germinate well in spite of adversity. Figure 23 illustrates the relationship between vigor and germination. As seeds age and begin to weaken and die, vigor declines before germination test results decline (Belcher 1978; Justice and Bass 1978).

Like germination tests, vigor tests are conducted under standardized conditions in order for the results to be repeatable and useful in the field. A vigor test cannot make up for poor practices that unnecessarily increase environmental variation in the field; such poor practices can be major sources of disparity between laboratory and field germination. Uniform sowing depth and watering, as well as sowing only on soil at the minimum acceptable soil temperature—all help make field germination more predictable.

The most common vigor tests in agriculture are the cold test, the accelerated aging test, the conductivity test, and the tetrazolium test. These 4 tests have not been used very much for forestry. In addition to these tests, speed of germination as expressed in a number of formulas has been put forward for use in forestry as a vigor test. Despite the potential benefit for tree seed nurseries, the science and technology are not advanced enough to permit the practical application of vigor testing with forest species.

Figure 22—Chapter 5, Seed Testing: seeds can be prechilled on a germination medium, in separate medium, or in a plastic bag.



The cold test is done by planting seeds in damp soil and then holding the germination tray at 10 °C for 7 days. This test mimics the cool damp conditions of soil in early spring. At the end of the period, the germination trays are transferred to the appropriate temperature for germination. The higher the percentage of germination, the more vigorous the seedlot is said to be. High-germinating lots have the needed strength or vigor to pass the period of stress and still have energy for high germination when conditions are favorable. This is analogous to the case of the tree seedlot that drops in germination following prechilling. Those that drop in germination after prechilling are weak.

The accelerated aging test is conducted with the stress of high temperature and moisture. The given weight of seeds is placed in a small box with a screen tray that suspends the seeds over a reservoir of water (figure 24). These boxes are then placed in an aging chamber at 40 to 43 °C for 72 to 288 hours, depending on the species. Whichever temperature is chosen in this range, the variation must be virtually nil to ensure repeatability of the results. The water-jacketed incubator has been determined by organized tests among laboratories to be the best device to give this necessary strong control over the test conditions. At the end of the period, the seeds are planted and tested for germination under the standard conditions.

The electrical conductivity test has been widely tested in agriculture but has not been adopted as routine practice except in a few specialized areas. In this procedure, seeds are soaked individually or in bulk. Deteriorated or dead seeds leak electrolytes more readily than high-vigor seeds. This greater leakage causes the water to have a higher conductivity, which can be measured with a conductivity meter (figure 25). Bonner and Agmata-Paliwal (1992) reported on the use of conductivity for tree seeds and found that results have poor repeatability for precise estimates but possibly would work for general estimates of classes as poor, low, intermediate, or high viability.

Several statistics have been put forward to use speed of germination as an indicator of vigor. The faster a seedlot completes germination or reaches its peak, the more vigorous it is said to be. The simplest indicator is days to 90% of total. For example, if the final germination is 88%, the indicator would be how many days it takes to reach 79% germination. A lot that reaches 79% in 12 days would be more vigorous than one that takes 16 days. To use this statistic, counts must be made quite frequently, even daily, or the data must be interpolated to determine the number of days to the specified germination.

Czabator's factor (1962), developed for use with southern pines, combines the maximum daily average germination, called the peak value, and the average daily germination at the end of the test to form one statistic called the germination value. Germination is counted frequently, at least every third day, and the cumulative germination on each day is divided by the number of days that the test has been run in order to compute the mean daily germination for that day. For example, if on day 22 the cumulative germination is 88, the mean daily germination is 4. This mean

Figure 23—Chapter 5, Seed Testing: as seed viability decreases, the proportion of live low-vigor seeds increases.

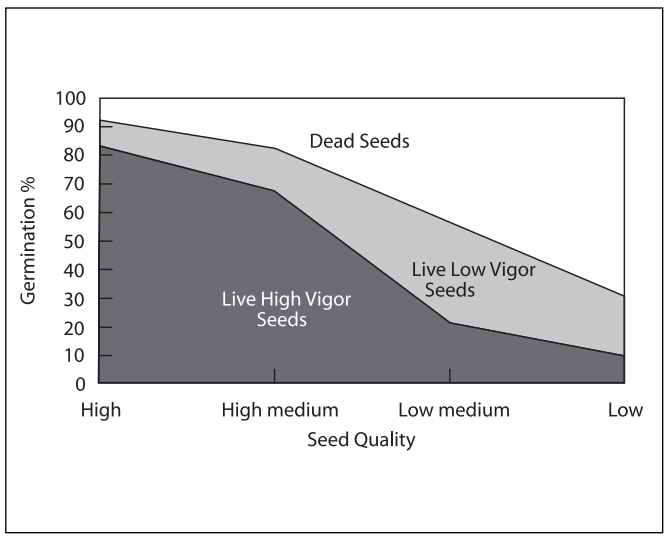
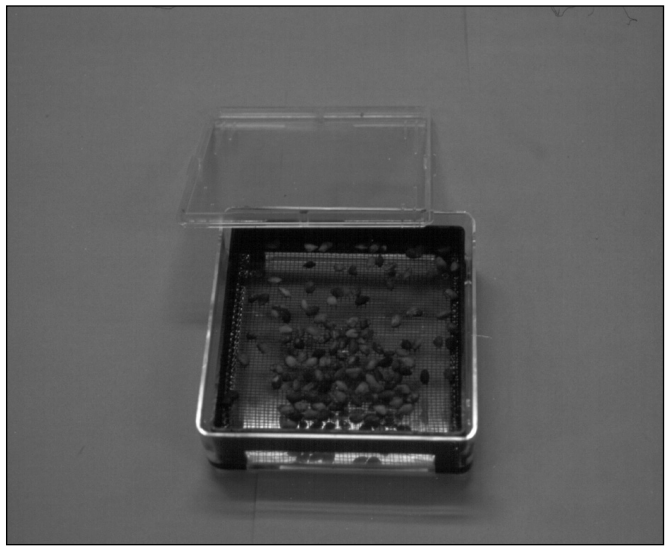


Figure 24—Chapter 5, Seed Testing: the accelerated aging test is conducted by placing seeds in a plastic box with a water reservoir and holding them at 40 °C for 72 hours.



daily germination increases with each day of germination until the period of maximum germination has ended and then decreases. The largest value of the mean daily germination is called the peak value. Figure 26 shows a graph of a typical germination. Initially only a few seeds germinate, followed by a period of rapid progress, and finally a slow-down period and an end of germination altogether. Germination value is computed by multiplying the peak value by the mean daily germination. Lots that have higher germination values are generally considered more vigorous.

Another characteristic of more vigorous lots is that they store for longer periods of time without loss of germination. Therefore, if 2 seedlots have equal germinations, the one with the lower vigor might be considered for first use, because the germination of this lot will likely decrease faster than the lot with higher vigor. This approach would give the greatest potential number of seedlings. Lower vigor seedlots will loose viability even under ideal conditions in the freezer.

Tetrazolium staining has been tried also as a vigor test (Moore 1976). Because of the highly subjective nature of this test and the great amount of experience it requires to administer, it has never been widely used as a vigor test and never successfully with forest plants. As stated in the next section, tetrazolium staining can be used to successfully estimate viability for very dormant species or for other hard-to-germinate species.

The problem with vigor analysis is that it has proven to be difficult to standardize, apparently because the test conditions are so exacting. In tests involving germination, the temperature must be very tightly controlled. Just a degree or two difference in temperature can change the speed of germination, effecting the value of those statistics that rely on germination speed. The accelerated aging test was difficult to standardize until chambers were developed that had virtually no variation in temperature. Difficulty in standardizing laboratory tests and the lack of clear and consistent interpretation to the field has prevented the operational use of vigor testing.

For a more complete list of literature references and a detailed explanation of the vigor testing procedures, refer to the Association of Official Seed Analysts' Seed Vigor Testing Handbook (AOSA 1983) and the International Seed Testing Association's Handbook of Vigour Test Methods (ISTA 1995). Bonner (1998) has also made a thorough review of vigor testing specifically for tree seeds.

Chemical Staining for Viability

The tetrazolium staining procedure mentioned in the vigor section is useful in estimating the viability of dormant seeds, especially very dormant ones. This test involves soaking the seeds first in water so that they imbibe fully and soften for cutting. A moistened seed will take up the stain more rapidly. A variety of methods are used to open seeds. It is extremely important that no damage occur to the embryonic axis when a seed is cut. The embryonic axis is the radical and the plumule. The meristematic regions are here, and their condition needs to remain unaltered until they are carefully examined. These are the areas where the embryo must

Figure 25—Chapter 5, Seed Testing: the conductivity meter is used to measure seed viability or vigor by estimating the amount of cations lost from deteriorating seeds.

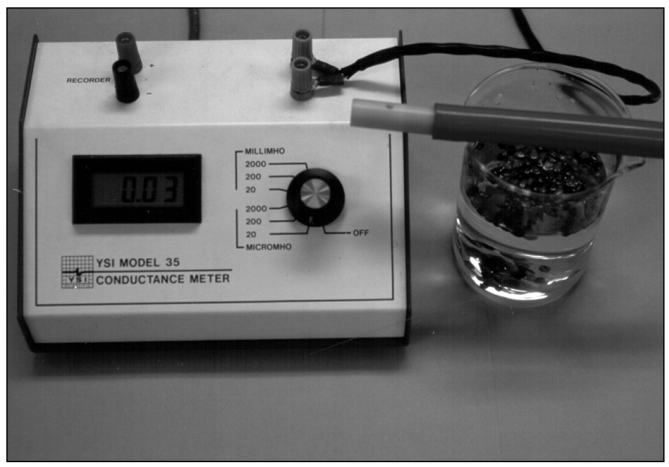
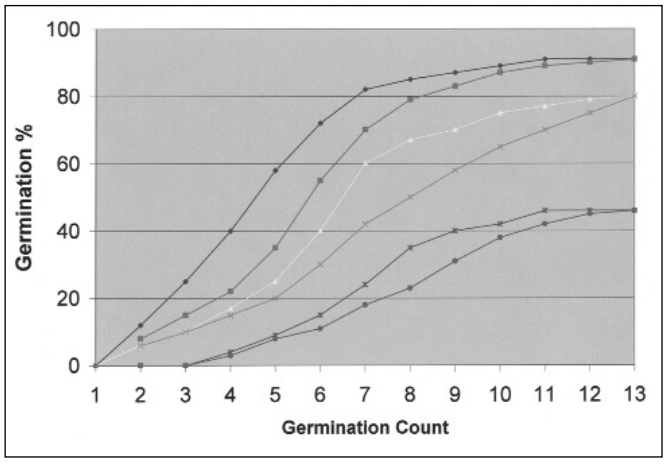


Figure 26—Chapter 5, Seed Testing: germination curves of 3 pairs of seedlots, with high, moderate, and low germination values. The upper curve in each pair represents the more vigorous lot in the pair because the germination is completed sooner.



grow in order to produce a normal seedling. Usually forceps and sharp single-edged razor blades are used to cut open the seeds (figure 27). For seeds with harder or stony seedcoats, a variety of vises, hammers, and clippers are used to cut through or remove the seedcoat (figure 28).

The solution that is used to make a tetrazolium (TZ) test is colorless. It is made by dissolving 2,3,5-triphenol tetrazolium chloride in a phosphate buffer at pH 7.4, which is the optimum pH for the TZ reaction. The buffer is necessary to compensate for any pH imbalance in the TZ salt, the water, or possibly the seeds. The colorless solution is taken up by the prepared seeds and then reacts with respiratory enzymes (that is, dehydrogenases) to form an insoluble light pink (magenta) precipitant. Tissues that are alive and respiring will stain, and those that are not alive will not. For a detailed discussion of this procedure, refer to the AOSA Handbook on Tetrazolium Testing (AOSA 2000). The TZ test can be completed in 4 to 48 hours, depending on the amount of preparation time required and the rate of staining.

Tetrazolium staining has proven useful with many species that have deep dormancy, including tuliptree (*Liriodendron tulipifera* L.), baldcypress (*Taxodium distichum* (L.) Rich.), Rocky Mountain juniper, and sumac (*Rhus* L.) species. However, for a few species with very deep dormancy, there will be no staining (Vivrette 1995) unless the seeds are prechilled.

Figure 27—Chapter 5, Seed Testing: seeds are cut open carefully to prepare them for tetrazolium staining.

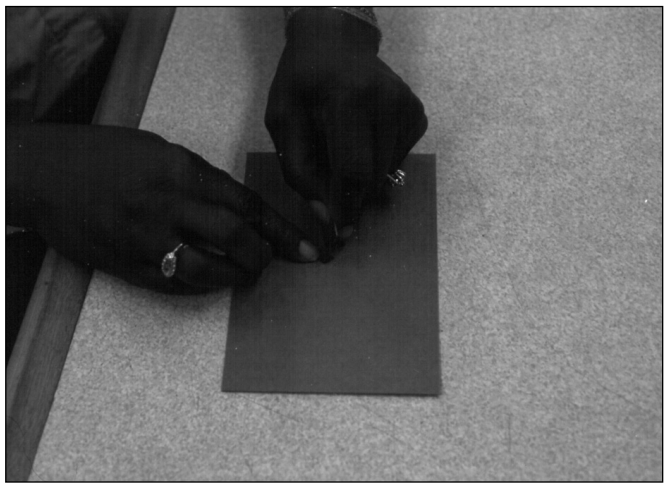


Figure 28—Chapter 5, Seed Testing: vises, hammers, or clippers are used to cut through or remove hard or stony seedcoats for conducting tetrazolium or excised embryo tests.

Excised Embryo Testing

The excised embryo test is done on the embryo after it is removed from the seed (Flemion 1948; Heit 1955). In this germination test, the embryo has been freed from the restriction of the seedcoat and nutritive tissue (figure 29). Therefore, a germination that would take many months and be incomplete can be complete in 10 to 14 days. The ashes (*Fraxinus* L.), maples (*Acer* L.), and cherries and plums (*Prunus* L.) are some of the genera that are tested by embryo excision. Because the embryos are very vulnerable to infection once excised, the test must be done under strictly clean (axenic) conditions. The work surface and all tools, hands, and germination dishes should be washed carefully, perhaps with absolute ethanol. If "clean" embryos mold easily, then cleaning procedures must be reviewed for effectiveness and the work area examined for sources of microbial contamination. Generally, however, sterilization procedures such as autoclaving are not required. The procedures for excising the embryos are similar to those used in preparing seeds for tetrazolium. Greater care is needed, however, because the embryo must be removed intact without any significant injury or broken apart. The main advantage of this method over the TZ test is that the evaluation is less subjective; the growing embryo is actually observed in most cases. Therefore, a direct reading on the growth potential of the seedlot can be obtained.

A complete excision is not always required. Russian-olive *(Elaeagnus angustifolia* L.) (Belcher and Karrfalt 1979) and western white pine (Hoff and Steinhoff 1986) respond well to only partial removal of the seedcoat. However, white pine seeds require prechilling before their seedcoats are cut open.

X-Radiography

X-radiography is very useful in forest seed analysis. It provides a very rapid and accurate analysis of the internal structure of seeds, identifying empty, insect-damaged, or poorly developed seeds (figure 30). It is an immense help in judging maturity, determining how many bad seeds should be remove, and detecting any mechanical injury. It is more accurate than cutting tests in many cases, requires much less time, and is nondestructive (AOSA 1979; Simak and others 1989). X-radiography was first applied to tree seeds by Simak in Sweden. The use of contrast agents has improved the ability of the x-ray test to discriminate between viable and nonviable seeds with some species (Kamra 1963; Simak 1957; Vozzo 1978). A contrast agent enters damaged areas of the seed differentially from nondamaged areas, making the damaged areas more radiopaque. They will then appear as bright areas on the radiograph. Aqueous solutions of heavy salts such as iodine or barium chloride and vaporous agents such as chloroform have been used as contrast agents.

Radiographs can be made on Polaroid® film, x-ray paper, or x-ray film. Polaroid film is useful if no darkroom is available, because the film is developed in the light, just like a Polaroid photograph. The disadvantages of Polaroid are high cost, short shelf life, and lack of detail. X-ray paper is fast to use but does require a simple darkroom. It is less expensive than Polaroid, has a shelf life of several years in cold storage (3 °C), and much better resolution. The best resolution is obtained with x-ray film. X-ray film, however, is more expensive and slower to develop (over 45 minutes) and a light table is required to see the images. Usually the film or paper is placed in a paper or vinyl cassette so that it may be handled in the light. This cassette can result in some loss of clarity of the image, especially with small seeds; using the film in the dark where the seeds can be laid directly on the emulsion gives a noticeably superior image.

Seed work is usually done with x-rays in the range of 10 to 30 kvp (that is, kilovolt potential), which is is the amount of penetrating power the x-rays have. The exact kilovolt potential depends on the equipment and the seeds in question. Trial and error is necessary to find the best combination. Too high a kilovolt potential and the seeds will not be visible or will appear too dark. Too low a kilovolt potential, and the image will lack detail and be too light. Some small seeds need to be x-rayed at a low kilovolt potential to give the correct penetration but need a long exposure to produce a radiograph with enough density to provide good contrast. X-ray inspection cabinets are manufactured that operate in this very low kilovolt potential range for examining small items such as seeds. They are designed for total protection of the operators, with complete lead shielding and safety interlocks on the door (figure 31).

X-radiography has proven useful for studying the seeds from many wild species, which often can be empty or poorly formed. Some laboratories test every lot of seeds they receive with x-rays and get a good initial evaluation. X-radiography can be of great value in evaluating germination test results, because it is much faster than cutting open

Figure 29—Chapter 5, Seed Testing: embryos of peach (*Prunus persica* L.) have been removed from their seedcoats for an excised embryo test of viability.

Figure 30—Chapter 5, Seed Testing: x-radiography can be used to quickly determine how many seeds are empty, damaged, or poorly developed.

seeds that failed to germinate. Empty seeds will never germinate, and damaged or poorly developed seeds will seldom germinate. The excised embryo or tetrazolium test for difficult-to-cut seeds can be speeded up by x-radiography. The seeds are first placed on the x-ray film or paper in a manner that will allow the comparison of the exact image to the exact seed. This is done by placing the seeds on an additional piece of paper before placing the paper on the x-ray film or paper. If orientation of the seed is important, as in double-seeded fruits such as dogwood, the seeds can be placed on adhesive tape and that then laid on the paper. The seeds should be oriented so that both seeds in the fruit can be viewed and the tape prevents them from turning. After the radiograph is made, the seeds are gently slipped off the x-ray paper so that the seeds are kept in order for cutting. Only those seeds that are morphologically sound in the radiograph need to be cut.

Other Quick Tests

As stated in the introduction, cutting tests are very limited in their application. However, they can provide useful information on full seed percentages and the condition of the internal structures. For example, color of the tissue cannot be determined in a radiograph, which is only black and white. Seeds that are cut and found to be dark are not likely to germinate. New and unfamiliar images in a radiograph require cutting the seed to determine what is actually in the seed. With slash and longleaf pines, cutting can reveal embryos that have initiated chlorophyll (turned green), a result of a seedlot having been held too long at high moisture. This is a sure sign of a weakened seedlot.

Hydrogen peroxide (H_2O_2) has been used as a quick test for western conifers (Ching and Parker 1958). In this test, the seeds are floated in solution of 1.0% hydrogen peroxide overnight. The radicle ends are then clipped and the seeds incubated in the dark at 20 to 30 °C for 10 to 12 days. Counts of germinates are made at 3 to 4 days and at 10 to 12 days. The hydrogen peroxide solution is changed at the first count.

Figure 31—Chapter 5, Seed Testing: a cabinet x-ray system is a safe and simple way to make radiographs of seeds.

Sowing Rates

A sowing rate is the amount of seeds sown in a unit area of nursery bed to produce the desired number of seedlings. The following formulas show how seed test data are used to determine this rate.

Weight of seeds to sow in a nursery bed (width x length) is equal to

(bed width x bed length x seedlings desired per area) ÷ (germination x seeds per weight x purity x survival factor)

Number of seeds needed to sow per area of nursery bed is equal to

(seedlings desired per area) ÷ (germination x survival factor)

In both of these formulas, the survival factor is the ratio of the number of seedlings expected to the number of viable seeds planted. It is derived from experience in the given nursery and should be constantly updated with new information collected from history plots. History plots are permanent sample plots in a nurserybed used for carefully monitoring the number of seeds sown and the number and quality of seedlings produced (Landis and Karrfalt 1987). For example, if 100 seeds are sown on a square foot, germination is 80% in the laboratory, and 60 seedlings actually grow on the square foot, then the survival factor is 60 ÷ 80 or .75 (75%).

Computing sowing rates for containers is somewhat different, because we must predict the probability of an empty cell in the container. The probability that a container cell is empty is equal to 1 minus the probability that at least 1 seedling is in the cell. Sowing 1 seed per cell, this probability is 1 minus germination. With a 90% germination, the probability of an empty cell following single-seed sowing is 0.1. In sowing 2 seeds per cell, the probability of no

seedling in a cell drops to .01, but now there are 81 cells (.90 × .90) out of 100 that will have 2 seedlings per cell. Double seedlings per cell requires thinning to 1 seedling per cell for proper growth. Thus, in container nurseries it is necessary to choose between empty spaces and thinning. In this example, to go from 10 empty cells to 1 empty cell per 100 cells, 81 seeds were wasted. For 10,000 seedlings, 8,100 seeds would be wasted, which would be 112 to 224 g (3.9 to 7.8 oz) of seeds when the seeds number 72,300/kg (32,900 seeds/lb). Thinning also requires more labor and may be dysgenic by favoring early germinating genotypes. Sowing extra containers is another strategy followed to compensate for empty cells. The empty cells are still present but enough seedlings are produced without the problems of thinning.

The purity and seed per weight are still important to the container grower, because they will be used to compute the amount of seed to prepare. The following formula can be used to calculate how many seeds are in a unit weight of seeds:

weight of seeds × purity × no. of seeds per unit weight

Example: 1 kg of seeds at 98% purity, 33,000 seeds/kg:
1 kg x 0.98 x 33,000 pure seeds/kg =
32,300 pure seeds

or 1 lb of seeds at 98% purity, 15,000 pure seeds/lb:
1 lb x 0.98 x 15,000 seeds/lb =
14,700 pure seeds

To sow 10,000 cells with 1 seed each, 10,000 seeds are needed, which is 10,000 seeds divided by 32,300 seeds/kg = 0.31 kg (10,000 divided by 14,700 = .69 lb). Double sowing 10,000 cells would take 2 x 0.31 = 0.62 kg (2 x .69 = 1.4 lb). Combining these steps yields the following formula:

(number of seeds to sow per cell x number of cells to sow) ÷ (purity x seeds per unit weight)

In the double-sowing example, this would be 2 × 10,000 ÷ .98 x 33,000 seeds/kg (.98 × 14,700 seeds/lb) for a total of 0.62 kg (1.4 lb) of seeds required.

Buying and Selling Seeds

Current test data are essential. To be current, the data should not be more than 9 months old. The more recent the test, the more likely it is to reflect the true condition of the seedlot when the buyer takes possession of it. Ideally the tests should be run by a disinterested third-party laboratory that is well qualified to do the tests. The results of informal analysis, such as the cut test, should never be accepted as the true measure of the worth of a seedlot.

Which tests are important to request, and how should they be used? Moisture content is important for 2 reasons. First, the seeds need to be at a proper storage moisture content to ensure viability. Orthodox seeds need to have a moisture content below 10% and recalcitrants usually above 25%. Second, it must be remembered that extra water can be added to the seeds and distort the true value of the lot. One kilogram of a seedlot with 10,000 seeds/kg (22,000 seeds/lb) at 7% moisture content would contain 70 g (2.5 oz) of water and 930 g (32.6 oz) of dry seeds. A similar lot of 10,000 seeds/kg at 9% moisture would have 90 g (3.2 oz) of water and 910 g (31.9 oz) of dry seeds. In an accurate comparison between the lots (that is, dried to equal moisture content of 7%), the mass of the seeds in the second lot is 20 g (2%) less than that of the first. Although both seedlots might appear to have seeds of the same size, the lot with higher moisture would actually have slightly smaller sized seeds. Because the water is free, adding extra moisture can be a good way for the seller to increase profits.

The number of pure live seeds per weight is a calculation that is often helpful in assessing the value of a seedlot. In this procedure, germination, purity, and seed weight are all considered. Consider a seedlot with germination of 90%, purity of 98%, seed weight of 18,600 seeds/kg (8,500 seeds/lb). The number of pure live seeds per kilogram is then .90 × .98 × 18,600 = 16,400 seeds/kg (7,500 seeds/lb). This is the same value as a lot that has 95% germination, 96% purity, and 18,000 seeds/kg (8,200 seeds/lb) (.95 × .96 × 18,000 = 16,400) but a higher value than a lot with 97% germination, 84% purity, and 17,400 seeds/kg (7,900 seeds/lb) (.97 × .84 × 17,400 = 14,200). Number of pure live seeds per weight tells the grower the potential number of seedlings and removes at least some ambiguity in comparing the value of different seedlots. If the maximum number of potential plants is the most important factor, the first 2 lots are superior to the third, although the third has a higher viability. Alternatively, as might be the case for a container nursery, the high germination could be the most important factor, and the third lot would be chosen over the first two, even though potentially fewer trees can be produced from it.

Minimum standards are usually set for all quality values. Those minimums depend on the type of nursery, the generally available quality for a species, the desirability of the seed source, and other factors. In general, the higher its quality, the more a seedlot is worth in the nursery. High germination

is of great value in a bareroot nursery but indispensable to the container grower, who seeks to avoid wasting seeds by double-sowing or having empty growing space in single sowing. However, for some species, 60% germination might well be typical and expecting 98% germination is not reasonable.

Test Limitations and Variation

Standardized laboratory tests are designed to give maximum values with minimum variation, allowing the results to be repeated. Without repeatability, there would be no standard by which to compare different seedlots. Assessments would become even more difficult if seed tests were conducted in random fashion to mimic field conditions. Although the correlation between laboratory and field germinations is frequently low, experience has shown that seedlots with higher germination scores will, over time, give more germination in the field. Further improvement in predicting field performance may result from improvements in the techniques of vigor testing.

Because seeds are biological, they usually are quite variable in size and performance. Natural things simply show more variation than is usually seen in manufactured items. Test results, therefore, can vary more than perhaps is expected and still be accurate. For example, a seed weight of 16,000 seeds/kg (7,300 seeds/lb) might be reported as 15,600 (7,100) in a second test, and both results are in fact accurate. Tolerance tables can guide decisions on whether test results are comparable. Some of these tables are suitable for all types of seeds, whereas others vary depending on the type of test and the kind of seeds tested.

Scheduling Seed Tests

When should a seed test be conducted? Tests are needed to formally determine the quality of the seedlot upon completion of the conditioning process. All variables then need to be measured: germination, seed weight, purity, and moisture content. Moisture needs to be monitored during storage to be sure it is being properly maintained. If there are no changes in moisture content, then seed weight and purity will not change and viability will change very slowly, if at all. Some annual monitoring of seed moisture is necessary to ensure that storage conditions are being adequately maintained. The viability can be retested at 3- to 5-year intervals with a current test always done no more than 6 to 9 months before sowing. If a longer time passes before sowing, some deterioration could occur, resulting in changes in germination. Determining viability in some seeds takes a long time, and thus it is important to schedule adequate lead time into the production schedule.

Commercial Trade of Tree, Shrub, and Native Plant Seeds

Official rules for testing seeds developed by the International Seed Testing Association or the Association of Official Seed Analysts are very important to the orderly buying and selling of seeds. These rules give standardized procedures that can be repeated with acceptable variation no matter what laboratory conducts the test. In addition, the seed testing associations conduct comparative tests among themselves to verify that the procedures are being applied uniformly and within tolerable limits of error. Such a system is important: it assures sellers that they are offering good seedlots for sale, and it reassures buyers by giving them reliable information on which to base their purchases. There are also consumer protection seed laws in some countries or states requiring that seeds offered for sale meet certain minimum standards or be accurately labeled as to their quality. Without a repeatable system of testing procedures, such laws would be impossible to enforce. Both the consumer and the reputable seed dealer would suffer. Uniformity of the rules combined with uniformity in applying the rules equals order in the marketplace.

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Chapter 6

Certification of Tree Seeds and Other Woody Plant Materials

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Introduction

Seed certification is a system that provides assurance to buyers that the seeds being purchased are what they are represented to be by the producer or seller. This certification of identity (and sometimes quality) is typically provided by an independent third party for a fee that is charged to the producer and becomes part of the production costs. The system is simple and effective; it is used all over the world in various, yet basically similar, forms for agricultural, horticultural, and forestry seeds or other propagules. This chapter will briefly describe how seed certification developed in forestry and how it is practiced today with seeds of woody plants. More detailed historical accounts of agricultural and forest tree seed certification in the United States can be found in Hackleman and Scott (1990) and Rudolf (1974).

Certification in Agriculture

Certification of agricultural seeds has been practiced in the United States since the early 1900s (Copeland and McDonald 1995; Hackleman and Scott 1990) and has been a positive force in the development of modern agriculture. Certification in individual states is typically controlled by an agency that is authorized by the state to carry out the procedures. The agencies are commonly called crop improvement associations, but some carry other designations. The organizational structures of these agencies may vary, but their goals are similar and they act cooperatively through the Association of Official Seed Certification Agencies (AOSCA 1994). AOSCA establishes minimum certification standards for all types of plant materials. The member state certification agencies may develop their own certification standards for different materials, but their standards must equal or exceed those of AOSCA. Agricultural seed certification is an assurance of the varietal (genetic) identity of the material, but it is also normally a *de facto* assurance of genetic quality. Developers of improved varieties of agricultural species (state land grant universities or private seed companies) widely publicize the results of their field trials, and the expected performance of new varieties is well known and documented before they reach the market. Seed buyers want the assurance from certification that their seeds are really the variety that the producer says they are. The slightly higher cost required for this assurance is gladly paid.

Certification in Forestry

Certification of forest reproductive material has developed in a slightly different manner from that of agriculture in this country. Most forest landowners do not have ready access to the performance data from field trials of selected forest materials. There are two primary reasons for this. First, field trial results in forestry are not as widely published as those in agriculture, and the publication outlets that are used are not widely seen by the general public. Second, much of the genetic improvement in forestry has been done by large forest industries and the USDA Forest Service, all of which originally intended that the improved materials would be planted on their lands only and not sold on the open market. So other than technical reports in forestry journals and a few government publications, these results have not been widely disseminated, although they are available.

The first efforts in genetic improvement in forest reproductive materials in this country came about through recognition that some seed sources were more suitable for planting in certain areas than others. Application of this principle in the 1930s and 1940s led to the establishment of seed control policies and seed zones to ensure that seeds and seedlings for reforestation came from the best origins

Figure 1—Chapter 6, Certification of Tree Seeds and Other Woody Plant Materials: current tree seed zones for Douglas-fir in western Oregon (adapted from Randall 1996).

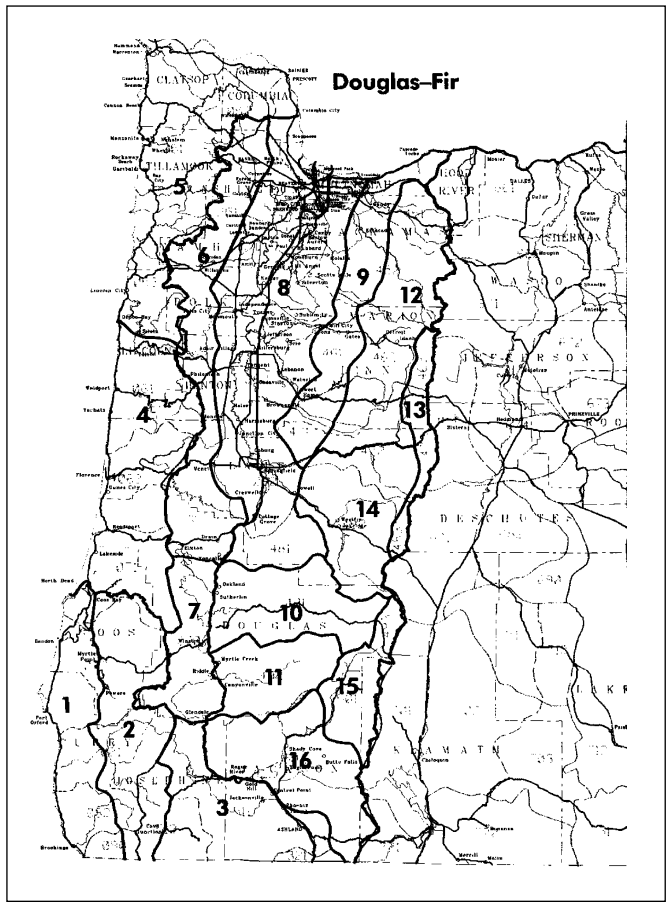


Figure 2—Chapter 6, Certification of Tree Seeds and Other Woody Plant Materials: current tree seed zones in use in Washington (adapted from Rudolf 1974).

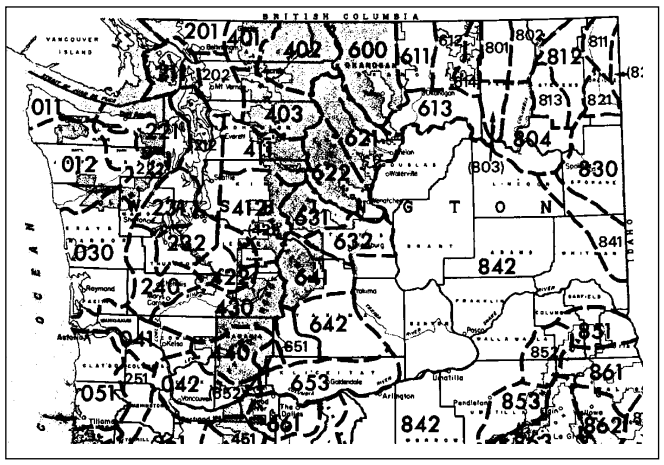


Figure 3—Chapter 6, Certification of Tree Seeds and Other Woody Plant Materials: geographic districts for source-identified certification of forest reproductive material in Mississippi (courtesy of MSIA 1979).

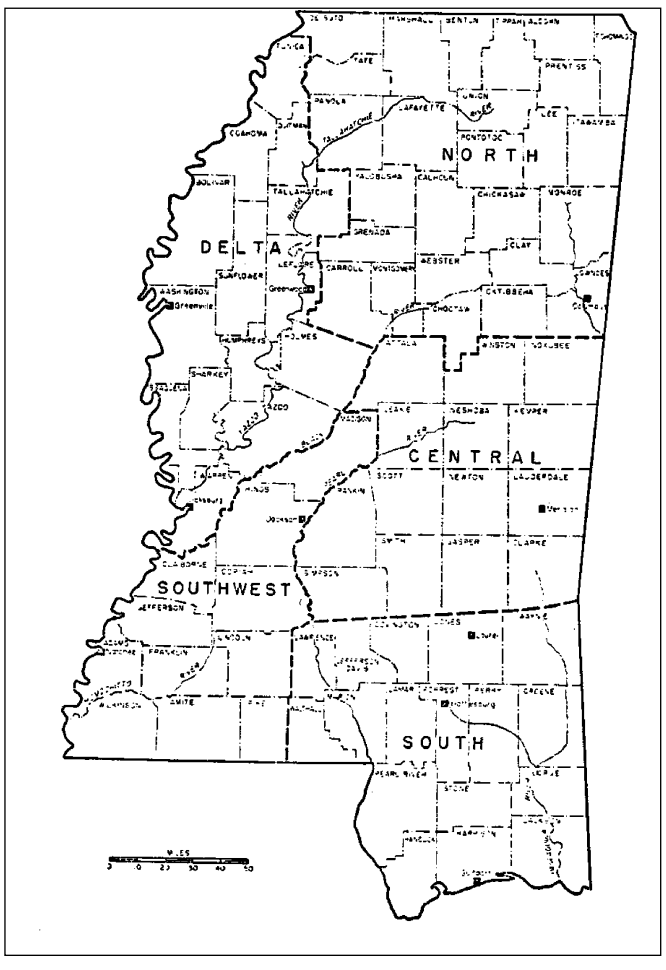
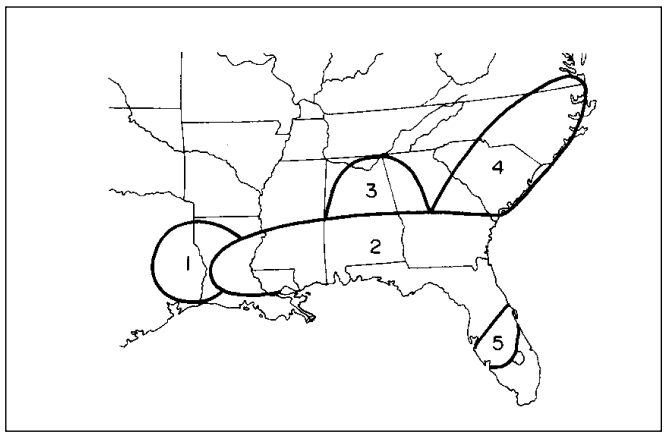


Figure 4—Chapter 6, Certification of Tree Seeds and Other Woody Plant Materials: the 5 seed collection and planting zones for longleaf pine (from Lantz and Kraus 1987).



(Rudolf 1974). The use of seed zones (figures 1–4) has been very effective, and they are still widely used today. The major impetus for forest seed certification, however, came from the expanded reforestation programs and rapidly developing tree improvement programs in the 1950s and 1960s. Establishment of seed orchards of major species with selected phenotypes and the subsequent progeny tests with their offspring has led to wide-scale use of improved families and clones in forest regeneration. When foresters wanted certification of this material, they turned to the state crop improvement associations, because these agencies were the only ones legally permitted in most states to perform certification services. As these services were extended to forestry material, the mechanisms for implementation developed differently in different parts of the country.

South Dakota established the first forest tree certification program in 1952 for stock selected for shelterbelt use (Rudolf 1974). Georgia established the next program in 1959 with comprehensive certification standards for tree seeds (GCIA 1959). The AOSCA (then known as the International Crop Improvement Association) adopted almost identical standards also in 1959 (Rudolf 1974), with later revisions in 1962, 1966, and 1970 (Hackleman and Scott 1990). Other states were not far behind. In 1994, AOSCA widened the scope of its tree seed certification standards to allow certification of material from all native plants—trees, shrubs, vines, forbs, and grasses (AOSCA 1994). These standards were designated for pre-variety germplasm certification and will be explained in a later section.

Pacific Northwest

An organized effort to improve tree seed supplies in the Pacific Northwest came about in the mid-1950s with the formation of the Northwest Forest Tree Seed Committee at Corvallis, Oregon (Edwards 1981). This group later became the Western Forest Tree Seed Council in affiliation with the Western Forestry and Conservation Association. The bumper cone crop of 1966 underlined the need for certification programs (Hopkins 1968), and the council and the Western Reforestation Coordinating Committee of the Western Forestry and Conservation Association took action. Through their efforts, the Northwest Forest Tree Seed Certifiers Association (NWFTSCA) was formed in 1966 to promote seed certification. This organization developed seed zone maps for Washington and Oregon and the framework for a seed certification system (Edwards 1981).

Certification was jointly administered by the Washington State Crop Improvement Association and the Oregon Seed Certification Service, a division of the Department of Crop and Soil Science at Oregon State University. The NWFTSCA provided review and advice to the agencies. Their system recognizes the following categories of reproductive material, which are indicated by standardized color-coded labels affixed to seed containers.

Audit class. Certifying authorities have reviewed records indicating seed lot origin and collection documentation on where and when the seeds were collected. Origins are usually less specifically identified than those in the source-identified class. ***Labels placed on the seed containers are brown and white.***

Source-identified class. Reproductive material comes from a seed zone defined by a legal description and from within a 154-m (500-ft) elevation band. The seed zones were defined on the Tree Seed Zone Map issued by the Western Forest Tree Seed Council in 1973. They are based on physiographic and geological provinces of Washington and Oregon as defined by Franklin and Dyrness (1973). Two subclasses are recognized: (a) *personally supervised production*—both the producer and the certifying agency have personal knowledge of the seed zone from which the seeds were collected and (b) *procedurally supervised production*—only the buyer and not the certifying agency determines if the collections are properly identified. ***Labels for both subgroups are yellow.***

Selected class. Reproductive material comes from trees that were selected for a specific character(s). Two classes are recognized: (a) *reproductive material obtained from selected trees* recognized to be superior for any number of traits, such as volume, form, or disease resistance and (b) *material from untested seed orchards and from seed production areas, and open-pollinated seeds* from individual selected trees. In this class, only the female parent is known. This class of material has promising traits that may be superior in the offspring, but such superiority has not been determined by testing. Details of the parents must be recorded. ***Labels are green.***

Tested class. Reproductive material comes from selected trees that have been tested for performance of specific characteristics, as determined by progeny or other applicable tests under specified conditions. The material from this class that performs best in the tests is presumed to be the ultimate in promised genetic superiority and is similar to the agricultural class "certified seed," indicating the highest degree of improvement. ***Labels are blue.***

To be able to sell certified material, the producer or collector must submit an application to the appropriate seed certifying agency, along with a fee, stating what material is to be certified. The application must spell out how the material will be produced or collected. The certifying agency will then notify the applicants if their plans are acceptable or in need of modification. The agency performs field and seed plant inspections, seed storage inventory audits, and whatever additional steps are necessary to ensure that the materials meet the agency's standards and can be tagged with the official agency labels. Cone collectors and buyers have slightly different registration and inspection procedures than seed orchard producers, but the agency controls are comprehensive. Procedures may be amended from time to time, so interested parties should check with their respective state certifying agencies to get the current regulations.

The species of greatest interest for certified collections have traditionally been Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western white pine (*Pinus monticola* Dougl. ex D. Don), ponderosa pine (*P. ponderosa* P. & C. Lawson), sugar pine (*P. lambertiana* Dougl.), and lodgepole pine (*P. contorta* Dougl. ex Loud.). Another dozen or more species, both hardwoods and conifers, are occasionally certified.

Most of the tree seeds sold in the Pacific Northwest are exported to countries in northern Europe that are members of OECD (Organization for Economic Cooperation and Development), a United Nations–based international economic development organization that has set up the Scheme for Control of Forest Reproductive Material Moving in International Trade. European countries that import tree seeds from the Pacific Northwest are required to have OECD certificates on their seeds; consequently, procedures were established in the Northwest to implement this scheme

(which varied only slightly from the standards already in place). The major importers have been Germany (Douglas-fir), the United Kingdom (Sitka spruce, *Picea sitchensis* (Bong.) Carr.), and Sweden (lodgepole pine) (Piesch 1977), with total presently somewhere around 4,500 kg/year (Pfeifer 1997). Because tree seeds are not covered under the Federal Seed Act, there are no officially collected data on the total amount of tree seeds exported from the United States. Details of the OECD Scheme and how it operates in the United States are provided in a later section of this chapter.

Southeast

Standards for tree seed certification in the Southeast began in the late 1950s as more and more attention was focused on seed source and the potentially superior material that could come from the newly established seed orchards. Much of this interest was in response to the results of a seed source study of southern pines established by Phillip Wakeley of the USDA Forest Service. His early results showed that these species could be greatly improved by careful selection of seed source (Wells and Wakeley 1966). Later results showed still more potential for genetic improvement programs (Wells 1983). Some seed zones for selected species were established within states (figure 3), and regional zones for the southern pines were established later (figure 4) (Lantz and Kraus 1987).

Instead of a collective effort, individual states developed their own standards, usually through committees of state, federal, and industrial interests under the aegis of state chapters of the Society of American Foresters. These committees then turned to their respective state seed certification agencies to administer the systems. Georgia and Florida were the first states to develop standards. Other states followed, basing their standards and procedures primarily on those of the states that had gone before. The following 3 classes of certified material were recognized by all states.

Source-identified material. Reproductive materials that can be from (a) *natural stands*, including seed production areas with known geographic origin or (b) *plantations of known provenance*. This class is equal to the source-identified class of the Pacific Northwest. ***Labels are yellow***.

Selected material. Reproductive materials must be from rigidly selected trees or stands that have promise but not proof of genetic superiority; progeny tests to supply the proof are not complete. This class is equal to the selected class of the Pacific Northwest. ***Labels are green.***

Certified material. These reproductive materials must be of known genetic identity obtained from trees of proven genetic superiority. This material must have proven its genetic superiority through progeny tests. This class of material is the same as the tested class in the Pacific Northwest system. ***Labels are blue.***

Most states wrote their standards to apply to seeds and seedlings of southern pines only, but Mississippi and Alabama also included sweetgum (*Liquidambar styraciflua* L.), sycamore (*Platanus occidentalis* L.), and eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.). Standards for cottonwood were for unrooted cuttings only (ACIA nd; MSIA 1979). The demand for certified material varied among states in subsequent years but was particularly strong in Georgia, where the state forestry commission vigorously promoted the use of certified seeds and seedlings of southern pines. Like the system used in the Pacific Northwest, certification in the Southeast requires application to the certifying agencies, fees, inspections, and possible audits. Most state systems in the Southeast are very similar, but details may vary. For more information, contact the respective state certification agencies.

Overseas sales of southern pine seeds were brisk in the 1950s and 1960s, but few, if any, of the lots were certified. In the 1980s the export market for southern pine seeds had decreased somewhat; however, new customers who wanted more assurance of quality were coming on the scene. This development stimulated interest in certification of these exports. Following the lead of the Pacific Northwest, producers and government officials in the Southeast turned to the OECD Scheme for Forest Reproductive Material, which was becoming a certification model acceptable throughout most of the world. Under the aegis of AOSCA, a committee comprising state and federal officials, seed producers and merchants, and university researchers was formed in 1986 to produce uniform regional standards that would meet (or exceed) both AOSCA and OECD standards of certification of forest materials. This action would also remove differences in state standards, thereby making cooperative action easier. In some cases, southern pine seeds were produced in orchards in one state, extracted and cleaned in another, and sold in still another. State certifying agencies had reciprocal agreements that allowed inspectors in one state to approve practices for seeds sold in a neighboring state, but differences in small details could cause problems. After 5 years of deliberations, agreement was reached on uniform standards, but apparently none of the states implemented the new standards. Certification in the Southeast continues to be carried out on demand by the respective state agencies, according to the standards adopted 20 or 30 years ago. Because the anticipated large demand for OECD-certified

material from the Southeast did not develop, seed producers and merchants have not been adversely affected by the lack of uniformity.

Organization for Economic Cooperation and Development

The United Nations Organization for Economic Cooperation and Development (OECD) was organized in 1960 to facilitate economic development in member countries. Membership included most of western Europe, Canada, the United States, Japan, Australia, and Turkey (Piesch 1977). The OECD Scheme for Control of Forest Reproductive Material Moving in International Trade was first published in 1967 and amended in 1974 (Hoekstra 1976). Additional revision is currently underway. The unit of approval for reproductive material is 1 of 7 kinds of "basic material": seed source, stand, seed plantation, seed orchard, parents of family(ies), clonal mixtures, and clone. All materials are tagged and accompanied by a certificate of provenance. The scheme describes the following 4 categories of certification possible for the materials.

Source-identified materials. Basic requirements are (a) the region of provenance where the material is collected and the origin of the basic material (indigenous or non-indigenous) shall be defined and registered by a Designated Authority and (b) the seed shall be collected, processed, and stored, and plants shall be raised under the control of a Designated Authority. This category is equal to the source-identified class of systems in the United States. ***Labels are yellow.***

Selected materials. Selected materials must conform to the 2 requirements above, and also they will be derived from basic material that conforms to certain requirements and has been approved and registered by a designated authority. The requirements pertain to selection criteria, uniformity, quality, isolation, and origin. This category is similar to the selected class of the systems in the United States. ***Labels are green.***

Materials from untested seed orchards. This material consists basically of seeds that are produced by a seed orchard of selected trees (category 2) for which progeny tests are not yet complete. These materials are potentially more valuable than those from category 2 because the mother trees are pollinated (it is hoped) by other selected trees. The original systems of the Pacific Northwest and Southeast did not contain this class but included these materials in the selected class. ***Labels are pink.***

Tested materials. This material is the same as class 3, except that progeny testing has been completed and (a) *the genetic superiority of the material is proven by the tests* and (b) *the results of the tests shall be registered by a designated authority.* This class generally corresponds to the tested class of the Pacific Northwest system and the certified class of most state systems in the Southeast. ***Labels are blue.***

The OECD scheme is virtually identical to the standards established in the United States except for class 3, the material (seeds) collected from orchards of selected material prior to completion of progeny tests. Oregon and Washington, wishing to continue export sales to OECD countries, added class 3 to their standards for the purpose of issuing OECD certificates. The USDA Forest Service has been appointed as the designated authority to implement the scheme in the United States. Because tree seeds are not covered in the Federal Seed Act, the Forest Service re-delegated its authority to implement the scheme to the states of Oregon and Washington under cooperative agreements with their seed certifying agencies (Hoekstra 1976). California, Ohio, and perhaps other states now have similar agreements in place (Karrfalt 1998). The same procedure would have been followed in the Southeast with the uniform regional standards if an agreement had been reached among all parties. This pathway is still open, of course, to individual states that wish to pursue separate cooperative agreements with the USDA Forest Service.

The OECD scheme is widely used as a model for certification standards in many non-member countries. It is currently being revised again; interested parties should contact the Cooperative Forestry Office of the USDA Forest Service in Washington, DC, for the latest information on the scheme.

European Union

The European Union (EU) also has a certification requirement for forest seeds imported into the member countries. All of these countries also participate in OECD and require both OECD and EU certificates and labels. Although the United States is not a member of EU, its seed dealers are affected when seedlots are exported to EU countries. The EU scheme differs from both OECD and North American systems in that only 2 categories of certification are recognized: selected and tested materials. The EU scheme does not recognize source-identified and audit classes from the Pacific Northwest system or source-identified class from the southern systems. Because the United States is not a member nation and because source-identified seed is the most common export from this country to Europe, these

seeds must receive a derogation (special exemption) and a special white label to signify their classification. Seed exports from the United States to Europe would be greatly simplified if the OECD and EU schemes were the same. Discussions are currently underway to revise the EU scheme, so there is hope that this harmonization will be realized in the near future.

Native Shrub and Grass Seeds

In the 1980s and 1990s, a surge of interest in rehabilitating rangelands arose in the western portion of the United States. The majority of the plant materials used in these projects are grasses and shrubs, not trees. Although some selection programs are underway to produce genetically superior materials within a limited number of species, practically all of the material being planted at present comes from general collections from natural stands. Because good results are obtained with local ecotypes, there is now a strong demand for source-identified certification of this material (Young 1994, 1995). Young (1994) listed 34 commercial seed dealers that were interested in collecting or producing certified grass or shrub seeds for reclamation and restoration plantings.

Although shrub seeds could conceivably come under certification standards for tree seeds, native grasses do not make a good fit in this regard. To meet this growing demand for certification, AOSCA has replaced their old tree seed certification standards with new pre-variety germplasm certification standards (AOSCA 1994). These standards allow certification of material from all natural plant populations of indigenous or non-indigenous species before any varieties that are developed in improvement programs are released. The standards recognize the following 3 types of materials.

Source-identified seeds:	***Labels are yellow***
Selected seeds:	***Labels are green***
Tested classes:	***Labels are blue***

All of these types are defined very much like the corresponding classes in tree seed standards that were described earlier. To satisfy OECD export standards, AOSCA will allow a pink label to go on Selected material if it is equal to the OECD class untested seed orchard. This class of material is collected from orchards for which progeny tests are not yet complete. Even though the current demand is for source-identified materials, the mechanism now already exists for certification of any improved native plant materials when producers are ready. For information on certification of native plant materials, including trees, consult the AOSCA Certification Handbook (AOSCA 1994) or state certification agency.

Federal Seed Act and Labeling Laws

The Federal Seed Act of 1939 is basically a truth-in-labeling law that governs interstate commerce and importation of agricultural seeds (Copeland and McDonald 1995). Movement of seeds within state boundaries is not covered under the act, therefore all states have their own seed labeling laws to govern intrastate sales. Presently fewer than 20 states include tree seeds under their labeling laws, and in most that do, enforcement is not strict. Because tree seeds are seldom, if ever, sold over the counter at retail stores, the public does not demand stricter enforcement. Laws do exist in some states, however, providing legal recourse for buyers who feel wronged. Label requirements differ; some states require only the species and date of collection, whereas others require germination test results and provenance data.

There has always been some confusion among foresters about the differences between certification and labeling (Zobel and Talbert 1984). Many believe that correct labeling is all that certification will deliver. Under labeling laws, seed officials normally step in to correct wrongs *after* they have caused damage to the buyer. The mere existence of inspections and penalties, however, promotes honesty in labeling. In certification programs, officials are on the scene to confirm identity and production of the material *before* it is delivered to the buyer. This certification activity has a cost, which is passed along to the buyer; it is, however, the best assurance that a buyer will receive what is being paid for.

Outlook for Certification

The outlook for certification of tree seeds, other forestry materials, and native shrubs and grasses is uncertain. Demand for tree seed certification in the Pacific Northwest formerly fluctuated with the size of the cone crops; large cone crops meant heavy demand for certification services. Currently, greatly reduced timber harvests on federal lands in the West have sharply cut the demand for seedlings from federal agencies and therefore for seeds. Demands for planting increase when large areas were denuded by wildfire, but this factor is not predictable. Forest industries are, for the most part, meeting their needs from their own seed orchards and are not applying for certification. The export market to Europe for seeds of western conifers would decline if European seed orchard production increases or if European environmental groups continue to effectively pressure foresters to plant only species native to Europe.

Tree seed certification in the South is quite dormant at the present. Export markets for southern pine seeds still exist, although not to the extent as in the 1960s, but most of these customers are not members of OECD or EU and do not require those certificates. Many of the pine seeds now sold overseas come from overseas seed orchards, primarily first-generation orchards that now produce excess seeds surplus to the producers' own needs. Among private forest landowners in the South, very little demand for certification is evident. The USDA Forest Service and forest industries that use most of their own improved seeds for planting are infrequent customers for certification services, and the Southern Region of the Forest Service's National Forest System is undergoing a reduction in timber harvest and replanting, much the same as the western regions.

The best potential for future certification of tree or other native plant seeds is in restoration or reclamation planting programs. These programs require relatively small seedlots from an extraordinarily large number of species, many of which have not been grown in nurseries before. There is also a trend toward wanting only local ecotypes for restoration planting (Young 1995) and source-identified certification to provide the assurance that proper seed sources are being used. The large number of shrub and grass seed dealers that are willing to get their products certified for source (Young 1994) and the increasing number of seed dealers that are selling tree seeds (at least 58 offering over 1,800 species) (USDA FS 1995) indicates that commercial sources are ready and willing—customers simply have to ask for certified materials. State certification agencies now have the standards and procedures to certify any or all of this material. From this perspective, there appears to be a promising future for certification of seeds and other materials from trees and other native plants.

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Chapter 7

Nursery Practices

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Contents

Introduction

Plant propagation is both a science and an art. In this chapter, we examine the science of plant propagation, which consists of a knowledge of plant physiology, nursery cultural practices, and the biological characteristics of the particular plant that we want to grow. The art of plant propagation cannot be taught, however, because it consists of certain technical skills that must be acquired through experience and often requires a certain "feel." This special quality is expressed in the saying that people who seem to be able to grow plants have a "green thumb" (Landis and others 1999). But before we get into the specific details of plant propagation, we first need to cover some basic nursery terms.

Terminology

A seedling is a plant grown from a seed, but the term is commonly used generically for many types of nursery stock, including transplants, rooted cuttings, and emblings (plants that are produced through micropropagation). Forest and conservation seedlings are traditionally divided into 2 basic stocktypes, depending on how they were propagated: bareroot seedlings and container seedlings. Bareroot stock is grown in soil in open fields (figure 1A), and the seedlings are removed from the soil during harvesting (figure 1B). Container seedlings are grown in an artificial growing medium in a controlled environment, such as a greenhouse (figure 2A), where most or all of the growth-limiting factors can be manipulated. Because the volume of growing medium in containers is relatively small, roots bind the medium into a cohesive "plug" by the time the seedlings are harvested (figure 2B). Therefore, container-grown stock are sometimes called "plug seedlings."

Another stock type is the transplant, a seedling that has been physically removed from its seedbed or container and then replanted in another location for additional growth. Traditionally, most transplants are bareroot seedlings that were grown for 1 or 2 years and then replanted into a transplant bed and allowed to grow for another year or two. Recently, container transplants are becoming much more popular. This new stock type, also called a plug transplant, is produced by transplanting a small container seedling into the bareroot nursery for an additional year or two of growth.

Bareroot seedlings have been traditionally described with a numerical code. The first number corresponds to the number of years in the seedbed, and the second number refers to the number of years in the transplant bed. Bareroot seedlings are generally produced in 1 to 3 years (1+0 to 3+0), and transplants require 2 to 4 years (for example, 1+1 or 2+2). The sum of the numbers gives the total number of years needed to produce that stock type. For example, a 1+2 transplant takes 3 years to produce.

There is no standard nomenclature for describing container seedlings, and each nursery and region uses its own system. Because most container seedlings are grown in a season or less, they are generally defined by the type and

Figure 1—Chapter 7, Nursery Practices: bareroot seedlings are grown in outdoor beds where they are exposed to local weather (**A**). During harvesting, the soil is removed from the roots and they are shipped to the outplanting site in the bareroot condition (**B**).

Figure 2—Chapter 7, Nursery Practices: container seedlings are grown in artificial growing media in a controlled environment where seedling growth is accelerated (**A**). By the end of the growing season, the roots have formed a cohesive "plug" (**B**).

volume of the growth container. For example, a "Styro " refers to a seedling that has been produced in a Styrofoam® block container with cells that are approximately 65 cm^3 (4 in^3) in volume. Plug transplants are described by the number of years in the transplant bed, so that a container seedling that is transplanted for an additional year of growth is called a "plug+1."

The Target Seedling

There is no one ideal type of seedling suitable for all purposes, and the ultimate use of the stock will control many aspects of the nursery program. Management objectives determine whether the seedlings will be used for plantation forestry or for ecosystem management purposes. Forest products companies demand plants that are genetically selected for commercial objectives: fast growth and desirable attributes such as fiber length or the ability to "self-prune." On the other hand, seedlings used in ecosystem management must reflect broad genetic diversity because they will be used to restore or maintain natural ecosystems. This distinction is critical because it not only affects target seedling specifications but the entire propagation system.

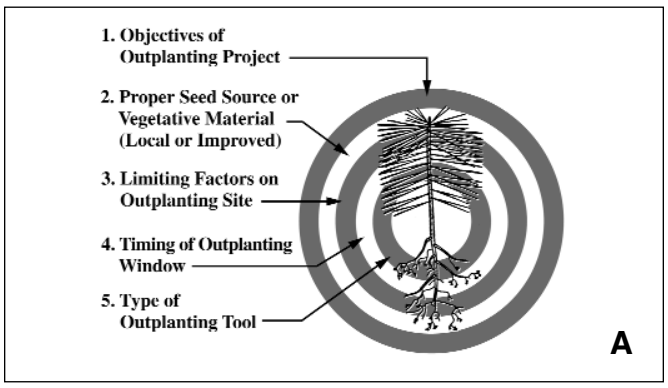
The true measure of seedling quality is performance on the outplanting site—both initial survival and subsequent growth. Because both the seedling user and the nursery manager are jointly responsible for successful plantations, they must work together to define the target seedling for that particular outplanting project (figure 3). Conditions on the outplanting site will determine both what to plant, and when and how to plant it. For example, the seedling user must specify the proper genetic origin for the seedlings (the seed source) and which environmental factors on the outplanting site will be most limiting to survival and growth. A very hot and dry site will require a different target seedling than an outplanting site in a rainy climate. Climate will also determine when to outplant. Planting windows are time periods when stresses are low and the chances for seedling survival and growth are optimal (figure 4).

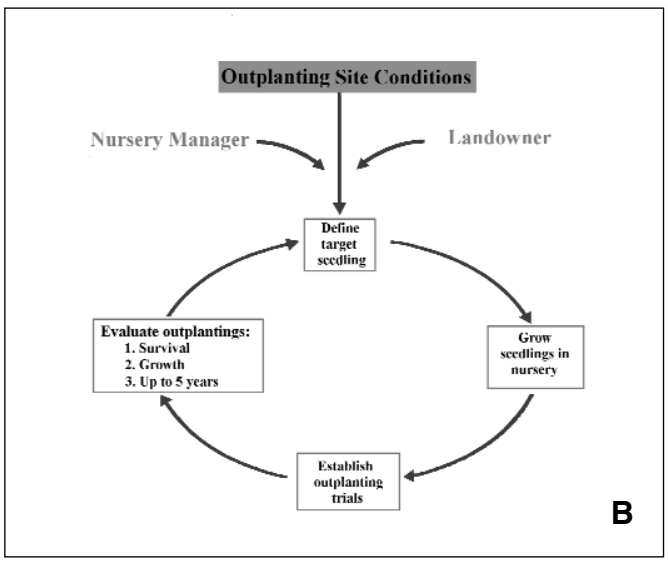
Target seedlings can be described in terms of (1) morphological factors, such as height and stem diameter, (2) physiological factors, such as root growth capacity and cold hardiness, and (3) genetic factors, such as seed source.

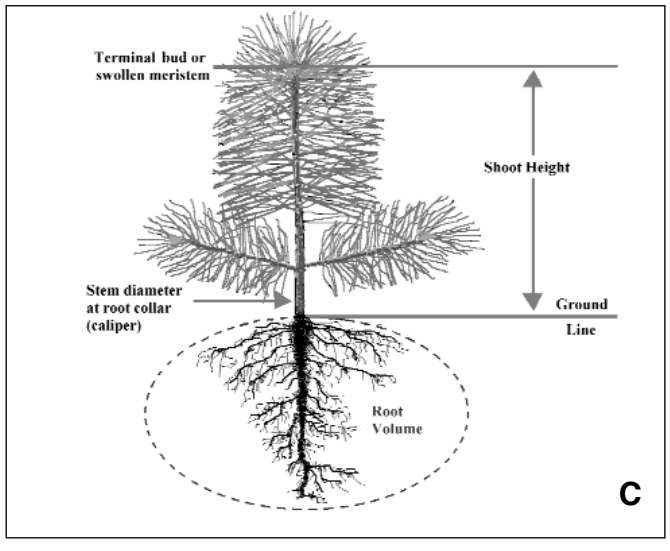
Morphological Specifications

Forest and conservation seedlings are described by traditional morphological dimensions, which are used by both nursery personnel and seedling users. The most common dimensions are shoot height and stem diameter. Shoot height is the vertical distance from the ground line to the tip of the terminal meristem or bud. Stem diameter, often called "caliper" or "root collar diameter," is the diameter of the main stem at the base of the shoot (figure 3C). Other seedling morphological specifications include root volume or length, ovendry (OD) weight, and shoot-to-root ratio (S:R). Though they require destructive sampling, seedling dry weights are useful indices of crop development. The S:R is a relative comparison of the size or weight of the shoot to

Figure 3—Chapter 7, Nursery Practices: the best species and stock type of seedling depends on customer objectives and especially conditions on the outplanting site (**A**). This ideal plant is known as the "target seedling" and has traditionally been described by morphological characteristics (**B**). This prototype seedling must be tested with outplanting trials and these survival and growth results are then used to fine-tune target seedling characteristics (**C**).







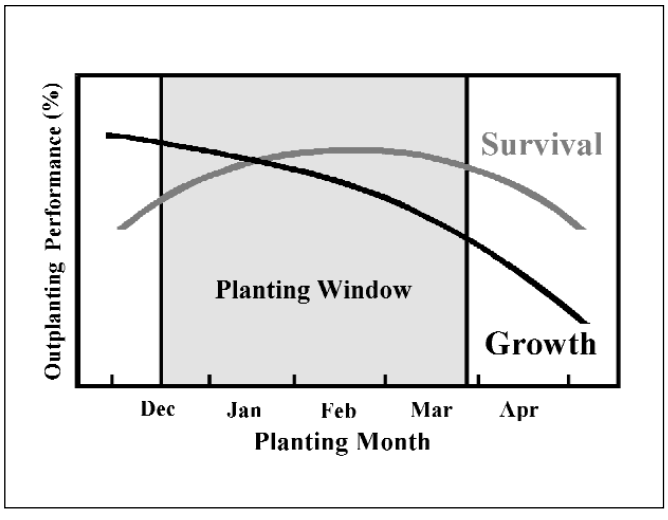
the root system and is sometimes specified by seedling users to match the stock type to conditions on the outplanting site.

Physiological Qualities

The most common measures of the physiological condition of forest and conservation seedlings are dormancy and hardiness. Dormancy refers to the state of relative metabolic activity, and seedlings reach maximum dormancy during the early winter. Hardiness is a general term for resistance to stress. Although cold hardiness is the most common type, hardiness can also refer to resistance to all types of stress, including high temperatures, dehydration, and physical handling.

Recently, nursery managers and foresters have been using 2 criteria to measure seedling quality. Root growth potential (RGP) measures a seedling's ability to produce new roots when growing in an ideal environment, such as a greenhouse. RGP tests are used operationally to establish lifting windows in the nursery and to help predict outplanting performance. The other common measure of physiological quality is the cold hardiness test, which measures the minimum temperature to which a seedling can be exposed without suffering observable cold injury. Because of their strong correlation with general stress resistance, cold hardiness tests have been used to establish nursery lifting windows and predict seedling tolerance to operational stresses such as dehydration and mishandling.

Figure 4—Chapter 7, Nursery Practices: seedling survival and growth is greatest during the "planting window," which is determined by conditions on the outplanting site, especially moisture and temperature (modified from South and Mexal 1984).



Genetic Considerations

Most seedlings grown for forest and conservation purposes are ordered by species, stock type, and seed zone or seed source. A seed zone is a geographic area that is relatively similar in climate and soil and often is described by a numerical code. Seed zones in mountainous terrain are also stratified by elevation (figure 5A). For example, the geographically diverse state of California has more than 80 different seed zones, with numerous elevation bands within each zone. All seeds and cuttings collected in a particular zone are labeled with that source code so that all seedlings produced from them will be planted back into the zone of origin. When a seedling order is sown in the nursery, information on species, seed zone, and elevation is included into a seedlot identification number. The seedlot number remains with this group of seedlings throughout their entire nursery tenure and is marked on the storage container when the seedlings are harvested for outplanting (figure 5B).

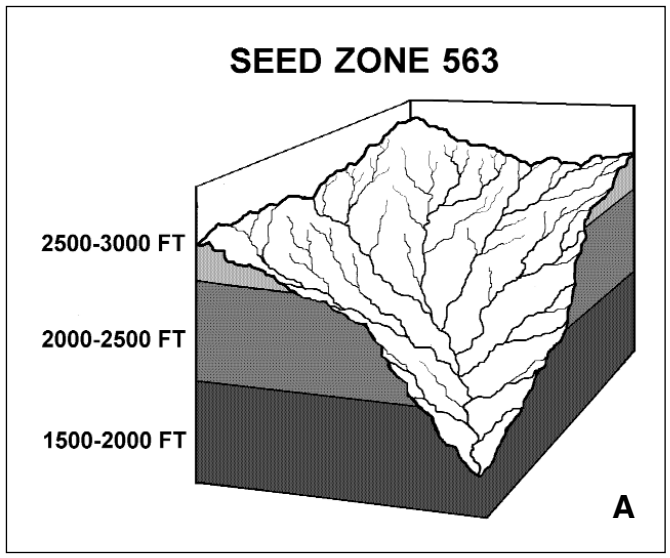
Types of Nurseries

Once the target seedling has been defined, the next step is to decide how best to grow it. Forest and conservation stock is propagated in either bareroot or container nurseries, and the choice is determined by several factors:

1. **Cost.** Container seedlings traditionally have been more expensive than bareroot stock, although, in recent years, the costs are becoming more comparable. Container nurseries also are more cost-effective at low seedling production levels.
2. **Species characteristics.** Most forest and conservation species can be grown as bareroot seedlings, although some do better in containers.
3. **Production time**. Because container seedlings can be produced more quickly than bareroot seedlings, they are often used to reforest burns and other sites that need to be planted quickly.
4. **Outplanting site condition.** Bareroot seedlings are used on typical reforestation sites, but container seedlings often are preferred for the more severe, hard-to-plant sites. Container stock has a wider outplanting window than bareroot stock.
5. **Personal preference.** Some customers tend to prefer one stock type over the other.

Because bareroot seedlings are grown in open fields, the soil, water supply, and climate of the nursery site must be suitable for propagation. The growth rate of bareroot seedlings and the length of the growing season are largely

Figure 5—Chapter 7, Nursery Practices: because plants are genetically adapted to local environmental conditions, forest and conservation nurseries use "seed zones" to ensure that seedlings will be ecologically adapted to the outplanting site (**A**). The seed zone and elevation are included in the seed source code, which will remain with the seedling throughout the nursery cycle (**B**).



controlled by the climate at the nursery site. Quality nursery soils are difficult to find in convenient locations, and good agricultural land is often expensive. Compared to container nurseries, bareroot nurseries usually require considerable capital to develop but have lower operating costs. A comprehensive discussion of site selection factors that should be evaluated when locating a bareroot nursery is presented in Duryea and Landis (1984) and Lantz (1985).

Container nurseries can be constructed on land with low agricultural value that would be unsuitable for bareroot seedling production. The amount of capital investment and

operating costs vary with the type of nursery. For example, fully controlled greenhouses require expensive structures and environmental controls, whereas open growing compounds are much less costly. Because container seedlings are grown at high densities, less land is required than for a bareroot nursery.

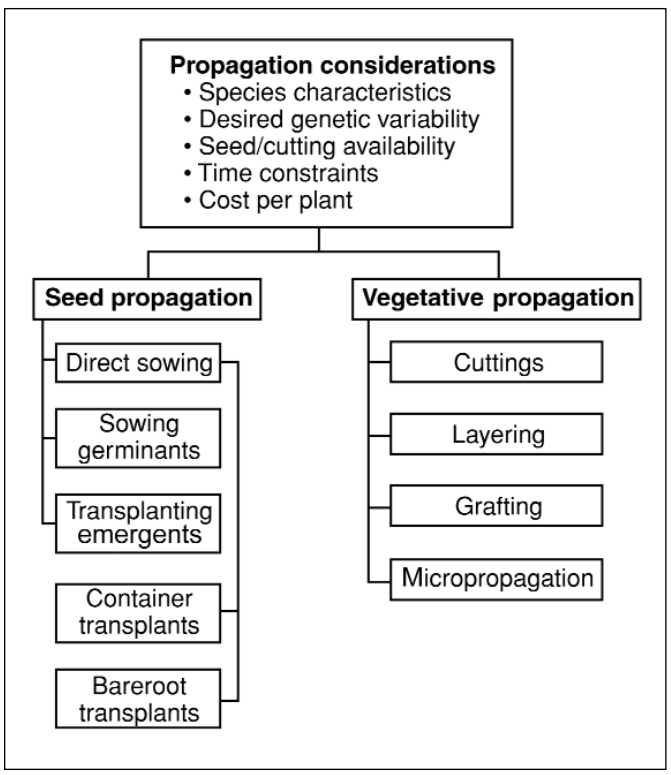
The decision whether to start a bareroot or container nursery must be carefully thought out because there are many considerations. It is helpful to list the various factors side-by-side for ease of comparison. A decision-making process is presented in the first chapter of volume one of the Container Tree Nursery Manual (Landis and others 1994).

Propagation Options

To determine which type of propagation method will be most effective and economical, both the biology of the plant and the objectives of the outplanting project must be considered (figure 6). As mentioned in the target seedling section, management objectives have a critical influence on the selection of propagation system. Most of the commercially important tree species used in plantation forestry can be grown from seeds, but a few are vegetatively propagated on a large scale to multiply selected clones. For example, on commercial forest land in the southeastern United States, southern pines are grown from genetically improved seeds. In the Pacific Northwest, forest product companies are vegetatively propagating fast-growing species such as redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.) and poplars (*Populus* spp.). Because biodiversity is a primary objective in ecosystem management and restoration, seed propagation is usually used, because it better captures and preserves natural genetic variation (table 1).

The availability of propagation material can also have an influence. Some species, such as western larch (*Larix occidentalis* Nutt.), produce seedcrops very irregularly; other species, such as Alaska-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach), produce seeds of poor quality. Availability is critical for emergency planting projects, such as fire restoration, when the crops must be grown in a very short time. As for economics, seed propagation is almost always much less expensive than vegetative propagation. All vegetative propagation techniques involve more hand labor than does seed propagation and also require special equipment and structures (table 1).

Figure 6—Chapter 7, Nursery Practices: nursery managers must consider many biological, operational, and economic factors before deciding on the best propagation system for a given plant species. The first and most important decision is whether to use seed or vegetative propagation.



Seed Propagation

Seed propagation is the most common means of producing forest and conservation seedlings in North America because of its many advantages (table 1):

1. **Cost.** Plants grown from seed are inexpensive.
2. **Ease of propagation.** Seed propagation is simpler and easier than vegetative propagation.
3. **Seedling vigor.** Plants grown from seeds often grow faster than those produced from cuttings.
4. **Phytosanitary restrictions.** It is easier to import and export seeds than vegetative material or whole plants.

There are 4 major ways to produce plants from seeds (table 2). Only direct seeding and transplanting are used in bareroot nurseries, but container seedlings have been produced by all 4 methods.

Direct seeding. Direct seeding is the most common and most economical method. After any required pretreatment, seeds can be sown directly into containers or seedbeds. Seeds are always sown by seedlot, and each lot is immediately labeled with some sort of marker that contains all pertinent information. The seedlot location is also permanently recorded in case the markers are lost. Seedlot identity is carefully maintained during the entire nursery operation to ensure that the seedlings are returned to the environment to

Table 1—Chapter 7, Nursery Practices: operational considerations when choosing propagation methods

Considerations	Seeds	Cuttings	Micropropagation
MANAGEMENT OBJECTIVES			
Fast growth	Most species, using genetically selected seeds from orchards	Good for certain fast growing species	Relatively new but offers enormous potential
Biodiversity	Best	Low, but can be increased with extensive collections	
Availability of propagules	Varies seasonally & yearly; some can be stored for long periods, others not	Collection is seasonal with most species	Collection from stock plants at nursery
EASE OF PROPAGATION			
Difficulty	Relatively easy	Some species root easily; others not	Currently possible for a few species
Specialized equipment & training	Minimal	Moderate (rooting benches)	Definitely
Timing	BR = seasonal C = year-round	BR = seasonal C= year-round	Year-round
Cost per plant	Low	Moderate	High

Note: BR=Bareroot nursery C=container nursery

which they are adapted. In the Pacific Northwest, some nurseries sow literally hundreds of different seedlots each year, reflecting the many diverse environments in that mountainous terrain. In the South, some nurseries propagate by families and the seedlots from each family are sown and cultured separately.

Many forest and conservation seeds have some type of seed dormancy that keeps them from germinating when placed under unfavorable environmental conditions. Growers need to understand the dormancy characteristics of the seeds that they are trying to germinate, because the type of presowing treatment differs for each. For example, some plants exhibit seedcoat dormancy, which means that the seeds are impermeable to the water and/or oxygen that the embryos need to initiate germination. Culturally, there are a couple of ways to overcome this problem. Scarification—any treatment that breaks down the seedcoats to allow penetration of water and oxygen—can be either mechanical or chemical. Mechanical scarification consists of physically scratching the seedcoat to reduce its thickness, and chemical scarification involves dissolving the seedcoat with caustic chemicals such as acids. Hot water or steam can also be used to soften hard seedcoats.

Another common presowing seed treatment is chilling or stratification, which consists of keeping seeds under a cool, moist environment for a specified period of time. The term stratification comes from the practice of placing layers of seeds between layers of insulating material that keep them moist and cool. A more popular form of stratification is called "naked stratification" because bare seeds are soaked and then placed in a plastic bag without any accompanying material. Bags are kept in a refrigerator for a specified period of time according to the requirements of the individual species. The plastic bag maintains the moisture around the seed but also allows oxygen to enter. Some nurseries place a tube in the mouth of the bag to stimulate better air exchange (see chapter 1 on seed treatments).

Planting germinants. The second method for sowing seeds is to pregerminate the seeds and sow the germinants directly into containers. This technique is particularly helpful with seeds that require long or variable cold, moist stratification treatments; seeds from large-seeded species; and seeds from lots of variable quality (table 2). For seeds that need cold, moist stratification, seeds can be mixed with a moisture-retaining material such as peat moss and placed in a plastic bag in a refrigerator. Another option is to place seeds on moisture-retentive material in a covered tray and keep them refrigerated. Stratifying seeds are checked every few days to see if the seeds have split and germination begun. It is very important to keep seeds moist but not too wet, because mold can develop. Spraying the germination tray with a hand sprayer works well. Germinating seeds are individually picked out of the tray, sown into a container, and then promptly covered with a seed mulch such as white grit to keep them from drying out. Seeds that require warm, moist stratification can be germinated in a greenhouse by

Table 2—Chapter 7, Nursery Practices: characteristics of seed propagation methods for forest and conservation species

Propagation method	Type of nursery	Best use	Advantages	Disadvantage
Direct seeding (seeds are sown with or without pretreatment)	Bareroot or container	Seeds of high quality with viability test information; uniformly shaped seeds with smooth seedcoats	Quick; minimizes seed handling; mechanical seeding possible; most labor efficient; sowing all at once	Requires seed of known high quality; dormant seeds must be pre-treated; Containers require thinning and/or consolidation
Planting germinants or "sowing sprouts" (pregerminated seeds are sown from stratification trays or bags)	Container	Very large or irregularly shaped seeds; seeds of unknown quality or low purity; valuable or scarce seedlots	Good use of growing space; efficient use of seed; can adjust for unknown seed quality	Slower & more labor intensive; sowing can take weeks or months to complete; irregular crop development due to staggered sowings
Transplanting emergents or "pricking out" (seeds are sown into trays & then young emergents are transplanted)	Container	Small or fragile seeds; seeds of unknown quality or low purity; valuable or scarce seedlots	Good use of growing space; efficient use of seeds can adjust for unknown seed quality; more uniform crop development	Slower & more labor intensive; poor technique results in stem deformation; potential disease problems in seed flats
Transplanting seedlings (established seedlings are re-planted into a transplant bed or container)	Bareroot or container	Producing stock with more caliper & larger root systems; hold-over stock	Transplants are more resistant to pests & weeds; increased yields per unit area	Increases cost of stock; requires more bed space than seedlings; "J" or "L" roots result from poor technique

Source: modified from Landis and Simonich (1984).

covering them with a moist layer of burlap. It is important to moisten the seeds frequently during this warm stratification period and then plant them as soon as they crack.

The timing of sowing and seed placement are critical; seeds sown too late or improperly placed may develop weak stems. Germinants must be sown before the radicle becomes too long and begins to curve and must be positioned with the radicle pointing downwards. It is best to dibble a small hole in the growing medium prior to sowing the seed so that the root can be oriented properly.

Transplanting emergents. This method involves growing seedlings to the primary leaf stage and then transplanting them to a container (often called "pricking out"). Transplanting emergents works best for seeds that have complex dormancy, are small in size, or come from lots of variable quality (table 2). In some container nurseries, seeds are sown in special trays and placed in a greenhouse to germinate. Small seeds are covered with a thin layer of sand as a mulch. After the seeds germinate and the young seedlings begin to emerge from the germination medium, they are carefully removed one at a time with a pointed instrument and transplanted into a hole made with a dibble in another container. The growing medium is firmed around the transplant to ensure good root contact, and then the seedlings are allowed to grow into shippable size.

When planting emergents, proper technique is extremely important so that seedlings do not become "J-rooted." One option is to clip off the bottom of the root to make planting easier. Another technique is to use a sharp, forked tool to insert the seedling into the container and then to cut off the root tip after the seedling is placed into the growing medium.

Transplanting seedlings. This propagation technique is used in both bareroot and container nurseries (table 2). Through the 1950s, transplanting was the principal way of producing bareroot seedlings because precision sowing equipment was unavailable. Today, transplanting is again growing in popularity because of the demand for larger seedlings with more-fibrous root systems.

Transplants are more expensive to produce than seedlings, but this expense can usually be justified under the new "free-to-grow" reforestation regulations that mandate quick establishment and growth.

Some bareroot nurseries grow seedlings specifically for transplanting, whereas others use smaller-grade stock from harvested seedbeds. Most nurseries transplant bareroot seedlings in the spring, but container seedlings are often transplanted in the summer or early fall. Mechanical transplanters use a vertical "shoe" to open the soil and a

wheel with clips to place the transplant into the slit at the proper spacing. Transplant beds have the same physical dimension as seedbeds but seedlings are planted in fewer rows and at much lower densities. Once they become established, transplants are fertilized and irrigated and are given the same root culture treatments as bareroot seedlings.

The first container transplants were made from surplus stock but now seedlings are grown specifically for this purpose. Typically, seedlings are grown in 33- to 66-cm^3 (2- to 4-in^3) containers for 4 to 6 months and are then transplanted to the beds. Miniplugs, the newest type of plug transplant, are grown in very small containers (around 16 cm^3 or 1 in^3) specifically for transplanting. Plug transplants are cultured and harvested in exactly the same manner as are bareroot transplants. Another new larger container stock type is made by transplanting miniplugs into much larger containers—for example, 328 cm^3 (20 in^3).

A complete discussion of seed propagation is provided in Landis and others (1999).

Vegetative Propagation

The second major plant propagation technique is vegetative propagation, which also is called asexual propagation because 2 parents are not required. A clone is defined as a group of genetically uniform individuals that were originally derived from a single parent by asexual propagation. The major benefit of vegetative propagation is that the offspring will very closely resemble the parent because their genetic code is identical (figure 7). Other benefits of vegetative propagation include the following:

1. The ability to obtain a high degree of crop uniformity.
2. The elimination of problems with seed availability, dormancy, and viability.
3. The ability to perpetuate genetically superior plants, such as fast-growing or disease-resistant clones.
4. The ability to "bulk-up" valuable, genetically improved seedlots.

In forest and conservation nurseries, rooted cuttings are the most common type of vegetative propagation, and there are 3 different types that are named for the type of tissue used. Hardwood cuttings (figure 8A) are collected during the dormant period from the last season's growth, stratified in cold storage, and planted ("stuck") in containers or bareroot beds. Semi-hardwood cuttings are collected after the active growth period from hardened woody tissue of the current season's growth. Softwood cuttings are collected from soft succulent new shoots of woody plants that have just begun to harden, normally in spring, but also at any time of the year in species having multiple flushes. Cuttings can be collected from plants in the wild or from mother plants established in the nursery for that purpose; rows of these mother plants are called stool beds. In bareroot nurseries, cuttings are planted in rows in formed seedbeds and cultured just like seedlings (figure 8B). In container nurseries, cuttings can be rooted in special trays and then transplanted into the growth containers or stuck directly into the containers (figure 8C). Rooting hormones are used to promote new root formation in recalcitrant species. Some nurseries sell unrooted cuttings of such easy-to-root genera as poplar (*Populus*) or willow (*Salix*).

Root cuttings are another type of vegetative propagation source that has been used for some species, such as quaking aspen (*Populus tremuloides* Michx.). Sections of lateral aspen roots, which are actually modified stems, are collected from trees in the wild and placed in growing medium in the greenhouse. After several weeks, shoots form on the roots and can be cut and stuck into growth containers.

Other vegetative propagation methods include air layering, grafting and budding, and micropropagation. Layering is uncommon but can be used for species such as those in the *Rubus* genus that grow as vines. Grafting and budding are normally used for fruit trees; they are too labor intensive

Figure 7—Chapter 7, Nursery Practices: plants propagated from seed appear different from their parents, because they contain a mixture of genetic characteristics **(Top).** Vegetative propagation, on the other hand, produces exact duplicates of the parent plant **(Bottom).**

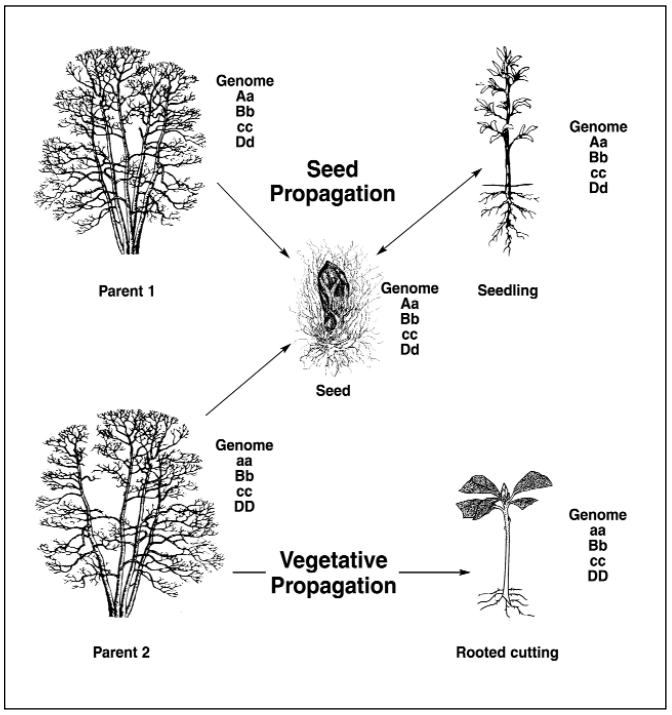
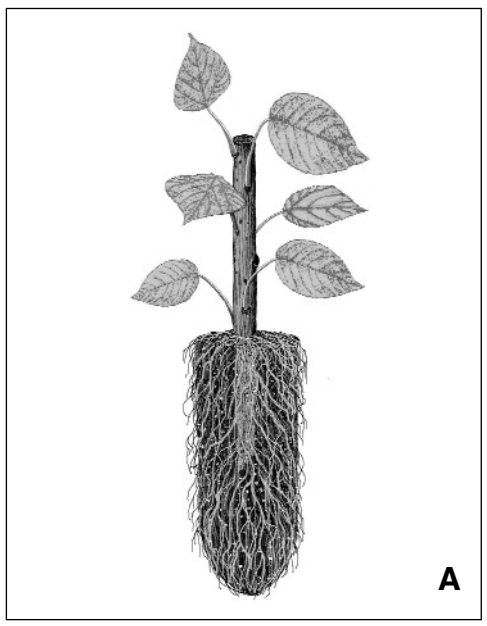


Figure 8—Chapter 7, Nursery Practices: hardwood cuttings are the most common vegetative propagation method used in forest and conservation nurseries (**A**). Hardwood or semi-hardwood cuttings are typically treated with rooting hormones and planted into bareroot beds (**B**) or containers (**C**).

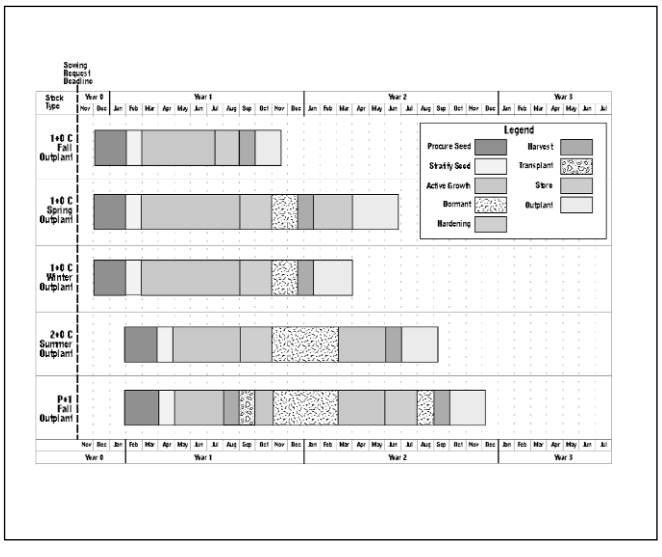


and thus too expensive to use for reforestation stock. Grafting is used in tree improvement programs to develop seed orchards. Micropropagation or tissue culture has been used for some forest species, but it requires specialized equipment and is therefore not currently practical for most species used in reforestation. A complete discussion of vegetative propagation is provided in Landis and others (1999).

Bareroot Nursery Cultural Practices

Bareroot seedlings take from 1 to as many as 4 years to produce, depending on the species, nursery climate, and stock type (figure 9). Southern pine seedlings are produced in 1 year, whereas some northern spruce transplants require 2 years in the seedbed and 2 more years in the transplant bed. Crop rotation requires at least 1 year longer to allow time for soil management. A typical crop rotation for a 2+0 ponderosa pine crop is 2 years with seedlings growing in the seedbed, followed by a 1-year rest or fallow period for the bed. The most comprehensive references on bareroot nursery management include Duryea and Landis (1984), Lantz (1985) and Williams and Hanks (1976). A complete discussion of the equipment needed to produce bareroot seedlings can be found in the *Bareroot Nursery Equipment Catalog* (Lowman and others 1992).

Figure 9—Chapter 7, Nursery Practices: growing schedule are used in crop planning to illustrate the time required for each phase of the nursery cycle from seed procurement to outplanting.



Soil Management and Seedbed Preparation

The bareroot nursery crop cycle starts with soil preparation. Next to water quality, the most important site quality factor in a bareroot nursery is the soil; maintaining or improving soil quality is an ongoing process. The best soil type for a forest and conservation nursery is sand to sandy loam at least 46 cm (18 in) deep.

A typical nursery crop cycle starts with either a cover crop, a green manure crop, or a year of leaving the soil fallow, depending on the objectives of the nursery manager. If the objective is to protect soil from wind and water erosion and control weeds, then cover crops are sown. Green manure crops are primarily grown to supply organic matter to the soil; they also serve as "catch crops" to capture mineral nutrients such as phosphorus and iron in a readily available form. The cover or green manure crop is plowed down in late summer to allow time for the organic matter to decompose (figure 10). If the objective is to eliminate weed growth and lower soil pathogen levels, then the land is kept fallow by repeated cultivation.

In addition to the organic matter supplied by the cover or green manure crop, many nurseries add organic amendments and fertilizers during the fallow year. Sawdust is a good soil amendment if nitrogen fertilizer is also added to promote decomposition; if no fertilizer is supplied, soil microorganisms will cause a nitrogen deficiency in the subsequent seedling crop. Many growers also add preplant fertilizers such as phosphorus or organic fertilizers during the rest or fallow year. Soil pH can be adjusted to the ideal range of 5.5 to 6.5 by adding dolomite to raise the pH or sulfur to lower it. Because phosphorus is immobile in the soil, phosphorus fertilizers are often incorporated into the soil at this time instead of as a top dressing during the growing season.

Figure 10—Chapter 7, Nursery Practices: the bareroot nursery cycle starts with soil preparation. Many nurseries sow a cover crop or green manure crop during the fallow year to protect the soil and maintain the organic matter level.

Seedbeds are prepared for sowing with a series of sequential cultivations, until the soil is worked into the proper crumb-like structure. Because of the frequent use of heavy equipment under wet conditions, soil compaction is a serious and recurring problem in forest and conservation nurseries. Many nurseries "deep rip" or "subsoil" their fields with long shanks during the rest or fallow year to a depth of 46 to 61 cm (18 to 24 in). Ripping is often done immediately after organic matter is applied so that it can be incorporated throughout the soil profile and prevent formation of hard, impermeable layers ("pans").

Many bareroot nurseries fumigate their seedbeds with soil sterilants such as methyl bromide/chloropicrin or methyl isothiocyanate. Fumigation is expensive, but eliminates all common nursery pests: pathogenic fungi, insects, nematodes, and weed seeds. The fumigants are either injected into or mixed with the soil and then covered with a plastic tarp or sealed with irrigation, allowing the gas to permeate throughout the soil. After several days, the tarp is removed or the soil seal broken to allow the gas to dissipate. Due to environmental concerns that have led to the phasing out of methyl bromide under the Montreal Protocol, nurseries are looking for alternatives to soil fumigation. One of these is encouraging the growth of beneficial microorganisms to make the soil suppressive to pathogens.

Sowing

Fall-sowing has been used to allow seeds to stratify naturally over the winter, but most nurseries sow in the spring as soon as soil temperatures are warm enough. In either case, the seeds are sown into preformed, raised seedbeds that are approximately 10 to 15 cm (4 to 6 in) high and 1.2 m (48 in) wide, a standard dimension that corresponds to all mechanized equipment. Seedbeds are laid out side-by-side between irrigation lines (figure 11).

The amount of seed to sow is calculated with a formula that takes both seed characteristics and "seedling factors" into consideration (figure 12):

Seed sowing rate = (desired seedbed density) ÷ (seed viability x nursery factor x seeds per weight)

Figure 11—Chapter 7, Nursery Practices: bareroot seedlings are grown in raised seedbeds that provide better drainage and warmer soil temperatures. Bed width is standardized to allow cultivation by tractor-drawn equipment (modified from *Bareroot Nursery Equipment Catalog* by Lowman and others 1992).

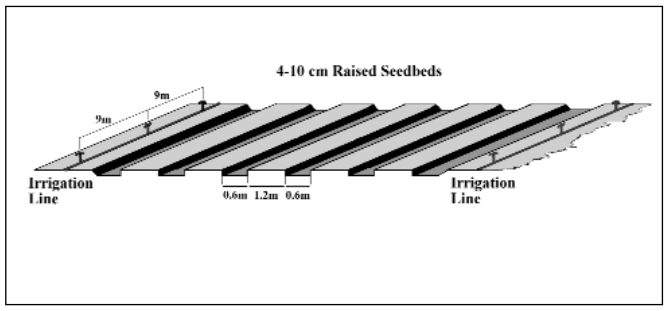
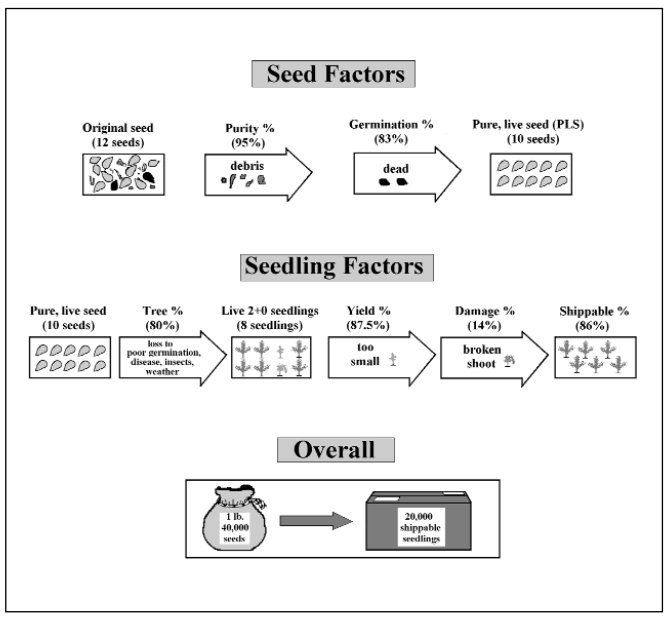


Figure 12—Chapter 7, Nursery Practices: seed use efficiency, the ratio of seeds sown to seedlings harvested, is a function of both seed quality and seedling losses during the growing season (from Thompson 1984).



Sowing seeds at the proper density is one of the most important cultural operations in a bareroot nursery because it controls the quantity and quality of the crop. Seedlings sown at too low a density grow large and out of proper shoot-to-root balance and thus waste valuable growing space. On the other hand, seedlings planted at too high a density often become stunted and spindly and are more susceptible to disease.

Seeds can be broadcast-sown by hand, but this is a critical operation and requires training and practice. Seeds are sown by making quick sideways movements with the hand, pressed into the seedbed with a roller, and then covered with a mulch. Seeds can be mechanically broadcast with a drop spreader, such as a fertilizer spreader, which is calibrated to distribute the proper amount of seeds per area of seedbed. Very small seeds are often mixed with a carrier, such as sand or sawdust, so that they will be distributed more evenly.

Most bareroot nurseries use mechanical seed drills that sow seeds in 6 to 8 rows per seedbed. To control seedling growing density, precision drills are capable of accurately placing seeds at specific distances in the row. Some seed drills automatically cover the seeds with soil, whereas others leave seeds exposed so that they can be covered with mulch, such as sawdust, pine needles, or hydromulch. Mulches serve several functions, including controlling soil erosion, retarding moisture loss, and reducing soil temperature.

Many nurseries apply chemical herbicides immediately after sowing. These pre-emergence herbicides selectively kill germinating weed seeds but do not harm the tree seedlings. Newly sown seedbeds are kept moist until germination occurs, which usually takes 3 to 4 weeks.

Irrigation and Fertilization

The ability to supply water and mineral nutrients for accelerated seedling growth is one of the most important cultural activities in forest and conservation nurseries. Nurseries have used both wells and surface impoundments as water sources; both are adequate as long as they are properly designed to deliver the right amount of water at the right pressure at the right time. Total nursery demand must be calculated to include water for other cultural activities such as cooling or frost protection as well as for seedling growth. The quality of irrigation water is critical and should have been checked before the nursery was ever developed. High pH values of water can be controlled with acid injection but high salt levels cannot be corrected economically.

Most bareroot nurseries pump water through semi-permanent sprinkler systems to keep the seedbeds at the proper soil moisture level. The amount of water to apply can be estimated from soil moisture measurements and predictions of evapotranspirational demand, but successful irrigation requires both good judgement and practical experience. Sprinkler irrigation also is used to cool the soil surface while new germinants are still succulent and to provide protection against late spring or early fall frosts.

Bareroot nurseries apply mineral nutrients needed for rapid seedling growth with chemical or organic fertilizers. Maintaining a slightly acid soil pH is important to ensure that all nutrients remain available. A presowing application of sulfur to lower pH or dolomite to raise it were discussed earlier, along with incorporation of phosphorus. Unless soil tests show other nutrient deficiencies, nitrogen and potassium are the only fertilizers that are typically applied during the growing season. These applications are called "top dressings," because they are applied over the top of the crop. Application rates are determined by experience or from chemical tests of the soil and seedling foliage, and the fertilizers applied by drop or rotary spreaders. Some nurseries inject soluble fertilizer solutions into the irrigation system or apply them through a spray boom behind a tractor. Suspected nutrient deficiencies, as indicated by symptoms such as chlorosis ("yellowing"), should always be confirmed by soil or foliage tests because symptoms can be caused by many factors.

Root Culturing and Top-Pruning

Root culturing is critically important. A tree seedling is only as good as its root system, because forest and conservation species need fibrous roots to absorb water quickly after outplanting. Root-pruning consists of undercutting seedbeds with a stationary or oscillating horizontal blade to sever the dominant tap root and promote new, more-fibrous root growth. Wrenching is a special type of undercutting that uses a thicker angled blade to shatter the soil profile and increase soil permeability and aeration (figure 13). During the hardening period, wrenching also is used to induce a temporary seedling moisture stress that retards shoot growth and induces dormancy. Lateral root pruning with a vertical blade or coulter is used to cut the lateral roots between the seedling rows. This piece of equipment is sometimes "belly-mounted" under the tractor, which allows precise placement by the tractor operator.

Some nurseries top-prune their seedlings to control shoot height and increase crop uniformity. The timing of this operation is extremely critical to ensure that the seedlings are not injured or stimulated to produce abnormal shoot growth. The window for top pruning usually lasts only a few weeks and must be scheduled each year based on seedling development.

Harvesting

Harvesting, or lifting, is done during the dormant period when seedlings are in a state of maximum dormancy and hardiness. This time period, known as the "lifting window"

Figure 13—Chapter 7, Nursery Practices: root culturing is important to develop a fibrous root system. These pine seedlings are being wrenched with a sharp-angled blade that is being pulled under the seedbed.

occurs during the late fall, winter, or early spring, depending on the climate of the nursery. Nurseries in milder climates can lift all winter, but nurseries located where the ground freezes have only 2 narrow lifting windows: one in the fall and another in the spring. Because the weather is often too wet in the spring, some nurseries must lift a significant portion of their crop in the fall.

The lifting operation consists of drawing an inclined, vibrating blade under the seedlings, usually at a depth of about 25 to 30 cm (10 to 12 in). The inclined blade lifts seedlings out of the seedbed and the vibrating action loosens soil from around their roots (figure 14A). Some nurseries hand-lift their stock after the seedlings are loosened: the seedlings are pulled from the seedbeds, the loosened soil shaken from the roots, and the seedlings placed in a box. The lifting boxes often are lined with wet burlap to keep the roots from drying out. Several different types of mechanical harvesters are also used to lift seedlings. Most use a digger blade to lift the entire seedbed onto a moving, vibrating belt that shakes soil from the roots; others have rubber gripper belts that pull the seedlings from the soil and transfer them to the work platform. Boxes or larger totes of seedlings are quickly transported to a pre-storage cooler to await grading and processing. In the South, some nurseries "field-pack" their seedlings, which involves bagging seedlings immediately after they are lifted and weighing them. The number of seedlings per bag is estimated from a ratio between the weight of seedling samples and the seedling count.

The time period from when seedlings are lifted until they are outplanted is one of the most critical in the entire

reforestation sequence. Tiny fibrous roots are especially prone to drying and can be killed by a few minutes of exposure to heat, direct sunlight, or drying wind. The lifting crew includes several people who are assigned to keep the seedling boxes wet until they can be moved to the pre-storage cooler (figure 14B). Progressive nurseries monitor seedling quality during the seedling harvesting/outplanting operation. The pressure chamber directly measures seedling moisture stress and is used to determine when weather conditions are too dry to lift and to identify potential problems.

Grading, Packing, Storing, and Shipping

Boxes of seedlings that are not field-packed are brought into the packing shed where they are graded and counted. Graders visually rate each seedling according to predetermined grading standards (figure 14 C and D). Bundles of "shippable" seedlings are placed on a moving belt and "culls" are discarded onto the floor and destroyed. Seedlings grown especially for transplanting are also graded in this manner, and some nurseries use a multiple grading system: shippable seedlings, transplants, and culls. Grading standards often are specified by the customer, depending on the intended use. Usually, the nursery manager negotiates these standards with the customer when the seedling order is taken. Grading standards usually consist of a range of acceptable shoot heights, a minimum acceptable stem diameter (caliper), and the length and fibrosity of the root system. Each seedlot is processed separately during the grading process and each box is marked with the proper seed source code (figure 5B).

Shippable seedlings are placed in moisture-retaining boxes or bags. The root systems of southern species are dipped in a clay slurry that coats them and prevents desiccation. For northern species, sphagnum moss or cedar shavings ("shingle toe") is sometimes added to the storage container to keep roots moist. These storage containers are transported to a cooler where they are kept at temperatures near freezing to maintain dormancy and cold hardiness. Cold storage facilities keep the ambient temperature near freezing, but it is important to monitor the temperature inside the storage container. The type of storage depends on the cold tolerance of the species and the length of the storage period. Southern pines will not tolerate freezing and can be cold-stored at slightly above freezing for only 1 to 2 weeks. Cold storage is prescribed for northern species when the storage period is 3 months or less. If the storage period exceeds 3 months, seedlings need to be kept in frozen storage with temperatures kept slightly below freezing. Research has shown that frozen storage can maintain high seedling quality for more than 6 months and also retards the development of storage molds. Hardwood seedlings are cold-stored in open bins under very high humidity. Sometimes, when cold storage is not available, hardwoods are "heeled-in" in outside beds until they can be outplanted. Heeling-in is effective because dormant hardwoods have lost their leaves and therefore lose little moisture through transpiration.

The period between leaving the storage area to outplanting of seedlings is one of the most critical in the entire nursery and reforestation process. Seedlings are susceptible to many abuses; desiccation and warm temperatures are the most serious. Cold is the primary environmental factor that maintains seedling dormancy, and even fully dormant seedlings can begin to grow after relatively short exposures to warm temperatures. Ideally, seedlings will always be shipped and stored on the outplanting site in refrigerated vans. If seedlings must be shipped in non-refrigerated trucks, then they should be covered with white or reflective tarps to keep them cool and retard desiccation. An excellent guide to all aspects of seedling handling that pertains to all species—not just southern pines—is provided by Lantz (1989) in *A Guide to the Care and Planting of Southern Pine Seedlings*.

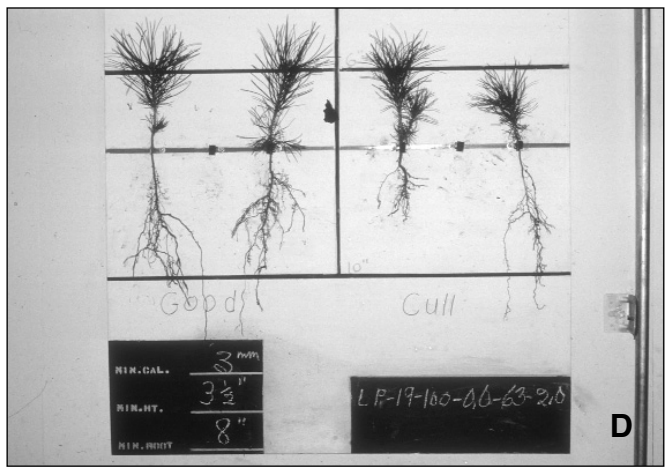
Container Nursery Cultural Practices

Container seedlings are grown in relatively small-capacity containers in special growth-promoting environments that can produce a shippable seedling in as little as 9 to 12 months (figure 2B). In the temperate zone, container crops are scheduled around the summer solstice, when solar energy and temperatures are at levels that promote rapid growth. Although many container nurseries typically grow just 1 crop per season, some can raise 2 or 3 crops by careful scheduling. The first crop is sown in late winter and grown in the greenhouse until outdoor conditions are mild enough to move seedlings outside. The second crop is sown just before the summer solstice so that the seedlings can still benefit from the intense sunlight of early summer and are left in the greenhouse through fall. In semitropical and tropical climates, container seedlings can be grown year-round and the growing schedule is primarily determined by moisture conditions on the outplanting site.

Propagation Environments

Several different types of growing environments are used to produce container seedlings. Fully controlled environments, such as the traditional greenhouse, are popular in colder climates and feature permanent sides and a full range of environmental control equipment. Semi-controlled environments, called shelterhouses, have sides that can be rolled up to promote better cross ventilation (figure 15A).

Figure 14—Chapter 7, Nursery Practices: harvesting equipment lifts bareroot seedlings by undercutting them and loosening soil from around the roots with vibration (**A**). During hand-lifting, workers pull seedlings from the seedbed and place them in tubs, being careful to avoid excessive exposure and desiccation (**B**). Seedlings are then taken to the packing shed where they are counted and graded (**C**) to predetermined morphological specifications that were agreed upon by the nursery manager and the customer: shoot height, stem diameter (caliper), and some measure of root size and fibrosity (**D**). Finally, the "shippable" seedlings are sealed into moisture-retentive bags or boxes for refrigerated storage (**E**).



Shelterhouses produce one crop per season, and the seedlings benefit from exposure to ambient conditions during the hardening phase. In milder climates, container seedlings can be grown in outdoor compounds (figure 15B). The type of growing environment will determine which cultural options are available and the resultant seedling growth rate. To reach the genetic potential of the crop, greenhouses and shelterhouses supply heating, ventilation, photoperiodic lighting, irrigation, fertilization, and even supplemental carbon dioxide. In open compounds, the ground is covered with weed barrier cloth and gravel to control weed growth, and the seedlings are raised on tables. Although temperatures cannot be controlled, the crop has the benefit of irrigation, fertilization, and sometimes even photoperiodic lighting.

Figure 15—Chapter 7, Nursery Practices: container seedlings are grown in a variety of propagation environments ranging from traditional greenhouses, to shelterhouses (**A**), and open growing compounds (**B**).

Types of Containers

There are many different types of containers, with capacities ranging from as small as 16 cm^3 (1 in^3) to more than 492 cm^3 (30 in^3). The most commonly used container types include Styrofoam® blocks, book planters, and several types made of molded hard plastic. Other growing containers, such as peat plugs and plastic bags, are sometimes used, but these lack vertical ribs on their insides for controlling root spiraling. The best type of container depends on available nursery equipment, the species of plant, and conditions at the outplanting site. Hardwood species must be grown in relatively larger containers than conifers because their large leaves intercept irrigation and create more shade competition with their neighbors. Foresters prefer seedlings grown in smaller containers for moist outplanting sites, but demand larger container stock for harsh dry conditions or sites with heavy brush competition. New container types are continually being developed. One of the newest innovations involves lining the container cavity with copper compounds that "chemically prune" the root system. Most containers can be used for more than 1 growing season and thus must be cleaned and sterilized between crops with hot water or chemical disinfectants.

Growing Media

Almost all container nurseries use some type of artificial growing medium instead of native soil. An ideal medium should be sterile, lightweight, porous, and consistent in quality. Several different brands of media are commercially available, and most are composed of sphagnum peat moss, vermiculite, and sometimes perlite, composted bark, or sawdust. Some nurseries mix their own growing media. Larger nurseries have specially designed mixers for blending the components, and some have customized equipment using cement mixers and so forth. Some components of growing media, such as vermiculite and perlite, are inherently sterile; sphagnum moss, however, may contain pathogenic fungi. Chemical fumigants or steam heat are typically used to sterilize media. Fertilizers or other chemical amendments are sometimes added to growing media during the mixing process. Dolomitic limestone is used to supply calcium and magnesium and raise the low pH. Slow-release fertilizers, such as Osmocote®, are composed of resin-coated pellets that release mineral nutrients in response to temperature and moisture.

Containers are filled with growing medium in several different ways. Smaller nurseries fill containers by hand. Automated filling machines that do everything from filling and tamping the medium to sowing and covering the seeds can also be used. A complete discussion of container types and growing media can be found in Landis and others (1990).

Sowing and Thinning

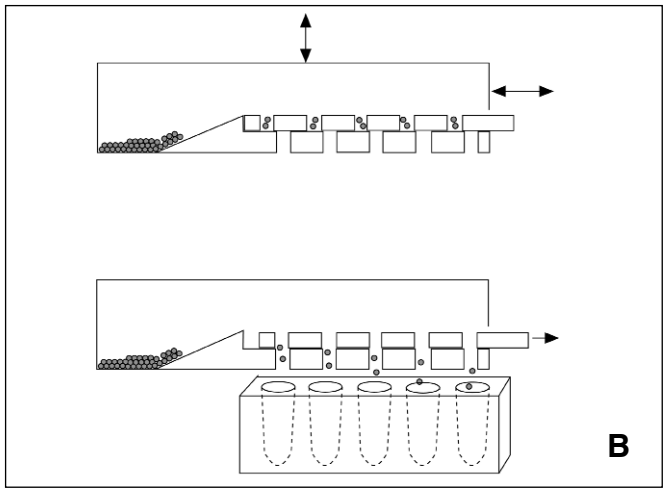
The number of seeds to sow per container cavity is calculated using the seed germination percentage, with the objective of having no empty cavities. Containers can be sown by hand, which is necessary for very large or irregularly shaped seeds, or with various sowing machines. The shutterbox (figure 16A) consists of a template with a set of predrilled holes that correspond to the pattern of the individual container cavities. The size of the holes in the shutter control the sowing rate, usually from 2 to 6 seeds per hole depending on seed quality (figure 16B). Vacuum seeders have plates or drums that hold a certain number of seeds until they are released into the containers. Precision sowing machines can accurately control the sowing density down to

1 seed per cavity. Although expensive, this equipment saves valuable seeds and eliminates the need for thinning.

The final stage in the sowing process consists of covering the sown seeds with some type of mulch such as perlite, grit, or coarse vermiculite. Light-colored mulches are preferred because they reflect sunlight and thus do not heat up as much as darker materials. Seed mulches restrict the growth of algae, mosses, and liverworts and also prevent weeds from becoming established. The depth of seed covering is very critical—if it is too deep, the seeds will not germinate; if it is too shallow, the seeds will dry out. The recommended depth is 2 to 3 times the width of the seeds.

Sown containers are moved into the growing area where they are placed on specially designed pallets or benches that promote air-pruning of the root system. Some benches are constructed on rollers so that they can be moved together when access is not required. This feature is popular because it saves valuable growing space. As in bareroot nurseries, the identification of each seedlot and its location is carefully monitored during the nursery process.

Figure 16—Chapter 7, Nursery Practices: shutterbox seeders are custom-made for each type of container (**A**). Sowing consists of filling the precisely spaced holes in the shutter with seeds (**B, top**) and then moving it laterally to allow the seeds to drop into the containers (**B, bottom**).



After 3 to 4 weeks, when seed germination is complete, workers thin multiple germinants down to 1 per cavity and remove any weeds that may be present. Extra seedlings are either pulled or clipped, depending on their size. Larger seedlings must be clipped because pulling them may uproot the crop seedling. If the sowing calculations were inaccurate, some containers may be empty. Resowing is an option, but late-sown seedlings would rapidly be overtopped by their neighbors and usually remain stunted. Single-cell containers such as the Ray Leach® system can be consolidated to remove empty cavities, saving valuable growing space.

Irrigation and Fertilization

Water quality is the most critical site selection factor for container nurseries, but because these nurseries can use a well-drained, slightly acid growing medium, they are better able to manage marginal water quality than are bareroot nurseries.

Eliminating water stress is crucial to achieving good seedling growth, and container nurseries use either stationary overhead sprinklers or mobile boom irrigation systems. Stationary systems consist of sprinkler heads set in a regular pattern that distribute water in a circular pattern (figure 17A), whereas mobile systems have a horizontally mounted boom that moves back and forth to deliver a uniform amount of water to the crop (figure 17B). Determining when and how much to irrigate is particularly difficult in a container nursery because seedlings use up water quickly in the small containers and it is difficult to directly observe moisture conditions. The best irrigation monitoring technique is to weigh containers between irrigations, as the relative wetness of the growing medium can be correlated to container weight.

Most container nurseries fertilize through the irrigation system, a process sometimes called "fertigation." Liquid fertilizer solutions are injected into the irrigation lines in the headhouse and applied to the crop through nozzles. The ability to supply all 13 essential mineral nutrients allows seedlings to grow at an exponential rate, and nutrient injection systems can supply the proper nutrient concentration and ratio at exactly the right time.

Hardening

When container seedlings have reached their desired height, the nursery manager changes the growing environment to initiate hardening. The most critical environmental

Figure 17—Chapter 7, Nursery Practices: container seedlings are typically irrigated either with stationary sprinklers (**A**) or moving irrigation booms (**B**).

factors for inducing hardiness and dormancy are cooler temperatures, mild moisture and nutrient stress, and shortened photoperiod. Seedlings in fully enclosed greenhouses are often moved to a shadehouse at this time, where the change in temperature and humidity aid the hardening process. Growers with shelterhouses permanently raise the sides to expose the crop to ambient conditions. At the same time, the photoperiod lights are shut off and the fertilizer mix changed to a special low-nitrogen hardening formula.

Harvesting, Grading, Storing, and Shipping

The harvesting method is related to the type of seedling storage. Some nurseries store their container seedlings outside to overwinter in sheltered storage, being particularly careful to insulate the root systems against cold. Seedling roots are much less cold-tolerant than shoots and can be damaged or even killed at temperatures that are only a few degrees below freezing. Other nurseries grade their seedlings and ship them directly to the outplanting site in the growth container. This procedure is necessary where freezer storage facilities are not available, but the seedlings still must be protected and maintained at the outplanting site.

Refrigerated storage is becoming increasingly popular. Like bareroot seedlings, container stock is usually harvested during the dormant period unless conditions on the outplanting site require otherwise. Cold hardiness tests can be used to determine when seedlings are ready for harvesting. Research has shown that these tests are a good indication of overall hardiness and dormancy. Nurseries pull seedlings from the growth container and wrap or bag them in bundles (figure 18A). The bundles are placed in moisture-proof boxes and stored under refrigeration (figure 18B). Container seedlings of cold-tolerant species can also be freezer-stored and treated essentially the same as bareroot stock. Container stock should be shipped to the outplanting site in refrigerated vans whenever possible and always kept out of direct sunlight and protected from drying winds.

Pest Management

The objective in both bareroot and container nurseries is to optimize the potentially limiting factors that control seedling growth to create the perfect propagation environment. Like all things in life, however, there is a trade-off. In this case, there is an increased risk of pests and abiotic stresses—increased succulence means greater risk of abiotic injury (frost injury is a prime example). The perfect propagation environment is also, unfortunately, a perfect breeding ground for many fungi, insects, and other pests.

A disease occurs anytime a seedling is not completely healthy. Both biotic pests and abiotic stresses can cause disease. Typical nursery pests include fungi, insects, and even weeds or moss, which compete with the seedling for light, nutrients, and water. Abiotic stresses include temperatures that are too high or too low and moisture and nutrient stresses. Although most people would think that biotic pests cause the most injury in nurseries, that is not the case (figure 19). Abiotic diseases are actually more common, especially in bareroot nurseries and open growing compounds, where seedlings are subject to the vagaries of the weather.

All pest problems can be prevented much more easily than they can be cured, so nurseries should set up a regular monitoring program. Nursery workers should constantly be on the lookout for anything unusual and notify the manager immediately if they notice a potential problem. Careful monitoring can distinguish between biotic and abiotic diseases (table 3) and make control much more effective. There

Figure 18—Chapter 7, Nursery Practices: many container seedlings are harvested by pulling them from the containers (**A**), wrapping them in plastic film or placing them in bags, and then storing them under refrigeration (**B**).

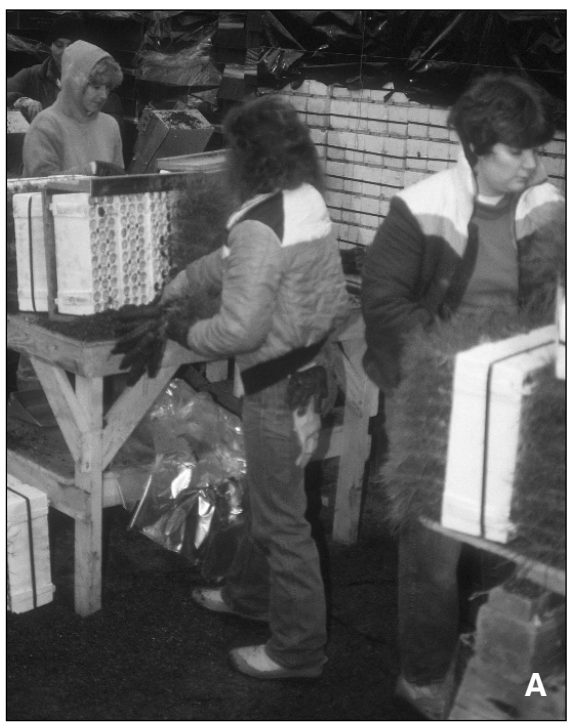
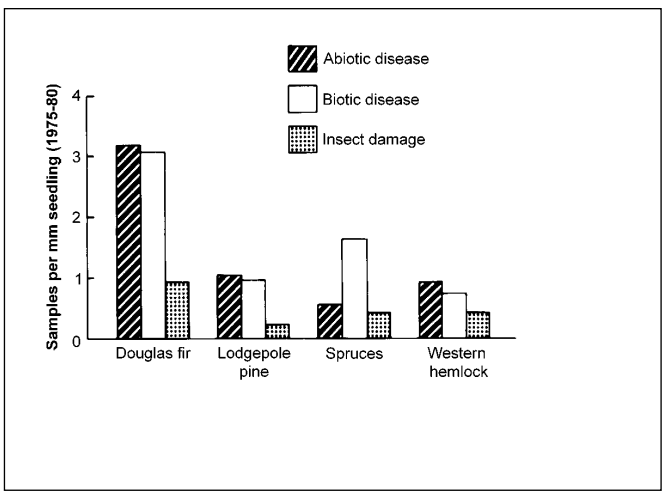


Figure 19—Chapter 7, Nursery Practices: abiotic diseases are usually more common than damage from biotic pests in forest and conservation nurseries (modified from Sutherland and others 1982).



are a couple of good references that can help improve diagnostic skills. For bareroot seedlings, readers are referred to *Forest Nursery Pests* (Cordell and others 1989), and for container seedlings, to volume five of the *Container Tree Nursery Manual* (Landis and others 1989).

Once a pest has been confirmed and the population has exceeded the allowable limit, growers should take immediate action. All controls should be part of an integrated pest management (IPM) program that uses cultural as well as chemical controls. Many pest problems, such as *Botrytis* blight, can be almost completely controlled using proper irrigation and sanitation measures. Fungicides and insecticides are often needed however, especially when a problem has gotten out of hand. Pesticides are usually injected through the irrigation system in container nurseries or with tractor-drawn sprayers in bareroot beds. In recent years, some new biocontrol agents have proven useful in controlling insect pests, such as fungus gnats in greenhouses.

Weeds are a much more serious concern in bareroot nurseries, where they must be controlled either mechanically

Table 3—Chapter 7, Nursery Practices: careful observation of disease development can aid in diagnosis

Characteristics	Abiotic disease	Biotic disease
HOSTS	Often affects several species, or ages of seedlings	Usually restricted to one species or age class
SYMPTOMS		
Patterns	Regular: spatially related to some environmental factor	Random locations at first
Rate of development	Rapid & uniform	Relatively slow & uneven
Signs	No evidence of a pest	Pests or indirect evidence present
Spread	Related to one incident, with no secondary spread	May spread over time under favorable conditions

Source: modified from Sutherland and Van Eerden (1980).

and chemically. Hand-weeding and mechanical cultivation can keep weed populations low and are especially effective if done before weeds are allowed to go to seed. Most nurseries apply a pre-emergence selective herbicide immediately after sowing and then at intervals during the growing season. Another option is to apply non-selective contact herbicides directly to the weeds with wick applicators or shielded sprayers.

Beneficial Microorganisms

Mycorrhizae develop from a symbiotic relationship between a beneficial fungus and the roots of the host seedling. Although mycorrhizae have been a popular topic for many years, there seems to be a variety of opinions as to their value in forest and conservation nurseries. Some people believe that mycorrhizae are essential for both nursery culture and successful outplanting, whereas other nursery and reforestation specialists are more skeptical. Almost 50,000 research studies have been done on mycorrhizae, and most confirm the benefits of reducing root disease and increasing seedling tolerance to drought and other environmental extremes. Results of operational nursery and field trials have been more variable, however, depending on the species of mycorrhizal fungus used and soil fertility and types of indigenous fungi on the outplanting site.

Inoculation with mycorrhizal fungi can be worthwhile, but the timing of inoculation and species of fungus should be matched to nursery and outplanting objectives (table 4). In particular, the fungal species should be selected for either the nursery or the outplanting site. There is no "all-purpose" fungus that will perform well under all conditions. Most fungal species that are adapted to wildland conditions will not survive under the high moisture and high nutrient nursery environment and vice versa. However, some genera of fungi, including *Thelephora, Laccaria,* and *Rhizopogon*, have strains or ecotypes that are adapted to either nursery or forest soils.

The species of fungus, type of inoculum, and timing of the inoculation will vary with the objectives of the treatment (table 4). Inoculants that are meant to prevent diseases or increase seedling growth in the nursery should be applied to seeds, incorporated into the soil or growing medium or applied as a spore suspension (figure 20). However, if the objective is to increase seedling survival and growth after outplanting, then a species of fungus adapted to the outplanting site should be applied late in the growing season or as a root dip during processing (table 4).

Therefore, when considering inoculation, it is extremely important to define objectives. Mycorrhizal fungi and other beneficial microorganisms can make a good seedling better but they shouldn't be expected to be a "cure-all" that will solve every nursery and outplanting problem.

Summary

Anyone considering propagating forestry and conservation species must be familiar with the unique characteristics of these plants. Unlike most other crops, seedlings from forest nurseries are typically outplanted on relatively harsh sites without subsequent care. This difference is significant because seedling quality is defined by environmental conditions on the outplanting site. There is no such thing as an "all-purpose" tree seedling. Bareroot and container seedlings have different applications, and the choice of approach depends on the available resources, the nursery climate, and the conditions on the outplanting site.

Table 4—Chapter 7, Nursery Practices: nurseries and seedling customers must consider their reasons for inoculating with mycorrhizal fungi because their objectives determine the species of fungus and the type and timing of inoculation

Type of mycorrhizal inoculation	Timing in the nursery crop cycle	Objectives of inoculation *	
		Nursery	Outplanting
Coating seeds with spores	Before sowing	1) Increased growth 2) Disease prevention	None
Incorporating mycelia into the growing medium	Before sowing	1) Increased growth 2) Disease prevention	None
Liquid drench with spores	Establishment or rapid growth phases	1) Increased growth 2) Disease prevention	None
Liquid drench with spores	Hardening phase	1) Disease prevention 2) Increased growth	1) Increased survival
Root dip with spores	During packing or before outplanting	None	1) Increased survival 2) Increased growth

* Regardless of the biological objectives, mycorrhizal inoculation may have marketing advantages.

Figure 20—Chapter 7, Nursery Practices: seedlings can be inoculated during the growing season with a liquid suspension of spores from a beneficial mycorrhizal fungus.

Forestry and conservations plants are typically propagated by seed, although vegetative propagation is used for some species. Direct seeding is by far the most common, although sowing germinants or transplanting is used for species that have complex germination requirements or other operational restrictions. Although specific practices differ for container and bareroot seedlings, a successful cultural regime must be designed to reflect the biological requirements of the species and the available resources of the nursery.

Seedlings must be properly handled and stored from the time they are harvested until they are outplanted. Exposure of the root system is particularly damaging to seedling quality. Because warm temperatures rapidly bring seedlings out of dormancy, refrigerated storage is recommended whenever possible. The time between removing the seedlings from the storage area and outplanting them is one of the most critical in the entire nursery and reforestation process. Seedlings are susceptible to many abuses, with desiccation from exposure to direct sun and overly warm temperatures the most serious. Seedling users need to understand that seedling quality only decreases after the seedlings leave the nursery and all mistakes and abuses are cumulative.

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Part II

Specific Handling Methods and
Data for 236 Genera

Pinaceae—Pine family

Abies P. Mill.

fir

D. George W. Edwards

Dr. Edwards retired from the Canadian Forest Service's Pacific Forestry Centre

Growth habit, occurrence, and use. The name *Abies* is derived from "abed," the Old World Latin name for the silver fir (Dallimore and Jackson 1967; Weber 1987). Theophrastus (371–286 BC) wrote of "silver firs" from Mt. Ida (today's Kaz Dag, Turkey) being used in shipbuilding, which may have been the lumber of *A. equi-trojani* (Thanos 2003b), but also may have been in reference to *A. cephalonica* Loud. and/or *A. pectinata* DC. (now *A. alba* P. Mill.) (Amigues 1993, cited in Thanos (2003b). The name *Abies* first appeared in Pliny the elder's *Historiae Naturalis* from about AD 77 (Liu 1971).

Firs are long-lived, on average achieving reproductive maturity at 20 years, with an average life-span of 60 years (Jacobs and others 1984). Fir trees in excess of 400 years old have been recorded in several species (Earle 1999), and noble firs 600 to 700 years old are known (Arno and Hammerly 1977; Franklin 1979; Franklin and Dyrness 1973), but such life spans are modest compared to those of other tree genera. Siberian fir (table 1) rarely, if ever, survives more than 200 years because the main stem decays out (Vidakovic 1991). In numbers of species, fir is second only to pine but lags behind spruce (*Picea* spp.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in terms of overall importance (Franklin 1982a).

All fir species are indigenous to the Northern Hemisphere (table 1), being widely distributed over the Eastern and Western Hemispheres (Liu 1971) chiefly in the temperate and frigid regions, from sea level to altitudes of 4,700 m. More than 70 species have been variously described (Liu 1971), although the number of those currently recognized is between 39 (Liu 1971) or 40 (Vidakovic 1991), 46 (Farjon 1990), ~50 (Welch 1991), and 55 (Rushforth 1987), depending on placements into varietal categories. Firs are found in 4 extensive regions (Franklin 1974b; Liu 1971; Miller and Knowles 1989; Welch 1991; Young and Young 1992):

- North America (Alaska to the Mexican border)—9 species
- Central America (Mexico, Guatemala, Honduras, and El Salvador)—8 species (Martinez 1948) or 6 species (Liu 1971)
- Mediterranean Basin, as well as lands bordering it, including southern and central Europe to the north, western Asia (Asia Minor, Caucasia, Syria, and Lebanon) to the east, and northwestern Africa (Morocco, Algeria, and Tunisia) to the south—8 species
- Siberia and eastern Asia (Amur, China, Korea, Japan, Taiwan, and the Himalayas)—17 species

The latitudinal range stretches some 53 degrees, from north of the Arctic Circle (north of 67°N, almost to Arkhangel'sk, Russia, on the White Sea) with Siberian fir (Liu 1971), to south of the Tropic of Cancer (south of 15°N, in El Salvador) with Guatemalan fir (FAO, in Anon. 1986). Fir has a long history in Mexico, with pollen from the middle Pleistocene Epoch (5 million years ago) (Graham 1999). The most widely distributed species is Siberian fir, then balsam fir, followed by subalpine fir (Liu 1971). Globally, some species—including Algerian fir (FAO, in Anon. 1986), bristlecone fir (Legg 1953; Little 1975; Talley 1974), Bulgarian fir (see table 1 footnotes for scientific name), Grecian fir, Spanish fir, (FAO, in Anon. 1969), Sicilian fir (Arena 1959a&b, 1960; FAO, in Anon. 1986); Gramuglio 1962; Köstler 1957) and Guatemalan fir (Anon. 1986; Donahue and others 1985; FAO, in Anon. 1986; Salazar 1991; Veblen 1978)—have restricted ranges or are rare and, in some ecosystems, endangered and threatened with extinction. No longer found on the island of Corsica, "silver fir" was described by Theophrastus (Thanos 2003b) as growing taller and better there than anywhere else in central and southern Italy. In 1986, 21 wild trees of Sicilian fir, a species that was considered extinct in 1900, were reported growing at Monte Scalone, Sicily; other plants grown from

Table 1—*Abies*, fir: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***A. alba* P. Mill.** *A. argentea* DC.; *A. candicans* Fisch. *A. nobilis* A. Dietr.; *A. Pardei* Gauss *A. pectinata* DC.; *A. picea* Lindl. *A. taxifolia* Desfont.; *A. vulgaris* Poir.	**European silver fir,** common silver fir, silver fir, Swiss pine	Mtns of central & S Europe, S to Corsica (~52°–38°N & ~3°W– 27°E)
***A. amabilis* (Dougl. ex Loud.) Dougl. ex Forbes** *A. grandis* A. Murr. *A. grandis* var. *densiflora* Engelm.	**Pacific silver fir,** lovely fir, amabilis fir, Cascades fir, white fir, silver fir, *sapin gracieux*	SE Alaska, coastal British Columbia, Coastal & Cascade Ranges of Oregon & Washington & rarely in Klamath Mtns of California (41°–56°50'N)
***A. balsamea* (L.) P. Mill.** *A. aromatica* Rafn. *A. balsamifera* Mich. *A. minor* Duham. ex Gord.	**balsam fir,** balsam, Canada balsam, eastern fir, balm of Gilead, blister fir, fir pine, silver pine	Labrador & Newfoundland & S to New York to central Wisconsin & Minnesota, N & W to Alberta (59°–38°50' N & 117°–53°W; generally S of 55°N, except in Alberta & Saskatchewan)
***A. bracteata* (D. Don) D. Don ex Poit.** *A. venusta* (Dougl.) K. Koch	**bristlecone fir,** Santa Lucia fir, silver fir, fringed spruce	Santa Lucia Mtns, Monterey Co., California (37°–36°N)
***A. cephalonica* Loudon** *A. panachaica* Heildr.; *A. lusombiana* Loudon *A. peloponesica* Haage	**Grecian fir,** Greek silver fir, Cephalonian fir, Mt. Enos fir	Higher mtns of continental Greece from Epirus & Thessaly S to Lagonia in Peloponnesos & SE to the Euboea; Turkey
***A. cilicica* (Antoine & Kotschy) Carrière** *A. selinusia* Carrière	**Cilician fir**	Turkey (Cilicia), N Syria, & Lebanon
***A. concolor* var. *concolor* (Gord. & Glend.) Lindl. ex Hildebr.** *A. lowiana* (Gord.) A. Murr. *A. grandis* var. *lowiana* (Gord.) Hoopes *A. concolor* var. *lowiana* (Gord.) Lemm.	**white fir,** white balsam, balsam fir, Rocky Mountain white fir, Colorado white fir, *piño real blanco,* concolor fir	Rocky Mtns from S Idaho & W Wyoming to S New Mexico W to N Baja California, Mexico, & S California N to central & NE Oregon (44°45'–30°N & 124°–105°W)
***A. concolor* var. *lowiana* (Gord. & Glend.) Lemmon** *A. lowiana* (Gord.) A. Murr. *A. concolor* (Gord. & Glend.) *A. concolor* var. *lasiocarpa* Engelm. & Sarg. *A. grandis* var. *lowiana* Mast.	**Sierra white fir,** Low white fir, Low silver fir, California white fir, Pacific white fir	Sierra Nevada of California & Nevada, Mt. Shasta, Siskiyou Mtns in SW Oregon, from about the divide between the headwaters of Umpqua & Rogue Rivers, Oregon, to mtns of Baja California Norte
***A. firma* Sieb. & Zucc.** *A. bifida* Sieb. & Zucc.; *A. momi* Sieb.	**Japanese fir,** *momi, momi* fir, Japanese silver fir	Mtns of central & S Honshu, Shikoku, & Kyushu, Japan (39°–30°N)
***A. fraseri* (Pursh) Poir.** ``*humilis* La Pilaye	**Fraser fir,** southern balsam fir, she-balsam, double fir balsam, double spruce, healing balsam	Appalachian Mtns of West Virginia, S Virginia, W North Carolina, & E Tennessee
***A. grandis* (Dougl. ex D. Don) Lindl.** *A. amabilis* A. Murr.; *A. excelsior* (Franco) *A. gordoniana* Carr. *A. lasiocarpa* Lindl. & Gord.	**grand fir,** lowland white fir, white fir, balsam fir, great silver fir, Oregon fir, western white fir, western balsam, *sapin grandissime, sapin du Vancouver*	W Montana & N Idaho to S British Columbia, Vancouver Island, S to Sonoma Co. in coastal California & E Oregon
***A. guatemalensis* Rehd.** *A. tacanensis* Lund. *A. guatemalensis* var. *tacanensis* (Lund.) Mart. *A. guatemalensis* var. *jaliscans* Mart.	**Guatemalan fir,** Guatemala fir, *paxaque, pinabete, romerillo*	Mtns of Guatemala, S Mexico, El Salvador; Honduras (19°30'–14°50'N & 104°–91°W)

Table 1—*Abies*, fir: nomenclature and occurrence (continued)

Scientific name & synonym(s)	Common name(s)	Occurrence
***A. holophylla* Maxim.**	**Manchurian fir,** needle fir, Sino-Korean fir	Khingan Mnts, & N part of Hebei* (N China Highlands), China; S. Sikhote Alin Mnts, Russia; Korean peninsula including Cheju Island (33°30'–49°N)
***A. homolepis* Sieb. & Zucc.** *A. brachyphylla* Maxim.	**Nikko fir,** *urajiro-momi, Dake-momi, Nikko-momi*	Mtns of central Honshu & Shikoku, Japan (37°–33°30'N)
***A. koreana* E.H. Wilson** *A. nephrolepis* Nakai	**Korean fir**	Confined to the volcanic island of Cheju & the Chiri-san Mtns, South Korea
***A. lasiocarpa* (Hook.) Nutt.** *A. bifolia* A. Murr.; *A. sub-alpina* Engelm. *A. sub-alpina* var. *fallax* Engelm.	**subalpine fir,** alpine fir, balsam fir, white fir, *piño real blanco de la sierras, sapin concolore*	W Northwest Territories, Yukon, & SE Alaska, S through British Columbia, SE Alberta to Oregon & in Rocky Mtns to Arizona & New Mexico; local in N California & NE Nevada (64°30'–32°25'N & 105°–145°W)
***A. lasiocarpa* var. *arizonica* (Merriam) Lemmon** *A. bifolia* (A. Murr.); *A. subalpina* Engelm.	**corkbark fir,** Rocky Mountain subalpine fir, Rocky Mountain alpine fir, alamo de la sierra, Arizona fir	SE Arizona E to S central New Mexico, & N to SW Colorado; reported locally in central Colorado
***A. magnifica* A. Murr.** *A. campylocarpa* A. Murr. *A. nobilis* var. *magnifica* Kell.	**California red fir**, red fir, golden fir, white fir, red bark fir, magnificent fir	Sierra Nevada, S Cascade Range, & N Coast Range in California & adjacent Nevada (43°35'–35°40'N
***A. mariesii* Mast.** *A. mayriana* Miyabe & Kudo	**Maries fir**, *Toddomatsu* fir, *Aomori-todo-matsu, O-shirabiso*	Mtns of N & central Honshu, Japan (41°–35°N)
***A. nebrodensis* (Lojac.) Mattei** *A. pectinata* Gilibert var. *nebrodensis* Lojac. *A. alba* Mill. var. *nebrodensis* (Lojac.) Svob.	**Sicilian fir,** *Abete delle Nebrodi*	Monte Cervo, Polizzo; Monti Nebrodi & Monte Scalane, Sicily
***A. nephrolepis* (Trautv. ex Maxim.) Maxim.** *A. sibirica* var. *nephrolepis* Trautv. *A. gracilis* Kom.	**Manchurian fir,** Khingan fir, Siberian white fir, Amur fir, Hinggan fir	E Siberia, through Lesser Khingan Mtns, Manchuria, W to Kansu of China & S to Chiri-san, South Korea (54°54'–35°30'N & 113°–140°30'E)
***A. nordmanniana* (Steven) Spach** *A. leioclada* (Stev.) Gord. *A. pectinata* var. *leioclada* (Stev. ex Endl.) Carr.	**Nordmann fir**, Caucasian fir, Crimean fir	W Caucasus & mtns connecting Caucasus with Armenian Highlands (44°–40°N & 46°–38°E)
***A. nordmanniana* ssp. *equi-trojani* (Asch. & Sint. ex Boiss.) Coode & Cullen** *A. bornmuelleriana Mattf.*	**Turkey fir**	Mt. Olympus, Bithynia (NW Turkey) to Paphlagonia (N Turkey), Asia Minor (~39°–42°N & 26°–38°W)
***A. numidica* de Lannoy ex Carrière** *A. pinsapo* var, *baborensis* Coss. *A. baborensis* Letourn.	**Algerian fir,** Algerian silver fir,	Kabylie Range, near summits of Mt Babor & Mt. Thabador, Kabylie. NE Algeria
***A. pindrow* (D. Don) Royle** *A. webbiana* Brandis	**west Himalayan fir,** west Himalayan silver fir, Pindrow fir	W Himalayas, India & Pakistan, N Afghanistan to Nepal & Tibet
***A. pinsapo* Boiss.** *A. hispanica* De Chamb.	**Spanish fir,** Spanish silver fir	Mtns of Malaga & Granada provinces, S Spain; Morocco (var. *marocana*)
***A. procera* Rehd.** *A. nobilis* (Dougl. ex D. Don) Lindl.	**noble fir**, red fir, white fir, noble red fir, feather cone fir, Oregon larch	Washington Cascade Range S through Cascade Range & high peaks of coast ranges to SW Oregon & NW California (48°30'–41°N)
***A. recurvata* Mast.** *A. ernestii* Rehd.; *A. beissberiana* Rehd. & Wilson	**Min fir**, *Min-kiang* fir	Mtns of Ming River Basin between Min-kiang & Sungpan Districts, Sichuan† Province; SW & C Kansu, NE Yunnan, China (~ 28°–39°N & 100°–106°E)

Table 1—*Abies*, fir: nomenclature and occurrence (continued)

Scientific name & synonym(s)	Common name(s)	Occurrence
***A. religiosa* (Kunth) Schltdl. & Cham.** *A. glaucascens* Roezl; *A. hirtella* Lindl. *A. lindleyana* Roezl	**sacred fir**, sacred Mexican silver fir, Mexican silver fir, *oyamel, pinabete*	Mtns of central & S Mexico, C. Michoacan to Veracruz & N & W Guatemala (~24°–15°N)
***A. sachalinensis* (Fr. Schm.) var. *sachalinensis* Mast.** *A. akatodo* Miyabe *A. veitchii* var. *sachalinensis* Fr. Schm.	**Sakhalin** [or Sachalin] **fir**, Japanese fir, *todo-matsu, akatodo*	Sakhalin & Kurile Islands, Kamchatka, Russia; Hokkaido, Japan (53°34'–41°30'N)
***A. sachalinesis* (Fr. Schm.) Mast. var. *mayriana* Miyabe & Kudo** *A. mayriana* Miyabe & Kudo	**Mayr Sakhalin fir**, *Ao-todomatsu, todomatsu, aotodo*	Hokkaido, Japan; Sakhalin & Kurile Islands of Russia (53°34'–41°30'N & from 10 m @ 45°N to 1650 m @ 44°N)
***A.* x *shastensis* (Lemmon) Lemmon** *A. shastensis* (Lemmon) Lemmon *A. nobilis* var. *robusta* Mast. *A. magnifica* var. *shastensis* Lemmon	**Shasta red fir**, Shasta fir, silvertip fir, golden fir, yellow-fruited fir	Oregon Cascade Range (~44°N), S through N Coast Ranges & S Cascade Range, California, & in S Sierra Nevada, California
***A. sibirica* Ledeb.** *A. hetrophylla* K. Koch; *A. pichta* Forbes *A. semenovii* Fedtsch	**Siberian fir**, Siberian silver fir, pitch silver fir	N & E Russia, Siberia to Kamchatka & Amur region, Alai Mtns & Turkestan; NE China (67°40'–42°15'N & 160°–40°E)
***A. squamata* Mast.**	**flaky fir,** *linpi lengshan*	High Mtns SW China, SE Xizang, W Sichuan, S Gansu & S Qinghay Provinces (26°–34°N & 98°30'–104°E)
***A. veitchii* Lindl.** *A. eichleri* Lauche; *A. sikokiana* Nakai	**Veitch fir**, Veitch silver fir, *shirabe, shirabiso,* Chinese silver fir	Mtns of Honshu & Shikoku, Japan (37°45'–34°N)

Sources: Anon. (1998), Dallimore and Jackson (1967), Donahue and others (1985), Earle (1999), Farjon and Rushforth (1989), Franklin (1974b), Liu (1971), Puri and Gupta (1968).
* Spelling of Chinese place names has changed over time. This name is given as Hopeh in Liu (1971) but is currently Hebei.
† Formerly spelled Szechuan or Szuchuan (Liu 1971).

Note: The following recognized fir species are not included in the table for lack of sufficient data (common names are given when known):

CENTRAL AMERICA: *A. colimensis* sp. nov. Rushf. & Nar.; *A. durangensis* Mart. (Durango fir); *A. flinckii* sp. nov. Rushf.; *A. hickelii* Flous et Gauss. (Hickel fir); *A. hidalgensis* sp. nov. Debr., Rácz & Guíz.; *A. neodurangensis* sp. nov. Debr., Rácz & Salaz.; *A. zapotekensis* sp. nov. Debr., Rácz & Ramír.; *A. vejarii* Mart. (Vejar fir).

EAST ASIA: *A. beshanzuensis* Wu (Baishan fir); *A. chengii* Rushf. (Cheng fir); *A. chensiensis* Van Tiegh. (Shensi fir); *A. delavayi* (Van Tiegh.) Franch. (Yunnan fir, or Delavay fir); *A. densa* Griff. (Sikkim fir); *A. fabri* (Mast.) Craib (Faber fir, sometimes also Yunnan fir); *A. fanjingshanensis* Huang, Tu et Fang (Fanjingshan fir); *A. fargesii* Franch. (Farges fir); *A. forrestii* Coltm.-Rog. (Forrest fir); *A. kawakamii* (Hay.) Ito (Taiwan fir); *A. spectabilis* (D. Don) Spach (east Himalayan fir or Webb fir); *A. yuanbaoshensis* Lu et Fu (Yuanbaoshan fir); *A. ziyuanensis* Fu et Mo (Ziyuan fir).

MEDITERRANEAN BASIN: *A.* x *borisii-regis* Mattf. (Bulgarian fir, sometimes Macedonian fir, or King Boris fir); *A. marocana* Trab. (Moroccan fir); *A. tazaotana* Cheval. (Tazaotan fir).

seeds or grafts have been established in various parts of Europe (FAO, in Anon. 1986). Bristlecone fir is found in sufficient numbers, and is distributed widely enough, that the potential for extinction remains low (Smith and Berg 1988), and research on genetics and population viability is underway (USDA FS 1992). The sacred fir, or *oyamel*, of Mexico is logged heavily. However, since 1975 has it become generally known that the bulk (the populations east of the Rocky Mountain crest) of North American monarch butterflies (*Danaus plexippus* L.) overwinter on the cool slopes of the transvolcanic ranges west of Mexico city forested with *oyamel* (Pyle 1992, 1999). Thus, the *oyamel*s may be preserved to protect the monarchs. The arboreal altitude record, 4,700 m, is held by flaky fir, with its distinctive reddish-brown bark that exfoliates in thin papery scales, found in the very dry regions of China near Tibet (Rushforth 1987).

Firs are easily distinguished from all other conifers by their disk-like leaf scars and erect, oblong-cylindrical, or cylindrical seed cones. These are borne in the uppermost regions of the crown and are essential to species identification (Farrar 1995). At maturity, the terminally winged seeds, ovuliferous scales, and bracts are shed (Dallimore and Jackson 1967; Farrar 1995), leaving the cone axis—the rachis—as a persistent, erect spike, a unique and distinctive feature of all firs (Hosie 1969). *Abies* is considered to be most closely related to the genus *Keteleéria;* species of this genus have upright, cylindrical cones that resemble those of firs, but *Keteleéria* cones do not disintegrate at maturity (Rehder 1958).

Nine fir species are native to North America; 7 introduced Asiatic and European species have become common in their use as ornamentals or Christmas trees (table 1) and others are being tested (Girardin 1997a). Table 1 is not a complete list of all fir species but covers only those firs for which widely accepted cone and seed information was available at the time of this revision. Brief descriptions, including cone and seed morphology, for nearly 2 dozen other firs found outside North America are available in a website maintained by Earle (1999). Older, still-valid descriptions of fir species with dates of introduction into North America (Rehder 1958) are used frequently by growers of exotic conifers, but readers should be aware that species nomenclature has changed in numerous cases. Information on 22 fir species recognized in China can be found in the *Flora of China* (Cheng and Fu 1987).

Firs play an important role in European forestry, although only European silver fir is distributed widely enough to be of more than local value (Handley 1982). Several North American firs, including white, grand, and noble firs have been planted in Europe but are only locally important (Handley 1982); subalpine fir is grown in Scandinavia (Dietrichson 1971), especially at high elevations in Norway (Hansen and Leivsson 1990). Introduction of the genus to New Zealand began in the mid-19th century; of some 30 fir species now grown there, white, grand, California red, Nordmann, Spanish, noble, and sacred firs have been suggested as "contingency" species, that is, alternatives to Monterey pine (*Pinus radiata* D. Don) (Miller and Knowles 1989).

It is in western North American that firs attain their greatest ecological and economic importance (Franklin 1982a). They are major vegetation components, especially in the boreal, Pacific Coast coniferous, and western montane/alpine coniferous forests. They are critical as cover for watersheds where heavy winter snowpack accumulates—this cover modifies snowmelt so that runoff continues throughout the spring and into summer (Franklin and others 1978; Laacke and Fiske 1983)—and the maintenance and regulation of high-quality streams (Hunt 1993). Firs provide cover, and their seeds and leaves are important as food for various birds, including northern spotted owl (*Strix occidentalis*) (Ripple and others 1991), osprey (*Pandion haliaetus*), and bald eagle (*Haliaeetus leucocephalu*s) (Hopkins 1979) and mammals including mule (*Odocoileus hemionus*) and white-tailed (*O. virginianus*) deer , elk (*Cervus elaphus*), and black (*Ursus americanu*s) and grizzly bears (*U. arctos*), moose (*Alces alces*), and mountain goat (*Oreamnos americanus*) (Agee 1982; Cooper and others 1987; Leach and Hiele 1956; Peek 1974; Steele and others 1981). Some of these animal species are sensitive, rare, or endangered (Laacke and Fiske 1983). Excellent sources of information on wildlife-cover values of fir forests are available (FEIS 1996).

Firs are found at all elevations, from sea level (grand fir on the Pacific Coast and balsam fir on the Atlantic Coast) to timberline (noble and subalpine firs); they attain their maximal development on relatively cool, moist sites (Franklin 1974b). Noble fir is one of the most windfirm trees (Earle 1999). The form, texture, and color of fir trees add to the high scenic values of their growing locations, many of which have become important recreation areas. Their attractive, highly symmetrical appearance make many species, particularly Fraser and Pacific silver firs, valuable in urban horticultural plantings, where their slow growth can be an advantage. Whereas the original *Woody-Plant Seed Manual* (USDA FS 1948) mentioned only 5 fir species used "to a very small extent" in reforestation in the United States,

9 species—Pacific silver, balsam, white, Fraser, grand, subalpine, red, Shasta red and noble firs—are now in regular use throughout their native ranges.

With 2 exceptions—Fraser fir, the remaining stands of which are extremely valuable for watershed protection as well as for their scenic beauty (Beck 1990), and the rare bristlecone fir—all North American firs have become commercially valuable as timber and/or pulp species. In general, fir wood is soft, odorless, and light in color and weight; it lacks resin ducts and usually kiln-dries without checking or collapse (but tends to warp). It is easily worked and finished to a good surface, and it takes paint and polish well (Dallimore and Jackson 1967). Although generally of low durability (Franklin 1982a) unless treated with preservative, fir wood can be used in projects that do not require high structural strength; balsam fir is used extensively for cabin logs. Noble fir wood (sometimes marketed as "Oregon larch") is the strongest (along with red fir) of fir woods and is more durable than that of most firs. The frames of Royal Air Force Mosquito fighter planes of World War II were build with noble fir (Pojar and MacKinnon 1994). Grand fir knots, steamed and carved, were made into fish hooks (Turner 1998). The many other products made in North America of fir wood include quality veneers, paneling, construction plywood, crates, container veneers, poles (after preservative treatment), moldings, window sash and door stock, Venetian blinds, ladder rails, and aircraft framing (because of its high strength-to-weight ratio) (Bakuzis and Hansen 1965; Frank 1990; Franklin 1974b, 1982a, 1990; Smith 1982). In the late 19th century, clear lumber of red fir was known as "butter wood" because, when made into boxes for cheese and butter, it did not influence their flavor (Young and Young 1992).

Japan, which imports large quantities of noble and Pacific silver firs for construction (Franklin 1982a), uses its indigenous Japanese fir for making boards, roof shingles, door plates, matches, wooden clogs, musical instruments, household utensils (furniture, packing boxes, and coffins), as well as using it in ship-building and cooperage (Liu 1971). The Yunnan and Faber firs (*A. delavayi* and *A. fabri*, see table 1 footnotes) are used for temple construction in the high mountains of Sichuan Province, China (Earle 1999). European silver fir is widely used throughout Europe also for construction, joinery, musical instruments, and (after preservative treatment) for poles. Guatemalan fir faces extinction in parts of its range (Donahue and others 1985; Salazar 1991) through overuse for building materials, roof shingles, interior paneling, weaving looms and "low-density" furniture, shipping crates, charcoal, firewood (Anon. 1998; Donahue and others 1985; Salazar 1991), and Christmas trees and boughs (FAO, in Anon. 1986). In Guatemala, sheep and other livestock destroy nearly all regeneration (Veblen 1978).

Fir pulp is used extensively for making printing papers and high-grade wrapping paper, with Pacific silver fir the mainstay in the Pacific Northwest and balsam fir in the northeastern United States. Red fir is preferred for sulfite and thermomechanical pulping (Laacke 1990b; Smith 1982). Wood residues not utilized elsewhere are considered to be an energy source (Smith 1982).

Fraser fir (in the East) and Pacific silver, white, red, and noble firs (in the West) are prized also for Christmas trees (Hopkins 1982; Laacke 1990a&b) and typically command high prices (Franklin 1974b; Young and Young 1992). The farm-gate value of Fraser fir Christmas trees cut in North Carolina in 1993 was 80 to 100 million dollars (Blazich and Hinesley 1994, 1995). Noble fir boughs account for some 75% of fir bough harvest in the Pacific Northwest (Douglass 1975; Murray and Crawford 1982), as well as in Denmark (Bang 1979 & Holstener-Jorgensen and Johansen 1975, both cited by Murray and Crawford 1982; Franklin 1982a). Guatemalan fir also provides yuletide greenery and Christmas trees in its native range (FAO, in Anon. 1986; Salazar 1991). The sacred fir, or *oyamel*, is so named because of its heavy use as greenery for celebrating religious events in Mexico. Throughout Europe, but particularly in Denmark, Nordmann fir is prized as an ornamental, for its decorative foliage, and for Christmas tree production (Gosling and others 1999; Poulsen 1996); seeds from sources from the northern Caucasus (Republic of Georgia) are preferred (Godwin 1997).

From bark resin blisters, oleoresin (known commercially as Canada balsam and Strasbourg turpentine) is obtained for varnishes, the mounting of light microscopy specimens and medicinal purposes (Dallimore and Jackson 1967; Frank 1990; Lanner 1983). After distillation to yield fine turpentine oil, the crude residue is sold as rosin (Liu 1971). The pitch and bark of subalpine fir were a very important source of medicines for native peoples of the interior of British Columbia (Pojar and MacKinnon 1994); the pitch also made an effective insect repellent (Turner 1998). The fragrant needles of balsam fir are stuffed into souvenir pillows sold in New England (Frank 1990). North American native peoples pulverized fir needles for use as a body scent (sometimes to mask their human scent to reduce the risk of being attacked by large predators) or as a perfume for clothing; used powdered fir needles (particularly those of subalpine fir) mixed with deer grease as a hair tonic and tint; sprinkled

finely ground needles on open cuts; boiled white fir needles to make a tea; and boiled bark resin to make an antiseptic for wounds or as a tea for colds (Hart 1976; Hopkins 1982; Pojar and MacKinnon 1994; Turner 1998). The Straits Salish of Vancouver Island made a brown dye for basketry of grand fir bark and a pink dye by combining it with red ochre (Turner 1998). Cone scales of east Himalayan fir (see table 1 footnote) have been used to make a purple dye (Rushforth 1987).

Most commercial "pine" scents are essential oils distilled from fir foliage (Hunt 1993); foliar loppings of European silver fir in Czechoslovakia yield 1,380 tonnes (13,612 tons) per year of essential oils (Cermak and Penka 1979). "Pine" aromatherapy and other perfumery oil is steam-distilled from Siberian fir foliage (Luebke 1994–2000). The essential and fatty oil contents of west Himalayan fir seeds are suitable also for commercial exploitation in India (Jain and others 1988). Oil chemistry of other fir seeds has been studied intensively (Carrillo and others 1994; Guo and others 1984; Hasegawa and others 1987; Iwai and Nishioka 1945; Kaneko and others 1985; Rutar and others 1989).

Geographic races. The genus *Abies* was established by Miller in 1754, but Spach, in 1842, made the first attempt at a generic classification (Farjon and Rushforth 1989). Taxonomically, it is a difficult genus (Liu 1971), with extensive genetic variation (Libby 1982) that is reflected in at least 14 formal classification attempts (and several other groupings of species) made in the past 160 to 175 years. Two earlier, more-notable monographic revisions of *Abies* (Franco 1950; Gaussen 1964) were superceded in the early 1970s by a more widely accepted classification (Liu 1971) using 2 subgenera. In this scheme, the subgenus *Pseudotorreya* has a single section for the species *A. bracteata*, while the subgenus *Abies* is divided into 14 sections, 3 of which contain continuously variable forms. Section Grandes contains the North American species *amabilis, concolor*, and *grandis*; section Nobiles contains *magnifica and procera;* and section Balsameae contains *balsamea, fraseri,* and *lasiocarpa*. However, this scheme has been criticized for its unrestrained use of geographical and ecological characters that grouped species merely because they occur together, producing artificial associations (Farjon and Rushforth 1989).

More recently, a new classification scheme based on the morphology of fruiting and vegetation that puts together species with similar ecological preferences from adjoining geographical regions has been proposed. This scheme divides the genus into 10 sections, 4 of which are further divided into a total of 9 subsections, including 3 new subsectional names (Farjon and Rushforth 1989); an historical review plus an evaluation of other attempts to classify firs are included. The new scheme is diagrammatically represented in table 2.

For North American firs, section Bracteata retains the single species *A. bracteata* as the type species, whereas section Amabilis includes *A. amabilis* as the type species. Section Balsameae, subsection *Laterales* (type *A. kawakamii),* includes *A. balsamea, A. bifolia,* and *A. lasiocarpa,* whereas subsection Medianae (type *A. sachalinensis*) includes *A. fraseri*. Section Grandes includes *A. grandis* (type) and *A. concolor*, as well as the Central American species *A. guatemalensis, A. durangensis,* and a new species *A. flinckii* (Rushforth 1989). Section Nobiles include*s A. procera* (type) and *A. magnifica*. Section Oiamel, which is divided into subsections Religiosae and Hickelianae, includes the other known Central American firs, including another new species *A. colimensis* (Rushforth 1989).

Note that this scheme places Fraser fir (*Abies fraseri)* in subsection Medianae and balsam fir *(A. balsamea*) in subsection Laterales; this separation is based on whether bract scales are exserted and the seed scales reniform (Medianae, Fraser fir), or bract scales are included and seed scales are cuneate-flabellate (Laterales, balsam fir) (Farjon and Rushforth 1989). Natural hybrids between these 2 species have been reported (see below) and bracts in balsam fir are not always completely "included" (hidden) (Lester 1968), so this separation does not appear to be justified.

Detailed taxonomy (as well as descriptions of cones, pollen, seeds, and seedlings) of 11 European fir species can be found in a recent monograph (Schutt 1991), whereas a more general text (Vidakovic 1991) includes 26 fir species. Other descriptions and drawings are available (Cope 1993; Rehder 1958; Rushforth 1983, 1984, 1986; Farjon 1990; Debreczy and Rácz 1995).

In North America, 2 sets of genetic complexes—grand and white firs, and noble and California red firs—create significant taxonomic confusion for students, foresters, and land-managers (Franklin 1982a). The geographic variation of the first set—grand fir and white fir (section Grandes, Farjon and Rushworth 1989; section Grandes, Liu 1971)—has been extensively studied. Although these 2 species are morphologically, ecologically, and chemically distinct, they are genetically plastic and intergrade and hybridize freely over a wide area (Daniels 1969; Foiles and others 1990; Hamrick 1966, cited by Franklin 1974b; Hamrick and Libby 1972; Klaehn and Winieski 1962; Laacke 1990a; Lacaze 1967; Steinhoff 1978). The variation can be continuous—

Table 2—*Abies*, fir: schematic of new infragenetic classification system

Section	Subsection	Species
Abies P. Mill.	—	***Abies alba*** (type) *A. cephalonica*, *A. cilicica*[1], *A. nebrodensis*, *A. nordmanniana* [2], *Abies x borisii-regis*
Piceaster Spach emended Farjon & Rushforth	—	***Abies pinsapo*** (type) [3] *A. numidica*
Bracteata Engelmann emended Sargent	—	***Abies bracteata*** (type)
Momi Franco emended Farjon & Rushforth (type: *Abies firma*)	***Homolepides*** (Franco) Farjon & Rushworth	***Abies homolepis*** (type) [4]
	Firmae (Franco) Farjon & Rushforth	*A. recurvata* (includes *A. recurvata* var. *ernestii*) ***Abies firma*** (type) ***A. beshanzuensis***
	Holophyllae Farjon & Rushforth	***Abies holophylla*** (type) *A. chensiensis* [5], *A. pindrow* [6], *A. ziyuanensis*
Amabilis (Matzenko) Farjon & Rushforth	—	***Abies amabilis*** (type) *A. mariesii*
Pseudopicea Hickel emended Farjon & Rushworth (type: *Abies spectabilis*)	***Delavayianae*** Farjon & Rushforth	***Abies delavayi*** (type) [7] *A. chengii*, *A. densa*, *A. fabri* [8], *A. fargesii* [9], *A. forestii* [10], *A. fanjingshanensis*, *A. spectablis*, *A. yuanbaoshanensis*
	Squamatae E. Murray	***Abies squamata*** (type)
Balsameae Engelmann emended Farjon & Rushforth (type: *Abies balsamea*)	***Laterales*** Patschke emended Farjon & Rushforth	***Abies kawakamii*** (type) *A. balsamea*, *A. bifolia*, *A. lasiocarpa*, *A. sibirica* (includes var. *semenovii*)
	Medianae Patschke emended Farjon & Rushforth	***Abies sachalinensis*** (type) (includes var. *mayriana* = *A. mayriana*) *A. fraseri*, *A. koreana*, *A. nephrolepis*, *A. veitchii* (includes var. *sikokiana*)
Grandes Engelmann emended Farjon & Rushforth	—	***Abies grandis*** (type) *A. concolor* (includes var. *concolor* & var. *lowiana*), *A. durangensis* [11], *A. flinckii* (= *guatemalensis* var. *jaliscans*), *A. guatemalensis*
Oiamel Franco (type: *Abies religiosa*)	***Religiosae*** (Matzenko) Farjon & Rushforth	***Abies religiosa*** (type) *A. colimensis*, *A. mexicana* [12], *A. vejarii*
	Hickelianae Farjon & Rushforth	***Abies hickelii*** (type) [13]
Nobiles Engelmann	—	***A. procera*** (type) *A. magnifica* (includes var. *shastensis*)

Source: (Farjon and Rushforth 1989).

1 Includes *A. cilicica* ssp. *isaurica*.
2 Includes *A. nordmanniana* ssp. *equi-trojani*.
3 Includes *A. pinsapo* var. *marocana*, and var. *tazaotana*.
4 Includes *A. homolepis* var. *umbellata*.
5 Includes *A. chensiensis* ssp. *salouenensis*, and ssp. *yulongxueshanensis*.
6 Includes *A. pindrow* var. *brevifolia* = *A. gamblei*.
7 Includes *A. delavayi* var. *nukiangensis*.
8 Includes *A. fabri* var. *minensis*.
9 Includes *A. fargesii* var. *sutchuensis*, and var. *faxoniana*.
10 Includes *A. forrestii* var. *georgi*.
11 Includes *A. durangensis* var. *coahuilensis*.
12 *A. mexicana* = *A. vejarii* var. *mexicana*.
13 Includes *A. hickelii* var. *oaxacana*.

hybrids between grand and white firs are intermediate in most characteristics—and white fir is usually referred to as "grandicolor" from northwestern California through central Oregon. However, regional races have evolved (Daniels (1969) and the major geographical units have been summarized (Franklin 1974b) as follows:

Species	Geographical location
A. grandis	Coastal lowlands of southern British Columbia, Washington, Oregon, and California, including lower elevations on the western slopes of the Cascade Range
A. grandis	Eastern slopes and higher elevations in the Cascade Range north of about 44° to 45°N latitude
A. grandis	Northern Idaho and interior of southern British Columbia
Intergrade	Klamath Mountains and Cascade Range of southwestern Oregon and northern California
Intergrade	Blue, Ochoco, and Wallowa Mountains of northeastern Oregon, west central Idaho
*A. concolor**	Sierra Nevada, California
A. concolor	Southern Rocky Mountains and southern California

*Now recognized as Sierra white fir (table 1).

No varieties of grand fir have been established, but 2 forms—the green coastal and the gray interior (Foiles and others 1990), reduced from the 5 climatic forms (Muller 1935, 1936, cited by Franklin 1974b)—are usually recognized. White fir is a highly variable species, the variation being significantly correlated with latitude of seed source for most morphological and growth characteristics (Hamrick and Libby 1972). At least 4 major morphological divisions—(a) central Oregon and northwestern California, (b) south-central Oregon and central and northeastern California, (c) southern California and Arizona, and (d) eastern Nevada and western Utah—have been designated (Hamrick and Libby 1972).

White and grand firs, as well as red and noble firs, are chemically distinguishable by their seedcoat terpenoids (von Rudloff 1976; Zavarin and others 1978, 1979), a method useful for identifying seed provenances (Zavarin and others 1979). Other chemo-systematic comparisons of leaf- and twig-oil terpenes have expanded the knowledge of geographic variation of Pacific silver, balsam, grand, and subalpine firs (Hunt and von Rudloff 1974; von Rudloff 1976; von Rudloff and Hunt 1977), and Greek (or Grecian) fir (Koedam 1981; Mitsopoulos and Panetsos 1987).

Noble, California red, and Shasta red firs form the second important interfertile complex of species (Franklin and others 1978; Sorensen and others 1990). Noble and California red firs readily produce hybrids (Barbour 1988; Little 1979) with seed and seedling characteristics similar to Shasta red fir where the ranges overlap (Franklin and others 1978; Sawyer and Thornburgh 1977; Silen and others 1965; Sorensen and others 1990). Populations in southern Oregon and northwestern California may represent hybrid swarms between the 2 species (Franklin and others 1978). Phenotypically, trees in southern Oregon to northwestern California often resemble noble fir but behave ecologically as Shasta red fir (Løfting 1966 and 1967, cited by Franklin 1974b). A latitudinal gradient in the Cascade Range, with a major discontinuity around 44°N, has been discerned (Franklin and Greathouse 1968a). The 2 species can be artificially cross-pollinated without difficulty as long as red fir is the female (ovuliferous) parent (Zavarin and others 1978). Noble fir exhibits high self-fertility that does not appear to affect germination but which can depress height growth (Sorensen and others 1976). Although no races of noble fir are known within its natural range, population differentiation and variation is reported (Maze and Parker 1983). Three horticultural varieties—cv. *glauca,* cv. *prostrata,* and cv. *robustifolia*—are recognized (Franklin 1990). When noble, Sakhalin, Maries, Japanese, and Grecian firs were used as female parents, height, dbh, and crown area were greater in the interspecific crosses than in intraspecific crosses (Mergen and Gregoire 1988).

Of all the interspecific crosses, progeny of Maries fir (as the female parent) showed the greatest growth; this species also had the least, whereas Sakhalin fir had the greatest, inbreeding depression (Mergen and Gregoire 1988). Effects of these crosses on seed and seedling characteristics were reported earlier (Mergen and others 1965). Geographic similarity (especially among Japanese, Korean, Maries, and Sakhalin firs) was suggested as a positive influence on hybrid survival and performance (Mergen and Gregoire 1988). Earlier, it had been suggested that a geographical, rather than genetic or physiological, separation occurred as the genus *Abies* evolved (Klaehn and Winieski 1962). Possible causes for incompatibility and results from other European inter- and intraspecific crossing experiments are reported (Kantor and Chira, 1965, 1971, 1972). However, many of the reported artificial crosses between noble fir and other true firs including balsam, white, subalpine, Min (or Min-kiang), and Sakhalin firs have not been repeated, and

their validity is questionable (Franklin 1990). Unsuccessful attempts to hybridize white and grand firs with European silver, Algerian, Nordmann, and Grecian firs indicate strong reproductive isolation between the North American representatives of the genus and their European counterparts (Kormutak 1997).

Pacific silver fir has an extensive range, occupying many soil types, and it can exist in areas of deep snow and minimal summer droughts (Packee and others 1982). Yet it is not a highly variable species, and no artificial hybrids with any other species have been described, although there is a cultivated dwarf form, Pacific silver fir var. *compacta* (Crawford and Oliver 1990). Despite this apparent lack of variation, strong family differences in germination responses among populations of Pacific silver fir on Vancouver Island, with important implications for maintaining genetic diversity in nursery seedling crops, have been reported (Davidson 1993; Davidson and others 1996).

For balsam fir, the most widely distributed fir in North America, apparently-continuous variation along altitudinal and geographic gradients has been reported (Lester1968; Myers and Bormann 1963) in which the putative variety *phanerolepis* (bracted balsam fir) is most important (Myers and Bormann 1963), but var. *fraseri* and var. *balsamea* have also been recognized (Frank 1990). The variety *phanerolepis* is most common in maritime Canada, the St. Lawrence Valley, and at higher elevations in mountains of the northeastern United States (Fernald 1909; Myers and Bormann 1963), although its taxonomic validity has been questioned (Myers and Bormann 1963). Natural hybrids have been discerned between balsam and Fraser firs (Myers and Bormann 1963; Robinson and Thor 1969), 2 closely related relics of an ancestral taxon (Robinson and Thor 1969; Jacobs and Werth 1984) that may have exhibited north–south clinal variation, although balsam fir var. *phanerolepis* is unlikely to be of hybrid origin (Robinson and Thor 1969; Jacobs and Werth 1984). Balsam fir var. *phanerolepis* and Fraser fir have been shown to be closely related and recently segregated taxa, with balsam fir var. *phanerolepis* being more closely related to balsam than to Fraser fir (Clarkson and Fairbrothers 1970). Using viable seed production as the criterion, balsam × Fraser fir and reciprocals, Fraser × bracted balsam fir and reciprocals, and bracted balsam × subalpine fir were found to be fully crossable (Hawley and Dehayes 1985a). This suggests that geographical rather than genetic isolation is likely more responsible for the taxonomic variation in these 2 firs (Hawley and Dehayes 1985a). After growing for 7 months indoors, hybrids from all these combinations were verifiable, with the hybrid seedlings not being characteristically intermediate between parents, but mostly resembling—but still distinguishable from—the paternal parent (Hawley and Dehayes 1985b). Interspecific crosses between balsam fir (as the maternal parent) and 10 other fir species (as paternal parents) have been claimed (Chiasson 1967), even though subsequent germination was very poor. A cultivar of balsam × Fraser fir (Fraser fir var. *prostrata*) is a dwarf shrub with horizontally spreading branches that is used ornamentally (Beck 1990).

Subalpine fir, the second most widely distributed fir in North America (covering 32 degrees of latitude), exhibits considerable variation, so much so that an (unsuccessful) proposal was made to reclassify it as a subspecies of balsam fir (Boivin 1959). In the West, subalpine fir was previously recognized as a separate, single species possessing 2 varieties, var. *arizonica*, the corkbark fir found only at the southern end of the range, and var. *lasiocarpa,* the typical subalpine fir, the remaining non-corky-barked trees (Fowells 1965; Little 1953). Differences in morphology, foliar volatile oils, and other factors have been cited as reasons for returning to the original designations of alpine fir as 2 species—that is, the subalpine fir (*A. lasiocarpa* Hooker) growing in the Cascade Range and the Rocky Mountain fir (*A. lasiocarpa* var. *arizonica*), growing in higher elevations in the interor—which are believed to have hybridized extensively (Hunt and von Rudloff 1979, 1983). It has been suggested (Hunt and von Rudloff 1979) that at the southernmost end of its range, coastal subalpine fir possibly hybridizes with noble fir, but no evidence for this has been reported.

Currently, corkbark fir is included under Rocky Mountain fir; corkbark fir seeds are about 70% larger than subalpine fir seeds (Fowells 1965). In central Alberta, on its eastern boundary where the range of Rocky Mountain fir meets and overlaps with that of balsam fir (Fowells, 1965, Hosie 1969), some studies obtained evidence of hybridization (Moss 1955; Roller 1967), whereas others suggested Rocky Mountain fir is a variety of balsam fir (Bakuzis and Hansen 1965). The controversy over the subalpine fir–Rocky Mountain fir–balsam fir complex (Hunt and von Rudloff 1979, 1983; Parker and Maze 1984; Parker and others 1981) continues.

The only unique populations of coastal subalpine fir are found in Alaska, at lower elevations, and appear to be isolated with no reported introgression between them and coastal mainland populations (Harris 1965; Heusser 1954). The Prince of Wales Island population has distinctive terpene patterns, but it is not known how, or if, these differ from those of neighboring populations (Hunt 1993). Three horti-

cultural and ornamental varieties of subalpine fir have been recognized—subalpine fir cv. *beissneri* (a dwarf tree with distorted branches and twisted needles), subalpine fir cv. *coerulescens* (with intensively blueish needles), and subalpine fir cv. *compacta* (a dwarf tree of compact habit) (Alexander and others 1990). Other fir varieties are described by Welch (1991).

Based on the mean yield of germinable seeds per cone as the crossability criterion in a study of 6 firs native to California (not including noble fir), plus 4 Eurasian and 2 Mexican firs, the long-held view that western true firs hybridize freely was challenged by Critchfield (1988). The only truly successful cross was white × sacred fir (from Mexico), species from 2 different taxonomic sections (independent of the classification scheme). Seedlings from white × grand fir were easily identified as hybrids, but crosses with Eurasian firs were uniformly unsuccessful. Nevertheless, the white × sacred fir cross, like several other successful crosses mentioned above, suggests that taxonomic sections in firs are not separated by reproductive barriers (as in *Pinus*), and that fir classifications should be reconsidered (St.-Clair and Critchfield 1988).

European experiences have been similar. In Germany, combinations of Veitch × European silver fir, white × Nordmann fir, white × grand fir, and white × noble fir showed marked hybrid vigor (heterosis effect) that was obtained almost always when white fir was a parent. Hybrids with long, green needles had the greatest growth vigor, needle color being a criterion of growth vigor even in seedlings (Rohmeder 1960a; Rohmeder and Eisenhut 1961; Rohmeder and Schönbach 1959). Seedlings from white × grand fir, Grecian × Nordmann fir, and Spanish × European silver fir crosses outgrew the offspring of the maternal species after 1 year (Kormutak 1991). Several of these crosses are between species from different taxonomic sections, providing support for the absence of reproductive barriers and/or the need to reconsider taxonomic sections (mentioned earlier). As in noble fir in North America, relative self-fertility of European silver fir in Germany is very high (0.72) (Moulalis 1986). Successful controlled crossings, unsuccessful controlled crossings, natural hybrids, intermediate populations, putative spontaneous hybrids, and putative controlled hybrids in firs have been summarized by Vidakovic (1991). The genetics and breeding of European silver fir have been thoroughly reviewed by Korpel and others (1982) and genetic variation in this species was further reported on by Bergmann and Kownatzki (1987). Since the 1980s, studies on fir genetics have gained momentum in Central America (Furnier and other 1996; Aguirre-Planter and others 2000), Europe (Fady and Conkle 1992, 1993; Fady and others 1991, 1992; Giannini and others 1994; Kormutak and others 1982, 1993; Mitsopoulos and Panetsos 1987; Parducci and others 1993, 1996, 1999, 2000; Parducci and Szmidt 1997, 1998, 1999) and Asia (Kawamuro and others 1995; Suyama and others 1992, 1996, 1997; Tsumura and others 1994; Tsumura and Suyama 1998). All of the reports cited here and throughout this chapter refer to other studies that are too numerous to include.

Elsewhere, Turkey fir (*A. bornmuelleriana*); the possible Grecian × Turkey fir hybrid (*A. equi-trojani*) (Liu 1971); and Nordmann fir are so variable in Turkey that *A. bornmuelleriana* and *A. equi-trojani* should be regarded as only races or ecotypes of *A. nordmanniana* (Arbez 1969a&b). Nordmann and Turkey fir can be distinguished in the nursery based on needle and bud characteristics (Arbez 1967). Bulgarian fir is recognized as one of several spontaneous hybrids (European silver × Grecian fir), as is Cilician fir (Grecian × European silver fir) (Korpel and others 1982). A monograph on Grecian fir is available (Panetsos 1975). Two varieties of European silver fir, var. *chlorocarpa* and var. *erythrocarpa*, are recognized in Bulgaria (Doikov 1973). Populations of Siberian fir in the former USSR have been differentiated on the basis of cone scale morphology (Vetrova 1992). Four species—west Himalayan fir, east Himalayan fir, Sikkim fir (often included with east Himalayan fir but quite distinct [Farjon 1990]), and Yunnan fir—are common in the Himalayas. A fifth—Faber fir, a Chinese species discovered in northeast Myanmar (Burma) on the Burma—Yunnan border, possibly a form of Yunnan fir—is not so common (Puri and Gupta 1968). Faber and Yunnan firs are closely related and were previously regarded as different forms of the same species (Dallimore and Jackson 1967) or as synonyms for the same species (Liu 1971). However, they have currently been given separate-species status (Farjon and Rushforth 1989). Other species have been described, such as Webb fir, which may be the western, high-altitude form of Sikkim fir, adding to the confusion (Puri and Gupta 1968). The high-altitude east Himalayan fir and the low-altitude west Himalayan fir are known to hybridize freely, forming intermediate populations with introgression at middle altitudes (Jain 1976).

Fir taxonomy in Mexico also is confused. Although *A. hickelii* has been suggested to be a synonym for *A. guatemalensis* (Dvorak 1997), others (Farjon and Rushforth 1989; Farjon 1990) classify it as a distinct species. Three more new species from western Mexico have been described (Debreczy and Rácz 1995). Levels and patterns of genetic variation in the firs of southern Mexico and

Guatemala have been reported (Aguirre-Planter and others 2000).

Because taxonomy remains confused in several instances, and because hybridization is probable, until the patterns of variation are better understood, the use of fir seed sources local to the reforestation site is the best practice. However, the specific or varietal name applied to the local population should not be relied on (Franklin 1974b). Geographic source has long been known to affect cone and seed characters in many fir species. Numerous studies have reported—sometimes contradictorily—that cone dimensions and (to a lesser extent) seed weight, germination, and seedling yields (as well as mineral contents in some species) may be under strong genetic control and related to provenance (Gambi and Stradajoli 1971; Giannini and Marinelli 1977; Gvozdikov 1980; Kociova 1974a&b; Laffers 1979; Singh and Singh 1981; Singh and others 1991; Ujiie and others 1991). For seeds of noble and Shasta red firs, the strong latitudinal gradients (or clines) in cotyledon number and in seed weight were considered promising indices of seed source/provenance (Franklin and Greathouse 1968b). Provenance selection is a key issue in Christmas tree production of noble, grand and Shasta red firs (Hupp 1984).

Isozyme analysis has effectively identified provenances of European silver fir (Konnert 1991) and has been used to study geographic variation of firs in Europe and to make comparisons with North American fir species (Konnert 1991; Kormutak 1988; Moller 1986; Schroeder 1989a,b&c). Thus, it was concluded that although European silver fir survived the last glaciation in 5 refugia, the species migrated to its present range from only 3 of them (Konnert and Bergmann 1995). By use of enzyme systems, Pascual and others (1993) showed that there is genetic divergence between Spanish and Moroccan populations of Spanish fir and that several true varieties of this species may exist. Enzyme linkages in balsam fir similar to those in other conifers might be used for taxonomic purposes (Neale and Adams 1981). A mating system study in balsam fir was described by Neale and Adams (1982). An isozyme study of Fraser fir on Mt. Rogers in Virginia revealed little or no population differentiation (Diebel and Feret 1991). Isozyme markers have revealed low levels of genetic variation within and high levels of genetic differentiation among Central American populations of Guatemalan fir, sacred fir, *A. flinkii*, and *A. hickelii* (see table 1 footnotes) (Aguirre-Planter and others 2000).

Flowering and fruiting. Fir strobili are unisexual and are typically borne on the uppermost branches. Both male (microsporangiate) and female (megasporangiate) strobili in grand fir develop from axillary buds (Owens 1984). The minimum age for production of female strobili is 20 years, that of male strobili, 35 years (Eis 1970). Usually, female strobili occur singly or in small groups on the upper side of the previous year's twigs on the highest branches, whereas male strobili cluster densely along the undersides of the previous year's twigs lower down in the crown. This arrangement promotes cross-fertilization but may reduce pollination (Singh and Owens 1982). However, both male and female strobili may be found on the same branchlet. Seed production in most fir species typically begins on trees 20 to 30 years old (table 3), although individual trees may produce some cones at a younger age, for example, 12 years in noble fir (Franklin 1974b) and 15 years in balsam fir (Roe 1948a). However, heavy cone production in noble fir begins when trees are 30 to 35 years old (Franklin 1982b). Seed production by Spanish fir in Czechoslovakia does not begin until trees are 50 years old (Holubcik 1969).

All firs require 2 years to complete their reproductive cycles; detailed descriptions of the cycles have been published for balsam, Pacific silver, grand, and subalpine firs (Owens and Molder 1977a&b, 1985; Powell 1970; Singh and Owens 1981, 1982), as well as descriptions of factors affecting seed production (Owens and Morris 1998). In Pacific silver fir, microscopic primordia are initiated in the axils of leaves inside vegetative buds during May of the first year; bud differentiation occurs about 2 months later, with bract initiation in mid-July and ovuliferous scales in mid-August; seed-cone buds become dormant in November. Microsporophyls are initiated between mid-July and early September, whereas microsporangia begin differentiation in September and are dormant by mid-October. Development of pollen-cone and seed-cone buds resumes early in April of the second year. While the single, large megaspore mother cell in each ovule is undergoing meiosis in early May, mature 5-celled pollen is forming (Owens and Molder 1977a&b).

Strobilus production, male and female, in balsam fir has been related to shoot vigor, the lowest number of female strobili occurring on whorl branches, and the most male strobili on internodal branches (Powell 1972). Even where the zones of male and female bearing overlap, the 2 sexes usually occur on different types of branch; when on the same branch, male strobili are confined to the weaker shoots. As the trees age, they appear to maintain a potentially female zone of constant size (number of whorls and internodes), while the uppermost boundary of the potentially male zone rises with increasing tree height. If the leader is lost, the male zone continues to rise while the female zone gets smaller, and the apical part of the crown can eventually become male (Powell 1972).

Table 3—*Abies*, fir: phenology of flowering and fruiting, and major characteristics of mature trees

Species	Location & elevation (m)	Flowering	Fruit ripening	Seed dispersal	Tree ht (m)	Age (yrs)*	Interval (yrs)
A. alba	Europe	May–mid-June	Mid-Sept–mid-Oct	Mid-Sept–mid-Oct	25–45	25–30	2–3†
A. amabilis	W Washington & Oregon (150–400)	Late Apr–May	Late Aug	Late Aug–Sept	35–65	30	3–6
	Vancouver Is., British Columbia (500)	Mid-May–June	Mid-Sept		—		
	Lewis Co., Washington (1,600)	June	—	Mid-Sept			
A. balsamea	—	Mid–late-May	Late Aug–early Sept	Mid-Sept	10–20	20–30	2–4
	Minnesota	Late Apr–early June	—	Early Oct	—	—	—
A. bracteata	Sta. Lucia Mtns, Monterey Co., California	Late Apr–early May	Late Aug	Mid-Sept	10–35	—	3–5
A. concolor	—	May–June	Sept–Oct	Sept–Oct	25–60	40	3–9
var. *lowiana*	Stanislaus NF, California (2,000)	Late May	—	Late Sept–late Oct	—	—	—
	Fremont NF, Oregon (1,600)	Mid-May–early June	—	—	—	—	—
A. firma	Japan	Late Apr–mid-May	Mid–late Oct	Late Oct–early Nov	30–45	—	4–6
A. fraseri	Roan Mtn, North Carolina	Mid-May–early June	Sept–mid-Oct	Sept–early Nov	10–25	15	3
A. grandis	Northern Idaho (750–1,100)	Mid-June	Aug	Early Sept	35–65	20	2–3
	W Washington & Oregon (100–400)	Mid-April–mid-May	—	Late Aug–mid-Sept	—	—	—
	Linn Co., Oregon (1,600)	Early–mid-June	—	Early Oct	—	—	—
	Mendocino Co., California (65)	Late March–early Apr	—	—	—	—	—
A. guatemalensis	Guatemala, S Mexico, Honduras, & El Salvador	—	Oct–mid-Dec	Nov–mid-Dec	20–30	—	2–3‡
A. homolepis	Japan	Mid-May–mid-June	Mid–late Sept	Mid–late Sept	20–30	—	5–7
A. lasiocarpa	San Francisco Peaks, Coconino Co., Arizona	Late June	Mid-Sept–early Oct	Late Sept–early Oct	10–35	50	2–3
	Northern Idaho (950)	Late June–early July	Mid-Aug	Mid-Sept	10–35	20	2–4
	Eastern Montana (2,100)	Early–mid-July	Late Aug	Early Sept	—	—	—
	Linn County, Oregon (1,750)	Late May–early July	—	Early Oct	—	—	—
A. magnifica	—	Late May–early June	Aug	Sept–Oct	30–55	35–45	2–3
A. mariesii	Japan	Mid–late June	Mid–late Sept	Late Sept–early Oct	10–25	—	5–7
A. nordmanniana	—	—	May	Sept–Oct	40–60	30–40	2–3
	Russian Georgia	—	After Oct 1	—	—	—	—
A. pindrow §	Himalayas	Late Apr–mid-May	Sept–early Oct	Oct–Nov	—	30–40	2–4
A. pinsapo	Czech Republic & Soslovakia	—	—	—	—	50	—
A. procera	Benton & Linn Cos., Oregon (1,350–1,550)	June	Mid–late Sept	Early Oct	45–80	12–15	3–6
	Lewis Co., Washington (1,600)	June–early July	Late Sept	Early Oct	—	—	—
A sachalinensis	Hokkaido, Japan	May–June	Sept–Oct	Oct	—	—	2–4
A. × shastensis	SW Oregon (1,850–2,000)	Mid–late June	Late Sept	Late Sept–mid-Oct	30–55	30–40	2–3
	N. California coast ranges (2,000)	—	Late Sept	Early–mid-Oct	—	—	—
	Shasta Co., California (1,700–2,000)	—	—	Mid-Oct	—	—	—
A. sibirica	W Siberia	—	—	—	—	—	2–8
A. veitchii	Japan	June	Sept–early Oct	Sept–Oct	20–25	30	5–6

Sources: Ahlgren (1957), Anon. (1950b, 1998), Bakuzis and Hansen (1965), Baron (1969), Beck (1990), Dallimore and Jackson (1967), Ebell and Schmidt (1964), Eis (1970), Eis and others (1965), Enescu (1960), Fowells (1965), Fowells and Schubert (1956), Franklin (1968, 1974b), Franklin and Ritchie (1970), Gordon (1978), Haig and others (1941), Hetherington (1965), Hughes (1967), Laacke (1990a&b), Laacke and Fiske (1983), Legg (1953), Leloup (1956), Little and DeLisle (1962), Løfting (1961), MacDonald and others (1957), MacLean (1960), Morris (1951), Munz and Keck (1959), Owens and Molder (1977b), Pearson (1931), Puri and Gupta (1968), Rudolf (1952), Sato (1940), Schmidt and Lotan (1980), Singh and Singh (1984a&b), Talley (1974), Tulstrup (1952), USDA Forest Service (1948), Wappes (1932), Zon (1914).

* Minimum age for commercial seed bearing.

† At higher elevations in central Europe, 4 to 6 years.

‡ Occasionally (Talley 1974).

§ Includes *A. delavayi*, *A. densa*. and *A. spectabilis* (Puri and Gupta 1968).

A

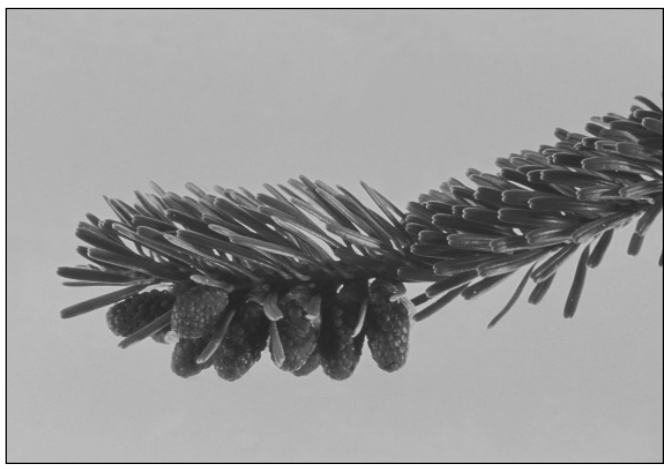
Thinning promoted fruiting in 150- to 170-year-old stands of Siberian fir in Siberia (Zelenin 1991), and best Sakhalin fir seeds occurred after heavy thinning (Sato 1940). In contrast, after a commercial thinning in a younger Siberian fir stand, the remaining trees produced such small amounts of pollen that seed quality was greatly reduced (Okishev and Pugachev 1983). Strobilus production in a Nikko fir seed orchard in Japan increased slightly following application of gibberellins $GA_{4/7}$ and GA_3, but girdling at the branch base was ineffective (Katsuta and others 1981).

Following bud burst in early spring, female strobili quickly elongate, and initially the bracts are highly conspicuous (figure 1). Enlarging male strobili have a miniature raspberry-like form (figure 2) until pollen is shed, when they become elongated and tassel-like. Wind-pollination in Pacific silver fir occurs by late May (Owens and Molder 1977a&b). Pollination durations may vary widely, from 18 days in a Nikko fir seed orchard in Japan (Itoo 1975) to a month in a Spanish fir forest in Spain (Arista and Talavera 1994a). Fir pollen is relatively heavy, so that pollination distances greater than 60 m may be the limiting factor for viable seed production in fir (and other coniferous species); although isolated trees may show an apparently good cone crop, the seedcrop may be poor (Anon. 1950a; Arista and Talavera 1994b). Parthenocarpy is known in balsam fir (Anon. 1950a) and Siberian fir (Nekrasova 1978a); without pollen, cones can be of normal size but what seeds form are without embryos. Controlled pollination techniques have been described for Fraser fir (Miller 1983), and fir pollen can be stored for at least 2 years under carefully controlled conditions (Kravchenko and others 1974; Lowe 1974).

For Pacific silver fir on Vancouver Island, development of the female gametophyte is complete at the end of June and fertilization occurs in mid-July. Embryonic meristems

Figure 1—*Abies amabilis,* Pacific silver fir: female strobili at the receptive stage (courtesy of D. Pigott).

Figure 2—*Abies procera, noble* showing the typical "raspberry" form (courtesy of Y. Tanaka.) fir: male strobili prior to pollen shedding (courtesy of D. Pigott).

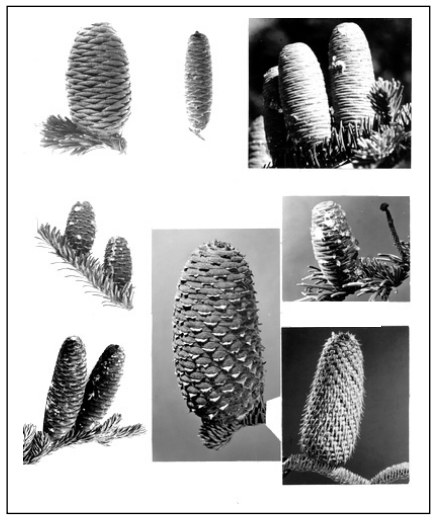


and cotyledons develop in early August and embryos mature late the same month or September. Seed dispersal usually begins mid-late September and most seeds have been shed by November (Owens and Molder 1977a&b). Similar phenologies have been described for grand fir on southern Vancouver Island (Owens 1984) and for Spanish fir in Spain (Arista and Talvera 1994b).

Mature fir cones are 7.5 to 25 cm long and typically ovoid to oblong-cylindrical. In many fir species, the fan-shaped ovuliferous scales outgrow the bracts early in the season, but the bracts remain highly conspicuous in noble fir, nearly covering the entire surface of the cone at maturity (figure 3). Typically, Shasta red fir bracts are also visible on the surface of mature cones, which makes them distinguishable from cones of California red fir, which have bracts that are shorter than the scales (Laacke 1990b). However, north of Mt. Lassen, where red and noble firs hybridize, red fir has exserted bracts (similar to those of noble fir). Adding to the confusion, exserted bracts are found also on a large southern Sierra Nevada population of red fir (Laacke 1990b). The bracts remain so prominent in bristlecone fir as to give this species its name.

Each scale bears 2 seeds on its adaxial (upper) surface, the ovules forming at the base of the scale near the attachment to the cone axis. The membranous wings form over the outer part of the scale. Scales near the tip and base of the cone usually lack fertile seeds. At maturity, seeds separate from the scale on which they form—a useful diagnostic in judging advancing ripeness—and seed dissemination involves abscission of the cone scales from the axis, leaving the rachis, the spike-like axis on the tree (figure 4) that may persist for several years. In Pacific silver fir, the scales become greatly distorted during drying in late summer, and

Figure 3—*Abies*, fir: mature female cones of *A. amabilis*, Pacific silver fir (**top left**); *A. balsamea*, balsam fir (**top middle**); *A. concolor*, white fir (**top right**); *A. fraseri,* Fraser fir (**middle left**); *A.* x *shastensis*, Shasta red fir (**middle center**); *A. grandis*, grand fir (**middle right**); *A. lasiocarpa*, subalpine fir (**lower left**); *A.procera*, noble fir (**lower right**).

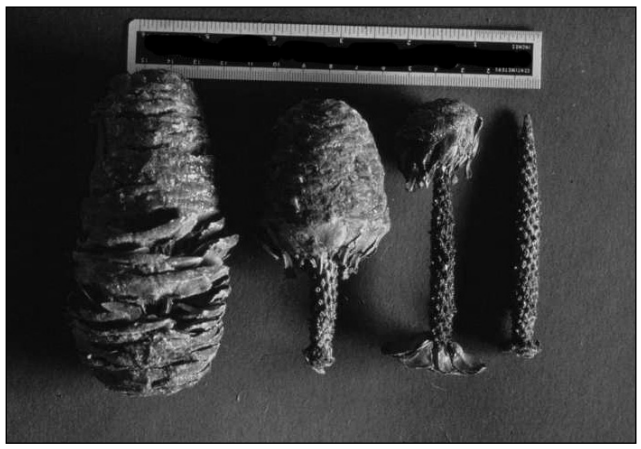


this twisting actively tears them from the axis. No such distortion occurs in noble fir, and seed dissemination requires branch movement by the wind or other agents to disturb the cone (Franklin and Ritchie 1970). Cone disintegration of other species such as grand fir and subalpine fir are intermediate.

Thus, pollination, fertilization, seed ripening, and dissemination all occur in the same season—in as little as 90 to 120 days—following the year of strobilus initiation (Franklin and Ritchie 1970). The chief agent of seed dispersal is the wind; seed rain density decreases as a function of distance from the parent tree, seedling mortality increases, and smaller-seeded species travel further (Carkin and others 1978; Franklin 1982b; Hofmann 1911; Houle 1992, 1995; Isaac 1930b; McDonald 1980; Savcenko 1966; Wolfenbarger 1946).

The majority of fir seeds are normally shed in October/November (table 3). Frequently these have the highest seed weight, maximum germination capacity and lowest occurrence of empty and immature seeds, plus higher seedling survival rates, than seeds shed earlier/later. In several firs, seed dispersal may extend well into winter (Anon. 1950b; Aussenac 1966; Hetherington 1965; Houle and Payette 1991; Roe 1946), the seeds becoming buried in, and germinating in, snowbanks (see also Pregermination treatments). Up to 50% of a Maries fir seedcrop may lodge in the foliage and only fall to the ground over winter (Smirnov 1991). The date of seed-fall of European silver fir in Italy

Figure 4—*Abies grandis*, grand fir: four stages in the abscision of ovuliferous scales from the cone axis (courtesy of D. Pigott)



became later with increasing altitude, but the amount of seeds fallen per square meter was greatest at intermediate altitudes of 900 and 1450 m and lowest at 800 and 1600 m. Seed quality in this species improved with increasing altitude because of a decrease in the percentage of empty and dead seeds (Giami 1970).

Fir seeds are large compared to most conifers, averaging 29, 46 and 83 seeds/g for Pacific silver, grand, and subalpine firs, respectively (Kolotelo 1997). In mature seeds (figure 5), the membranous wings are large—20 to 23.5 mm long in Manchurian fir (Voroshilova 1983)—ovoid or oblong, 1 to 1.5 times the length of the seed, and up to twice the seed width. The wing is usually translucent, uniformly light brown or tan, sometimes with a magenta edge. Seeds are completely covered by the wing on the adaxial face, but only on 2 margins on the abaxial face (Cermak 1987) by narrow flaps (figure 6). The soft seedcoat is brown, tan, or rarely cream and, in the outer, softer parts (sarcotesta) (Cermak 1987) where the seed is covered by the wing, large resin vesicles develop from cavities that differentiate in the outer layers of the integument (Owens and Molder 1977b). Vesicles appear on the seed surface as small, dark patches, their number, character, and placement varying with the species. Vesicle position (figures 7–9) and chemical contents in European silver fir have been described (Cermak 1987). The seedcoat of white fir is thinner than that of red fir and contains more vesicles, the number varying between 5 and 12/seed, although 7 to 9 are more common (Kitzmiller and others 1975). About 20% of the fresh weight of European silver fir seeds is resin (Cermak 1987), 90 to 95% of which is monoterpene hydrocarbons (principally limonene) (Cermak 1987; Cermak and Penka 1979; Penka and others 1977).

A

Figure 5—*Abies*, fir: mature seeds of *A. amabilis*, Pacific silver fir (**top left**); *A. balsamea*. balsam fir (**top center**); *A. fraseri*, Fraser fir (**top right**); *A. grandis*; grand fir (**bottom left**); *A. lasiocarp*a, subalpine fir (**bottom center**); *A. magnifica*, California, red fir (**bottom right**).

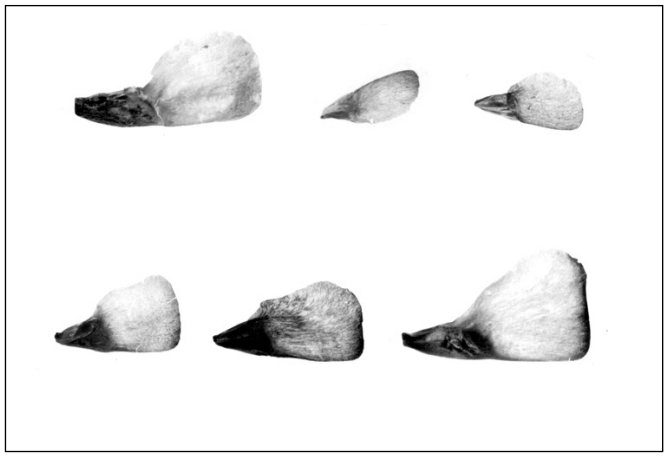
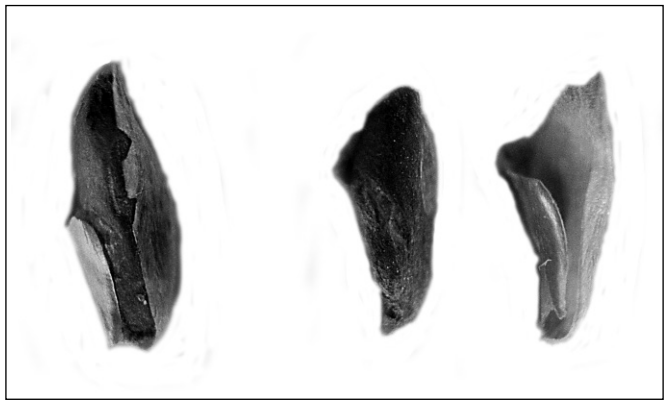


Figure 6—*Abies procera,* noble fir: abaxial view of seed showing (**left**) a seed with wing, but with integument still attached (indicated by the prominent flaps wrapping around the long margins) and which would be regarded as a "pure seed" commercially; a naked seed (**center**) without wing or integument; and the intact integument (**right**) removed from the seed at center. This wing attachment to the seed is typical for fir (Edwards 2002); scale bar is in millimeters.



The role of resin has been linked to inhibiting precocious germination, that is, to promoting dormancy, of mature fir seeds at the time of seedfall (Rohmeder 1951). It might also provide some form of protection for the embryo and megagametophyte against excessive drying (Gunia and Simak 1970). Germination of non-stratified European silver fir seeds was increased after resin removal by low-temperature vacuum distillation (Zentsch 1960), and resin extracted from this species inhibited germination in pine and spruce seeds (Dässler and Zentsch 1959; Rohmeder 1951). Damaging the vesicles during processing of fresh European silver fir seeds and allowing the resin to "contaminate" undamaged seeds reduced their germination (Gunia and Simak 1970). The germination-reducing effect of resin leakage in other species was greater when damage occurred before the seeds had been stratified (Arista and others 1992; Kitzmiller and others 1973, 1975), lending support to the suggestion that the resin may be chemically transformed during chilling rather than simply being evaporated (Gunia and Simak 1970). Leaking resin quickly oxidizes and may then be toxic to the embryo (Bouvarel and Lemoine 1958), and/or provide a good medium for mold development (Gunia and Simak 1967, 1970; Kitzmiller and others 1973). Whatever the precise role of the resin, fir requires careful handling of cones and seeds from the time they are picked (Dalskov 1960; Gunia and Simak 1970). Although fragile, the seedcoat can account for up to 60% of the total dry weight in noble fir seeds (Kandya and Ogino 1986).

Most of the bulk in a mature fir seed is occupied by the fleshy, nutritive megagametophyte tissue. Whereas the seedcoat proportion does not vary greatly, the weight of the megagametophyte and embryo varies widely among individual seeds and is more closely correlated with how quickly the seeds germinate (Kandya and Ogino 1986). The embryo extends almost the length of the megagametophyte (figure 10), and this extension—relative to the megagametophyte length—is a good index of seed ripening (Dobbs and others 1976; Oliver 1974) (see also table 6). Embryonic cotyledons, which may vary in number from 3 to 14, are well-differentiated, but the radicle apex is difficult to discern as it is encased by the protective root cap.

Seedcrops large enough to justify commercial collections generally occur every 2 to 4 years (table 3), but inter-

Figure 7—*Abies alba*, European silver fir: diagrammatic view of the adaxial surfaces of a pair of seeds on an ovuliferous scale. **CA** = cone axis; **OS** = ovuliferous scale; **Br** = bract; **S1, S2** = seeds; **W1, W2** = wings. A cross section through the seeds (indicated by the dotted line) is shown in figure 8 (after Cermak 1987).

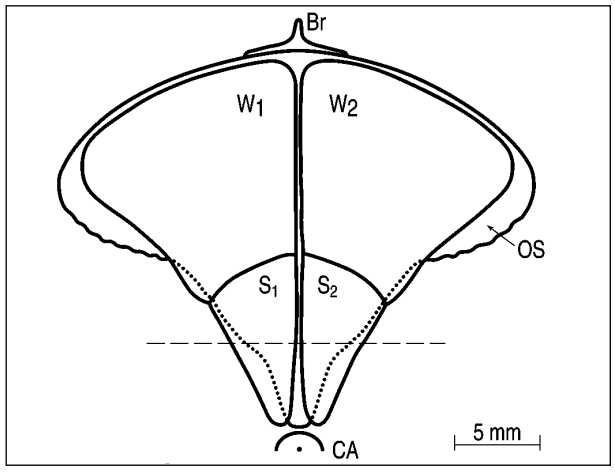


Figure 8—*Abies alba*, European silver fir: diagrammatic cross section of a seed (**S1** in figure 7). **OS** = ovuliferous scale; **Br** = bract; **W** = wing; **m** = median plane of the ovuliferous scale; **e** = embryo; **meg** = megagametophyte ("endosperm"). **A, B, D,** and **E** indicate individual resin vesicles located on the adaxial (**ad**) or abaxial (**ab**) surfaces, and medial (**med**) and marginal (**marg**) edges of the seed (after Cermak 1987).

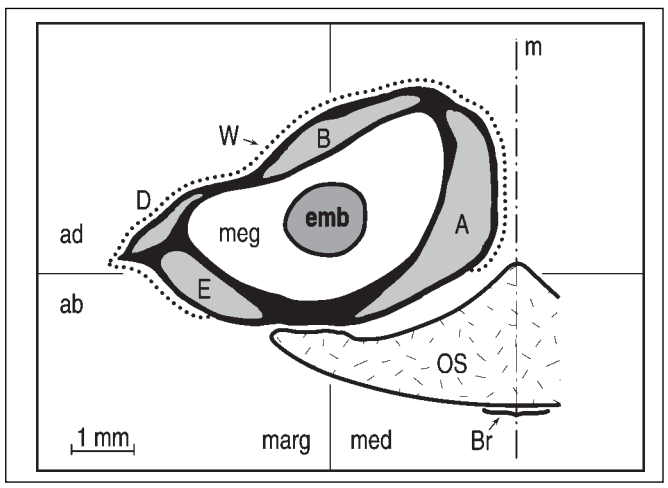
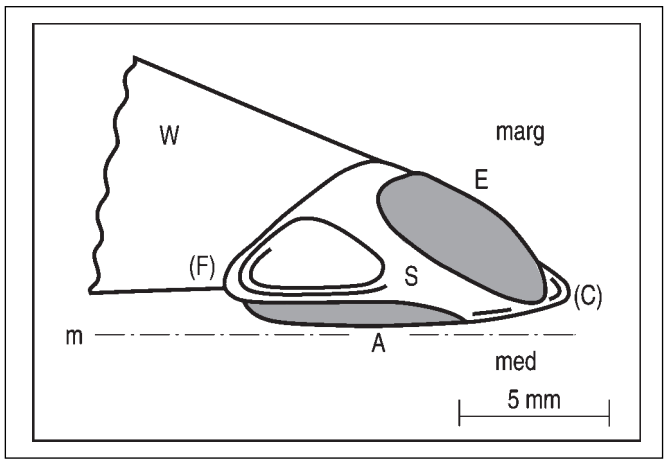
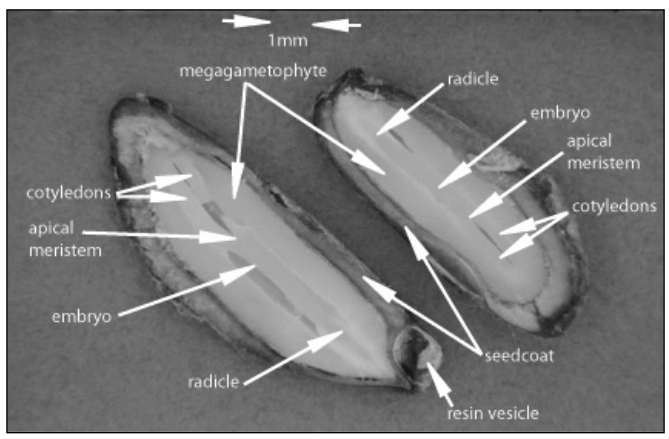


Figure 9—*Abies alba* European silver fir: digrammatic view of the abaxial surface of 1 seed. **W** = wing; **m** = median plane of the ovuliferous scale. Resin vesicles appear on the medial (**A**) or marginal (**E**) sides of the seeds, and at both ends (**C** and **F**) (after Cermak 1987).



vals may vary considerably due to numerous factors. Strobilus production in balsam (Powell 1977) and Spanish firs (Arista and Talavera 1995) occurs in alternate years. This was previously thought to be due to an endogenous rhythm unrelated to environmental factors (Greenbank 1963), but it has been shown that good cone crops in grand fir require both a cool, moist summer the year before seed maturation and a warm, dry summer the year of seed matu-

Figure 10—*Abies grandis*, grand fir: longitudinally sectioned mature seeds showing embryos (**e**) occupying 90+% of the corrosion cavity in the megagmetophytes (meg) ("endosperm." **C** = cotyledons; **AP** = apical meristem; **R** = radicle; **H**= hypocotyl/shoot axis: **V** = resin vesicle; **SC** = seedcoat. Scale bar is in millimeters (courtesy of D. Pigott).



ration (Eis 1973). Thus, large crops are unlikely in consecutive years. Other environmental requirements must be met also, which is why lapses of several years between heavy crops is more the rule. For example, the interval between heavy crops of white fir in California is commonly 5 years (McDonald 1992) but may vary from 3 to 9 years (Fowells and Schubert 1956). Henderson (1982) found that for subalpine fir, only 1 year over a 28-year period produced a "bumper" crop, whereas 4 other years were "good." Several true firs in Oregon and Washington produce good crops on a 3-year cycle (Franklin 1968), with noble fir averaging medium or better crops 50% of the time over its range, although some sites may go as long as 6 years without significant cone production (Franklin 1982b). Crop year can have a large effect on seed weight and cotyledon number in noble fir (Sorensen and Franklin 1977); cotyledon number in Sakhalin fir was weakly correlated with provenance (Okada 1966).

Several methods for forecasting cone crops have been devised. One, for Maries fir, is based on bud counts the previous year (Matsuura 1963); another uses visual estimates of the number of cones on individual Sierra white fir trees and the proportion of trees bearing cones (McDonald 1992); a photographic method is more accurate than visual rating for red fir (Gordon 1962). Crop production in grand fir can be estimated using a regression equation that employs the number of cones on the top 2 whorls of the crown, and the num-

ber on the south side of the tree (Kulhavy and Schenk 1976).

Cone length and seed yield are significantly correlated in grand fir (Ching 1960), and cone length and seed weight are correlated with mean temperature during maturation in Sakhalin fir (Okada 1983). The fertile length, or "effective size," of balsam fir cones ranges from 60% in small cones to 83% in large cones and, because larger cones are borne higher in the crown, the upper branches bear a greater proportion of the potential seed yield than they bear of the cone crop (Powell 1979). The fertile length of a European silver fir cone represents 74% of the total cone length, and the average yield of potentially fertile seeds varies from 122 (small cones) to 272 (large cones) (Nanu 1979a).

Total seed set (including damaged seeds) can be estimated for subalpine fir (Kulhavy and others 1976) and other firs (Douglass 1969) from the number of exposed seeds—sound and insect-damaged—when cones are cut in half lengthwise. The number of filled seeds exposed when cones are cut in half longitudinally is used in British Columbia to judge whether the crop is worth collecting; for Pacific silver fir at least 8 to 12, for grand fir at least 12 to 14, and for subalpine fir at least 4 to 6 filled seeds must be exposed on one cut face of the cone (Edwards 1986a; Eremko and others 1989). These numbers apply just prior to collection, because insects or disease may decrease counts if there is a significant time lag between cone examination and cone collection.

Tree age and size affect seed quality, sometimes in contradictory ways. Best seeds were obtained from younger (40- to 50-year-old) trees of the rare Sicilian fir in Italy (Arena 1960) and balsam fir in Michigan (Benzie 1960), than from trees more than 150 years old. European silver fir trees between 40 and 100 years old were judged best (Magini 1953), but Bosnian sources of this species showed no decrease in fertility with age (Panov 1949). West Himalayan fir at 200 years in Pakistan still produced enough seeds for adequate natural regeneration (Haq 1992), although viable seeds did not exceed 15% of the crop.

Almost 90% of white fir cones are borne on dominant trees, 12% on codominants, and almost none on intermediate and suppressed trees (Fowells and Schubert 1956). In white fir, cone production peaks in trees with 75 cm dbh, then gradually decreases as diameter increases (Fowells 1965). Seed-bearing white fir trees over 60 cm dbh are targets for the fir engraver beetle (*Scolytus ventralis* LeConte), which weakens and damages tops and thus may seriously impair cone production in old-growth stands (Hopkins 1982). Most cones occur on branches of the second and third nodes from the apex of balsam fir trees (Powell 1979). Similarly, cones occur at the very top of dominant Siberian fir trees over 28 cm dbh (Kolomiec 1950). In Siberian fir, the frequency of fruiting is correlated also with height, diameter, and trunk volume (Nekrasova and Ryabinikov 1978): all trees with a dbh of 24 cm or larger bear cones (Atimetov 1968). For European silver fir, seed numbers per tree generally increase with dbh, whereas the 1,000-seed weight peaks at dbh 40 to 50 cm, then decreases. Nursery seedlings surviving into their second growing season increased with parent-tree dbh up to 50 to 60 cm, so cones should be collected from trees 35 to 50 cm dbh (Souleres 1965). Germination in Himalayan fir seeds is optimal from trees in the 1.3- to 2-m dbh class (Puri and Gupta 1968). Cone diameter, 1,000-seed weight, and germination varied significantly with dbh of west Himalayan fir trees (Arya and others 1994).

Proper form and timing of nitrogen fertilizer has increased the frequency and size of balsam fir seedcrops—producing bigger and heavier cones and better quality seeds—in both natural stands and seed orchards (Arnold and others 1992; Edwards IK 1986; Sheedy 1974, 1978). Similar effects have been reported for European silver fir (Huchler 1956). Foliar levels of phosphorus and magnesium were identified as the nutritional elements most limiting cone yields in a Fraser fir seed orchard; the relative nitrogen status of high-yielding trees was superior to that of low-yielding trees. However, increasing the level of the most limiting nutrient may not increase cone production because other internal and external factors play a more decisive role (Arnold and others 1992).

Causes of reduced seed production. Despite producing abundant amounts of pollen, firs typically are poor seed producers, the reasons (in decreasing order of importance) being infrequent cone initiation, insect infestation, frost damage to cones and ovules, inadequate pollination, and several other minor causes (Owens and Morris 1998). The main factor affecting the number of cones produced is the proportion of initiated female strobili that develop into fully mature cones (Eis 1970; Nekrasova 1974; Owens and Molder 1974, 1977a&b; Owens and Morris 1998; Powell 1973; Shea 1989a&b). In a good crop year, an average grand fir tree produces over 40 cones (Foiles and others 1990). Cool wet weather may interfere with pollen dispersal (Franklin 1974a). Lack of pollination, incomplete development, and abortion, in balsam fir may cause more empty seeds than insect damage (Fye and Wylie 1968). Self-pollination in noble fir may reduce seed yield by 31%; although seed weight, germination, and seedling survival are not affected, seedlings of selfed parents show a 24%

inbreeding depression of 3-year height growth (Sorensen and others 1976). Late frosts up to 6 to 8 weeks after bud burst, that is, late May and early June (Fowells and Schubert 1956; Franklin and Ritchie 1970) may cause total abortion of female strobili in several species. Additionally, some primordia may become latent or differentiate as vegetative structures, depending on environmental and physiological factors during their development. Aerial contaminants may reduce seed yields also (Loffler 1988; Sidhu and Staniforth 1986).

High percentages of empty seeds have been observed in collections of numerous fir species (Franklin 1974b; Keen 1968; Khutortsov 1987; Nanu 1979b). The proportion of empty seeds increases in poor seed years, up to 90% in Siberian fir (Nekrasova 1978b) and to 63% plus 36% insect damaged in noble fir (Scurlock and others 1982). Cone crops of noble fir must be medium size or larger for sound seed to exceed 10% (Franklin 1982b).

The proportion of high-quality germinable seeds is often reduced by frequent infestations of insects that damage both cones and seeds (Hedlin 1974; Hedlin and others 1980). Insect predators appear wherever firs grow worldwide and about 50 insect species have been identified as damaging agents to fir cone and seedcrops (table 4). Tortrix moths are a major pest in China (Zhang 1982). Damage caused by cone midges, moths, maggots, and seed chalcids (*Megastigmus* spp.) usually is extensive, but cone moths (*Barbara* spp. and *Dioryctria* spp.) (figure 11) and cone maggots (*Earomyia* spp. and *Hylemya* spp.) that mine through the cones, injuring more than 1 seed (Hedlin 1966; Hedlin and Ruth 1974; Keen 1968; Pfister and Woolwine 1963) cause the most conspicuous destruction. The insect complex colonizing white fir cones comprises 3 feeding guilds—cone and seed miners, seed miners, and scale and bract feeders (Shea 1989a&b). These include at least 11 different insects (Shea 1989a&b):

- cone and seed miners—*Dioryctria abietivorella* Grote, *Eucosma* probably *siskiyouana* (Kearfoot), *Cydia* probably *bracteatana* (Fernald), and *Barbara* spp.
- seed miners—*Megastigmus pinus* Parfitt, *M. rafni* Hoffmeyer, and *Earomyia abietum* McAlpine
- scale and bract feeders—*Asynapta hopkinsi* (Felt), *Dasineura* probably *abiesemia* Foote, *Resseliella conicola* (Foote), and *Lasiomma* (*Strobilomyia*) *abietis* (Huckett)

Seed-mining guild insects cause the major seed damage in most years and, as cone crop size decreases, the proportion of cones with more than 1 insect species increases, together with an increase in co-occurrence of members of different guilds (Shea 1989a&b). In contrast, the larvae of seed chalcids (figure 12), which are the most common insects destroying coniferous seeds across the North American continent (Speers 1974a), destroy 1 seed each (Nanu 1980; Speers 1967). By means of seed x-radiography, not only can the degree of damage be estimated readily (Kulhavy and others 1976; Overhulser and Tanaka 1983; Speers 1967; Tanaka 1982), but larvae of *Megastigmus* spp. can be distinguished from those of *Resseliella* spp. (Gagov 1976).

In poor seed years, insects may totally destroy seedcrops of white fir in the western United States (Keen 1968), Fraser fir in the eastern United States (Speers 1968), and Siberian fir in western Siberia (Kolomiec 1950). Damage generally is

Figure 11—*Abies grandis,* grand fir: almost-mature cones attacked by the insect *Barbara* spp. (courtesy of D. Pigott).

Figure 12—*Abies, Fir: seed chalcid.*

Table 4—*Abies*, fir: insects affecting cone and seed production

Insect*	Common name	Host tree species
Adelges piceae Ratz.	balsam woolly aphid	*A. balsamea, fraseri*
Argyresthia fundella F.R.	—	*A. alba*
Asynapta spp.†	bract feeder	*A. concolor, lasiocarpa*
Barbara spp.	fir cone moth	*A. alba, concolor, grandis, lasiocarpa, magnifica, nephrolepis*
Camptomyia spp.	—	*A. alba*
Cartodere spp.	—	*A. alba*
Cryptophagus (micrambe) abietis (Pay.)	—	*A. alba*
Cydia bracteatana Fernald	fir seed moth	*A. concolor*
Dasineura spp.	fir seed midges	*A. concolor, grandis, lasiocarpa, procera*
Dendroctonus spp.	—	*A. guatemalensis*
Dioryctria spp.	cone moth	*A. alba, amabilis, balsamea, A. cephalonica, A. concolor, A. grandis, nephrolepis, nordmanniana, A. pindrow, pinsapo*
Earomyia spp.	seed maggot	*A. alba, concolor, grandis, lasiocarpa, magnifica, A. nordmanniana, procera*
Epinotia nigricana H.-S.	—	*A. alba*
Eucosma siskiyouana Kearfott	cone and seed miner	*A. concolor*
Evetria margarotana Wocke	—	*A. alba, borisii-regis, cephalonica, sibirica*
Hylemya spp.	cone maggot	*A. bracteata, concolor, grandis, lasiocarpa, nephrolepis*
Lasiomma spp.	fir cone maggot	*A. concolor, grandis, lasiocarpa, nephrolepis*
Laspeyresia spp.	—	*A. alba, borisii-regis, cephalonica, concolor, magnifica*
Leptoglossus occidentalis Heid.	western conifer seed bug	*A. grandis*
Lestodiplosis holstei L.	—	*A. alba*
Lonchea viridana Meig.	—	*A. alba, borisii-regis, cephalonica*
Lycoriella cellaris Leng	—	*A. alba*
Megastigmus spp.	seed chalcid	*A. alba, amabilis, balsamea, borisii-regis, A. bracteata, cephalonica, concolor, fraseri, grandis, guatemalensis, A. lasiocarpa, magnifica, bornmuelleriana var. equitrojana A. sibirica pinsapo, procera,*
Pegohylemia spp.	—	*A. alba, balsamea*
Ptilinus fur L.	—	*A. alba*
Resseliella spp.	cone scale midge	*A. alba, borisii-regis, cephalonica, cilicica, concolor, A. grandis, nordmanniana*
Spermatolonchaea viridana L.	—	*A. cilicica*
Zeiraphera rufimitrana Foote	—	*A. alba*

Sources: Androic (1960, 1976), Annila (1982), Arista and Talavera (1995), Bess (1946), Blais (1952), Bradley and others (1981), Bryant and Hudak (1968), Canakcioglu (1969), Donahue and others (1985), Durzan (1979), Eremko and others (1989), Fang and others (1988, 1989), Fedde (1973a&b), Gagov (1976), Gonzalez and others (1983) [in Donahue and others 1985]), Gordon (1970), Greenbank (1963), Hall (1981), Hedlin (1966), Hedlin and Ruth (1974), Hedlin and others (1980), Hussey (1954, 1957, 1960), Hussey and Klinger (1954), Jesperson and Lomholdt (1983), Kailidis and Georgevits (1970, 1972), Kayacik (1964), Keen (1968), Koerber (1963), Kolomiec (1950), Kulhavy and Schenk (1976), Kulhavy and others (1976), Lanz (1942, 1943), Legg (1953), Mackay (1949), Matic (1972), Miller (1986), Miller and Ruth (1989), Moody (1988), Nanu (1979b), Nanu and others (1986), Nekrasova (1978b), O'Connor and O'Connor (1984), Overhulser and Tanaka (1983), Pfister and Woolwine (1963), Powell (1973), Pribylova (1975), Puri and Gupta (1968), Rahman and Chaudhry (1986), Schooley (1975, 1976, 1978), Scurlock and others (1982), Shea (1989a&b), (Skrzypczynska 1982, 1984, 1985, 1989a&b), Skrzypczynska and others (1988, 1990, 1995), Speers (1968, 1969), Talley (1974), Tanaka (1982), Toth (1973), Woodwell (1961).

* Insect names, in alphabetical order, are listed as cited by sources. No attempt has been made to rationalize synonyms, because sources rely on different nomenclature authorities.
† For simplicity and conciseness, where several species in a single genus have been identified, insects are grouped by genus, for example, *Asynapta* spp.

higher in poor crop years (Speers 1967), because adult female insects have fewer cones on which to concentrate (Lanz 1943). Even in good cone crop years, the number of emerging adult insects may be positively correlated with the flowering intensity of the food plants, with the most important factor influencing the size of the insect population being the amount of seeds produced (Annila 1982). Little in-depth research on the biology, ecology, and effective control of fir seed and cone insects has been done (Gara 1982).

Although cone and scale midges cause no significant loss, seed or gall midges may reduce seed yields (up to 72%) (Skrzypczynska 1985) by fusing seeds to the scales, although germinability of galled noble fir seeds was not reduced (Franklin 1974b). Likewise, larvae of *Spermatolonchaea viridana* L. (table 4) cause deformations on the cone scales and seed wings of Cilician fir in Turkey but do not affect the seeds (Kayacik 1964).

Most insects damage seeds directly, but the spruce budworm—*Choristoneura fumiferana* (Clemens), a defoliating insect—also attacks balsam fir by feeding on pollen in

developing male strobili (Bess 1946; Blais 1952; Greenbank 1963). Also, the budworm girdles the basal parts of developing female strobili (Powell 1973), thereby reducing the formation of female buds and hence the cone crop for the following season (Powell 1973; Woodwell 1961). Severe defoliation decreases tree vigor, food reserves, and cone production (Hall 1981; Schooley 1975, 1976, 1978), and the trees become susceptible to secondary attacks (by root rot and beetles), a condition referred to as Stillwell syndrome (Moody 1988).

In some localities, Douglas squirrels (*Tamiasciurus douglassi*) and red squirrels (*T. hudsonicus richardsoni*) cut and cache large quantities of cones of Pacific silver, grand, and subalpine firs. They may sever the twigs that support the current cones, and also those that bear the female buds for the next year's crop (Franklin 1964; McKeever 1964; Smith 1968). In the Northeast, voles and mice (*Clethrionomys gapperi*, *Peromyscus maniculatus, P. leucopus*, and *Microtus pennsylvannicus*) prefer spruce (*Picea glauca, P. rubens*) and pine (*Pinus strobus, P. resinosa*) seeds to balsam fir seeds, even in extreme hunger (Abbott 1962; Abbott and Hart 1960). However, a titmouse (*Parus ater*) is known to eat European silver fir seeds, causing many problems in Slovakian nurseries (Bauer and Tichy 1960). Titmice, voles (*Clethrionomys rutilus*), mice (*Apodemus* spp.), and shrews (*Sorex* spp.) can destroy 60 to 80% of the Siberian fir seedcrop in Siberia (Vladyshevskii and Shtarker 1982).

Several fungi associated with fir seeds usually make their presence apparent during stratification and germination (table 5), but it has not been shown if the cones become infected before harvest or during harvest, handling, transporting, or processing. The fungal pathogen *Caloscypha fulgens* (Pers.) Boud. was found in 25% of stored grand fir seedlots, but not in Pacific silver fir (Sutherland 1979). Dwarfmistletoes (*Arceuthobium* spp.) attack firs, especially red and white firs, to such an extent that stand control measures can be required (Hawksworth and Wiens 1965; Parmete and Scharpf 1963). Infected trees show less growth and

Table 5—*Abies*, fir: fungi and other organisms isolated from fir cones and seeds

Organism	Host tree species
Alternaria spp.	*Abies* spp.*
Aspergillus spp.	*Abies* spp.
Botrytis cinerea Pers.: Fr.	*A. amabilis*
Caloscypha fulgens (Pers.) Boud.	*A. grandis*
Cephalosporium spp.	*Abies* spp.
Ciboria rufo-fusca (O. Weberb.) Sacc.	*A. alba, nordmanniana*
Cladosporium spp.	*A. grandis, magnifica, × shastensis*
Cylindrocarpon spp.	*A. amabilis, sibirica, Abies* spp.
Fusarium culmorum (Wm.G. Sm.) Sacc.	*Abies* spp.
Fusarium moniliforme J. Sheld.	*A. grandis, nordmanniana*
Fusarium oxysporum Schlechtend.: Fr.	*A. grandis, procera*
Fusarium roseum Link: Fr.	*A. grandis, procera*
Fusarium semitectum Berk.& Ravenel var. *majus* (Wollenweb.)	*A. amabilis*
Fusarium spp.	*Abies* spp.
Geniculodendron pyriforme G.A. Salt	*A. amabilis, grandis*
Heterobasidion annosum (Fr.:Fr.) Bref.	*Abies* spp.
Lirula macrospora (R. Hartig) Darker	*Abies* spp.
Melanospora zamiae Corda	*Abies* spp.
Mucor spp.	*Abies* spp.
Papulospora spp.	*A. amabilis, grandis*
Penicillium spp.	*A. amabilis, grandis, magnifica, × shastensis, procera*
Phoma spp.	*Abies* spp.
Rhacodium therryanum Theum.	*A. sachalinensis*
Rhizoctonia solani Kühn	*A. balsamea, fraseri, grandis*
Sclerotium spp.	*A. mariesii, Abies* spp.
Trichoderma spp.	*A. amabilis, grandis, Abies* spp.
Tricothecium roseum (Pers.:Fr.) Link	*A. grandis*
Truncatella hartigii (Tub.) Steyaert	*Abies* spp.
Virus-like particles	*A. alba, homolepis*

Sources: Anderson (1985), Bloomberg (1969), Buchwald and others (1961), Edwards and Sutherland (1979), Eremko and others (1989), Flachmann and others (1990), Hayashi and Endo (1975), Heit and Natti (1969), Kolotelo (1994), Littke and Browning (1991), Ono (1974), Prisyazhnyuk (1960). Fungal nomenclature mainly according to Farr and others (1989).

* Individual tree species not determined.

vigor (Laacke 1990a&b) and produce fewer seeds with lower viability (Hawksworth 1978).

Collection of cones. Fir seeds ripen in 2 recognizable phases, the first being the accumulation of organic materials, and the second involving metabolic changes within the seeds, so that germinative capacity continuously increases up to (or almost up to) seed dispersal (Edwards 1969; Franklin 1974b; Pfister 1967; Speers 1962; Weyerhaeuser 1958; Yanagisawa 1965). In noble fir, germination increases to a peak, accompanied by an increase in seed dormancy (Edwards 1969, 1982a), then levels off before seed dispersal (Edwards 1969; Franklin 1965; Rediske and Nicholson 1965); a similar trend occurs in Turkey fir (Beskok 1970). In contrast, in grand (Pfister 1966; Snyder 1976) and Fraser firs (Speers 1962) germination continues to increase right up to seed dispersal. For this reason, seeds should not be removed from fir cones—particularly cones collected early—immediately after collection, because low seed viability may result (Edwards 1969; Rediske and Nicholson 1965; Speers 1962) due to curtailment of the second phase of ripening.

The period for cone collection, from the time organic accumulation ends until seed dispersal begins, typically ranges from 4 to 6 weeks, depending on location. Calendar dates are unreliable and vary with locality—especially elevation—and weather patterns, but if cone storage facilities are available, collections in the West may begin by mid- to late-August. Knowledge of local ripening conditions (degree-day summations are useful) and the use of the few known ripeness indices (table 6) can aid the decision to begin collecting (Edwards 1982a).

Judging when to start cone collection can be a major difficulty. In many tree genera, not all fruits mature simultaneously, maturation date varying among cones on the same tree (cones on the southern aspect of the crown generally ripening earlier), among trees within the same stand, from stand to stand in the same year, and from one year to the next (Edwards 1980a; Franklin 1965). The extent to which collections can be made in advance of seed dispersal is largely governed by the fact that fir seed development ceases if the cones are detached from the parent tree too soon, especially if the primary organic-accumulation phase is incomplete. Early-collected cones are more sensitive to handling method, but this sensitivity declines in later collections (Edwards 1980a). Cone maturity indices are very important for firs, therefore.

In firs, cone and seed color (common maturity indices in many conifers) may be more closely related to seed source and to individual parent tree than to ripeness. For example, mature cones of white fir may be either green or purple, with green cones having (on average) 25% fewer viable seeds, and the seeds weighing 15% less, than seeds from purple cones, although there were significant interactions with elevation of the seed source (Farris and Mitton 1985). Similarly, in the former Yugoslavia, mature seeds of white fir from violet cones germinate better than those from yellow cones (Stilinovic and Tucovic 1971). Quality of Siberian fir seeds is better from trees with light-green cones than that of trees with dark-green cones (Kirgizov and Mosin 1980). Progressively southern sources of European silver fir in Bulgaria have darker colored and more germinable seeds (Gagov 1973).

Nevertheless, workable indices of fir maturation have been devised for some species based on changes in cone color, seedcoat color, or the development of color in the seed wing (table 6), although this remains subjective and depends on the experience of the collector (Rudolf 1940). When cones of noble fir in Denmark begin to change from green to yellowish brown and bend down the branches because of their weight, natural seedfall is 2 to 3 weeks ahead; thus at the first signs of cone scale separation, the cones are collectable (Dalskov 1960).

Two interrelated parameters—cone moisture content and cone specific gravity—are more objective and reliable indices (Rediske 1961). There is some general agreement (table 6) that maturity is reached when specific gravity of cones has fallen below 0.9, indicating a moisture content below 50%. Either of these 2 parameters must be measured only on freshly picked cones, and because cone moisture content is not easily determined in the field, specific gravity is usually the measurement of choice. Thus, if cones of white and red firs (and of other conifers) float in kerosene, a 50:50 mixture of kerosene and linseed oil, or any mineral/lubricating oil of specific gravity 0.85 to 0.80, the crop is ready to be picked (Lanquist 1946). However, cone specific gravity is of little use in judging maturity in Japanese fir (Yanagisawa 1965).

Although no documented use of the following attribute has been found outside British Columbia, one criterion for judging when to begin fir cone collections is to allow a sample of longitudinally cut seeds to dry out overnight at room temperature. Then, if the megagametophyte tissue shows very little or no shrinkage away from the testa in most (if not all) of the seeds, they are sufficiently well developed for cone collections to begin (Dobbs and others 1976; Edwards 1980a, 1982a; Eremko and others 1989). Shrinkage of the megagametophyte indicates that the seeds are still high in moisture content and that collection should be delayed.

Table 6—*Abies*, fir: cone and seed maturity indices identifying earliest collection date

Species	Cones	Seeds
A. amabilis	Green with yellow tinge, turning gray or purple	Seedcoat cream or tan; wing light brown/pale purple, with brown margin; megagametophyte opaque & firm; embryo yellow/yellow-green, 90% extended; rudimentary cotyledons well developed*
A. balsamea	Turning purple; moisture content < 60%	—
A. concolor	Specific gravity 0.85–0.96	Wing uniform brown, deep magenta edge; seed detached/loosely attached to cone scale; embryo pale yellow-green, 9 of 10 fully elongated
A. firma	Turning yellow-brown, losing luster	—
A. fraseri	Blue-green turning brown	Distinct seedcoat color visible
A. grandis	Light brown; specific gravity <0.90 In BC: turning gray or purple.	Wing purple-brown (green-colored cones only); seed detached from cone scales In BC: seedcoat cream or tan; wing light brown/pale purple, with brown margin; megagametophyte opaque & firm; embryo yellow/yellow-green, 90% extended; rudimentary cotyledons well developed
A. guatemalensis	Turning dark green or purple; resin droplets visible on exterior	Wings yellow
A. homolepis	Turning yellow-brown & losing luster	—
A. lasiocarpa	Green with yellow tinge, turning gray or purple	Seedcoat cream or tan; wing light brown/ pale purple, brown margin; megagameto-phyte opaque & firm; embryo yellow/ yellow-green, 90% extended; rudimentary cotyledons well developed
A. magnifica	Specific gravity < 0.75.	Wing uniform brown, deep magenta edge; detached/loosely attached to cone scale; embryo pale yellow-green, 8 of 10 fully elongated
A. mariesii	Turning brown & losing luster.	—
A. procera	Light brown; specific gravity < 0.90	Wing uniform brown; detached from cone scale; embryo 90% extended & firm; crude fat content 25 mg/g dry weight †
A. sachalinensis	Turning brown & losing luster	—
A. veitchii	Turning brown & losing luster	—

Sources: Anon. (1998), Bakuzis and Hansen (1965), Donahue and others (1985), Eremko and others (1989), Franklin (1965, 1974b), Oliver (1974), Pfister (1967), Snyder (1976), Speers (1962), Stoeckeler and Jones (1957).

* Using 10 × lens.

† Rediske and Nicholson (1965).

The ratio of embryo length to the length of the cavity in the megagametophyte (figure 10) is also widely employed in British Columbia for judging when to collect (Eremko and others 1989). Embryos do not have to be fully elongated to be germinable, but seeds with embryos less than 50% extended germinate less vigorously and predictably. This extension can be determined readily by field personnel equipped with a sharp knife, a 10 × lens and a little training (Dobbs and others 1976; Eremko and others 1989), and it can be recorded easily on x-ray film. Thus, when a majority of the embryos—94% in white fir seeds (usually some 3.5 weeks before seedfall) and 84% in red fir (2 weeks before seed dispersal)—are fully elongated, provided other criteria are satisfactory (table 6) the cones are ripe enough to collect (Oliver 1974).

Because megagametophyte tissues do not mature as quickly as the embryos, collections should be delayed until these tissues have achieved a firm consistency (similar to the meat of a coconut), that is, they have lost their earlier watery, translucent appearance. Megagametophyte tissues will then exhibit little or no shrinkage or curling and retain a relatively firm, fresh appearance when longitudinally sliced seeds are left uncovered overnight at room temperature. The current prescription is to delay collections until embryos are at least 90% extended (figure 10), by which time the megagametophyte tissue has matured sufficiently also (Edwards 1982a; Eremko and others 1989) (table 6). As previously mentioned, another useful criterion of seed maturation is the degree to which the seeds have abscised/detached from the ovuliferous scales on which they developed. Seed

detachment indicates that they have ceased, or have greatly reduced, the accumulation of organic materials and that the seedcoats are undergoing the final stages of their development and becoming impermeable, usually signaled by the attainment of a distinct seedcoat (and seedwing) color.

Chemical indices of maturity have been explored. The crude fats and lipids that—together with protein bodies—are the main storage structures in fir seeds (Kovac and Wrischer 1989) reach high levels in mature seeds of several fir species (Bennett 1966). At a seed crude-fat content of 250 mg/g (dry weight), noble fir cones were judged to be ripe enough to collect, but that some artificial ripening (the "after-ripening" phase) prior to seed extraction was required to achieve maximum seed quality (Rediske and Nicholson 1965). A later study on maturing noble fir seeds was unable to substantiate the pattern of crude fat accumulation (Edwards 1969). Metabolism of fir seed lipids during germination has been linked to the glyoxalate cycle (Firenzuoli and others 1968).

As a general recommendation, no single criterion should be relied on when judging maturity of fir seeds. Rather, several characteristics such as seedcoat and wing color, seed detachment from cone scale, and embryo color and extension should be assessed before large-scale cone collections are undertaken (Oliver 1974; Snyder 1976).

Because fir cones disintegrate and seeds disperse at maturity, then making cone collection impossible, it is necessary to collect in advance of full seed ripeness. Collections may be by hand from standing (Seal and others 1965) or recently felled trees, or from squirrel-cut cones on the ground or from squirrel caches. Extensive collections in the western United States used to be made by climbing open-grown trees in 40- to 70-year-old stands, and some cones are still collected this way, but caution is required because fir stems are relatively brittle and tops may break out (Franklin 1974b). Cones collected by climbing should not be thrown to the ground, even in sacks, because of the danger of resin vesicle damage discussed earlier. Collections made close to the time of natural seed dispersal—when the cones are lighter (drier), the seeds are riper, and the seedcoats tougher—still require care to avoid resin vesicle injury (Dalskov 1960).

Synchronizing cone collections with felling operations, so that cones can be collected from newly felled trees reduces this danger, but the cones may disintegrate upon impact with the ground (making gathering time consuming) and may be difficult to separate from the branch debris (Pigott 1994). Squirrel-cut or -cached cones are easier to collect and the seeds are more likely to be ripe for 2 reasons: squirrels in the Pacific Northwest (at least) do not begin to cut in quantity until cones are approaching maturity, so that full seed development can be achieved because the cones are typically cached in cool, moist microsites (Franklin 1974b; Halvorson 1986; Pedro White and White 1986). However, red squirrels in the Rocky Mountains and Douglas squirrels in the southern Cascades have been seen to cut and begin caching white fir cones before they were fully mature (Fowells and Schubert 1956; Lanner 1983); red squirrels also cut immature subalpine fir cones (Lanner 1983). The high crude-fat content of conifer seeds, especially that of fir seeds, probably resists spoilage in the caches (Halvorson 1986). Although there is no direct evidence that seeds collected in this way are inferior, some squirrel-cut fir cones may have been bruised, and the seeds damaged, on impact with the ground. Also, the parent trees from which they were cut will not be known. Because squirrels collect far more cones than they can eat, they later fail to find all the cones they have cached. Thus only a portion of the caches are found by human collectors and there is no danger of depriving the animals of their winter food supply (Pedro White and White 1986).

Shooting-out cone-laden tops of fir trees with a rifle has been used with some degree of success, with smaller crews collecting many (if not more) cones than by climbing. However, there are inherent dangers in this technique, especially in the vicinity of other work crews, and/or near urban areas (Dobbs and others 1976). Cone harvesting by mechanically shaking the trees was unsuccessful on both noble and grand firs (Anon. 1970).

One technique developed in the past 2 decades is the aerial cone-rake, a device designed to be lifted by helicopter and lowered over the crowns of cone-bearing trees (figure 13). In the process of retrieving the device, cones and cone-laden branches are raked from the tree by a circle of tines and collected in a basket (figure 14. When the basket is full, the device is lowered to a cone-dump site and the cones and slash sorted by hand (Wallinger 1986) (figure 15). By this means, larger volumes of cones per day—up to 10 hl (28 bu) of Pacific silver fir, 10 hl or more of grand fir, but only 2 to 5 hl (5 to 15 bu) of subalpine fir—can be collected in a much shorter time than by traditional methods (Eremko and others 1989; Portlock 1996), making the technique economically viable. There are additional advantages in that cone collection can begin closer to seed dispersal, that is, full maturity, and cones can be collected from areas that have no road access. The technique works best on tree species (such as fir) that bear cones in the upper third of the crown. Cone rakes have been used to collect over 90% of all fir cones collected in British Columbia (Wallinger 1986). All aspects

Figure 13—*Abies procera*, noble fir: aerial collection using a cone rake (courtesy of D. Pigott).

Figure 14—*Abies procera*, noble fir: cones collected by aerial cone rake (courtesy of D. Pigott).

of the application of the technique, as well as aerial clipping/sawing, and aerial topping for cone collection, have been comprehensively reviewed (Camenzind 1990).

Cone and seed processing. Seed germinability of a number of species, including white (Oliver 1974), grand (Pfister 1966), Nordmann (Muller 1971), and noble firs (Edwards 1969; Franklin 1965; Rediske and Nicholson 1965) can be improved by storing the cones under cool, moist conditions for several weeks after collection. In contrast, cones of red fir need to be collected as close as possible to seed fall (Oliver 1974). Artificial ripening of early-collected seeds allows cone collections to be started sooner, thus extending the collection period, so that immature cones from logging operations can be used (Edwards 1982a). The maximum period of collection prior to the onset of natural seed dispersal appears to be around 6 weeks, but it is safer to think in terms of only 4 weeks. Warmer, drier summers (after pollination) may allow earlier starts to cone collection than cool, wet summers. In most years, the beginning of August is probably the earliest any cones should be collected, and only then if storage facilities can provide the cool, slow-drying conditions required. Because water loss is an intrinsic part of the maturation process (Pollock and Roos 1972) in orthodox seeds (see chapter 1), the cones need to be dried, preferably slowly, so that mold build-up and heating are avoided.

The period of cone storage is governed by the natural disintegration of the cones; once they have fallen apart they can be regarded as fully mature (Edwards 1969; Muller 1971). Well-spaced (not stacked) sacks of cones should be stored for periods of several weeks or months in drying sheds with good air circulation, for cones mature best in cool (<10 °C), shaded conditions (Edwards 1969; Franklin 1965; Rediske and Nicholson 1965). Storing grand fir cones with their bases in water or nutrient solutions gave higher seed weights and increased germination (Pfister 1966), but storing grand and noble firs cones in damp peatmoss was deleterious (Franklin 1965; Pfister 1966). For immature cones that are high in moisture, rebagging the cones as they arrive at the storage station and reducing by half the amount of cones in each sack will promote good curing. Periodic inspection for deterioration and turning the material within the sacks are good cone storage practices. Spreading balsam fir cones on mesh-bottomed trays is advantageous also; cones should not be more than 6 cm deep and they may

Figure 15—*Abies grandis*, grand fir: bagging aerially collected cones at a dump site; note the wooden box by picker's knee, this is a cone-volume measuring device (courtesy of D. Pigott).

need turning at least once each day, especially if they settle onto the trays in a compact mass (Carman 1953). No deterioration in seed quality was found when Pacific silver fir cones were stored for 6 months (October to March), either in a covered shed exposed to ambient external temperatures or in a refrigerated compartment at 2 °C prior to seed extraction, provided the cones had been properly handled in the field (Leadem 1982). Therefore, fir cones may be among the last to be scheduled for seed extraction, December or even later, by which time full seed maturity has been achieved and the cones have completely disintegrated, making seed extraction simpler. It cannot be over emphasized that fir seeds should not be extracted from the cones immediately after collection, especially from early-collected cones, otherwise viability is likely to be low.

Cones should be placed in proper storage facilities as soon as possible after harvesting and on no account should they be left untended at the collection site or in a vehicle for more than a few hours. Especially for premature collections, interim collection facilities in the field are essential to allow for continuing maturation (Dobbs and others 1976; Eremko and others 1989; Stein and others 1974; see also chapter 3). Incompletely ripened fir seeds store poorly, with serious losses in germinative capacity (Muller 1971; Yanagisawa 1965). Even when collected close to full maturity, fir cones that are not placed in suitable interim storage which will permit continued loss of moisture, the heat of respiration is liable to cause an increase of the surrounding temperature and non-dormant seeds may sprout before the cones can be processed. Such viviparous germination has been observed in subalpine fir (figure 16 and 17) and in other conifer species (Edwards 1980a). Although interim storage is a minor component of seed collection costs, it is important and yet is often poorly addressed (Pigott 1994). Cones should be moved to a more permanent storage location as soon as other operations permit, but for reasons similar to the above, long-distance transportation should be avoided. Turpin (1963) recommended field extraction using an inexpensive, easily erected structure so that only the extracted seeds of European silver, white, grand, and Sierra white firs are shipped.

Processing fir cones (table 7) is similar to processing cones of other conifers, except that if the fir cones have been stored for 2 to 3 months, they will have disintegrated naturally, the seeds will have separated from the scales, and the kiln-drying and tumbling steps can be dispensed with. In British Columbia, storage of the cones of Pacific silver, grand, and subalpine firs not only conditions the cones, but also, if the cones are dried to a target-moisture content of 15%, damage through seedcoat abrasion is reduced and makes the seed wings become more brittle and easier to break off (Rooke 1997).

Figure 16—*Abies lasiocarpa*, subalpine fir: viviparous germination, with seeds germinating in the cone before they could be extracted (courtesy of D. Pigott).

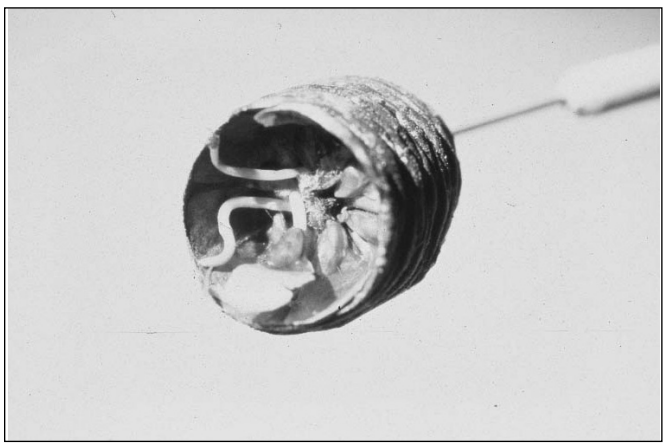


Figure 17—*Abies lasiocarpa*, subalpine fir: viviparous germination, with seeds germinating while still attached to the ovuliferous scales (courtesy of D. Pigott).

When additional drying is required, cones should be air-dried for 3 weeks or more at 20 to 30 °C (Franklin 1974b) where ambient conditions permit. If kiln drying is absolutely necessary, temperatures between 30 and 38 °C for up to 14 hours are used (table 7), but care must be taken to avoid damage through too rapid or prolonged drying. When possible, kiln-drying should be avoided so that any possibility of heat damage to the seeds is eliminated.

Partially or wholly disintegrated cones are tumbled or passed over vibrating screens (Carman 1953; Rooke 1994) to separate the seeds from the cone axes, scales, and bracts.

Table 7—*Abies*, fir: cone drying schedules

Species	Air-drying* period (days)	Kiln-drying period	
		Time (hr)	Temp (°C)
A. amabilis	60–180	6–14 †	30–38
A. balsamea	20–30	0	—
A. concolor	7–14	0	—
A. firma	14	(†)	48
A. fraseri	30–45	0	—
A. grandis	60–180	6–14 †	30–38
A. guatemalensis	< 60§	0	—
A. homolepis	14	(‡)	48
A. lasiocarpa	60–180	6–14†	30–38
A. magnifica	8–21	0	—
A. mariesii	14	(‡)	48
A. procera	60–180	6–14 †	30–38
A. sachalinensis	14	(†)	48

Sources: Anon. (1998), Edwards (1982a), Franklin (1974b), Heit (1968a), Heit and Eliason (1940), Jones (1962), Leloup (1956), Speers (1967).

* At ambient air temperature; cooled (<10°C) conditioning facilities are superior.

† If air-drying not possible, but cones should not be processed immediately after harvest.

‡ In a rotary kiln; seeds removed from heat as soon as they fall through the tumbler mesh.

§ In the shade.

Screening is more gentle and less damaging to seedcoat resin vesicles. Nordmann fir seeds can be extracted by passing the cones between series of rotating and fixed teeth, the spacing of which gradually decreases (Saralidze and Homeriki 1964). The separated seeds are then de-winged, a step during which fir seeds can be easily damaged (Allen 1958; Franklin 1974b; Roe 1948b; Weyerhaeuser 1957), thereby exacerbating losses of viability during storage (Rediske 1967). Small lots are best de-winged by hand (Roe 1948b), but even this can rupture some vesicles in noble fir (Edwards 1982a). Grand fir seeds de-winged by hand germinated significantly better than those commercially processed (Wang 1960). When mechanical processes must be used on large lots, one common technique for true firs is to break the wing at or near the point that it extends beyond the seedcoat, relying on friction in a mass of seeds agitated by gentle rolling of the seed mass (Rooke 1994). Using a spiral screw or auger, or drawing the seeds through tubing connected to a vacuum cleaner, may achieve the same goal. Some machines employ rotary screens that permit the wing, but not the seed, to protrude and to be broken by a brush. Some wings may be removed during the initial vibratory-screening to separate seeds from other cone parts (Carman 1953). Special processing and sowing machinery designed for European silver fir in Poland are based on morphological measurements of the seeds (Czernik 1993).

All these methods, which are performed on dry seeds and can be quite effective in breaking the seedwing, provide for impact damage to the resin vesicles and to the seedcoat itself. Prolonged de-winging, or de-winging fir seeds in a mixture that includes a considerable amount of hard, sharp debris such as cone scales, can cause considerable injury. When subalpine fir seeds were run through a brush de-winger 3 times, 50% of their original viability was lost (Allen 1958). A simple, efficient 2-step process using a scalper treatment followed by pneumatic separation was recommended for white and red fir seeds by Kitzmiller and others (1975). The scalper did less damage than hand de-winging, and although the pneumatic separator inflicted some injury, it eliminated most of the impurities remaining after the scalper treatment.

As described earlier, the fir seedwing forms on the adaxial (upper) surface of the developing seed and is attached to the seed by an integument. Two narrow flaps wrap around the long margins of the seedcoat toward the abaxial surface, thereby gripping the seed (figure 6). Most integuments remain attached to dry seeds after normal de-winging but often loosen and separate from the seedcoats when they become wet during a germination test. This suggests that the seeds might be de-winged when wet, but no documented use of the method is known for fir seeds.

Gravity table cleaning can be very efficient and gentle (Rooke 1994). An aspirator sorter works well for cleaning and for separating filled and empty seeds of Pacific silver, grand, and subalpine firs (and other conifer seeds), although small-filled seeds generally accumulate in the empty seed fraction, whereas large-empty seeds separate out with the filled seeds (Edwards 1979). Prior seed sizing improves the efficiency of this technique.

The IDS (incubating-drying-separating) method (see chapter 3) works well on seeds of other Pinaceae (Bergsten 1993; Karrfalt 1997; Simak 1984) and has been used to remove seeds infested with *Megastigmus spermotrophus* Wachtl. (Sweeney and others 1991). A variant of the IDS method known as density separation processing (DSP) is used to upgrade seed quality of Pacific silver and subalpine firs in British Columbia. In 12 seedlots of Pacific silver fir, an average gain in germination of 24% and an increase in potential seedlings of 48% was obtained, but gains in seedlots of subalpine fir were smaller (Kolotelo 1993). The method does not work on all seedlots, especially those with a high proportion of immature seeds, and seedlots from sources above 1,000 m elevation (Kolotelo 1994); the reasons for this are not known. Another approach to flotation sorting has been described (Edwards 1978). Separation in other liquids, such as petroleum ether (Lebrun 1967) or absolute alcohol (Simak 1973) cannot be recommended because the ether is highly flammable and alcohol is phytotoxic to true fir seeds (Edwards 1980b).

Another advantage of processing fir cones late in the year during cold weather is that low temperatures solidify any resin that has leaked from the vesicles in the seedcoat or may be present as an impurity from other sources. This makes the resin less likely to gum-up processing machinery as well as making it easier to separate from the seeds. Resin/pitch is relatively dense, so it sinks and seeds float in a water separator. Seeds may be chilled as a first step in cleaning to reduce resin problems, but additional chilling may be required as the seeds warm up (Rooke 1994). When de-winging and cleaning to the desired level of purity are complete, seed moisture contents should be checked, adjusted as required, prior to cold storage. In the past, recommended processing standards of 20 to 35% viability used to be common for commercial lots of North American fir species (WFTSC 1966), and fir seed quality traditionally was low, rarely exceeding 50% germination (Franklin 1974b). This was often the result not only of poor (by present standards) seed processing methods that failed to remove many unfilled or partially filled seeds, but also of inadequate methods for overcoming dormancy.

Typical cone and seed yields and numbers of fir seeds per unit weight are listed in table 8.

Seed storage. Fir seed storage has been intensively researched (Barton 1961; Holmes and Buszewicz 1958, 1962; Magini 1962; Wang 1974) and is summarized in table 9. Fir seeds are orthodox in storage behavior, meaning that they store well at low temperatures and moisture contents. Most experts agree, however, that the seeds lose viability quickly unless special precautions are taken, possibly because of the high oil and resin contents that (when oxidized) may be toxic to the embryo (Bouvarel and Lemoine 1958). Guatemalan fir seeds have been found to lose their viability in a few weeks; one report states that they cannot be dried below 12% moisture content and are considered recalcitrant (Anon. 1998). However, other workers recommend drying them to 6 to 8% moisture, which permits storage for nearly a year (Donahue and others 1985) (table 9). The embryonic radicle usually dies first in stored European silver fir seeds (Gogala and Vardjan 1989).

One decision that must be made is whether the seeds are to be stored for a few months or for a year or more, because lower temperatures will be required for longer periods (Tocci 1966). For example, it may be pointless to store large volumes of seeds for periods longer than the interval between good cone crops (Edwards 1982a). Although the superiority of sub-freezing conditions as low as –17 °C has been amply demonstrated (they are commonly used for long-term storage of fir and other orthodox seeds), higher temperatures (never above 4 °C) can suffice for short-term storage. Fir seeds store well for 3 to 10+ years in sealed containers (Allen 1957; Gradi 1966), but such containers are not a panacea if the seeds have not been properly prepared (Gradi 1966; Tumbarello 1960). Experiences with fir-seed storage durations and conditions have been amply reported (Allen 1957; Carrillo and others 1980; Isaac 1930a, 1934; Issleib 1956; Larsen 1922; Roe 1948b; Rohmeder 1953; Rudolf 1952; Schubert 1954; Vilmorin 1944; Vlase 1960), and cryopreservation of fir seeds also has had some success (Jorgensen 1990; Neuhoferova 1994; Stanwood and Bass 1978).

In principle, storage temperature is of greater significance when seed moisture content is high and, conversely, has less effect when moisture content is low (Barton 1953; Magini and Cappelli 1964a&b). At low moisture contents, seed storage becomes almost independent of temperature, an inverse relationship demonstrated by Danielson and Grabe (1973) in a 2-year trial with noble fir seeds that (a) deteriorated rapidly when moisture content was above 12%, irrespective of storage temperature; (b) maintained viability at 12% moisture when stored at –18 °C, but not at +5 or +20 °C; (c) maintained viability at 6 to 9% moisture when stored at –18 and +5 °C; and (d) maintained viability at 4% moisture when stored at –18, +5, and +20 °C. For firs in general, the critical safe moisture level appears to lie between 5 and 8% of seed fresh weight (Wang 1974).

Table 8—*Abies*, fir: cone measurements and yields of cleaned seeds

Species	Cone wt/vol		No. of cones		Seed wt/ cone wt		Seed wt/ cone vol		Seeds/	Seeds/wt Range		Seeds/wt Average		
	kg/hl	lb/bu	/hl	/bu	g/kg	oz/100lb	kg/hl	oz/bu	cone	/kg	/lb	/kg	/lb	Samples
A. alba	36	28	—	—	55	89	2	25	—	17,400–41,000	7,900–18,600	22,500	10,200	>72
A. amabilis	—	—	—	—	—	—	3.7	48	400	17,200–36,400	7,800–16,500	24,250	11,000	66
	—	—	—	—	—	—	—	—	—	21,800–45,900	9,900–20,800	30,450*	13,800 *	8
A. balsamea	45	35	2,700–5,500	1,000–2,000	—	—	2.9–3.6	37–46	134	66,150–208,400	30,000–94,500	131,400	59,600	42
A. concolor	39–45	30–35	—	—	32	51	1.3–2.5	17–32	185	18,950–39,100	8,600–17,720	24,500	11,100	46
A. firma	—	—	—	—	—	—	—	—	—	20,500–30.900	9,300–14,000	25,150	11,400	>12
A. fraseri	—	—	2,500–2,700	900–1,000	—	—	2.5–3.7	32–48	—	117,950–173,650	53,500–78,750	134,050	60,800	10
A. grandis	—	—	700	250	—	—	1.9–2.5	24–32	115	26,250–63,500	11,900–28,800	40,600	18,400	144
	—	—	—	—	—	—	—	—	—	—	—	44,550*	20,200*	12
A. guatemalensis	—	—	—	—	—	—	—	—	—	30,000–43,000	13,600–19,500	36,500	16,500	>2
A. homolepis	54–64	42–50	800	300	—	—	—	—	67–89	32,200–49,000	14,600–22,200	43,650	19,800	19
A. lasiocarpa	—	—	—	—	—	—	1.7	22	—	52,700–108,700	23,900–49,300	76,750	34,800	19
	—	—	—	—	—	—	—	—	—	—	—	47,600*	21,600*	4
var. *arizonica*	—	—	—	—	—	—	1.2–1.9	16–24	—	38,800–56,200	17,600–25,500	49,200	22,300	8
A. magnifica	32–39	25–30	—	—	40	64	1.4	18		8,800–19,600	4,000–8,900	14,100	6,400	36
A. mariesii	33–41	26–32	850	312	—	—	—	—	52–65	42,100–65,050	19,100–29,500	50,700	23,000	>6
A. nordmanniana	40–50	31–39	—	—	125	196	4.8–5.8	62–75	—	11,550–19,000	5,700–8,600	15,650	7,100	>24
A. procera	—	—	200	80	—	—	1.7–3.6	22–46	500	20,300–42,100	9,200–19,100	29,800*	13,500*	>36
A. sachalinensis	—	—	—	—	—	—	—	—	—	65,050–118,000	29,500–53,5000	97,000	44,000	>29
A. x shastensis	—	—	—	—	—	—	—	—	—	11,250–24,700	5,100–11,200	16,100*	7,300*	36
A. veitchii	—	—	—	—	—	—	—	—	—	50,700–173,750	23,000–78,800	99,200	45,000	17

Sources: Anon. (1998), Ching (1960), den Ouden and Boom (1965), Eis and others (1965), Fowells and Schubert (1956), Franklin (1974b), Ghent (1958), Heit (1968a), Lalu (1993), Lanquist (1946), Leloup (1956), MacDonald and others (1957), Rafn (1915), Rafn and Son (nd), Roe (1948b), Seal and others (1965), Soljanik (1950), Speers (1962), Tulstrup (1952), Wappes (1932).

* Seeds were 100% sound, separated by x-radiography.

Table 9—*Abies*, fir: experiences with seed storage conditions (recommended conditions are in **bold face**)

Species	Moisture content (% fresh wt)	Storage temp (°C)	Possible storage period (yr)
A. alba	5–7	–3 to 7	2–6
	5–8	**–10 to –17**	**15**
	< 9	–15	4–5
A. amabilis	**6–8**	**–17**	**> 5**
A. balsamea	5–8	+0.5 to +4	5
	6–8	**–17**	**13**
A. cephalonica	9–11	+ 4	1–2
A. concolor	**5–8**	**0 to –18**	**7**
	6–10	–18	3
A. firma	—	–2 to –4	> 6
A. fraseri	10–15	–12	—
A. grandis	5–8	–7	> 2
	7–10	–4 to –10	3
	11	–4	10 +
	9–11	+4	1–2
	< 9	**–15**	**> 5**
A. guatemalensis	6-8	+3 to +4	<1
A. homolepis	—	–2 to +4	> 6
A. lasiocarpa	**5–8**	**–17**	**> 5**
A. magnifica	9–11	+5	5
A. mariesii	—	–2 to +4	> 6
A. nordmanniana	9–11	+4	2
	< 9	**–15**	**> 5**
A. procera	6–9	0 to –18	7
	6–9	**–4**	**> 10**
A. sachalinensis	—	–2 to +4	> 6
A. × shastensis	11	–4	> 10

Sources: Allen (1957), Edwards (1982a), Franklin (1974b), Gradi (1966), Heit (1941, 1968b), Hofman and Vackova (1966), Holmes and Buszewicz (1962), Issleib (1956), Jones (1962), Loffler (1985), Machanicek (1965), Mormann (1956), Radulescu (1968), Speers (1974b), Tillisch (1952), Tokarz (1974).

Pregermination treatments. Dormancy in fir may be both physical and physiological, but it apparently does not reside in the embryo, because embryos excised from unstratified noble fir seeds grow just as well as those from stratified seeds (Edwards 1969). Reasons for fir seed dormancy may be poor oxygen exchange or an inhibitor, because chipping the seedcoat to expose and remove a sliver of megagametophyte was as effective as (or more so than) stratification in stimulating germination of seeds of noble, Pacific silver, and grand firs (Edwards 1969) and European silver fir (Gogala and Vardjan 1989). Stratification also probably overcomes dormancy by reducing the mechanical restraint of the tissues surrounding the embryo (Edwards 1962, 1969; Jones and others 1991; Speers 1962; Wang 1960). Length of treatment is usually 21 to 28 days for laboratory tests (AOSA 1998; ISTA 1993), but other reported periods range from 14 to 120 days, and longer periods are the rule for nursery sowing (table 10). Longer treatments should be approached with care because they may result in more fungal/bacterial damage and premature germination (Edwards 1982a; Grittanuguya 1962; MacGillivray 1955; Zentsch 1960) and are best at lower seed moisture levels, as demonstrated for various hybrid firs (Wright 1950) (see also stratification–redry method below).

As with many tree seeds, dormancy among the firs is quite variable. Although stratification is routinely prescribed for European silver and Fraser firs, there are reports (Speers 1967; Zentsch and Jahnel 1960) that some seedlots of both species show little or no dormancy. The only way to determine whether or not a lot is dormant is to perform 2 germination tests—one with stratified seeds and one with unstratified seeds (Edwards 1962). The response to stratification may be regarded as an indicator of the degree of dormancy in the lot; after stratification, more-dormant seedlots germinate more rapidly than less dormant lots. In some instances, stratification has increased total germination as well as germination rate (Jones and others 1991; Pfister 1966; Speers 1968), although this may have been due partially to the seeds' germinating before development of the

Table 10—*Abies*, fir: nursery practices

Species	Stratification time (days)	Sowing season	Bareroot production: Seedling density /m²	Seedling density /ft²	Sowing depth cm	Sowing depth in	Mulch[a]	Stock type	Container production: Container type[b]	Stock type
A. alba	0	Fall	270–430	25–40	2[c]	3/4[c]	Pine needles	—	—	—
	30[d]–80	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2, 5	1+0
A. amabilis	28[f]	Mar–Apr	270–540	25–50	0.5–1	1/4–1/2	Straw[g]	3+0, 3+1	—	—
	—	—	—	—	—	—	None	1+0, 2+0, 3+0	—	—
	—	Late Apr–early May	330/row	100/row	—	—	—	3+0, 3+1	—	—
	30[d]–120[h]	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
	30[d]–120[h]	Jan–Mar (1+0)	—	—	—	—	—	—	313A&B, 410A, PCT410, 412A, 415B&D, 615A	1+0, P+1[3]
	30[d]–120[h]	Early Mar–early April	—	—	—	—	—	—	313A, Styro 2, 5,& 7	1+0, 2+0, P+1
	30[d]–120[h]	Apr–early May (2+0) outdoors	—	—	—	—	—	—	415B,D, 412A	2+0
A. balsamea	0	Fall	220–54	20–50	—	—	—	—	—	—
	28–60[h]	Late Mar–early Apr	—	—	—	—	—	—	Styro 2, 5, 7	1+0, 2+0, P+1
A. bracteata	0	Fall	—	—	0.5	1/4	—	2+0	—	—
	14–28	Feb-Mar	—	—	—	—	—	—	313A, 415B, D, 615A	1+0, 2+0, 2+1, P+1
A. concolor	0	Fall	270–430	25–40	2[c]	3/4[c]	Pine needles, peat moss, none	2+0, 2+2, 3+0, P+1	—	—
	28–60[f]	Spring	220–540	20–50	—	—	Straw[g], none	1+0, 2+0, 2+1	—	—
	14[d]–80[h]	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
	14[d]–80[h]	Feb–mid-Apr	—	—	—	—	—	—	313A, 410A, 415B,D, 412A, 615A, Styro 2,5,7; Leach 1,2	1+0, 2+0, 2+1, P+1
	—	Apr–early May (2+0) outdoors	—	—	—	—	—	—	415B, 412A	2+0
A. firma[i]	3 0–60	Apr–early May	—	—	—	—	—	2+2	—	—
A. fraseri	0	Fall	220–540	20–50	0.3–0.5	1/8–1/4	Sawdust	3+0, 4+0	—	—
	28–60	Late Mar–early Apr	270	25	—	—	—	—	—	—
	28[d]–60[h]	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
	40—60	Mid-March–early May	330	100	—	—	—	—	—	—
	28[d]–60[h]	Jan (1+0)	—	—	—	—	—	—	415B, D, 615D	1+0
	28[d]–60[h]	Feb–early Apr	—	—	—	—	—	—	313A, 415B,D, 615D, Styro 2, 5, 7	1+0, 2+0, P+1
	28[d]–60[h]	Apr–early May (2+0) outdoors	—	—	—	—	—	—	415B, 412A	2+0
A. grandis	0	Fall	270–430	25–40	2[c]	3/4[c]	None, sawdust	2+0, 2+1, 3+0	—	—
	0[i]–42[f,g]	Spring (early Apr–early May)	215–270	20–25	0.5–2	1/4–3/4	pine needles	1+0, 2+0, 3+0, P+1	—	—
	28[d]–120[h]	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
	28[d]–120[h]	Jan–early Feb (1+0)	—	—	—	—	—	—	313A, 410A, 415B,D, 615A	1+0
	28[d]–120[h]	Early Feb–Apr	—	—	—	—	—	—	313A, 410A, 415B,D, 412A, 615A, Leach 1,2, Styro 2,5,7	1+0, 2+0, 2+1, P+1
	28[d]–120[h]	Early Mar (greenhouse)–early May (2+0) (incl outdoors)	—	—	—	—	—	—	412A	2+0, P+1
A. homolepis	30–60	Spring	—	—	—	—	—	2+2	—	—
	60–80	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2,5	1+0
A. koreana	60–80	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2,5	1+0
A. lasiocarpa var. *arizonica*	0	Fall	—	—	0.3	1/8	Leaf mold	—	—	—
	30[d]–80[h]	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2,5	1+0, 2+0

Table 10—*Abies*, fir: nursery practices (Continued)

Species	Stratification time (days)	Sowing season	Bareroot production: Seedling density /m²	Seedling density /ft²	Sowing depth cm	Sowing depth in	Mulch[a]	Stock type	Container production: Container type[b]	Stock type
A. lasiocarpa	30[d]–120	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
var. *lasiocarpa*	30[d]–120	Jan–to early Feb (1+0)	—	—	—	—	—	—	313B, 410A, 415B,D, 615A	1+0
		Jan–Mar	—	—	—	—	—	—	313A,B, 410A, PCT410,	1+0, 2+0, 2+1, P+1
	30[d]–120	Early Mar–late May (2+0)	—	—	—	—	—	—	410A, 412A, 415B,D,415B, 615A	1+0, 2+0, 2+1, P+1
	30[d]–120	(incl outdoors)								
A. magnifica var. *magnifica*	30–42[f]	Mid-Mar–early May	215–430 (330/row)	20–40 (100/row)	0.5–1.5	1/4–1/2	None	1+0, 2+0, 2+2 P+1	—	—
	30[d]–60[h]	Jan	—	—	—	—	—	—	415B,D, 615A	1+0
	—	Late Mar–early Apr	—	—	—	—	—	—	Styro 2,5,7	1+0, 2+0, P+1
A. nordmanniana	0	Fall	220–540	20–50	2[c]	3/4[c]	Pine needles, none	—	—	—
	50–70[f]	Spring	540	50	1–2.5	3/8–1	Peat moss	3+0	—	—
	14[d]–80[h]	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2,5,7	1+0, 2+0
A. pindrow	30[d]–80	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2,5	1+0
A. procera	0	Fall	220–540	20–50	2[c]	3/4[c]	Pine needles, none	1+0, 2+0, 3+0	—	—
	0[i]–42[f]	Spring	320–430	30–40	0.5–1.5	1/4–1/2	None	2+0, 3+0, 2+0	—	—
	28[d]–120[h]	Early Mar–early May	220–380	20–35	0.5–1.5	1/4–1/2	None	2+0, 3+0, 2+0	—	—
	28[d]–120[h]	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
	28[d]–120[h]	Jan–early Feb (1+0)	—	—	—	—	—	—	313B, 410A, 415B,D, 615A	1+0
	28[d]–120[h]	Feb–Apr	—	—	—	—	—	—	313B, 415B,D, 410A, 615A, Styro 2,5, Leach 1,2	1+0, 2+0, 2+1, P+1
	28[d]–120[h]	Early Mar (greenhouse)	—	—	—	—	—	—	313A	2+0, P+1
	28[d]–120[h]	Apr–early May (2+0) (incl outdoors)	—	—	—	—	—	—	415B,D, 412A	2+0
A. sachalinensis	30–60[k]	Spring	—	—	—	—	—	2+2	—	—
A. x shastensis	0[i]–42[f]	Spring	220–430	20–40	1–1.5	3/8–1/2	None	1+0, 2+0, 2+1, 3+0	—	—
	30[d]–45[h]	Late Feb–Apr	—	—	—	—	—	—	410A, 412A, Styro 5, Leach 1,2	1+0, 2+0, P+1

Sources: Adkins (1984), Adkins and others (1984), AOSA (1998), Asakawa (1968), Barton (1930), Bongio (1997), Bouvarel and Lemoine (1958), Curtis (1997), Fenimore (1997), Franklin (1974b), Garren (1997), Gates (1997), Hanson (1997), Heit (1964, 1967, 1968b), Heit and Eliason (1940), Helson (1997), Henry and Blazich (1990), Holmsgaard and Kjaer (1951), ISTA (1993), Kusisto (1997), Lehar (1997), Leloup (1956), MacDonald (1998), Moore (1997), Nagao and Asakawa (1963), NBV (1946), Pelton (1997), Rafn (1915), Rafn and Son (nd), Riskin (1997), Rutar (1991), Snyder (1997), Speers 1962, Stubley 1998, Thompson 1997, Toumey and Stevens (1928), Triebwasser (1997), Trimble (1997), Tulstrup (1952), USDA Forest Service (1948), Vacowicz (1997), Wedman (1997), Wong (1997), Wright (1950), Zemanek (1997).

a Depth of mulch: peat moss, 0.5–1.5 cm (_–_ in); pine needles, 3–4.5 cm (1_–1_ in); sawdust, 0.5 cm (_ in); straw, 5 cm (2 in).

b Containers are all PSB type; Styro = Styroblocks, PCT = copper treated. The various containers listed have the following volumes: 313A, 52 ml (3.6 in^3); 313B, 65 ml (3.9 in^3); 410A & PCT 410, 80 ml (4.9 in^3); 415B, 93 ml (6.3 in^3); 412A, 126 ml (7.7 in^3); 415D, 172 ml (10.5 in^3); 615A, 336 ml (20.0 in^3); Styro 2, 39 ml (2.3 in^3); Styro 5, 77 ml (4.7in^3); Stryo 7, 121 ml (7.4in^3); Leach 1, 50 ml (3 in^3), Leach 2, 164 ml (10 in^3).

c Seeds covered with 1 cm nursery soil plus 1 cm sand.

d For 28–30 days only if intending to strat-redry.

e Some container transplants grown as P+2, P+3, P+4.

f Stratified in wet vermiculite, wet sand, or 1.5- to 2-day running-water soak and naked stratification.

g Used overwinter on first-year seedlings.

h Some free moisture left in plastic bag for long stratification.

i Light may be beneficial to germination.

j When not stratified, soaked 2 days before sowing.

k Alternatively, bury the seeds in snow for 50 days.

extensive fungal and bacterial molding common to more-slowly-germinating unstratified seeds (Edwards 1969). In noble fir, an increasing response to stratification as the seeds matured suggested that dormancy increased also, and that dormancy and maturity are interrelated (Edwards 1969). Whereas much of the variability in dormancy among seedlots may be attributable to seed origin, crop year, and time of collection, it may also be due to methods of cone processing, seed cleaning, and seed storage (Franklin 1974b; Wang 1960).

Laboratory and nursery stratification is often performed by refrigerating previously hydrated seeds in plastic bags or other containers—the "naked stratification" method (Allen and Bientjes 1954) favored in many nurseries for its ease of seed handling. More traditionally, dry seeds (at storage moisture contents) are placed on a moist medium (filter paper, vermiculite, or wet sand) and refrigerated. The moist filter paper method produced higher germination in noble fir because it was believed that the preliminary water soak that is the first step in the naked stratification procedure damaged the seeds by too-rapid tissue hydration, a phenomenon well-documented in legumes (Jones and others 1991). Soaking temperature in this noble fir study was 4 °C. However, no direct evidence for the damage, particularly its location, was provided. It is unlikely that any damage occurred in the tissues of the embryo. When noble fir seeds were soaked in water at 25 °C, after 48 hours most of the water was still in the seedcoat: the outer region of the megagametophyte had become moist, but the embryo was still dry (Edwards 1969). It was found that noble fir embryos require hydration of between 48 and 72 hours, even at room temperature, before they absorb enough moisture to be safely excised (Edwards 1969). Furthermore, when dry noble fir seeds are placed on a moist medium and refrigerated, they absorb water slowly during the entire chilling period and achieve a higher moisture content than seeds soaked in water at room temperature for the same length of time (Edwards 1971). Thus, in the above comparison, the moisture content of soaked seeds averaged 36%, whereas that of seeds chilled on moist filter papr averaged 43% (Jones and others 1991). This difference, small as it may appear, may have been significant due to the moisture content in soaked seeds possibly being less than adequate for optimal stratification to occur. In the development of the stratification/redry method (see below), it was found that if fir seeds were initially hydrated only to 35% moisture content (the same moisture content achieved after redrying), subsequent stratification was far less effective (Edwards 1986). If noble fir seeds are sensitive to imbibitional damage as claimed (Jones and others 1991), then the stratification/redry method—which involves a preliminary soak at room temperature—must repair such damage since germination is greatly increased. However, no evidence for this repair, or the initial imbibitional-damage phenomenon, has been documented.

In any event, crop year, seed source, seed vigor (as distinct from seed quality), as well as chilling method and germination temperature played roles in the response of different seedlots of Pacific silver fir to stratification (Leadem 1986). Stratification response of Nordmann fir was also believed to be strongly seedlot dependent (Poulsen 1996). For balsam fir seeds, prolonged soaking in cold water containing a fungicide was deleterious (Kozlowski 1960), but changing the water weekly produced germination similar to that after stratification (Rudolf 1950). Best results with Manchurian fir occurred when soaked seeds were stored in snow for 1 to 2 months (Pavlenko 1972).

Stratification temperature range is often specified as 1 to 5 °C (Franklin 1974b), although testing laboratories typically use a narrower window of 3 to 5 °C. Stratifying grand and subalpine fir seeds at 2 °C was optimal (compared to –2, 5, and 7 °C), especially during extended chilling (Edwards 1982a). Fir seeds will germinate during stratification if left for a sufficient length of time (Allen 1960; Edwards 1969; Blazich and Hinseley 1984; Roe 1948b; Vabre-Durrieu 1956). Such observations reinforce the idea that stratification is incipient germination. In this regard, it should be remembered that late-dispersed seeds of numerous high-elevation firs (plus some other conifers) germinate in snow banks (Anon. 1951; Franklin and Krueger 1968; Gordon 1970; Hetherington 1965; Irmak 1961; Roe 1946; Stein 1951). Snow absorbs 99% of the infra-red (IR) radiation from sunlight, and dark-colored seeds embedded in snow may reach several degrees above freezing by absorbing these IR rays. However, these germinants seldom establish as seedlings when the snow melts (Gordon 1970; Stein 1951).

Despite the fact that lower than normal levels of seed moisture were known to benefit extended treatments of hybrid fir seeds (Wright 1950), fir seed research continued to focus on stratification temperature and duration and not on moisture level during treatment. Since the 1980s it has been demonstrated conclusively that seeds of Pacific silver, grand, subalpine, and noble firs stratified at 2 to 5 °C in plastic bags for 4 weeks (moisture content 45% or higher), then air-dried to moisture contents between 25 and 35%, can be returned to the same refrigerator for (a) another 12 months (at 25%) without significant decreases in subsequent germination or (b) a further 3 to 6 months (at 35%) with greatly enhanced germination rate and germination capacity (Edwards 1980b, 1981, 1982a,b, &c, 1986b, 1997; Leadem 1986, 1988b, 1989; Tanaka and Edwards 1986). When air-

dried to 35% and refrigerated for a further 3 months, all viable grand fir seeds germinated within 2 weeks (Edwards 1980b). This is the result of achieving a synchronicity in germination achieved by the reduced moisture content that places the embryos under a moisture stress. This stress prevents less-dormant seeds in the mixture from germinating, while allowing more-dormant seeds to achieve a ready-to-germinate state when the extended chilling ends. Subsequently, sowing the seeds on a non-moisture-limiting medium permits all the viable seeds to germinate at the same time (Edwards 1981, 1982b, 1986b). In addition, the reduced moisture content "protects" the energy supplies of the megagametophyte from being respired as rapidly as in seeds undergoing traditional stratification at high moisture content (Leadem 1993).

This process, which has become known as the stratification-redry method, differs from traditional stratification as shown diagrammatically in figure 18. During routine stratification (upper), seeds are soaked for 24 to 48 hours at room temperature, drained, chilled at 2 °C for 4 to 8 weeks in their "fully imbibed" state (moisture content around 45% or higher) until they are sown in the nursery. In the new process (lower), seeds are soaked for 24 to 48 hours at room temperature, drained, and chilled for 4 weeks while fully-imbibed (as in the old method). Then, the stratified seeds are removed from the refrigerator and air-dried to 30 to 35% moisture content. Next, they were returned to the refrigerator for an additional 1 to 3 months of chilling for the most rapid and complete germination. Alternatively, when dried to 25% moisture content and returned to the refrigerator, they can be kept for up to an additional 12 months until they are sown. The procedure has been described in detail (Edwards 1982b, c, 1986, 1997) and is now used operationally in British Columbia (Leadem and others 1990). An almost identical procedure has been described for Nordmann fir seeds (Jensen 1997; Poulsen 1996), and control of moisture level during stratification has been recommended for Guatemalan fir (Donahue and others 1985).

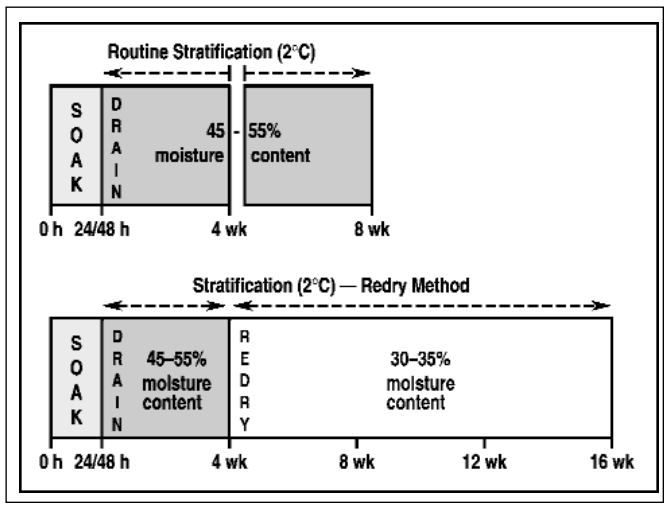
As described above, seeds air-dried to 25% moisture content can be "stored" in the refrigerator for up to a year without losing the beneficial effect of the initial stratification, that is, they remain in a ready-to-germinate state. Stratified seeds of noble and Pacific silver firs have been dried to 5 to 9% moisture content and stored for 1 year, after which they germinated significantly better than the original controls (Hall and Olson 1986). For the seedling grower, these methods allow stratification to begin well in advance of nursery sowing date and/or make the sowing date more flexible (Edwards 1980b, 1981, 1982a, 1986b). Two additional beneficial effects of redrying (to either 35 or 25%) observed in the laboratory were that fungal and bacterial molding of seeds was greatly reduced and that emerging radicles were more positively geotropic than in germinants from routinely stratified seeds. This latter is important in that germination in firs is epigeal (figure 19) and a vigorous healthy radicle is essential for successful seedling establishment.

There is little reported evidence of the use of gibberellins increasing fir seed germination, but a combination of stratification for 40 to 60 days and treatment with 200 ppm GA_3 worked well for Guatemalan fir seeds (Salazar 1991). Use of gibberellin GA_{4+7} improved dark-germination of Fraser fir at 30/20 °C over a 42-day test but was ineffective (light or dark) at 20/15 °C unless the seeds were first hydrated for 20 hours (Henry and Blazich 1988). The beneficial effect of an auxin has been reported in Sakhalin fir (Yoshida 1960).

Germination tests. Stratification treatments for 10 fir species regarded as consistently dormant are prescribed in seed testing rules (AOSA 1998; Edwards 1987; ISTA 1993), whereas double (paired) tests (with and without stratification) are recommended for 8 other species in which dormancy varies among seedlots. West Himalayan fir might be added to the list of species requiring double tests (Khattak and Ahmad 1980), but Korean fir is consistently dormant (Jakimova 1965). The officially prescribed stratification period for all fir species is either 21 or 28 days, the longer period being favored by the AOSA rules for 6 species.

Alternating temperatures of 30 °C with light for 8 hours and 20 °C for 16 hours without light are standard for most fir species, with 3 notable exceptions. For Pacific silver fir, the current AOSA prescription is for 25 °C (light) for 8 hours and 15 °C (dark) for 16 hours. However, seeds of this species germinate more slowly but more completely at 15 °C (light) for 8 hours and 10 °C (dark) for 16 hours (Leadem 1986). Similarly, subalpine fir seeds stratified for 8 weeks germinate well under a 25/15 °C regime (Hansen and Leivsson 1990; Leadem 1989), whereas Fraser fir seeds stratified for 12 weeks germinate well at 20 °C for 8 hours with light for 1 hour (only) during the latter part of this warm period, followed by 10 °C (dark). If stratified for 8 weeks only, Fraser fir seeds should be tested at the standard 8/16 hours 30/20 °C, with a 1-hour light treatment during the higher temperature (Adkins 1984; Adkins and others 1984; Henry and Blazich 1990). The involvement of phytochrome has been demonstrated in the germination responses of Fraser fir (Henry and Blazich 1990) and is suspected in several other firs (Li and others 1994; Nagao and Asakawa 1963; Messeri and Salvi 1964), making it essential to use fluorescent-only lighting for laboratory tests (Asakawa 1959; Blazich and Hinseley 1984; Nagao and Asakawa 1963).

Figure 18—*Abies*, fir: schematic comparison between traditional stratification (**upper**) and the newer stratification–redry method (**lower**).



The germination substrate is usually kept at its maximum moisture-holding capacity so the test samples are not under any moisture stress but without excess free water present. Full germination of Pacific silver and grand fir seeds was unaffected unless the medium was moistened to below 40% of maximum holding capacity (Edwards unpublished data). However, completeness of germination, and germination rate of west Himalayan fir seeds was highly sensitive to moistening the filter paper with PEG (polyethylene glycol) solution (Singh and others 1986). Many laboratories use a paper/blotter substrate as this allows easy evaluation of the radicles (figure 20), but porous mineral substrates such as perlite, vermiculite, and Sponge Rok® may be employed also. Tests conducted according to standard laboratory prescriptions usually terminate after 21 or 28 days, although those on unstratified seeds may continue for 35 or 42 days. As a means of predicting operational sowing requirements in nurseries, some agencies test stratified true fir seeds in fumigated soils at temperatures of around 24 °C during the day and 18 °C at night (Johnson 1984).

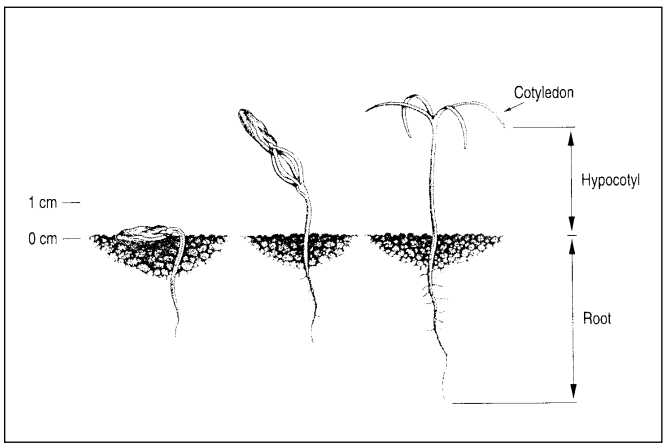
By the time newly harvested fir seeds have been processed, there is often insufficient time to complete standard germination tests that require a minimum of 3 weeks for completion, and more than twice this duration if the seeds must be stratified, before they are required for sowing the following spring. To provide more rapid estimates of seed quality, several so-called quick tests have been developed. The simplest is the cutting test, but it is also the least reliable because it fails to detect seeds damaged during handling and processing or that have died during storage. The cutting test invariably overestimates seed quality in grand (Rohmeder 1960b) and European silver fir seeds (Enescu 1968; Ducci and Paci 1986).

Where equipment is available, x-radiography quickly determines percentages of filled seeds of several fir species (Edwards 1982a,b&c; Speers 1967) and provides indirect indications of seed viability (Allison 1980) that are more accurate in fresh than in stored seeds of white fir (Eden 1965). When barium chloride was used as an contrast agent, x-radiography tended to over-estimate the viability of poor-quality seeds and under-estimate that of high-quality seeds of Siberian fir (Scerbakova 1964). When chloroform was used as the contrast agent, there was fairly good agreement with standard tests for seedlots of Pacific silver fir below 30% germination, but in general the germination capacity was over-estimated (Edwards 1982a; Leadem 1984).

Hydrogen peroxide has been used *in lieu* of stratification to stimulate germination in subalpine (Shearer and Tackle 1960), European silver (Simak 1970), and grand firs (Gyimah 1977), but not in Pacific silver fir (Edwards 1982a; Edwards and Sutherland 1979). For a rapid viability test, hydrogen peroxide gives results in 5 to 9 days with viable seeds producing visible radicles. The results correlate well with the standard germination test for noble, grand, and white fir lots between 24 and 64% germination (Ching and Parker 1958), but the method under-estimates germination capacity in lots below 30% (Edwards 1982a; Leadem 1984). As with other rapid viability assessments, the hydrogen peroxide test does not provide any information about the speed of germination, or the requirement for stratification (Johnson 1984).

Official prescriptions for tetrazolium chloride (TZ) staining tests of fir have been developed (AOSA 1998; Buszewicz and Holmes 1957; ISTA 1993; Knierim and Leist

Figure 19—*Abies amabilis*, Pacific silver fir: germinant and seedling development at 3, 5, and 7 days after germination.



1988). Tetrazolium test results often correlate with seedling emergence experienced in nursery sowings (Franklin 1974b). Tetrazolium agreement with standard germination tests can vary among lots of many species (Ducci and Paci 1986; Flemion and Poole 1948; Leadem 1984; Rohmeder 1960b), and a "best estimate" of 2 methods (for example, hydrogen peroxide and TZ) has been proposed for rapid tests (Edwards 1982a). An excised embryo method that requires about 1 week for assessment of European silver fir has been described (Nyholm 1956), but no official prescriptions for fir have been developed. Although "quick tests" may be completed in a matter of hours, or days, compared to weeks required for standard germination tests, not only do they over-estimate (Franklin 1974b; Rohmeder 1960b; Stein 1967) or underestimate (Edwards 1982a; Leadem 1984) viability of fir seeds, they are more time (and labor) consuming, and a single skilled analyst can complete fewer quick tests per month than standard germination tests. They also require a high degree of skill and experience to perform them consistently and well. Their technology was described as unreliable for firs (Edwards 1982a), and it remains so.

Although a number of vigor tests have been devised for agricultural and vegetable seeds (AOSA 1983; ISTA 1995), no tests have been adapted, or are widely used, for firs. However, it is known that stratification broadens the temperature range for optimal germination of Pacific silver (Davidson and others 1984) and grand firs (Wang 1960), and that the stratification/redry method (described earlier) broadens the range even further (Davidson and others 1984). This temperature-range broadening is a sure sign of increased vigor (Grabe 1976). One distinction between seed vigor and seed germination can be seen in the effects of long-term seed storage, which causes a reduction in plant percentage in the nursery before it affects germination percentage (Giannini and Murazio 1972; Muller 1977, 1980). Seed vigor was related to germination rate, seed protein levels, and seed respiration, all of which were thought to have potential for development as quantifiable indices of this variable in subalpine fir (Leadem 1988a&b, 1989).

Figure 20—*Abies lasiocarpa*, subalpine fir: stages in seed germination, from an ungerminated seed (**lower left**) to a 3-day-old germinant (**upper right**) (courtesy of D. Pigott).

Nursery practice. Fir seedlings are grown as both bareroot and container stock. A 1997 survey found 20 nurseries growing almost 21 million seedlings of 16 (including 6 non-native) fir species for reforestation purposes. Several other exotic firs are grown, especially in the northeastern United States, for Christmas trees (Girardin 1997a&b). For bareroot sowing in the past, most Pacific Northwest and California nurseries stratified for 1 to 2 months (table 10) at 0 to 3 °C, and sowed between mid-April to mid-May (exceptionally as late as June), favoring a seedling density of 270 to 330 seedlings/m^2 (25 to 30/ft^2) (Lavender 1979) (table 10). Bareroot sowing rates for Pacific silver, grand, subalpine, and noble firs in British Columbian nurseries usually were lower—220 to 240/m^2 or 260 to 300/linear m of seed bed (20 to 23/ft^2 or 79 to 91/linear ft of seed bed)—to produce more open-grown plants (Arnott and Matthews 1982).

Although seeds of European silver, balsam, and Fraser firs normally may be fall-sown in bareroot beds without stratification (table 10) as are seeds of noble and white firs raised in European nurseries (Franklin 1974b)—spring-sowing of stratified seeds has been recommended for balsam (Roe 1948b), and European silver firs (Neubacher 1959; Paiero and Piussi 1964; Vlase and Iesan 1959). Fall-sowing of freshly collected fir seeds may not be possible because seed processing is incomplete, so sowing the following spring provides the earliest opportunity. Spring-sowing of stratified seeds is the traditional standard for most western North American species (table 10), which minimizes losses from birds, rodents, and adverse weather (Lanquist 1946). Merely soaking grand fir seeds can be beneficial (Hofman 1966). Sowing unstratified seeds of grand and noble firs in January to March or stratified seeds in April gave satisfactory results in the United Kingdom (Faulkner and Aldhous 1959). Most bareroot nurseries use a seedling caliper between 2.5 and 5 mm (metric measure only) for culling purposes.

Fir seedling production in Canadian nurseries is now entirely from container systems (figure 21), a method widely used in the United States also. In container nurseries, sowing usually occurs in the spring, as early as January or as late as June (for stock being grown for $1^1/_2$ seasons) (table 10). Nearly all container-grown firs are started in greenhouses to provide warm temperatures for germination and early growth and then moved to cooler shadehouses during the hotter part of the summer; alternatively, the greenhouse covers (or sides) may be removed. January-sown seedlings maybe ready for mid-October planting, but more optimal dormancy and frost-hardiness is achieved by delaying planting until mid-November. However, high-elevation sites then may be inaccessible, so cold storage is required to keep stock dormant until spring planting. If noble fir seedlings are to be fall-planted, it is important to switch to cool conditions by mid-summer to achieve adequate cold-hardiness (Owston and Kozlowski 1981). Although stock quality varies widely according to planting site requirements, 1+0 seedlings 7.5 to 10 cm tall with 2.5-mm caliper are acceptable provided the root plugs remain intact on extraction from the containers (Owston 1979).

Many container nurseries stratify fir seeds by soaking them in cold water, then draining them and placing them in large plastic bags. Water temperature is normally uncontrolled and is ambient for the local supply. Seeds to water ratio (by volume) should be at least 1:3. Running water soaks, or water changes during longer soaking periods, are quite common and are used especially to help clean seeds of pathogens (Campbell and Landis 1990). One nursery follows the initial soak with a brief dip in 1% hydrogen peroxide to control fungal infections, but the efficacy of this has not been verified. After draining, no more than 2 to 2.5 kg (5 lb) of seeds are placed in plastic bags that are either loosely tied (Jones and others 1991) or have a breather tube inserted (before the tops of the bags are tied) to ensure gas exchange with the outside air (Johnson 1984). Hanging the bags from a bar in the chilling facility assures that free water will continue to drain to the bottom, and several pin pricks in the bag will allow any excess moisture to drain away. At least once weekly (several times being preferred by some operators) the seeds are rolled within the bags to bring those from the center or bottom of the mass near the top. This provides maximum exposure to the air and ensures that moisture remains evenly distributed and all seeds achieve the chilling temperature. Water is added if the seeds appear to be drying. Several nurseries now use the stratification/redry method (see the section entitled Pregermination Treatments), or a variation thereof, for improving germination in 12 species (table 10). Not every user succeeds with this technique, possibly due to differences in seedlot dormancy, because—as with routine stratification—the stratification/redry method has a greater effect on more-dormant fir seeds, less-dormant lots not benefiting as well.

Container seedlings of grand and noble firs grow quickly and evenly, so that 10- to 15-cm-tall plants can be obtained about 20 weeks after sowing without using extended photoperiods. By artificially increasing daylengths to 18 hours, similarly sized Pacific silver fir seedlings (figure 21) can be produced, but subalpine fir plants generally set bud early and achieve no more than 6 cm of height (Arnott and Matthews 1982; Gates 1994). When 5-month-old container-grown Fraser fir seedlings were naturally chilled outdoors through mid-November (fluctuating temperatures and natural photoperiods), then returned to a greenhouse, at 15 months they were taller than conventionally grown 3+1 and artificially chilled plants (Seiler and Kreh 1987).

Most containers are made of Styrofoam® blocks with cavities (Sjoberg 1974) or trays of individual plastic cells; cavity and cell volumes vary widely (table 10). In general, smaller containers are used for early sowing if the stock is to be transplanted. Later sowings use bigger containers to produce bigger plants, some of which may be transplanted also (table 10). The principles of container nursery technology are well established (Landis and others 1989, 1990a&b, 1992, 1995), and the concept is now widely accepted.

Herbicides are not used at most container nurseries, whereas bareroot facilities employ a range of chemicals; recommendations for some of these (and for damping-off control) have been published (Imai and others 1955; Roe 1948b; Sanftleben 1989; Sato 1962; Singh and Bhagat

Figure 21—*Abies amabilis*, Pacific silver fir: seeds germinating in a container nursery; wooden toothpicks (left-rear of cavities) were used to mark the progression of germination for a research trial (courtesy of C. L. Leadem).

1989). Pesticide use changes over time, so nursery operators should seek the advice of local extension agents for current recommendations.

In bareroot beds, irrigation control may be combined with wrenching, side pruning, and undercutting to assist in achieving seedling dormancy. Undercutting is often repeated, for example at 2-week intervals beginning in late July/early August for 1+0 bareroot stock. For 2+0 seedlings, a combination of sidepruning, wrenching, and undercutting before new growth gets underway (late February/early March), and at other times during the second growth season, is practiced. In contrast, irrigation control is seldom used to regulate the growth cycle in container nurseries because seedlings of many fir species are drought-intolerant. Some nurseries recommend a moist growing regime, as if growing spruce stock, whereas others may reduce irrigation late in the growing season when target heights are assured. Induction of seedling dormancy and better height control are achieved by the use of black-out control (short photoperiods) in several nurseries. Black-out followed by a 4-week rest period and then 1 to several weeks of 23-hour photoperiods may give a slight increase in height growth. Several cycles of black-out and extended photoperiod can induce multiple flushes in 1+0 seedlings of Pacific silver and subalpine firs to ensure that they reach target height as 2+0 crops. However, the second year reflush (in late March as the greenhouse temperature is raised) is sensitive to molding because the emerging new foliage tends to collect a large drop of water.

Extended photoperiods (16- to 23-hour days) during the accelerated growth phase, beginning 4 weeks after sowing for early-sown stock and continuing almost the entire season, are used in many container facilities. Except where high sunlight is encountered, shading usually is not employed. Greenhouse roofs may be removed during the summer to increase light levels and improve cooling. Shading bareroot seedbeds for 2 months after germination and hoeing or hand pulling to control weeds is advised for European silver fir (Vlase and Iesan 1959), but open beds receiving full light are best for noble fir (Schwenke 1956, 1961).

Lifting dates for 1+0 container stock vary from August for “hot” (that is, immediate) planting or transplanting, to mid-November/December for planting the following spring. Depending on weather conditions (such as snowmelt), lifting from bareroot beds may extend from December through March.

Fir seedlings are shippable as 1+0 plugs (85% of total container production), 2+0 plugs, and P+1 (transplanted from containers to outside beds); in addition, some container transplants may be shipped as P+2, P+3, or even older stock (table 10) depending on the species and customer requirements. Plug stock may be transplanted both spring and fall (August), fall transplantation giving larger seedlings but at the risk of damage during the first winter. Bareroot 2+1 seedlings are reported to perform better when transplanted in the fall.

Shippable heights for container seedlings vary between 13 cm (5 in) for 1+0, and 15 cm (6 in) to 26+ cm (10+ in) in 2+0. Transplants from containers may be between 20 cm (8 in) to 46 cm (18 in), averaging 30 to 36 cm (12 to 14 in). Root caliper generally varies from 2.5 to 3.5 mm for 1+0 stock of all fir species and up to 6 mm for 2+0. Sizes of shippable bareroot stock are not well defined, depending largely on contract requirements.

To overwinter stock in bareroot beds, some nurseries find mulches such as peat moss, pine needles, sawdust, and straw beneficial, especially during the first winter (table 10). Protection of 1+0 seedlings can be accomplished also by sowing seeds between rows of transplants (Anon. 1977). Germination and seedling survival of west Himalayan fir was improved by sowing the seeds 15 to 20 mm ($^1/_2$ to $^3/_4$ in) deep (Singh and Singh 1984), then covering the beds with 10 to 15 cm (4 to 6 in) of humus (Singh and Singh 1990); other aspects of nursery culture of this species have been reviewed (Sharma and others 1987).

Vegetative propagation of Fraser fir, which is easy to graft and air-layer and readily produces roots on stem cuttings, is transforming the production of this species for the all-important (4 to 5 million trees annually) eastern North America Christmas tree market (Blazich and Hinesley 1994, 1995). A genetically improved balsam fir Christmas tree, with increased foliage density and higher frost resistance, has been field tested (Girardin 1997b).

Micropropagation techniques have been applied to selected firs, and regeneration of somatic embryos using seed explants of European silver fir (Gebhart 1990; Hartmann and others 1992), and Pacific silver fir (Kulchetscki and others 1995) have been obtained. However, the problems encountered with Fraser and balsam firs make cloning of these 2 species by micropropagation a future development (Blazich and Hinesley 1994).

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Fabaceae—Pea family

Acacia L.

acacia

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Growth habit, occurrence, and use. The acacias include about 1,200 species of deciduous or evergreen trees and shrubs widely distributed in the tropics and warmer temperate areas (Guinet and Vassal 1978). Nearly 300 species are found in Australia and about 70 in the United States. Some 75 species are of known economic value, and about 50 of these are cultivated. Certain species of acacias—Cootamundra wattle (*A. baileyana* F. Muell.), Karoo thorn (*A. karroo* Hayne), golden wattle (*A. pycnantha* Benth.), and others—rank among the most beautiful of all flowering trees, and many have been planted in the warmer regions of the United States (LHBH 1976; Menninger 1962, 1964; Neal 1965). Acacias produce many benefits: collectively they yield lumber, face veneer, furniture wood, fuelwood, and tannin; and such products as gum arabic, resins, medicine, fibers, perfumes, and dyes; some are useful for reclamation of sand dunes and mine spoils, and for shelterbelts, agroforestry hedgerows, and forage; and some serve as a host for the valuable lac insect (ACTI 1980; Prasad and Dhuria 1989; Turnbull 1986). They are valuable not only to the forest but also to pastures and agricultural crops for the nitrogen that is fixed in their root nodules (Hansen and others 1988).

Green wattle, introduced to Hawaii about 1890, has been declared noxious for state land leases (Haselwood and Motter 1966). A fast-growing tree of no local value, it spreads rapidly by seeds and root suckers, crowding out other plants. More than 90 years ago, Maiden (1908) commented on the pestiferous nature of several varieties of this species in Australia. Only acacia species that do not spread by suckering should be selected for planting. Also to be avoided under most circumstances are the thorny acacias—such as sweet acacia and gum arabic tree—which are widely dispersed rangeland pests. These 2 species are know to exert allelopathic effects on plants growing near them (Hampton and Singh 1979; Singh and Lakshminarayana 1992). Reliable seed data are available on 8 species (table 1), all of which grow naturally or are widely planted in the United States or associated territories.

Flowering and fruiting. Acacia flowers are perfect or polygamous; most of them are yellow, some are white. They usually appear in the spring or summer. The fruit is a 2-valved or indehiscent legume (pod) that opens in the late summer. The 1 or more kidney-shaped seeds (figure 1) that develop per fruit are usually released by the splitting of the legume. The seeds contain no endosperm (figure 2). Acacias begin bearing seeds between 2 to 4 years of age (Atchison 1948; Turnbull 1986). There are good seedcrops nearly every year and seed production can be quite high. Individual trees in a mangium plantation were reported to produce 1 kg (2.2 lbs) of seeds (about 100,000 seeds) annually (ACTI 1983). Seeding habits of 8 acacias are listed in table 2.

Collection, cleaning, and storage. Ripe acacia legumes are usually brown. They can be picked from the trees, or fallen legumes and seeds can be collected from underneath the trees. Collections from the ground may include legumes more than a year old. Seeds can be extracted by hammermilling, trampling, or placing the

Figure 1—*Acacia,* acacia: seeds (3 to 12 cm): *A. melanoxylon*, blackwood (**top**); *A. decurrens*, green wattle (**left**); *A. koa*, koa (**right**).

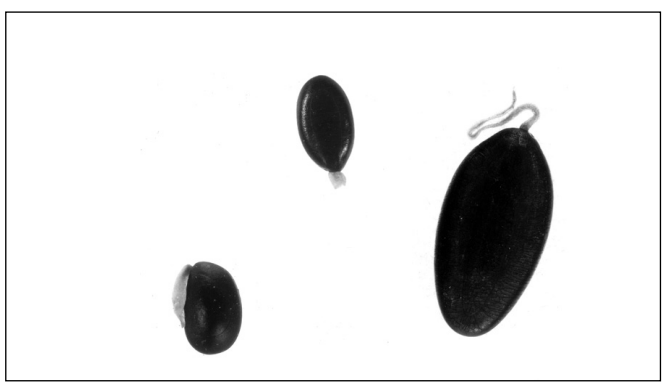
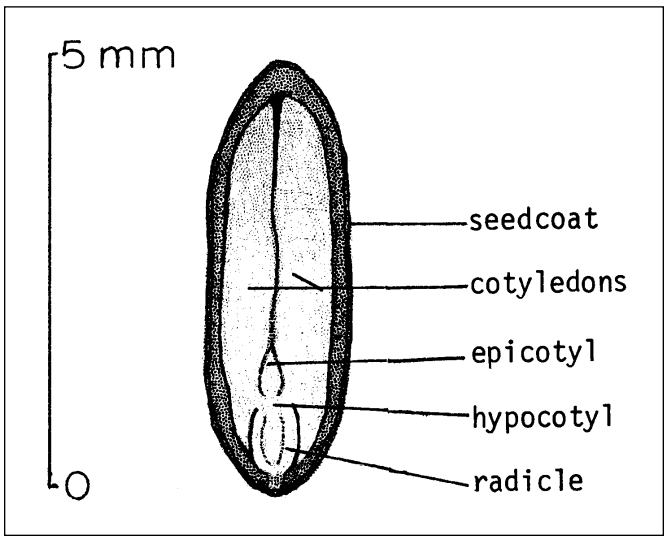


Table 1—*Acacia,* acacia: nomenclature, occurrence, and height

Scientific name & synonym(s)	Common names	Occurrence		Height at maturity (m)
		Native	US	
***A. auriculiformis* A. Cunningham ex Benth.**	**earleaf acacia**	Australia	Florida & Puerto Rico	12–30
***A. decurrens* Willd.** *A. decurrens* var. *normalis* Benth.	**green wattle**, black wattle, Sidney black wattle	Australia	California & Hawaii	8–18
***A. farnesiana* (L.) Willd.** *Vachellia farnesiana* (L.) Wright & Arn.	**sweet acacia**, *huisache*, aroma	France & Italy	S US, Puerto Rico, & Virgin Islands	3–5
***A. koa* Gray**	**koa**	Hawaii	Hawaii	24–34
***A. mangium* Willd.** *Mangium montanum* Rumph.	**mangium**	Indonesia, New Guinea, & Australia	Hawaii & Puerto Rico	12–30
***A. mearnsii* de Wildeman** *A. decurrens* var. *mollis* Lindl.	**black wattle,** green wattle, black wattle	Australia	California & Hawaii	15
***A. melanoxylon* R. Br. ex Ait. f.**	**blackwood**, Australian black wood, Tasmanian blackwood, black acacia, Sally wattle	Australia	California & Hawaii	24–36
***A. nilotica* (L.) Willd. ex Delile** *A. arabica* (Lam.) Willd. *Mimosa nilotica* L	**gum arabic tree,** Egyptian thorn, red heat	Asia & Africa	Puerto Rico & Virgin Islands	3–20

Source: Anderson (1968), Barrett (1958), Fagg (1992), Munoz (1959), Parrotta (1992), Turnbull (1987), Whitesell (1974).

Figure 2—*Acacia melanoxylon*, blackwood: longitudinal section through a seed.



legumes in a cloth bag and flailing it against the floor. Seeds are sometimes separated by feeding the legumes to cattle and collecting the seeds from the manure (NFTA 1992). Blowers and shakers will remove legume fragments and debris satisfactorily for most species. The weights of cleaned seeds for 8 species are listed in table 3 (Goor and Barney 1968; Letourneux 1957; Mangini and Tulstrup 1955; Salazar 1989; Turnbull 1986; Whitesell 1964, 1974). Seeds of blackwood collected and cleaned in Uruguay had a purity of 93% (Whitesell 1974).

Acacia seeds are among the most durable of forest seeds and need not be kept in sealed containers, although it is still advisable to do so. If kept in a cool, dry place, the seeds of most acacia species will germinate after many years of storage. For example, 63% of green wattle seeds germinated after 17 years in storage (Atchinson 1948). Seeds of blackwood, which were air-dried to a constant weight and then stored in sealed containers, retained viability unimpaired for at least 3 months; seeds stored in the open still retained 12% viability after 51 years (Whitesell 1974). Koa seeds lying on the ground are known to have retained their ability to germinate for as long as 25 years (Judd 1920).

Pre-germination treatments. The seeds of most species have hard coats that cause poor germination unless they are first scarified by briefly treating them with sulfuric acid or soaking in hot water (Gunn 1990; Kumar and Purkayastha 1972; Natarajan and Rai 1988; Rana and Nautiyal 1989). Hot water treatment is the most practical. The seeds are placed in hot or boiling water, the source of heat removed, and the seeds allowed to soak for 3 minutes to 24 hours (Clemens and others 1977). Blackwood seeds subjected to 90 to 100 °C water for 3 minutes and than stratified at 4 °C for 4 to 6 weeks germinated at a rate of

Table 2— *Acacia,* acacia: phenology of flowering, fruit ripening, and seed dispersal

Species	Location	Flowering	Fruit ripening	Dispersal
A. auriculiformis	Florida	Mar–Apr	Jun–Jul	Aug–Dec
A. decurrens	California	Feb–Mar		
A. farnesiana	Puerto Rico	Nov–Feb	Mar–Sep	Mar–Dec
A. koa	Hawaii	Jan–Jul	Jun-Jul	Feb; Jun–Nov
A. mangium	Puerto Rico	Mar–Apr		May–Aug
A. mearnsii	California	Jun & later	Jun–Oct	Jun–Oct
A. melanoxylon	California	Feb–Jun	Jul–Nov	Jul–Dec or later
	Hawaii	May–Jun		
A. nilotica	Puerto Rico	Almost continuously	All year	All year

Sources: Parrotta (1992), Turnbull (1986), Whitesell (1974).

Table 3—*Acacia,* acacia: legume (pod) and seed data

Species	Legume size (cm)		Cleaned seeds/wt	
	Length	Width	/kg	/lb
A. auriculiformis	5–10	1.3	30,000–158,000	14,000–72,000
A. decurrens	10	—	53,000–88,000	26,000–40,000
A. farnesiana	4–7	2.0	7,600–13,000	3,000–6,000
A. koa	3–6	1.5–2.5	5,300–16,300	2,000–7,000
A. mangium	3–12	1.3	80,000–110,000	36,000–50,000
A. mearnsii	5–8	—	33,000–74,000	15,000–34,000
A. melanoxylon	4–13	1.0	44,000–88,000	20,000–40,000
A. nilotica	5–15	0.8–1.6	5,000–16,000	2,000–7,000

Sources: ACTI (1983), Fagg (1992), Goor (1968), Letourneux (1957), Magini and Tulstrup (1955), NFTA (1987a,b), Salazar (1989), Turnbull (1986), Whitesell (1974).

over 98% and grew 25% faster than control seedlings in the first 3 months (De Zwaan 1978). Some species also appear to require 2 to 4 months of "after-ripening" in dry storage before good germination may be obtained (Whitesell 1974). Germination is epigeal.

Germination testing. Prescriptions for official testing for acacias call for clipping, nicking, or filing through the seedcoats and soaking in water for 3 hours, or soaking seeds in concentrated sulfuric acid for 1 hour, then rinsing thoroughly (ISTA 1993). Germination should then be tested on moist blotter paper at alternating 20/30 °C or constant 20 °C for 21 days. Germination tests of acacias can also be made in flats with sand or soil. Results of tests for 8 species of acacias are given in table 4**.**

Nursery and field practice. After proper pretreatment, the small-seeded acacias should be covered with 6 to 12 mm (1/4 to 1/2 in) of soil. Optimum sowing depth for sweet acacia seeds was found to be 2 cm (3/4 in) (Scifres 1974). A 2:1 mixture of soil and sand proved to be a better germination medium for gum arabic tree than other mixtures of soil, sand, and manure (Bahuguna and Pyare 1990). The use of sawdust in germination mixtures was found to inhibit the germination of mangium (Newman 1989b). Sowing is done in spring in the warm temperate zone of the United States mainland and year-round in tropical areas, except during dry periods. Earleaf acacia can be grown from cuttings treated with indole acetic acid (IAA) with a high degree of success (Huang 1989). Seedlings of mangium and earleaf acacia inoculated with Bradyrhizobium and Rhizobium bacterial strains nodulated, but only the Bradyrhizobium strains fixed nitrogen (Galiana and others 1990). Blackwood is preferably outplanted as small 1.25-cm ($^{6}/_{10}$-in) stumps lifted from a seedbed 1 year after planting (Parry 1956) or as transplanted seedling 20 to 25 cm (7.8 to 9.8 in) high (Streets 1962). The best survival for koa planted in Hawaii is obtained with potted seedlings. Mangium is usually planted as potted (plastic nursery bags, or polybags) seedlings but may be planted bareroot (Webb and others 1984). Container seedlings 20 cm (7.8 in) high were recommended for earleaf acacia (Wiersum and Ramlan 1982).

Table 4—*Acacia,* accacia: pregermination treatments, germination test conditions, and results

Species	Seed source	Pretreatment	Germination test conditions: Medium	Temp (°C)	Duration (days)	Germination (%)
A. auriculiformis	Puerto Rico	None	Soil	—	21	56
	Puerto Rico	Hot water	Soil	—	14	30
	Java	Warm water	Soil	—	85	—
A. decurrens	—	—	—	—	—	74
A. farnesiana	Puerto Rico	Abrasion	Paper	79	30	56
A. koa	Hawaii	Hot water	Soil	—	30	18
A. mangium	Australia	Hot water	—	—	10	80
A. mearnsii	—	—	Soil	60	14	72
A. melanoxylon	Tasmania	Hot water	Paper	77	60	70
	Tasmania	Hot water	Paper	77	30	74
	Victoria	Hot water	Paper	77	90	93
	Uruguay	None	—	—	30	4
	Uruguay	H_2SO_4	—	68	21	48
	Uruguay	Abrasion	—	68	28	26
	—	—	Soil	—	15	52
A. nilotica	—	Hot water	—	75	85	—
	—	Hot water	Soil	—	30	74

Sources: ACTI (1983), Francis and Rodriguez (1993), Newman (1989a), Parrotta (1992), Webb and others (1984), (1986), Whitesell (1974).

Plantable seedlings of gum arabic tree were produced in India by planting pretreated seeds in May in polybags containing a nursery mixture in full sun and fertilizing them twice (Kumar and Gupta 1990). The use of straw mulch increased the emergence of direct-seeded sweet acacia in old fields (Vora and others 1988).

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A

Aceraceae—Maple family

Acer L.

maple

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Growth habit, occurrence, and use. Maples—members of the genus *Acer*—are deciduous (rarely evergreen) trees; there are 148 species (de Jong 1976; Van Gelderen and others 1994). The majority of species originate in central and eastern Asia, China, and Japan (de Jong 1976; Van Gelderen and others 1994; Vertrees 1987). There are several taxonomic treatments available for the genus. Vertrees (1987) and Van Gelderen and others (1994) should be consulted for a discussion and comparison of the different classifications. Van Gelderen and others (1994) recognize 16 sections, some of which are further divided into 2 to 3 series. The publications by De Jong (1976), Van Gelderen and others (1994), and Vertrees (1987) are filled with interesting information and are wonderful reference books for the genus *Acer*.

Based on the classification of Van Gelderen and others (1994), there are 9 species in the United States and Canada (tables 1 and 2). In addition, there are 8 taxa closely related to sugar maple—these include black maple, Florida maple, bigtooth maple, and whitebark maple—as well as a number of subspecies for others. Van Gelderen and others (1994)

Table 1—*Acer,* maple: nomenclature, occurrence, and uses

Scientific name & synonym(s)	Common name(s)	Occurrence
***A. circinatum* Pursh**	**vine maple,** mountain maple	SW British Columbia to N California E side of Cascades W to Pacific Coast
***A. ginnala* Maxim.**	**Amur maple,** Siberian maple	NE Asia; introduced to N & central Great Plains
***A. glabrum* var. *glabrum* Torr.**	**Rocky Mountain maple,** dwarf maple, mountain maple	SE Alaska, S to S California, E to S New Mexico, N to Black Hills, South Dakota
***A. grandidentatum* Nutt.**	**bigtooth maple**, sugar maple	SE Idaho, S to SE Arizona, E to S New Mexico & northern Mexico, N to W Wyoming
***A. griseum* (Franch.) Pax**	**paperbark maple**	Central China & Japan
***A. macrophyllum* Pursh**	**bigleaf maple,** broadleaf maple, Oregon maple	Pacific Coast from W British Columbia S to S California
***A. negundo* L.** *Negundo aceroides* (L.) Moench.	**boxelder,** ashleaf maple, California boxelder	Throughout most of US & prairie provinces of Canada*
***A. palmatum* Thunb.**	**Japanese maple**	Japan, China, & Korea
***A. pensylvanicum* L.** *A. striatum* DuRoi.	**striped maple,** moosewood	Nova Scotia, W to Michigan S to Ohio, E to S New England, mtns of N Georgia
***A. platanoides* L.**	**Norway maple**	Europe & the Caucasus; introduced to central & E US
***A. pseudoplatanus* L.**	**planetree maple,** sycamore maple	Europe & W Asia; introduced to central & E US
***A. rubrum* L.** *A. carolinianum* Walt.	**red maple,** soft maple, swamp maple	Throughout E US & southern Canada from SE Manitoba & E Texas to Atlantic Coast
***A. saccharinum* L.** *A. dasycarpum* Ehrh.	**silver maple,** river maple, soft maple	New Brunswick, S to NE Florida NW to E Oklahoma, N to central Minnesota
***A. saccharum* Marsh.** *A. saccharophorum* K. Koch	**sugar maple,** rock maple, hard maple	New Brunswick, S to central Georgia, W to E Texas, N to SE Manitoba
***A. spicatum* Lam.**	**mountain maple**	Newfoundland, S to New Jersey, W to Iowa, N to Saskatchewan, S in Appalachian Mtns to N Georgia

Sources: De Jong (1976), Dirr (1990), Fischer (1990), Olson and Gabriel (1974), Rehder (1940), Van Gelderen and others (1994), Vertrees (1987), Viereck and Little (1972).

* Introduced into subarctic interior Alaska, where it forms a small tree and produces viable seeds (Viereck 1996).

Table 2—*Acer,* maple: height, seed-bearing age, and seedcrop frequency

Species	Height (m) at maturity	Year first cultivated	Minimum seed-bearing age (yrs)	Years between large seedcrops
A. circinatum	9	1826	—	1–2
A. ginnala	6	1860	5	1
A. glabrum var. *glabrum*	9	1882	—	1–3
A. griseum	8	1901	—	—
A. macrophyllum	35	1812	10	1
A. negundo	23	1688	—	1
A. palmatum	6	1820	—	—
A. pensylvanicum	11	1755	—	—
A. platanoides	31	Long ago	—	1
A. pseudoplatanus	31	Long ago	—	1
A. rubrum	28	1656	4	1
A. saccharinum	28	1725	11	1
A. saccharum	31	Long ago	22	3–7
A. spicatum	9	1750	—	—

Sources: Burns and Honkala (1990), Dirr (1990), De Jong (1976), Olson and Gabriel (1974), Vertrees (1987).
Note: *A. rubrum, A. negundo, A. pensylvanicum,* and *A. saccharinum* are dioecious to varying degrees. The other species are monoecious, but male and female flowers may occur in different parts of the tree.

actually classify the 4 species mentioned above as subspecies of sugar maple. Eight of the 16 sections of the genus are represented in North America (Van Gelderen 1994). Additionally, a number of species (table 1) have been introduced for use as ornamentals (Burns and Honkala 1990; Dirr 1990; Dirr and Heuser 1987; Fischer 1990; Van Gelderen and others 1994; Vertrees 1987). The native species range in size from trees that dominate forest canopies to medium to tall understory shrubs or small trees (table 2). Boxelder has been introduced into Alaska, where it survives and reproduces; however, it does dieback periodically under extreme winter temperatures (Viereck 1997).

The native maples all regenerate vegetatively by basal sprouting, but the ability to do so varies among species and with plant age (Burns and Honkala 1990; Fischer 1990). Vine, Rocky Mountain, striped, and mountain maples frequently layer, giving them the potential to develop relatively complex clones of varying size and morphology (Hibbs and Fischer 1979; O'Dea and others 1995; Post 1969; Zasada and others 1992).

Some species of maple are important sources of firewood, pulpwood, high-quality lumber, and veneer (Alden 1995; Burns and Honkala 1990). Four species have been used to produce maple sugar and syrup—sugar, black, red (Jones 1832; USDA FS 1982), and bigleaf maple. Sugar maple is the most important of these species because it has the highest sugar content. In the western United States, bigleaf maple produces adequate quantities of sap, but its sugar content is low compared to the sap of sugar and red maples, and the flow is erratic (Burns and Honkala 1990).

Maples are very important for wildlife, providing browse and cover for a variety of mammals, important sites for cavity-nesting birds, and food for seed-eating mammals and birds (Burns and Honkala 1990). Maples are also important substrates for various lichens and mosses. Their occurrence on mountain slopes makes them useful in the protection of watersheds. Boxelder is an important species for shelterbelt planting.

Many of the maples have ornamental value because of their attractive foliage or interesting crown shape, flowers, or fruit; native and introduced maple varieties with desirable features such as a particular foliage color or attractive bark have been propagated specifically for ornamental use (Dirr 1990). For an interesting discussion of variation in form and leaf morphology in Japanese maples, see the wonderfully written and illustrated book by Vertrees (1987).

Flowering and fruiting. There is substantial variation within the genus in terms of gender of trees. Some species—for example sugar, black, and bigleaf maples—are monoecious with flowers that appear perfect but are functionally either male or female. In the monoecious species, the functionally male and female flowers often occur in different parts of the crown (Burns and Honkala 1990; De Jong 1976).

Other species—for example boxelder and red, striped, silver, and bigtooth maples—are primarily dioecious, but some individual trees are monoecious to varying degrees. In natural populations of red maple, the sex ratio tends to be male-biased. The ratio may vary somewhat between geographic areas within the species range. Sex ratio was also

found to be highly skewed to males in red maples just beginning to flower. Change of sexual expression does occur in these dioecious species but only in a small percentage of the population. Variation in sex expression was related to site conditions in boxelder (Freeman and others 1976), but the relationship of gender to site has not been well-established for all species. There do not appear to be consistent differences in growth rate between males and females. Sakai and Oden (1983) reported that monoecious silver maples were larger than dioecious trees and exhibited a different size distribution pattern. Male boxelder trees showed no growth advantage over females despite the increased amount of carbon needed for fruit production (Willson 1986). However, it was observed that female trees that were previously male had a higher mortality rate than trees that were consistently male or trees that were previously female (Barker and others 1982; De Jong 1976; Hibbs and Fischer 1979; Primack and McCall 1986; Sakai 1990b; Sakai and Oden 1983; Townsend and others 1982).

Flowering and pollination occur in spring and early summer (table 3). Dichogamy (male and female parts in the same flower or different flowers on the same tree mature at different times) is common in maples and has been described for sugar maple and other species (De Jong 1976; Gabriel 1968). Insect and wind pollination both occur, but the relative importance of each differs among species (De Jong 1976; Gabriel 1968; Gabriel and Garrett 1984).

The fruit is composed of 2 fused samaras (a term used interchangeably with seeds here), which eventually separate on shedding, leaving a small, persistent pedicel on the tree. The fused samaras may be roughly identical in appearance or differ in physical size; both samaras may or may not contain viable embryos (Abbott 1974; Greene and Johnson 1992). Parthenocarpic development occurs but differs in the strength of expression among species; this phenomena may explain size differences in paired samaras (De Jong 1976). Samara pairs may occur singly or in clusters of 10 or more. The fruits of the maples vary widely in shape, length of wings, and angle of divergence of the fused samaras (figure 1) (Carl and Snow 1971; De Jong 1976; Greene and

Figure 1—*Acer*, maple: samaras of *A. platanoides*, Norway maple (**top left**); *A. circinatum*, vine maple (**top right**); *A. saccharum*, sugar maple (**second row left**); *A. grandidentatum*, bigtooth maple (**second row center**); *A. spicatum*, mountain maple (**second row right**); *A. saccharinum*, silver maple (**third row left**); *A. macrophyllum*, bigleaf maple (**third row center**); *A. negundo*, boxelder, (**third row right**); *A. glabrum* var. *glabrum*, Rocky Mountain maple (**bottom left**); *A. rubrum*, red maple (**bottom center**); *A. pensylvanicum* (**bottom right**).

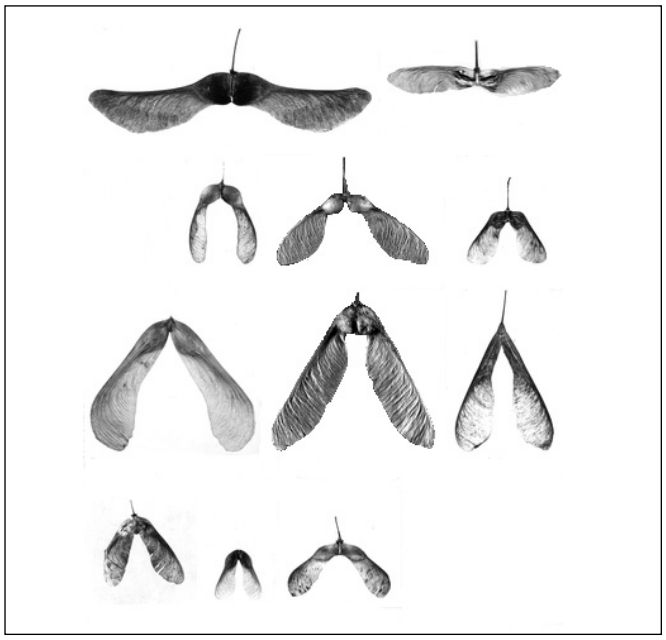


Table 3—*Acer*, maple: phenology of flowering and fruiting

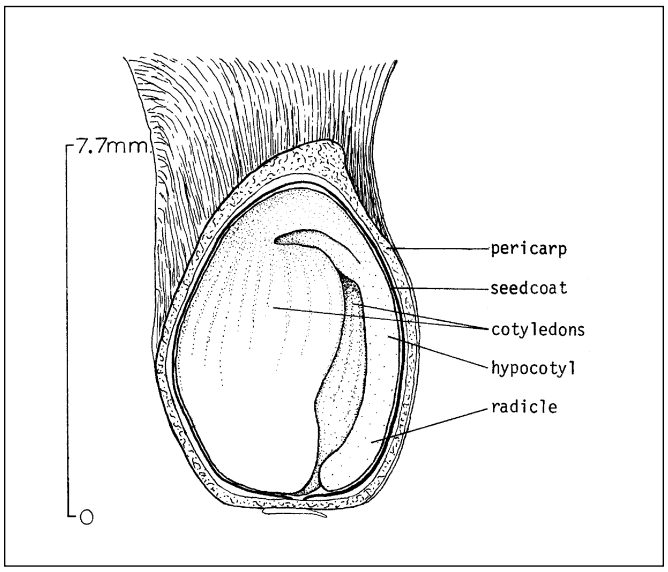
Species	Flowering	Fruit ripening	Seed dispersal
A. circinatum	Mar–June	Sept–Oct	Oct–Nov
A. ginnala	Apr–June	Aug–Sept	Sept–Jan
A. glabrum var. *glabrum*	Apr–June	Aug–Oct	Sept–Feb
A. macrophyllum	Apr–May	Sept–Oct	Oct–Mar
A. negundo	Mar–May	Aug–Oct	Sept–Mar
A. palmatum	May–June	Aug–Sept	Sept–Oct
A. pensylvanicum	May–June	Sept–Oct	Oct–Feb
A. platanoides	Apr–June	Sept–Oct	Oct–Nov
A. pseudoplatanus	Apr–June	Aug–Oct	Sept–Nov
A. rubrum	Mar–May	Apr–June	Apr–July
A. saccharinum	Feb–May	Apr–June	Apr–June
A. saccharum	Mar–May	Sept–Oct	Oct–Dec
A. spicatum	May–June	Sept–Oct	Oct–Dec

Sources: Dirr (1990), Burns and Honkala (1990), Olson and Gabriel (1974).

Johnson 1992; Sipe and Linnerooth 1995). Each filled samara typically contains a single seed without endosperm (figure 2). However, polyembryony has been observed in sugar and bigleaf maples (Carl and Yawney 1972; Zasada 1996). Maple seeds turn from green or rose to yellowish or reddish brown when ripe; the color of mature samaras can vary among species. Pericarps have a dry, wrinkled appearance when fully mature (Al'benskii and Nikitin 1956; Anon. 1960; Carl and Snow 1971; Harris 1976; Rehder 1940; Sargent 1965; Vertrees 1987).

The embryo with associated seedcoats is contained within the pericarp (figure 2). The surface of the pericarp is usually glabrous (except that of bigleaf maple, which has dense, reddish brown pubescence). The pericarp can be extremely hard (particularly when it has dried out) and difficult to cut open. Development of the samara in black maple has been described in detail by Peck and Lersten (1991). Both the pericarp and seedcoat have been identified as causes of dormancy. The cavity (locule) in which the embryo occurs may have concave or convex walls. There are 2 types of embryo folding: (a) incumbent folding, in which the hypocotyl is against the back of one cotyledon, and (b) accumbent folding, in which the hypocotyl is against the edges of the folded cotyledons. Of the native maples, vine and sugar maples are classified as incumbent and the others (except bigtooth maple, which was not classified) are accumbent. The cotyledons may be green while still in the pericarp (Carl and Yawney 1972; De Jong 1976; Dirr and Heuser 1987; Olson and Gabriel 1974; Peck and Lersten 1991; Vertrees 1987).

Figure 2—*Acer circinatum*, vine maple: longitudinal section of a seed showing bent embryo. On drying the seed shrinks, leaving space between the seedcoat and the pericarp.



During the maturation process, the pericarp and wing change color as seed biochemistry, anatomy, and moisture content change (Carl and Yawney 1966; Peck and Lersten 1991; Vertrees 1987). Both anatomical and physiological studies indicate that green samaras photosynthesize, thus contributing to the carbon balance and growth of the fruit (Bazzaz and others 1979; Peck and Lersten 1991).

The native species can be divided into 2 groups based on timing of seed dispersal (table 3) (Burns and Honkala 1990). Silver and red maples release samaras in late spring and early summer, whereas the other species disperse theirs in late summer and fall. The summer-dispersing species appear to release seeds over a period of about 1 month (Bjorkbom 1979). The fall-dispersing species release samaras in a more protracted manner, usually over 2 months or more (Bjorkbom 1979; Garrett and Graber 1995; Graber and Leak 1992). In sugar maples, seedfall has been observed in every month of the year, but seeds dispersed during the summer months are usually empty (Garrett and Graber 1995). Bigleaf maples in western Oregon and Washington may retain seeds through March.

The mechanics of samara flight following release from the tree have been studied in considerable detail (Green 1980; Greene and Johnson 1990, 1992; Guries and Nordheim 1984; Matlack 1987; McCutchen 1977; Norberg 1973; Peroni 1994; Sipe and Linnerooth 1995). The remainder of this paragraph briefly summarizes the main points of these papers. Maple seeds spin when they fall. There are 2 components to flight—the initial free-fall before spinning and the spinning itself. Depending on species, the initial phase covers a distance of 0.4 to 0.8 m. The terminal velocity attained during spinning varies from 0.8 to 1.3 m/sec and is related to the size of the seeds. Within an individual species, descent rate of individual samaras varied from 0.6 to 1.7 m/sec, depending on seed size and shape. These are the main factors determining how far seeds will fly during primary dispersal under different wind conditions. In relatively strong winds, the free-fall phase may not occur. Wind conditions for early summer dispersal of red and silver maples may differ substantially from those of fall dispersal of seeds because the fully developed canopy can affect within-stand wind conditions. Secondary dispersal after flying may occur over a fairly long distance if seeds fall into moving water or a short distance if seeds are cached by rodents or moved by rainwater or snowmelt.

The maximum dispersal distance for maple seeds is reported to be at least 100 m under open conditions as might occur in a large gap or clearcut (Burns and Honkala 1990). Dispersal distance and patterns of seed rain will vary within

stands due to tree distribution and stand microclimate. For example, seed rain around an individual red maple within a hemlock–hardwood forest dropped from 340 seeds/m^2 (range, 200 to 450/m^2) at the base of the tree to about 50/m^2 (range, 0 to 100/m^2) at 10 m from the base (Ferrari 1993). The large variation in seed rain at each distance indicates that microclimate, location of seeds within the tree crown, and other factors create a relatively heterogeneous pattern of seed deposition.

The weight of maple seeds varies substantially among species (table 4) (Green 1980; Guries and Nordheim 1984). Some examples of within-species variation in seed weight are given below. The average dry weight of sugar maple seeds varied from 0.09 to 0.03 g in a collection from across the eastern United States; the heaviest seeds were from New England area and the lightest from the southern part of the range (Gabriel 1978). In the central Oregon coastal range, the dry weight of bigleaf maple samaras varied from 0.25 to 0.65 g; embryo dry weight accounted for 30 to 40% of total samara weight (Zasada 1996). Sipe and Linnerooth (1995) found that average weight of silver maple seeds varied from 0.10 to 0.16 g. Peroni (1994) found that the dry weight of red maple samaras from 10 North Carolina seed sources varied from 0.013 to 0.016 g. Townsend (1972) reported a 2- to 3-fold variation in red maple fruit weight for seeds collected throughout the species' range.

Seed production can vary significantly among years for a single stand or between stands in a given year in quantity, quality, biomass, and seed weight as a percentage of total litterfall (Bjorkbom 1979; Bjorkbom and others 1979; Burns and Honkala 1990; Chandler 1938; Curtis 1959; Garrett and Graber 1995; Godman and Mattson 1976; Graber and Leak 1992; Grisez 1975; Pregitzer and Burton 1991; Sakai 1990). Although separated geographically and conducted in stands differing in composition, seed production studies over 11 to 12 years in Wisconsin and New Hampshire reported similar results. In Wisconsin, the quantity of sugar maple seedfall in a pure stand of sugar maple varied from 0.1 to 13 million seeds/ha and percentage of filled seeds from 3 to 50% during a 12-year period. Seed production exceeded 2.5 million seeds/ha in 5 of 12 years (Curtis 1959). In a mixed hardwood stand in New Hampshire in which sugar maple made up 69% of the basal area, production varied from 0.2 to 11.9 million seeds/ha; viability was generally related to size of the seed crop and ranged from 0 to 48%. Seed production exceeded 2.5 million seeds/ha in 6 of 11 years (Graber and Leak 1992). In northern Wisconsin, good or better seed years occurred every other year in red maples over a 21-year period and every third year for sugar maples over a 26-year period (Godman and Mattson 1976). In a gradient study of sugar maple stands from southern Michigan to the Upper Peninsula, production of reproductive litter (seeds and flower parts) varied by a factor of 2 and 4 for 2 seed years. The southern stands were more productive one year, whereas the northern stands were more productive the other year (Pregitzer and Burton 1991). Flower and seedcrops in red and sugar maples were related and the former could be used to predict seedcrops (Bjorkbom 1979; Grisez 1975). Fertilization has been shown to alter seed production in maples (Bjorkbom 1979; Chandler 1938). Long and others (1997) reported that liming affected seedcrop size but not periodicity in sugar maple in Allegheny hardwood forests. They also reported that good sugar maple seedcrops occurred the year after a June–July period with a relatively severe drought index (that is, when plants were subjected to a high level of moisture stress).

Table 4—*Acer*, maple: seed yield data

	Cleaned seeds/weight			
	Range		Average	
Species	**/kg**	**/lb**	**/kg**	**/lb**
A. circinatum	7,710–12,220	3,490–5,530	10,210	4,620
A. ginnala	22,980–44,640	10,400–20,200	37,570	17,000
A. glabrum var. *glabrum*	17,280–44,860	7,820–20,300	29,680	13,430
A. macrophyllum	5,970–8,840	2,700–4,000	7,180	3,250
A. negundo	18,120–45,080	8,200–20,400	29,610	13,400
A. pensylvanicum	21,430–34,400	9,700–15,600	24,530	11,100
A. platanoides	2,810–10,300	1,270–4,660	6,320	2,860
A. pseudoplatanus	6,480–15,910	2,930–7,200	11,290	5,110
A. rubrum	28,070–84,420	12,700–38,200	50,520	22,860
A. saccharinum	1,990–7,070	900–3,200	3,930	1,780
A. saccharum	7,070–20,110	3,200–9,100	15,540	7,030
A. spicatum	33,810–60,330	15,300–27,800	48,910	22,130

Source: Olson and Gabriel (1974).

Most studies of seed production are conducted in pure stands or those with a majority of the stems of the desired species. However the availability of seeds when species make up only a minor component of the stand is of interest when estimating seeds available for further colonization. An example of this is provided for a New Hampshire sugar maple–yellow birch–beech stand (Graber and Leak 1992). In this study covering 11 years, the total production of red and striped maples, both minor components, was 0.6 (0% viability) and 0.5 million seeds/ha (40% viability), respectively (Graber and Leak 1992). Seed quality of species present in low number may be limited by pollination. Ferrari (1993) provided information on production and dispersal of seeds from an isolated red maple in a hemlock–hardwood forest in upper Michigan.

Abbott (1974) and Grisez (1975) found that seed production in red and sugar maples was related to dbh. The following listing provides some indication of this relationship for red maple (Abbott 1974):

Tree dbh (cm)	Seeds/tree (thousands)
5	11.9
12	54.3
20	91.4
31	955.8

Reductions in the potential seedcrop can result from biotic and abiotic factors. The strong summer winds and rain associated with thunderstorms in the northern hardwood forests often litter the forest floor with immature seeds and flower parts. Post-zygotic abortion occurring soon after fertilization was the primary cause of empty seeds; in addition, insects affected the quality of more than 10% of seedfall (Graber and Leak 1992). Furuta (1990) found that aphid infestations had an adverse effect on seed production in the Japanese maple *A. palmatum* subsp. *amoenum* (Carr.) H. Hara. Carl and Snow (1971) suggest that heavy aphid infestations affect seed production in sugar maple. Experimental defoliation reduced seed production in striped maples during the year of defoliation but not in the following year (Marquis 1988). Once seeds have been dispersed, seed predation by small mammals can greatly reduce the seed pool before germination (Fried and others 1988; Graber and Leak 1992; Myster and Pickett 1993; Tappeiner and Zasada 1993; Von Althen 1974).

Collection of fruits. Minimum seed-bearing age differs among species. Intervals between mast years vary by species, but some seeds are usually produced every year (table 3) (Burns and Honkala 1990). Seeds may be picked from standing trees or collected by shaking or whipping the trees and collecting the samaras on sheets of canvas or plastic spread on the ground. Samaras may also be collected from trees recently felled in logging operations. Samaras from species such as boxelder and vine, sugar, bigleaf, silver, and Norway maples can be gathered from lawns and pavements and from the surface of water in pools and streams. After collection, leaves and other debris can be removed by hand, screening, or fanning. The following weights were reported (Olson and Gabriel 1974) for samaras:

	Weight/volume of samaras	
Species	kg/hl	lb/bu
vine maple	15.3	11.9
bigleaf maple	5.9	4.6
sugar maple	13.1	10.2

Seed collection for most species occurs when the samaras are fully ripened and the wing and pericarp have turned tan or brown in color (Carl 1982a; Carl and Yawney 1966). However, for maples that are difficult to germinate—such as vine maple, striped maple, and the Japanese maples—it is recommended that seeds be collected before they have dried completely, when the wing has turned brown but the pericarp is still green (Dirr and Heuser 1987; Vertrees 1975, 1987).

Although the seeds of most maples are glabrous, those of bigleaf maple are often densely pubescent. The pubescence may irritate the skin and cause some respiratory tract congestion when airborne. Individuals who might be sensitive to this material should use rubber gloves and a face mask.

Extraction and storage of seeds. Maple seeds are generally not extracted from the fruits (samaras) after collection, except when seeds are used in research on seed dormancy or lots of particularly valuable seeds that are difficult to germinate. De-winging reduces weight—wings account for about 15 to 20% of samara weight (Greene and Johnson 1992; Sipe and Linnerooth 1995)—and bulk for storage. The separation of filled and empty samaras for sugar maple can be accomplished on small lots by floating the samaras in n-pentane (filled seeds sink). This practice had no apparent effect on long-term seed viability (Carl 1976, 1982a; Carl and Yawney 1966). Removal of empty samaras, which can be done readily on a gravity table, improves seed handling, storage, sowing, and control of seedbed density.

After dispersal, maple seeds (with the exception of silver maple seeds and some red maple seeds) lie dormant in

the forest floor for at least 3 to 5 months before germinating (Fried and others 1988; Houle and Payette 1991; Marquis 1975; Sakai 1990b; Tappeiner and Zasada 1993; Wilson and others 1979). Sugar and bigleaf maples usually germinate fully in the spring and summer after dispersal. Seeds of vine, striped, red, and mountain maples and the Japanese maples may lie dormant for 1 to 2 or more growing seasons before germinating (Marquis 1975; Peroni 1995; Sakai 1990b; Tappeiner and Zasada 1993; Vertrees 1987; Wilson and others 1979). In the southern United States, however, one test has indicated that seeds of red maple will maintain viability only for a few months when buried in the litter (Bonner 1996). Thus, with the exception of silver maple and possibly red maple seeds in some areas, seeds of all maples are "stored" naturally in the forest floor for varying lengths of time.

The critical factors in seed storage are temperature and seed moisture content. The moisture content of samaras depends on the stage of seed development and species. Beginning in late August, the moisture content of sugar maple seeds declined from about 160% (dry weight basis) to between 30 to 40% at dispersal (Carl and Snow 1971). The moisture content of sycamore maple seeds decreased from 750% (100 days after flowering) to 125% (200 days after flowering). Moisture content at dispersal for other species has been reported to be 7 to 50% for bigleaf maples (Zasada and others 1990); 80 to 100% for silver maples (Becwar and others 1983; Pukacka 1989), 30 to 35% for Norway maples (Hong and Ellis 1990), and 125 to 130% for sycamore maple (Hong and Ellis 1990).

Moisture content for seed storage defines into 2 groups—seeds that can be stored at relatively low moisture contents (orthodox seeds) and those that must be stored at relatively high moisture contents (recalcitrant seeds). Silver and sycamore maple are clearly recalcitrant (Becwar and others 1982, 1983; Bonner 1996; Dickie and others 1991; Hong and Ellis 1990; Pukacka 1989). Seeds of these species can be stored for about a year (Bonner 1996), and seed moisture content should be maintained at about 80% (dry weight) (Dickie and others 1991; Pukacka 1989).

Orthodox seeds can be stored for longer times and at lower moisture contents than recalcitrant seeds. Viability of sugar maple seeds did not decrease over a 54-month storage period when seeds were stored in sealed containers at a moisture content of 10% (dry weight) and a temperature range of –10 to 7 °C. Similarly, viability did not decrease significantly at 17% moisture content and –10 °C. Seeds stored in open containers at the same temperature lost viability more rapidly than those in sealed containers (Yawney and Carl 1974). Sugar maple seed moisture content can be reduced slowly from 100% (dry weight basis) at the time of collection to 20% with little effect on viability (Carl and Yawney 1966). Under stress conditions (seeds maintained at 52 °C), longevity of Norway maple seeds increased linearly as seed moisture content declined from 23 to 7% (fresh weight); seeds died when dried to moisture contents of 4 and 2.5% (Dickie and others 1991). Viability of bigleaf maple seeds declined from 73 to 62% when they were stored for 1 year in sealed containers at 1 °C and at a moisture content of 16% (dry weight); viability was reduced from 73 to 12% when seeds were stored at –10 °C (Zasada and others 1990).

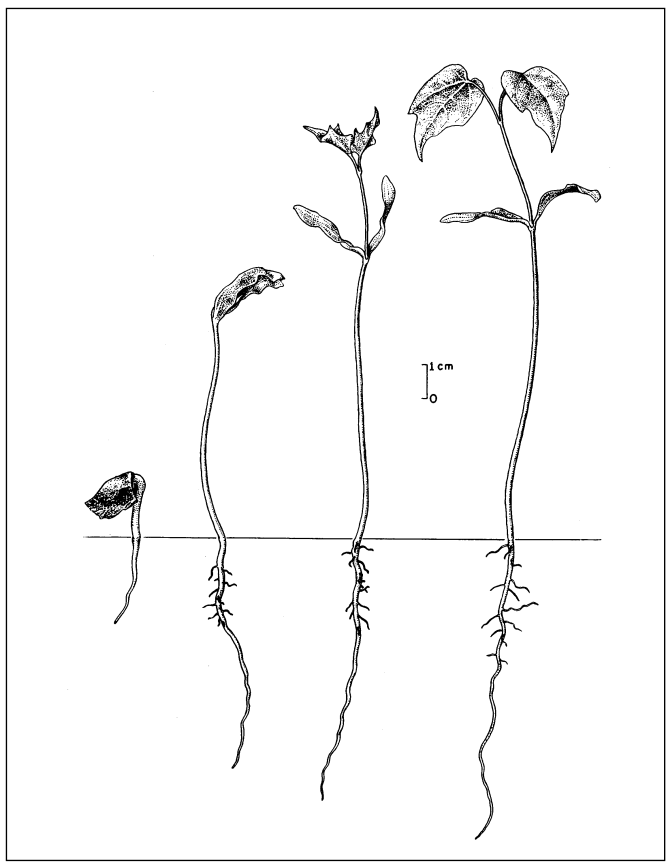
It was previously believed that bigleaf maple seeds could not be stored for even short periods (Olson and Gabriel 1974). Based on recent work by Zasada and coworkers (Zasada 1992, 1996; Zasada and others 1990) in the central Oregon coastal range, an important consideration in storing these seeds seems to be collecting them before autumn rains begin, when the seeds are at their lowest water content. When collected at this time, some seedlots have moisture contents of 7 to 15% (dry weight basis), whereas seeds collected at other times have moisture contents of 25 to 35%. Once autumn rains begin, seeds attached to the tree increase in moisture content and, if they stay on the tree, can germinate under the right conditions. Although more work is required to determine the optimum storage conditions, the limited data suggest that seeds collected at the lowest moisture content behave more like orthodox seeds whereas those collected after autumn rains have increased moisture contents and some characteristics similar to recalcitrant seeds. The pubescent pericarp may play an important role in the moisture content of samaras.

For the other native maples, the fact that they remain viable for 1 year or more in the forest floor or nursery bed suggests that they could be stored for extended periods. Temperatures of 1 to 3 °C and seed moisture contents when dispersed should retain viability for several years.

Pregermination treatment and germination. Germination is epigeal for most species (figure 3), but silver maple and *A. tataricum* L. exhibit hypogeal germination (Burns and Honkala 1990; De Jong 1976; Harris 1976).

Under field conditions, maple germination falls into 3 general types, with red maple exhibiting a combination of 2 types. The first general pattern includes the 2 late spring/early summer seed dispersers (table 3)—red and silver maples—which is the best example. All seeds of this species must germinate before they dry below a moisture content of about 30% (fresh weight) or they die (Pukacka 1989). In red

Figure 3—*Acer platanoides*, Norway maple: seedling development at 1, 3, 7, and 19 days after germination.



maples, the percentage of non-dormant seeds varies with the seed source and among trees in a given geographic area; indeed, this species shares some characteristics with the second type of germination (Abbott 1974; Farmer and Cunningham 1981; Farmer and Goelz 1984; Marquis 1975; Peroni 1995; Wang and Haddon 1978).

The second pattern is typified by sugar and bigleaf maples. Seeds are dispersed in the fall and early winter, stratify during winter and spring, and germinate as soon as temperature thresholds are reached. Both can germinate at constant temperatures just above freezing. In the relatively mild climate of western Oregon, bigleaf maple germinants begin to appear in late January. Bigleaf maple seeds that remain on the tree until late February or March can germinate on the tree (Zasada 1992; Zasada and others 1990). Sugar maple seeds have been observed to germinate under the snow in the spring (Godman and others 1990).

The third pattern has been observed in vine and striped maples (Tappeiner and Zasada 1993; Wilson and others 1979) and may occur in Rocky Mountain and mountain maples. Japanese and paperbark maples and other maples from Asia also exhibit this pattern (Dirr and Heuser 1987; Vertrees 1987). Seeds are dispersed as in the second pattern, but germination occurs over several years. In Massachusetts, less than 1 and 25% of striped maple seeds germinated, respectively, in the first and second years after sowing at the time of natural seedfall (Wilson and others 1979); in coastal Oregon 70 to 80% of vine maple seeds germinated in the second growing season after fall-sowing, with the remainder germinating in the first and third growing seasons (Tappeiner and Zasada 1993). Delayed germination of vine maple has also been observed in nursery beds (Vertrees 1975; Zasada 1996). Vertrees (1987) observed that Japanese maple germinants appeared over a 5-year period after a single sowing.

Methods for testing germination and pre-sowing treatments in nurseries are related in general to the germination patterns described above (tables 5 and 6). Silver maple seeds are not dormant (Pukacka 1989). Some red maple seeds may germinate without stratification, but stratification is necessary for seeds from some populations (Abbott 1974; Farmer and Cunningham 1981; Farmer and Goelz 1984; Peroni 1995; Wang and Haddon 1978). The group represented by sugar and bigleaf maples requires 30 to 90 days of stratification. Germination paper, sand, perlite, and sphagnum moss were all suitable stratification media for sugar maple seeds (Carl and Yawney 1966). Seeds will germinate completely at stratification temperatures. To assure that seeds have been stratified long enough, it may be advisable to wait until the first germinants appear before moving them to warmer temperatures to increase germination rate or sowing in the nursery. The optimum temperature for stratification in general is 0 to 3 °C, but some species will germinate well after stratification at temperatures up to 10 °C (Nikolaeva 1967).

The species that exhibit delayed germination are, under field conditions, exposed to warm and cold conditions and thus a warm period of incubation followed by cold stratification may stimulate germination. These species may also germinate better after a treatment that physically breaks the seed pericarp and testae (tables 5 and 6). Soaking seeds in warm water for 1 to 2 days is often recommended when they are completely dried out and the seedcoat has become very hard (Browse 1990; Dirr and Heuser 1987; Vertrees 1987). Seed testing rules recommend tetrazolium testing and excised embryo tests for the more difficult to germinate species (ISTA 1993).

Table 5—*Acer*, maple: warm and cold stratification treatments for internal dormancy

Species	Warm period		Cold period	
	Temp (°C)	Days	Temp (°C)	Days
*A. circinatum**	20–30†	30–60	3	90–180
*A. ginnala**	20–30†	30–60	5	90–150
A. glabrum	20–30†	180	3–5	180
A. macrophyllum	—	—	1–5	40–60
*A. negundo**	—	—	5	60–90
A. palmatum (dry seeds)	Warm water‡	1–2	1–8	60–120
A. palmatum (fresh seeds)	—	—	1–8	60–120
A. pensylvanicum	—	—	5	90–120
A. platanoides	—	—	5	90–120
A. pseudoplatanus	—	—	1–5	40–90
A. rubrum§	—	—	3	60–90
A. saccharinum	—	—	—	0
A. saccharum	—	—	1–5	40–90
A. spicatum	—	—	5	90–120

Sources: Browse (1990), Dirr and Heuser (1987), Harris (1976), Olson and Gabriel (1974), Vertrees (1987).

Note: Even after standard pretreatment, seedlots of *A. griseum* may require 2 to 3 years for complete germination.

* Mechanical rupture of the pericarp may improve germination. This is necessary in *A. negundo* when seeds are very dry; a warm soak as for *A. palmatum* may suffice.

† The benefit of warm incubation prior to stratification is not well-documented. Seeds may go through at least 1 warm/cold cycle before germinating under field conditions.

‡ Water temperature at start of incubation is 40 to 50 °C and allowed to cool gradually. Some recommend a 21 °C incubation period following warm water treatment and a 90-day stratification period.

§ Requirement for stratification is highly variable. In all seedlots, some seeds will germinate without stratification.

Optimum temperatures for germination are not clearly defined. Although most species have their best germination at higher temperatures within the optimum range (table 6), this is not always the case. Studies with red and striped maples have shown that, for seeds from some sources, germination is faster at lower than at higher temperatures (Farmer and Cunningham 1981; Farmer and Goelz 1984; Wilson and others 1979).

Germination occurs on a wide variety of substrates and a full range of light conditions (Burns and Honkala 1990; Fischer 1990; Olson and Gabriel 1974). Under field conditions, germination often occurs in association with leaf litter and other organic substrates on relatively undisturbed seedbeds. Germination paper, sand, perlite, and sphagnum moss support good germination in controlled environments. Red maple was shown to be more sensitive to the acidity of a substrate than sugar maple (Raynal and others 1982).

The morphological and physiological basis for seed dormancy in maples varies among species and includes pericarp-and-seed-coat-imposed dormancy and embryo dormancy (Farmer 1996; Young and Young 1992). The type of dormancy may change as seeds mature. There may be little relationship between dormancy of the mature seed and that of a seed with a fully developed embryo that is not yet mature in a biochemical sense (Thomas and others 1973). Thus for some species it may be best to collect and sow immature seeds as suggested by Vertrees (1975, 1987) for vine and Japanese maples and more generally by Dirr and Heuser (1987) for species with the third germination pattern mentioned above. The type of dormancy imposed by the pericarp and seedcoat (such as that in vine and striped maples) may be released by removing the pericarp and all or part of the testae (figure 2) or by physically breaking the pericarp without actually removing the embryo (table 5) (Wilson and others 1979). Some of the delayed field germination described above is caused by the impenetrability of the seedcoat after embryo dormancy has been released (Dirr and Heuser 1987; Wilson and others 1979).

Nursery practice. Maple seedlings can be produced as container stock or as bareroot seedlings. Bareroot seedlings seem to be the most common when all species of maples are considered. Pre-sowing treatment and sowing time are based on the characteristics of the seeds being sown, convenience, and experience. Cutting tests or x-radiography to determine the presence of embryos are advised for some of the introduced species because poor seed quality is common (Dirr and Heuser 1987; Hutchinson 1971; Vertrees 1987). The information reviewed above on dormancy and germination pattern suggest a number of options for sowing. The least amount of seed handling is required when seeds are sown immediately after collection and allowed to stratify "naturally" before germination. Silver and red maple

Table 6—*Acer,* maple: germination test conditions and results for stratified seeds

Species	Germination test conditions: Temp (°C) Day	Temp (°C) Night	Days	Germination rate: Amount (%)	Time (days)	Total germination (%)
A. circinatum	30	20	38	12	10	19
A. ginnala	30	20	38	50	10	52
A. glabrum	10–16	10–16	—	40	30	—
*A. macrophyllum**						
Source 1	2–3	2–3	120	15–66	60–90	100
Source 2	2–3	2–3	120	0–13	60–90	100
Source 3	2–3	2–3	120	8–92	60–90	100
A. negundo	—	—	24–60	14–67	14–48	24–96
A. pensylvanicum†	5	5	90	—	—	82
	23	23	60	—	—	76
A. platanoides	4–10	4–10	—	—	—	30–81
A. pseudoplatanus	—	—	—	24–37	20–97	50–71
A. rubrum‡						
Low elevation (U)	15	5	—	—	—	55
Low elevation (S)	15	5	—	—	—	89
High elevation (U)	15	5	—	—	—	13
High elevation (S)	15	5	—	—	—	54
A. saccharinum	30	30	5–18	72–91	3–13	94–97
A. saccharum	2–3	2–3	90	80	75	95
A. spicatum	—	—	—	32	31	34

Sources: Olson and Gabriel (1974), Farmer and Goelz (1984), Farmer and Cunningham (1981), Vertrees (1987).

Notes: Germination rate indicates the number of seeds germinating in the time specified and total germination all of the seeds germinating in the test. The length of germination tests are not same for all species.

Seeds of *A. griseum* and *A. palmatum* are very difficult to germinate and seed quality is usually poor. Cutting tests are recommended to determine potential viability. Tetrazolium tests could be used to determine if seeds are alive; knowing this one can sow and wait several years for seeds to germinate. Because the delay in germination appears related to a very hard pericarp, removing the pericarp can improve germination.

* Seed sources from central Oregon coastal range. Germination rate greatly increased when seeds moved to 20 to 25 °C when germination in stratification begins (Zasada 1996).

† Germination of seeds with testa removed over radicles. Seeds with testae did not germinate at 23 °C even after 5 months of stratification, whereas seeds kept at 5 °C germinated completely after 6 months (Wilson and others 1979).

‡ Seed sources from Tennessee, total germination at higher temperatures was lower than shown here (Farmer and Cunningham 1981). Similar trends were observed with red maple from Ontario (Farmer and Goelz 1984). U = stratified seeds, S = unstratified seeds.

seeds are sown after collection in late spring, whereas seeds of other maples are sown in the fall when they are mature and the nursery beds mulched (Harris 1976; Olson and Gabriel 1974; Yawney 1968). If stratification requirements are not satisfied with this method or if secondary dormancy is imposed, there may be a substantial number of seeds that do not germinate in the first growing season. Treatment of seeds may result in more uniform germination. For example, Webb (1974) proposed soaking sugar maple seeds for 24 hours before stratification to promote more uniform germination.

For difficult species such as vine and striped maples, which germinate over a several-year period, it has been recommended that seedcoats be either physically broken to promote more uniform germination or soaked in warm water, or given both treatments to reduce the number of seeds not germinating during the first growing season (Browse 1990; Olson and Gabriel 1974; Vertrees 1975, 1987). Vertrees (1987) describes several sowing methods for Japanese maples. The choice of a method depends on degree of maturity, length of time seeds have been stored, and the time desired for sowing. It is also recommended that nurserybeds in which these seeds are sown be maintained for several years so that late-germinating seeds are not destroyed; this is particularly true when seed supplies are limited.

Maple seeds are usually sown 0.6 to 2.5 cm ($^1/_4$ to 1 in) deep, either broadcast or using drills. Seedbed densities from 158 to 1,520/m^2 (15 to 144/ft^2) have been recommended (Carl 1982b; Olson and Gabriel 1974; Vertrees 1987; Yawney 1968). Densities in the range of 158 to 320/m^2 (15 to 30/ft^2) appear most satisfactory for the production of vigorous seedlings. In some instances, seedbeds require treatment with repellents against birds and mice and treatment with fungicides to prevent damping off (Olson and Gabriel 1974; Vertrees 1987). Shade is recommended during the period of seedling establishment (Olson and Gabriel 1974).

Sometimes maple seedlings are large enough to plant as 1+0 stock, but frequently 2+0 or even 2+2 stock is needed to ensure satisfactory results. In general, the larger the planting stock, the better the survival.

Container seedling production is less common than bareroot production, but is used by some producers (Tinus 1978). Container seedlings grown in a greenhouse will usually be larger than those grown outdoors in containers or in a nursery bed (Wood and Hancock 1981). Container production would probably be best achieved with stratified seeds that are just beginning to germinate; this can be easily achieved for species like bigleaf and sugar maples that germinate during stratification. Various sizes and types of containers can be used. One grower uses a container that is 4 cm (1.6 in) in diameter and 15 cm (6 in) deep to produce 30- to 40-cm-high (12- to 16-in-high) stock in 1 growing cycle. These seedlings can be outplanted or transplanted to nursery beds or larger containers for production of larger stock for ornamental purposes.

Artificial sowing in field situations is an alternative to planting seedlings. Successful germination and early growth have been demonstrated for bigleaf maple and vine maple under a variety of forest conditions (Fried and others 1988; Tappeiner and Zasada 1993) and red maple (Brown and others 1983). One drawback to sowing under forested conditions is heavy seed predation by various small mammals.

Desirable maple genotypes can also be propagated vegetatively by rooting stem cuttings and various types of layering (Dirr 1990; Dirr and Heuser 1987; O'Dea and others 1995; Post 1969; Vertrees 1987; Yawney 1984; Yawney and Donnelly 1981, 1982). Methods for rooting and overwintering cuttings before outplanting are available for sugar maple (Yawney and Donnelly 1982) and Japanese maples (Dirr and Heuser 1987; Vertrees 1987).

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Fabaceae—Pea family

Adenanthera pavonina L.

peronías

J.A. Vozzo

Dr. Vozzo retired from the USDA Forest Service's Southern Research Station

Other common names. jumbie-bead

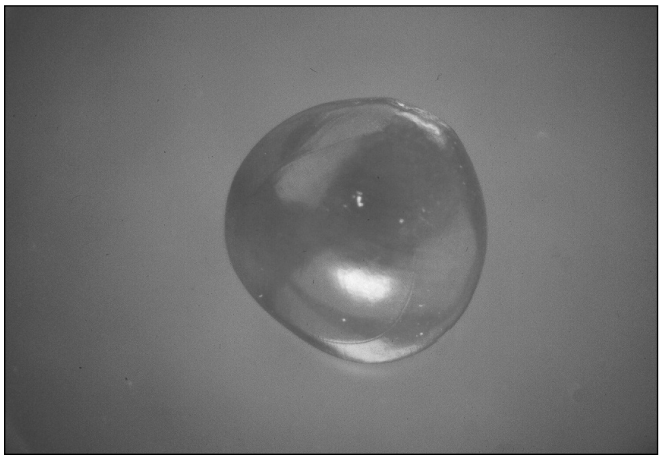
Occurrence and growth habit. Originally from tropical Asia, this genus has spread to parts of tropical Africa and America that have 1,300 to 2,100 mm of rainfall, soil pH 5.0 to 7.5, and nutrient-rich soils with moist but well-drained profiles. It maintains a common abundance relative to other competitors (Francis and Liogier 1991). *Peronıas—Adenanthera pavonina* L.—has large bipinnate leaves, 30 to 60 cm in length, and narrow, erect flower clusters with shiny scarlet seeds. The medium-sized deciduous tree can be 13 m tall and 45 cm in trunk diameter, with brown, smooth bark (Little and Wadsworth 1964). Two other species—*A. microsperma* Teysm. & Binn. and *A. bicolor* Moon —are similar but smaller (Neal 1965). Only a small number of species are included in the genus. Gunn (1984) recognizes only the following 5 species—*A. abrosperma* F. v. *Mueller, A. bicolor, A. intermedia* Merrill, *A. pavonina* L. var. *microsperma,* and *A. pavonina* L. var. *pavonina*. Only *A. pavonina* var. *pavonina* is commonly found in the American tropics, where it has naturalized in Puerto Rico (Francis and Liogier 1991).

Use. The mature trees are good shade trees but not particularly ornamental (Neal 1965), although they are valued for their attractive feathery foliage and bright red seeds in Nyasaland (Streets 1962). Peronıas is also planted as a hedge in Asia, where it is called peacock flower fence (Bailey 1941). Its sapwood is light brown and hard, and its heartwood is hard and red. The heavy, hard wood (specific gravity 0.6 to 0.8) makes durable, strong furniture. It is used locally for poles and firewood as well as a source of red dye (Little and Wadsworth 1964). It gets its Asian common name—red sandalwood—from its use as a substitute for sandalwood. The red seeds are known as "Circassian seeds" and used for bead work. An interesting (but questionable) use is as commercial weights for goldsmiths and silversmiths, who claim each seed weighs a uniform 4 grains (Neal 1965).

Flowering and fruiting. Flowers are borne on racemes (either lateral or terminal) on short stalks 3 mm long and may be pale yellow to white. The small, inconspicuous flowers have a sweet smell and form axillary clusters during the hot, humid season. The fruits mature in the dry season and remain on the tree several months as dark brown legumes (pods) that measure 10 to 20 mm wide and 15 to 20 cm long and are twisted. They readily split and show seeds (figures 1 and 2) attached to the smooth, yellow interior. There are about 3,500 seeds/kg (~1,580/lb) (Bailey 1941; Little and Wadsworth 1964; Neal 1965; Troup 1921). Seeds store well with no special techniques required (Francis 1994).

Germination. Although presoaking is helpful, seeds will germinate with no pre-germination treatment. Several reports do, however, suggest that germination is enhanced by hot-wire scarification (Sandiford 1988) and sulfuric acid exposure (Ahmed and others 1983; Xu and Gu 1985). Francis and Rodriguez (1993) report 86% germination of mechanically scarified seeds held for 6 days on blotter paper at ambient temperature (24 to 30 °C). Germination is epigeal (figure 3).

Figure 1—*Adenanthera pavonia*, peronías: seed.



A

Nursery practice. Although there are no printed reports of nursery practices, seeds readily germinate along moist roadsides. Peronıas will readily propagate from cuttings planted during rainy periods (Troup 1921).

Figure 2—*Adenanthera pavonia,* peronías: cross section of a seed.

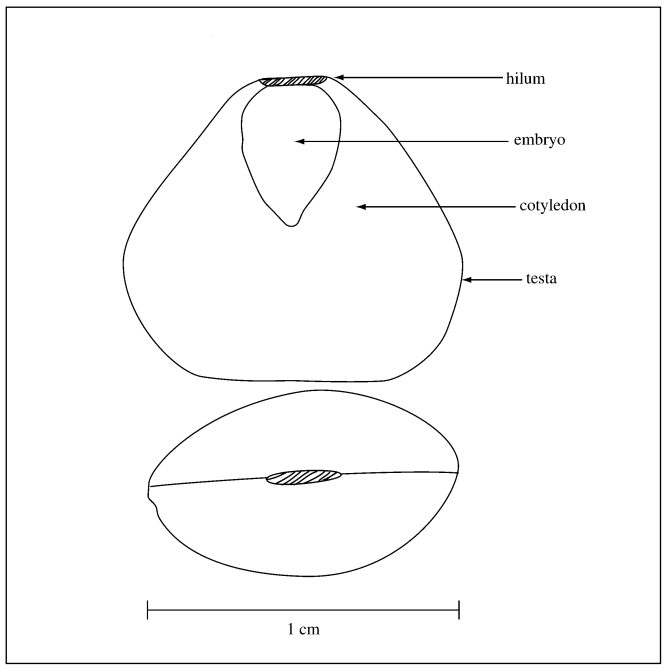
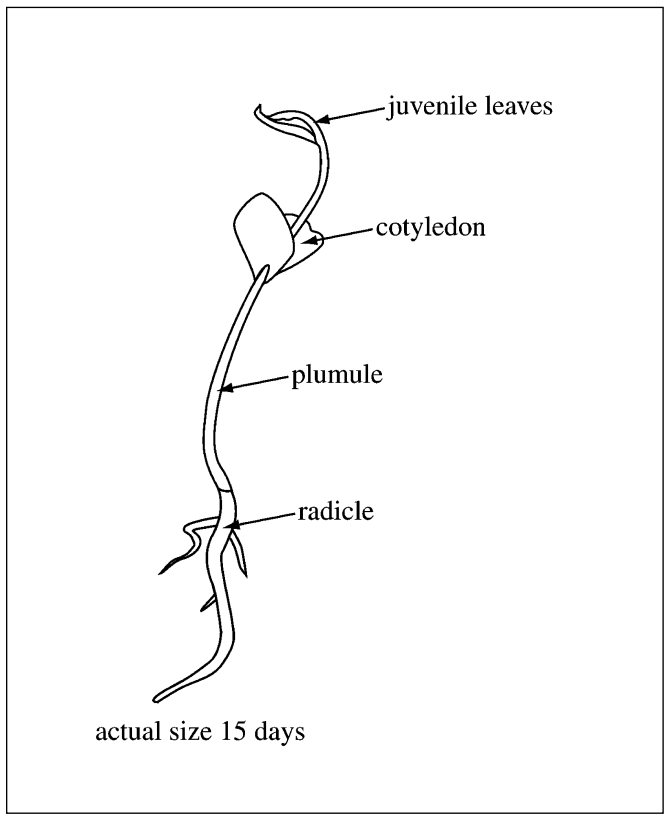


Figure 3—*Adenanthera pavonia*, peronías: seedling, 15 days.



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Hippocastanaceae—Horsechestnut family

Aesculus L.

buckeye

Paul O. Rudolf and Jill R. Barbour

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Growth habit, occurrence, and use. The buckeyes—which occur in North America, southeastern Europe, and eastern and southeastern Asia—include about 25 species of deciduous trees and shrubs (Rehder 1940). They are cultivated for their dense shade or ornamental flowers, and the wood of some species is occasionally used for lumber and paper pulp. They also provide wildlife habitat. The shoots and seeds of some buckeyes are poisonous to livestock (Bailey 1939). Seven of the 9 species described (table 1) are native to the United States. The horsechestnut was introduced into this country from southern Europe, and the Himalayan horsechestnut occurs naturally in the Himalayas.

Seven of these 8 species are not used much in reforestation, but all are used for environmental forestry planting. Himalayan horsechestnut is used extensively for reforestation and the nuts are fed to sheep and goats (Maithani and others 1990). This is also true of horsechestnut, which has been widely planted as a shade tree in Europe and also in the eastern United States, where it sometimes escapes from cultivation (Bailey 1939). Ohio and yellow buckeyes are sometimes planted in Europe and the eastern United States, the former having been successfully introduced into Minnesota, western Kansas, and eastern Massachusetts. California buckeye is also occasionally planted in Europe and to a somewhat greater extent in the Pacific Coast states. A natural hybrid—*A.* × *bushii Schneid. (A. glabra* × *pavia),* called Arkansas buckeye—occurs in Mississippi and Arkansas (Little 1953). At least 5 other hybrids are known in cultivation (Little 1953).

Flowering and fruiting. Buckeye flowers are irregular in shape and white, red, or pale yellow in color; they are borne in terminal panicles that appear after the leaves. The

Table 1—*Aesculus,* buckeye: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***A. californica* (Spach) Nutt.** *A. octandra* Marsh	**California buckeye**	Dry gravelly soils; lower slopes of coastal range & Sierra Nevada in California
***A. flava* Ait.**	**yellow buckeye,** sweet buckeye, big buckeye	Moist, rich soils; SW Pennsylvania, W to S Illinois, S to N Georgia, & N to West Virginia
***A. glabra* Willd.**	**Ohio buckeye,** fetid buckeye, American horsechestnut	Moist, rich soils; W Pennsylvania to SE Nebraska, S to Oklahoma, then E to Tennessee
***A. glabra* var. *arguta* (Buckl.) B.L. Robins.** *A. arguta* Buckl. *A. glabra* var. *buckleyi* Sarg. *A. buckleyi* (Sarg.) Bush	**Texas buckeye**	Limestone & granite soils; S Oklahoma, E & central Texas to Edwards Plateau
***A. hippocastanum* L.**	**horsechestnut,** chestnut, bongay	Native to Balkan Peninsula of Europe; planted extensively in US
***A. indica* (Wall. ex. Cambess) Hook.**	**Himalayan horsechestnut**	Himalayas between 1,524 to 3,050 m
***A. parviflora* Walt.**	**bottlebrush buckeye**	SW Georgia & Alabama
***A. pavia* L.**	**red buckeye,** scarlet buckeye, woolly buckeye, firecracker plant	Moist, rich soils; Virginia to Missouri, S to Texas & Florida
***A. sylvatica* Bartr.** *A. neglecta* Lindl. *A. georgiana* Sarg. *A. neglecta* var. *georgiana* (Sarg.) Sarg.	**painted buckeye,** dwarf buckeye, Georgia buckeye	Coastal plain & outer piedmont, from SE Virginia to Georgia, Alabama, & NW Florida

Source: Rudolph (1974).

flower spikes are 15 to 20 cm tall by 5 to 7.5 cm wide (Browse and Leiser 1982). The flowers are polygamo-monoecious, bearing both bisexual and male flowers. Only those flowers near the base of the branches of the cluster are perfect and fertile; the others are staminate (Bailey 1939; Rehder 1940).

The fruit is a somewhat spiny or smooth, leathery, round or pear-shaped capsule with 3 cells (figure 1), each of which may bear a single seed. Sometimes only 1 cell develops and the remnants of the abortive cells and seeds are plainly visible at maturity. When only 1 cell develops, the large seed is round to flat in shape. The ripe seeds (figure 1) are dark chocolate to chestnut brown in color, with a smooth and shining surface and have a large, light-colored hilum resembling the pupil of an eye. They contain no endosperm, the cotyledons being very thick and fleshy (figure 2). When ripe in the fall, the capsules split and release the seeds. The times of flowering and fruiting for 7 species of buckeyes are given in table 2. Other fruiting characteristics are listed in table 3.

Normally, horsechestnut and Ohio buckeye will set viable seeds almost every year. Bottlebrush buckeye rarely sets seed except in very hot, dry, late summers (Browse 1982).

Collection of fruits; extraction and storage of seeds. The fruits may be collected by picking or shaking them from the trees as soon as the capsules turn yellowish and begin to split open or by gathering them from the ground soon after they have fallen. The fruits may be dried for a short time at room temperature to free the seeds from any parts of the capsules that may still adhere to them, but great care must be taken not to dry them too long. When this occurs, the seedcoats become dull and wrinkled and the seeds lose their viability. There is ample evidence that buckeyes are recalcitrant in nature (Bonner 1969; Pence 1992; Tompsett and Pritchard 1993). Moisture contents at the time of shedding have been reported as 49% for horsechestnut (Suszka 1966) and 56% for red buckeye (Bonner 1969). The seeds of this genus should be sown at once in the fall or stratified promptly for spring-sowing.

Figure 1—*Aesculus,* buckeye: capsules and seeds of *A. glabra*, Ohio buckeye (**topleft**); *A. pavia*, red buckeye (**top right**); *A.hippocastanum*, painted buckeye (**middle left**); *A. sylvatica*, horsechesnut (**middle right**); *A. california*, yellow buckeye (bottom).

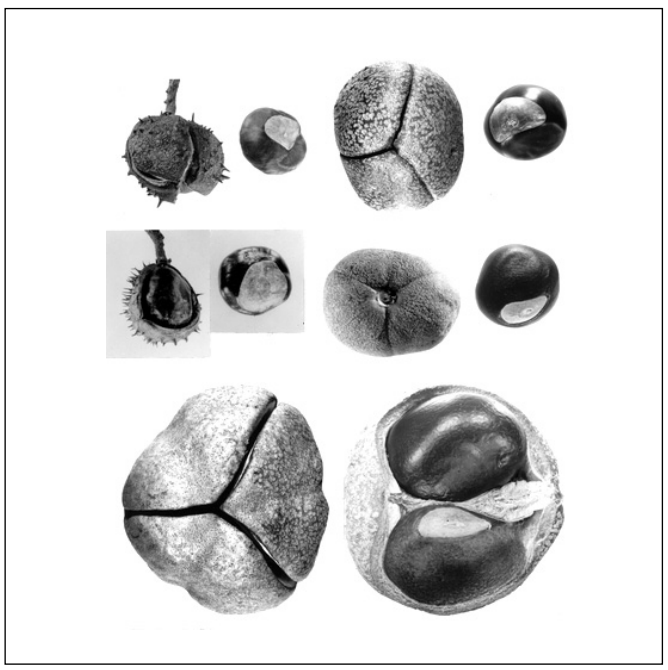
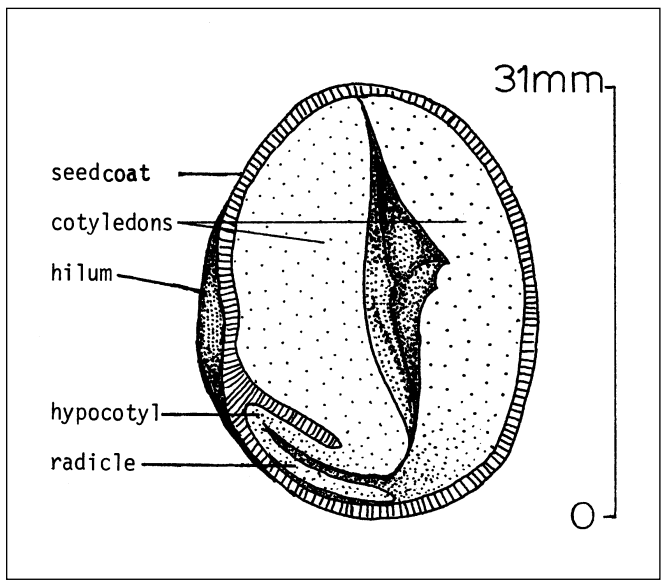


Figure 2—*Aesculus glabra*, Ohio buckeye: longitudinal section through a seed.



Buckeye seeds must be stored with moisture contents close to what they are shed with, but even then their viability cannot be maintained very long. Initial viability of fresh seeds of horsechestnut was maintained for 6 months when they were stored in polyethylene bags at 1 °C. This storage condition is the same as cold moist stratification because of the high moisture content of fresh seeds (Suszka 1966). When seeds were stored at –1 °C in sealed packages without added moisture for 13 months, germination dropped from 85% to 60%; after 15 months, however, germination was only 25% (Widmoyer and Moore 1968). Data on number of cleaned seeds per weight are listed for 7 species in table 4. Purity and soundness usually are close to 100% (Rudolf 1974). Nonviable seeds will float in water and can be discarded (Browse 1982).

Pregermination treatments. Seeds of Ohio, yellow, and painted buckeyes and horsechestnut require stratification or prechilling to induce prompt germination (Rudolf 1974). Stratification has been done in moist sand or sand-peat mix-

Table 2—*Aesculus,* buckeye: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
A. californica	S California	Apr–Sept	Sept–Oct	Nov & Dec
A. flava	—	Apr–June	Sept	Sept
A. glabra	—	Mar–May	Sept–mid-Oct	Early Sept–late Oct
var. *arguta*	Texas	Mar–Apr	May–June	—
	Minnesota	May	Sept–Oct	Sept–Oct
A. hippocastanum	Europe & NE US	Late Apr–early June	Mid-Sept–early Oct	Mid-Sept–mid-Oct
A. parviflora	SW Georgia, Alabama	July-Aug	Oct–Nov	Oct–Nov
A. pavia	South part of range	Mar–Apr	Sept–Oct	Sept–Nov
	North part of range	May–June	Sept–Oct	Sept–Nov
A. sylvatica	—	Apr–May	July–Aug	July–Aug
	Minnesota	May	Sept–Oct	Sept–Oct

Sources: Brown and Kirkman (1990), Harrar and Harrar (1962), Little (1953), Loiseau (1945), NBV (1946), Radford and others (1964), Rehder (1940), Rudolf (1974), Sargent (1965), Sus (1925), Turner (1969), van Dersal (1938), Vines (1960), Wyman (1947).

Table 3—*Aesculus,* buckeye: height, year first cultivated, flower color, seed-bearing age, seed crop frequency, and fruit ripeness criteria

Species	Height at maturity (m)	Year 1st cultivated	Flower color	Min seed-bearing age (yr)	Years of large seedcrops	Fruit ripeness criteria	
						Preripe color	Ripe color
A. californica	4.5–12	1855	White to rose	5	1–2	—	Pale brown
A. flava	7.5–27	1764	Yellow	—	—	Yellowish	Yellowish
A. glabra	9–21	1809	Pale greenish yellow	8	—	Green	Yellowish
var. *arguta*	2–11	1909	Light yellowish green	8	1+	Yellow	Yellowish green
A. hippocastanum	7.5–24	1576	White tinged with red	—	1–2	Green	Yellowish brown
A. parviflora	4.5–6	—	White	—	—	—	—
A. pavia	2.5–8.5	1711	Bright red	—	—	—	Light brown
A. sylvatica	7.5–20	1826	Pale yellow, red veins towards base	8	1+	Yellow-green	Yellowish tan

Sources: Brown and Kirkland (1990), Rehder (1940), Rudolf (1974), Sargent (1965)

Table 4—*Aesculus,* buckeye: seed data

Species	Place collected	Cleaned seeds/weight*			
		Range		Average	
		/kg	/lb	/kg	/lb
A. californica	El Dorado & Contra Costa Cos., California	18–36	8–16	26	127
A. flava	Kentucky & North Carolina	60–66	27–30	62	28
A. glabra	—	106–148	48–67	128	58
var. *arguta*	Carver Co., Minnesota	71–104	32–47	88	40
A. hippocastanum	W Europe	51–75	23–34	64	29
A. parviflora	SW Georgia, Alabama	40–60	18–27	51	23
A. pavia	Oktibbeha Co., Mississippi	—	—	117	53
A. sylvatica	Greene Co., Georgia, & Carver Co., Minnesota	68–126	31–57	88	40

Sources: Browse (1982), NBV (1946), Rudolf (1974).
* This value varies not only with seed size but also with moisture content, which is initially rather high in *Aesculus* seeds. One sample of *A. flava* seeds showed a moisture content of 95% (dry-weight basis) after it had been kept at room temperature for 36 days after collection.

tures at 5 °C for about 120 days, and by storage in sealed containers at 1 °C for 100 days or longer (May 1963; Rudolf 1974; Suszka 1966). In contrast, fresh seeds of California and red buckeyes can germinate satisfactorily without pretreatment (Rudolf 1974). Red buckeye seeds requires no stratification even though germination is delayed until spring. Cool winter temperatures suppress the germination, thus preventing autumn emergence (Browse 1982).

Bottlebrush buckeye seeds exhibit a type of epicotyl dormancy in so far as the root system continues to develop, but the shoot becomes dormant after it has emerged (Browse 1982). Further development of the shoot system does not occur until the spring (Browse 1982).

Presowing treatments of horsechestnut seeds increased germination 3 to 15% over the control. The treatments yielded the following germination rates: exposure to 50 °C, 92% germination; soaking with slight drying, 92%; exposure to 35 °C, 87%; exposure to high pressure, 87%; soaking in cobalt nitrate, 85%; soaking in chlorocholine chloride, 80%; and control, 77% (Tarabrin and Teteneva 1980).

Stratification benefits Himalayan horsechestnut. There was a 5-fold increase in germination at 30 °C from 12% for the control to 60% following stratification for 15 days (Maithani and others 1990). Prolonging the stratification period to 30 days resulted in 79% germination (Maithani and others 1990).

Germination tests. Stratified buckeye seeds have been germinated in sand or on wet paper at diurnally alternating temperatures of 30 and 20 °C. Results are summarized in table 5. Official testing rules for red buckeye (AOSA 1998) call for germinating unstratified seeds for 28 days on the top of wet paper at the 30/20 °C regime. A recommendation for germinating seeds of horsechestnut without stratification is to soak them in water for 48 hours and cut off one-third of the seed at the scar end without removing the seedcoat. The portion with the scar should then be germinated in sand flats for for 21 days at the same 30/20 °C regime (ISTA 1993).

Nursery practice. Under natural conditions, seeds of most buckeye species germinate in the early spring. California buckeye, however, germinates just after winter rains have begun, usually in November. In the nursery, buckeye seeds usually are sown in the fall as soon after collection as possible to prevent drying and loss of viability. If desired, however, the seeds of species having embryo dormancy can be stratified or placed in cold, moist storage promptly and then sown in the spring (Rudolf 1974; Suszka 1966). Himalayan horsechestnut seeds without any treatment showed 80% germination after 133 days (Maithini and others 1990). Seeds sown after 30 days of cold stratification showed 68% germination in 78 days (Maithini and others 1990). The seeds should be sown about 5 cm (2 in) apart in rows 15 cm (6 in) apart (NBV 1946) and covered with 2.5 to 5 cm (1 to 2 in) of soil. The seeds should be sown with the scar underneath so that the radicle emerges in the correct position to produce a normal seedling (Browse and Leiser 1982). If the seeds are variable in size, it is better to grade them so that small sizes are discarded or sown separately, as these rarely make large 1-year seedlings (Browse 1982).

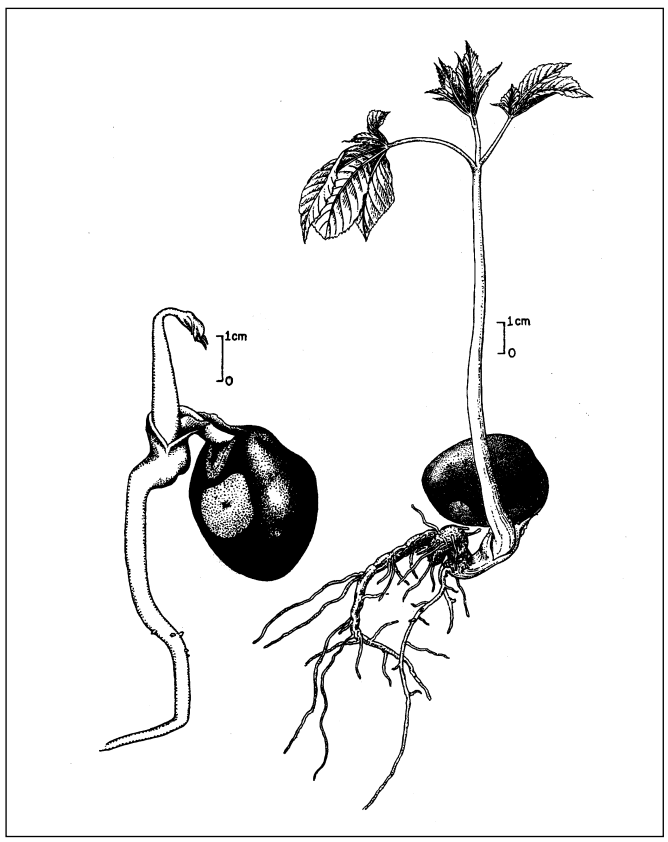
Germination is hypogeal (figure 3) and usually is complete 3 to 4 weeks after spring sowing (NBV 1946). A tree percentage of 70 has been obtained (Rudolf 1974). The beds should not be over-watered because the seeds rot rather easily (Rudolf 1974). Ordinarily, 1+0 stock is large enough for field planting.

Table 5—*Aesculus,* buckeye: cold stratification periods, germination test conditions, and results

Species	Cold stratification* (days)	Daily light (hrs)	Germination test conditions				Germinative energy		Germinative (%)
			Medium	Temp (°C) Day	Temp (°C) Night	Days	Amount (%)	Time (days)	
A. californica	0	—	Sand	30	20	20	—	—	56
A. flava	120	—	Sand	30	20	40	62	27	76
A. glabra	120	—	Sand	30	20	40	—	—	59
var. *arguta*	120	8	Sand	24	17	30	—	—	76
A. hippocastanum	120	—	Sand	30	20	30	—	—	89
A. pavia	0	8	Kimpak	30	20	30	62	20	70
A. sylvatica	90	—	Sand	—	—	30	—	—	78

Sources: May (1963), NBV (1946), Rudolf (1974), Suszka (1966), Widmoyer and Moore (1968).
* Cold stratification temperatures ranged from – 0.5 to 5 °C.

Figure 3—*Aesculus californica*, California buckeye: seedling development at 2 and 4 days after germination.



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A

Simaroubaceae—Quassia family

Ailanthus altissima (P. Mill.) Swingle

ailanthus

John C. Zasada and Silas P. Little

Dr. Zasada retired from the USDA Forest Service's North Central Research Station; Dr. Silas Little (deceased) retired from the USDA Forest Service's Northeastern Forest Experiment Station

Synonyms. *Toxicodendron altissimum* Mill., *Ailanthus glandulosa* Desf.

Other common names. Tree-of-heaven ailanthus, tree-of-heaven, copaltree.

Growth habit, occurrence, and use. Native to China, this 12.5- to 25-m-tall deciduous tree is described as "the most adaptable and pollution tolerant tree available" (Dirr 1990). Although it was originally considered a desirable ornamental tree, its desirability and usefulness are now questioned (Dirr 1990; Feret 1985) and many consider it an "invasive alien pest." It is sometimes planted for shelterbelts, for game food and cover, and, rarely, for timber as in New Zealand. Ailanthus was introduced into cultivation in England in 1751 (Feret 1985; Illick and Brouse 1926) and brought to America in 1784 (Little 1974). It has become naturalized in many parts of the United States—from Massachusetts to southern Ontario, Iowa, and Kansas, and south to Texas and Florida, as well as from the southern Rocky Mountains to the Pacific Coast (Feret and Bryant1974; Feret and others 1974; Little 1979). In some localities, ailanthus is so well-established that it appears to be a part of the native flora. Wood properties are summarized by Alden (1995) and silvics by Miller (1990). There are a number of other *Ailanthus* species grown in other parts of the world for various purposes (Alam and Anis 1987; Beniwal and Singh 1990; Feret 1985; Rai 1985; Ramikrishnan and others 1990).

Ailanthus is an aggressive, intolerant pioneer species with rapid juvenile growth of 1 to 1.5 m/year. It invades severely disturbed sites, harsh environments, and poor soils. It suckers from roots and can form dense stands, making it difficult for native species to colonize. Stands may be maintained by root suckering but it does not regenerate from seed under its own canopy (Bordeau and Laverick 1958; Miller 1990). One or more potent inhibitors of seed germination and seedling growth are produced in the bark, leaves, and seeds (Heisey 1990; Lawrence and others 1991). Heisey (1990) concluded that allelochemicals in ailanthus may have potential as naturally produced herbicides.

Flowering and Fruiting. The tree is mainly dioecious, with some monoecious individuals (Dirr 1990; Miller 1990). Flowers are usually unisexual, but perfect flowers do occur in some individuals (Feret 1973). Flowering has been observed in seedlings 6 weeks after germination (Feret 1973).

Commercial "seed" consists of the 1-celled, 1-seeded, oblong, thin, spirally twisted samaras. These samaras, with seeds near the middle, are 8 to 12 mm wide and 33 to 48 mm long (Feret and others 1974) and light reddish brown in color (figure 1). Flowering occurs from mid-April to July (Little 1974). Seeds ripen in large panicles in September to October of the same season and are dispersed from October to the following spring (Illick and Brouse 1926). Ailanthus is a prolific seeder: 15- to 20-year-old trees bear considerable quantities. Seeds have no endosperm (figure 2).

Collection of fruits; extraction and storage of seeds. Ailanthus seeds have been found in soil seedbanks in stands with no individuals present in the overstory. This suggests that seeds may be stored in the soil for some period of time after parent trees have disappeared from a site (Dobberpuhl 1980).

Figure 1—*Ailanthus altissima*, ailanthus: samara.

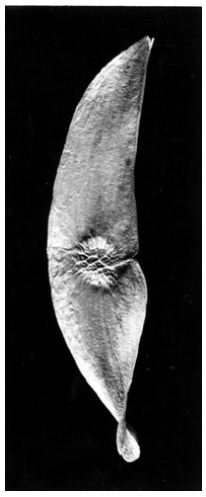
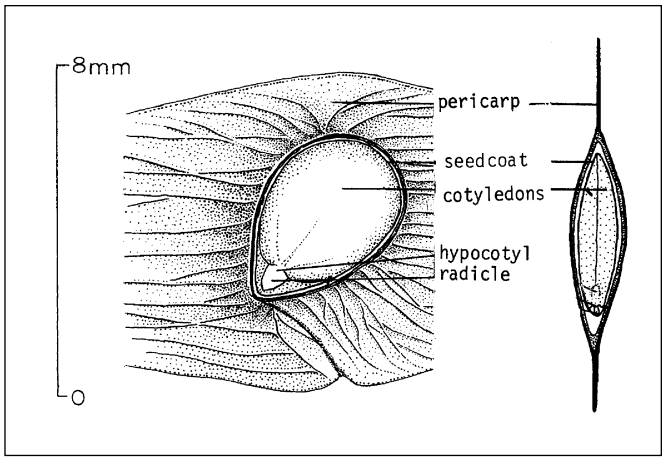


Figure 2—*Ailanthus altissima*, ailanthus: longitudinal section through a seed.



Ailanthus fruits are picked from standing trees by hand or flailed or stripped onto canvas at any time during the late fall and early winter. After collection, the fruits should be spread out to dry (to lose superficial moisture). They may then be run through a macerator and fanned to remove impurities, or they may be flailed or trampled in a burlap bag and run through a fanning mill (Little 1974).

Forty-five kilograms (100 lb) of fruit yields 13.6 to 40.9 kg (30 to 90 lb) of cleaned seeds (Little 1974). Seeds with wings attached weigh from 22,700 to 75,500/kg (10,300 to 34,300/lb), with an average of about 38,700/kg (17,500/lb) (Feret and others 1974; Little 1974). Cleaned seeds (without wings) weigh from 29,000 to 43,000/kg (13,200 to 19,500) with a mean of 37,200/kg (16,900/lb) (Al'benskii and Nikitin 1956). Germination capacity of seedlots is normally in the 75 to 96% range (Al'benskii and Nikitin 1956; Graves 1990; Little 1974).

Seeds should be stored with low moisture contents at temperatures of 1 to 3 °C, and in sealed containers (Heit 1967). However, seedlots stored in sacks for over a year at temperatures ranging from –6 to 40 °C still had germination of 75% (Little 1974). In Russia, seeds are stored in boxes at 0 to 4 °C, layers about 2.5 cm (about 1 in) thick being separated and topped by layers of dry sand half as thick (Shumiliana 1949). Although sensitive to moisture and fluctuating temperatures, seeds can be successfully stored for long periods in sealed containers at low moisture contents in a refrigerator (Heit 1967).

Germination. Stratification appears to improve germination in most cases, although varying amounts of germination occur in unstratified seeds (Bordeau and Laverick 1958; Dirr 1990; Graves 1990; Little 1974; Shumilina 1949). Graves (1990) found that although total germination was not affected by stratification, germination rate was greater in stratified seeds. Thirty to 60 days of stratification at 1 to 5 °C is usually recommended (Dirr 1990; Little 1974; Shumilina 1949); however, Graves reported 70, 77, and 96% germination after stratification at 5 °C for 0, 4, and 12 days, respectively. Seed testing rules recommend temperatures of 20 to 30 °C with no stratification (pericarp removal may increase germination rate); first evaluation at 7 days and a test duration of 21 days (ISTA 1993). Ailanthus seed germination was little affected by salt concentrations representative of roadside environments where salt is applied in winter; seeds of native oaks and birch were more sensitive (Bicknell and Smith 1975). Other *Ailanthus* spp. are more difficult to germinate than tree-of-heaven (Ramakrishnan and others 1990).

Nursery practice. Seeds can be sown immediately after collection if conditions permit or they can be stratified and sown in the spring with drills. Broadcast seeds should be covered with 1.3 cm ($^1/_2$ in) of soil. Fifteen to 25% of the viable seeds sown produce usable 1+0 seedlings (Little 1974). Thus, 0.45 kg (1 lb) of seeds may yield 3,000 usable plants (Van Dersal 1938). Greenhouse studies indicate that ailanthus could be grown in containers (Feret and Bryant 1974; Feret and others 1974; Heninger and White 1974). Maximum seedling growth occurs at a soil temperature of 19 °C (Heninger and White 1974). Ailanthus can be produced vegetatively from root cuttings (Dirr and Heuser 1987).

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Fabaceae—Pea family

Albizia Durazz.

albizia

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Growth habit, occurrence, and use. The albizias include about 50 species of medium- to large-sized deciduous trees and climbers distributed throughout tropical and subtropical Asia, Africa, and Australia (Rock 1920). Many species have been introduced into the United States, and the 4 listed in table 1 are important. Silktree was introduced into the southern United States in 1745 and planted widely for ornamental purposes. Currently it is considered invasive. The species is also valuable for wildlife cover and browse (Wick and Walters 1974). Siris is planted in Hawaii for shade and ornament (Neal 1965) and was introduced into Puerto Rico during the Spanish colonial era. Its yellowish brown heartwood is moderately hard, coarse-grained, strong, and fairly durable and is used for a variety of purposes, including furniture-making, in its native Asian range (Parrotta 1987a). White siris is planted in Hawaii (Neal 1965) and was introduced into Puerto Rico in 1927 as an ornamental and fuelwood species. In Puerto Rico, white siris has become naturalized and is now common on severely disturbed sites and old fields. The light brown heartwood is moderately hard, straight-grained, strong, and durable and is used in the species' native range as an all-purpose timber (Parrotta 1987b). Raintree (formerly known as *Pithecellobium saman)* is valued for timber and wildlife habitat and as an ornamental. The wood is used for paneling, furniture, and specialty items. The tree was introduced into Florida and Hawaii (Little and Wadsworth 1964; Magini and Tulstrup 1955) and is now considered invasive.

Flowering and fruiting. The flowering and seeding dates of *Albizia* species are listed in table 2. Flowers of siris are greenish-yellow to whitish, those of silktree are light pink, and those of white siris are whitish (Little and Wadsworth 1964; Wick and Walters 1974). All species bear their flowers in clusters near the tips of branches. The fruits of all species are flat, linear, 6- to 12-seeded legumes (pods) (figure 1) and ripen within a year after the trees flower (Little and Wadsworth 1964; Rock 1920; Wick and Walters 1974). Silktree legumes are about 15 cm long; siris and white siris legumes are up to 20 cm long. When mature, the legumes of tall albizia are reddish brown, whereas those of

Table 1—*Albizia,* albizia: nomenclature, occurrence, and growth habit

Scientific name & synonym(s)	Common name(s)	Occurrence		Growth habit
		Native	US	
***A. julibrissin* Durz.** *Acacia julibrissin* (Durraz.) Willd. *A. nemu* Willd.	**silktree,** albizia, mimosa tree, powder-puff tree	Iran to Japan	Southern US	Deciduous ornamental
***A. lebbeck* (L.) Benth.** *Acacia lebbek* Willd. *Mimosa lebbek* L.	**siris,** woman's-tongue	Pakistan to Burma	Puerto Rico & Hawaii	Deciduous forest tree, ornamental
***A. procera* (Roxb.) Benth.** *Acacia procera* Willd. *Mimosa elata* Roxb. *M. procera* Roxb.	**white siris,** tall albizia	India to Melanesia & Hawaii	Puerto Rico	Deciduous forest tree
***A. saman* (Jacq.) F. Muell.** *Pithocellobium saman* (Jacq.) Benth. *Samanea saman* (Jacq.) Merr.	**raintree,** saman, monkey-pod	Central & South America & West Indies	S Florida & Hawaii	Evergreen tree (deciduous in Hawaii)

Sources: Walters and others (1974), Wick and Walters (1974).

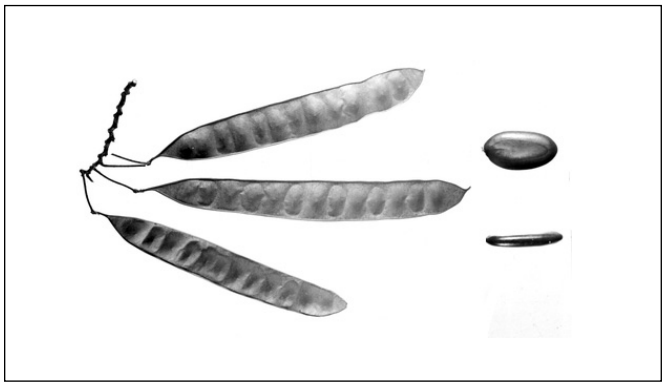
A

Table 2—*Albizia,* albizia: phenology of flowering, fruit ripening, and seed dispersal

Species	Location	Flowering	Fruit ripening	Seed dispersal
A. julibrissin	S US	June–Aug	Sept–Nov	Sept–Nov
A. lebbeck	Puerto Rico	Apr–Sept	All year	All year
A. procera	Puerto Rico	Aug–Sept	Jan–June	All year
A. saman	—	Spring–fall	Fall–spring	All year

Sources: Little and Wadsworth (1964), Rock (1920), Wick and Walters (1974).

Figure 1—*Albizia julibrissin*, silktree: legumes and seeds.



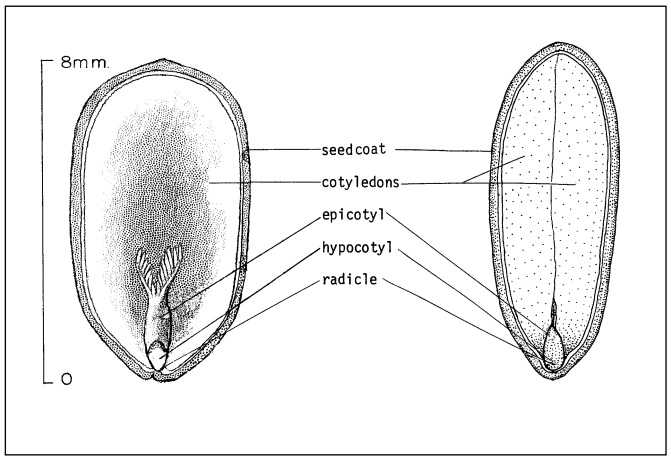
the other 2 species are straw-colored. The light brown seeds of all species are released from the dehiscent legumes from legumes that are still attached to the tree or from fallen legumes, which may travel considerable distances in high winds (Parrotta 1987a; Rock 1920; Wick and Walters 1974).

Collection, extraction, and storage. Collection of albizia seeds should begin as soon as the legumes mature. Siris seeds are particularly prone to predation by insect larvae, especially those of bruchid beetles (Parrotta 1987a). The legumes may be picked or shaken from the trees and collected on canvas. Seeds are readily extracted from the legumes by flailing or threshing. A seed cleaner or a fanning mill can be used to separate seeds from the remaining debris. Silktrees average about 24,000 clean seeds/kg (11,000/lb) (Wick and Walters 1974); siris, 7,000 to 11,000 seeds/kg (3,000 to 5,000/lb) (Parrotta 1987a); white siris, 17,000 to 25,000 seeds/kg (8,000 to 11,000/lb) (Francis and Rodrıguez 1993; Parrotta 1987b); and raintrees, 4,400 to 7,720 seeds/kg (2,000 to 3,500/lb) (Walters and others 1974). Albizia seeds are orthodox in nature. Air-dried seeds of siris and white siris generally retain high germination rates for at least 1 to 2 years in storage at room temperature or under refrigeration (Parrotta 1987a). No definitive information is available on how long silktree seeds can be stored, although a small sample of seeds kept in loosely corked bottles in a laboratory for almost 5 years had a germination rate of almost 90% (Wick and Walters 1974).

Germination. Germination of albizia seeds is slow because of their impermeable seedcoats (figure 2). Dormancy can be broken either by mechanical scarification, sulfuric acid scarification, or soaking in water (Francis and Rodrıguez 1993; Parrotta 1987a). The easiest, safest, and usually most effective means for breaking dormancy in siris and white siris is immersion of the seeds in boiling water for 1 to 3 minutes, soaking them in water at room temperature for 24 hours, then sowing the seeds immediately (Parrotta 1987a). Germination rates for scarified seeds range from 50 to 99% and germination begins within 2 to 4 days after sowing (Francis and Rodrıguez 1993; Parrotta 1987a&b). Raintree seeds will often germinate without pretreatment, but a 10-minute soak in sulfuric acid will increase the percentage and rate of germination (Walters and others 1974). Germination as high as 92% has been reported for this species (Neal 1965; Rock 1920). Germination in albizias is epigeal (figure 3).

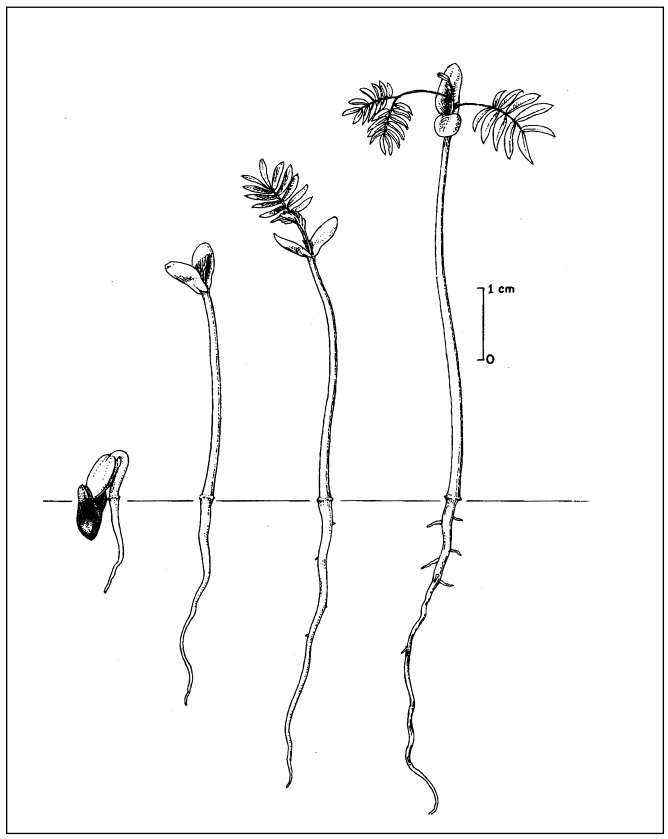
Nursery practice. Germination and seedling growth of albizia is favored by shallow sowing, up to 2.5 cm (1 in)

Figure 2—*Albizia julibrissin*, silktree: longitudinal section through a seed.



depth, in loose, moist soil under full sun (figure 3). Seedling growth is rapid; siris and white siris seedlings reach plantable size (20 cm in height) usually within 2 to 3 months after sowing under nursery conditions in Puerto Rico (Parrotta 1987a). Raintree seeds are sown in March in Hawaii for outplanting as $^{3}/_{4} + 0$ stock the following winter. A sowing depth of 2.5 cm (1 in) and density of 160 to 215 seedlings/m^2 (15 to 20/ft^2) are recommended, with 75 to 85% shading of the beds (Walters and others 1974). Plantations can be established by direct sowing (for siris and white siris) or by using container seedlings (for all species). Stumped seedlings or stem, branch, and root cuttings can also be used to propagate siris and white siris (Parrotta 1987a).

Figure 3—*Albizia julibrissin*, silktree: seedling development at 1, 3, 5, and 8 days after germination.



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A

Euphorbiaceae—Spurge family

Aleurites moluccana (L.) Willd.

Indian-walnut

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Synonyms. *Aleurites javanica* Gand., *A. triloba* Forster & Forster f.

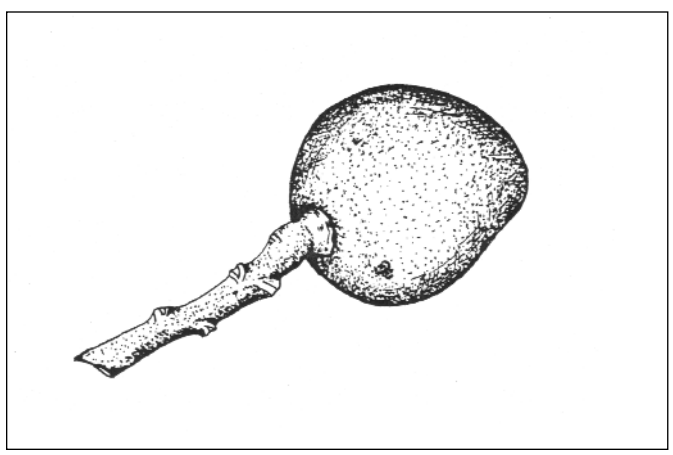
Other common names. Kukui, candlenut-tree, *tutui, nuez, nuez de India, lumbang, sakan, lama*.

Growth habit, occurrence, and uses. Indian-walnut is well-known as kukui, the state tree of Hawaii. On the Islands, it is a large, evergreen, spreading tree of moist lowland mountains up to an elevation of 671 m. It may grow to a height of 24 m and a bole diameter of 0.9 m (Little and Skolmen 1989). This species is a probable native of Malaysia, as its name suggests that it came from the Moluccan Islands. It can be found on islands throughout the Pacific region, and it has been introduced to other tropical areas, including Puerto Rico and the Virgin Islands (Little and Skolmen 1989).

The tree was introduced by early Hawaiians for its oily, nutlike seeds. Oil pressed from these seeds was once widely used for fuel in stone lamps, for paints and varnishes, and for medicines. In past years, as much as 37,850 liters (10,000 gal) of the oil was exported annually, but the industry has become unprofitable in Hawaii (Little and Skolmen 1989). The trees are still grown for production of the oil in the Philippines and other parts of the Pacific region (Eakle and Garcia 1977). In addition, the leftover oil cake can be used as fertilizer or cattle food. Local uses also included folk medicine and dyes, and a waterproofing substance can be made from the tree's sap and green fruits (Little and Skolmen 1989). Indian-walnuts have been utilized in shade, ornamental, and protection plantings in Hawaii (Little and Skolmen 1989).

Flowering and fruiting. Indian-walnut's flowers are borne in terminal cymes 9 to 15 cm long. The white individual flowers are about 10 mm long. Flowering is monoecious, with many more male flowers than female on the cymes (Little and Skolmen 1989). Fruits are round to ellipsoidal in shape, 5 to 6 cm long, and 5 to 7 cm wide, with fleshy to leathery husks (figure 1). There are 1 or 2 elliptical seeds per fruit. The seeds are 2.5 to 3.5 cm long, and the shells are hard, rough, and black (Dayan and Reaviles 1995; Little and Skolmen 1989). Flowering and fruiting occurs intermittently in Puerto Rico (Little and others 1974).

Figure 1—*Aleurites moluccana*, Indian-walnut: fruit (drawing from Little and others 1974).



Collection, extraction, and storage. Fruits may be collected from the ground after shedding or picked from the trees. In the Philippines, it is common practice to let the fruits decay for 3 to 5 days after collection and then remove the husks by hand under running water. The seeds are then dried in the sun for 3 or 4 days to a low moisture content; there are about 116/kg (53/lb) (Dayan and Reaviles 1995). Empty or deteriorated seeds can be removed by water flotation (Tamesis 1958; Eakle and Garcia 1977). There are no long-term storage data on Indian-walnut, but the seeds are apparently orthodox in storage characteristics. Dayan and Reaviles (1995) reported that seeds dried to 10 to 12% moisture can be successfully stored at room temperature for 7 months.

Germination. Indian-walnut germinates slowly, apparently due to dormancy imposed by the hard seedcoat (Eakle and Garcia 1977). Several pretreatments have been

used to speed germination. In early tests in the Philippines, seeds were heated by burning grass over a layer of seeds or by planting imbibed seeds in drums of moist soil exposed to the sun (Tabat 1925; Tamesis 1958). The heat and moisture were thought to cause the seedcoats to crack. Sometimes, very good germination could be obtained by planting untreated nuts and keeping the seedbeds very moist; this method produced 86% germination 5 months after planting (Tabat 1925). Eakle and Garcia (1977) tested numerous acid scarification treatments with sulfuric, nitric, and hydrochloric acids, but none were successful. Dayan and Reaviles (1995) recommend manual cracking of the nuts, followed by an overnight soak in tap water.

Nursery practice. Seedborne fungi may be a problem for Indian-walnut, so treatment with a good fungicide prior to planting is recommended. For container production, a 1:1:1 ratio of sand, top soil, and dried organic matter should be used as a medium (Dayan and Reavile 1995). Direct seeding has also been successful in the Philippines. Seeds are allowed to start germination in a drum of moist soil heated by the sun, then removed for direct planting in the field when they start to crack open (Tamesis 1958).

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A

Betulaceae—Birch family

Alnus P. Mill.

alder

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Growth habit and occurrence. Alder—the genus *Alnus*—includes about 30 species of deciduous trees and shrubs occurring in North America, Europe, and Asia and in the Andes Mountains of Peru and Bolivia. Most alders are tolerant of moist sites and thus are commonly found along streams, rivers, and lakes and on poorly drained soils; in addition, some species occur on steep slopes and at high elevations. The principal species found in North America are listed in table 1. Many changes in the taxonomy of alder have been made over the years; in this summary, species are referred to by their currently accepted names although in many cases the information was published originally under the synonyms (and alternative common names) listed in table 1.

Although some cultivated European alder is used commercially in the eastern United States, red alder is the largest native species. It is also the most extensively utilized of the native species. Management interest and research activity on red alders have increased dramatically during the past 2 decades, and the resulting information accounts for the majority of new information added to the previous summary on alder seeds prepared by Schopmeyer (1974).

Alders are pioneer species favored by high light levels and exposed mineral soils; in addition, their ability to fix atmospheric nitrogen facilitates establishment on geologically young or disturbed sites with low levels of soil nitrogen (Harrington and others 1994). Dense stands of naturally regenerated red alders established quickly on mudflows associated with the eruption of Mount St. Helens. The trees grew rapidly and soon overtopped other pioneer species such as poplars in the nitrogen-deficient soils (Heilman 1990). Sitka alder plays a similar role in primary succession following deglaciation in Alaska.

Use. Seedlings have been planted successfully for reforestation of coal mining spoil banks (Lowry and others 1962). Soil fertility is improved through fixation of atmospheric nitrogen by microorganisms in the root nodules (Tarrant and Trappe 1971). Alders also have been planted for wildlife food and cover (Liscinsky 1965) and for ornamental use. European and red alders have been considered for use in biomass plantings for energy (Gillespie and Pope 1994) and are considered excellent firewood. In recent years, harvest and utilization of red alder has expanded greatly on the Pacific Coast of North America, where the species is used for paper products, pallets, plywood, paneling, furniture, veneer, and cabinetry (Harrington 1984; Plank and Willits 1994). Red alder is also used as a fuel for smoking or curing salmon and other seafood and its bark is used to make a red or orange dye (Pojar and MacKinnon 1994). The soft, even-grained wood lacks odor or taste and has been traditionally been used by native peoples, and more recently other woodworkers, to make bowls, eating utensils, and other items (Pojar and MacKinnon 1994). In addition, alder exports have grown from almost nothing in 1990 to more than 153,000 m^3 (or 65 million board feet) of lumber annually (Tarrant and others 1994). Several options exist for managing alder in both mixed (Miller and Murray 1978) and pure stands (Tarrant and others 1983), and a summary of management principles and alternative strategies are available for red alder (Hibbs and DeBell 1994).

Geographic races and hybrids. Considerable geographic variation exists among populations of red (Ager and others 1993; Ager and Stettler 1994; Dang and others 1994; Hamann and others 1988; Lester and DeBell 1989), speckled (Bosquet and others 1988), American green (Bosquet and others 1987), and European alders (Funk 1990; Hall and Maynard 1979). Disjunct populations of red alder have been located in Idaho (Johnson 1968), and growth of such populations and those at the extremes of species' range differs markedly from that of most populations (Lester and DeBell 1989). Natural hybridization is common in alder, and zones of introgression between some species can occur where ranges overlap (Ager and Stettler 1994). Artificial hybridization has been conducted with numerous species, including

Table 1—*Alnus,* alder: nomenclature and occurrence

Scientific name(s) & synonyms	Common name(s)	Occurrence
***A. glutinosa* (L.) Gaertn.** *A. alnus* (L.) Britt. *A. rotundifolia* Mill.; *A. vulgaris* Hill *Betula alnus* var. *glutinosa* L.	**European alder,** black alder, European black alder	Native of Europe, northern Africa, & Asia; naturalized locally in parts of E Canada & NE US, cultivated in E, central, & S US
***A. incana* (L.) Moench** *Betula alnus* var. *incana* L.	**mountain alder,** European speckled alder, hoary alder, gray alder	Native of Europe & the Caucasus area; occurs in North America only under cultivation
***A. incana* ssp. *rugosa* (Du Roi) Clausen** *A. incana* var. *americana* Reg. *A. glauca* Michx. *A. rugosa* (Du Roi) Spreng. var. *americana* (Reg.) Fern *A. rugosa* var. *tomophylla* (Fern.) Fern. *Betula alnus* var. *rugosa* Du Roi	**speckled alder,** tag alder, swamp alder, *aulne blanchâtre*	E & central Canada, N central US & in Appalachian Mtns to West Virginia & Maryland
***A. incana* ssp. *tenuifolia* (Nutt.) Breitung** *A. incana* var. *occidentalis* (Dippel) Hitch. *A. incana* var. *virescens* S. Wats. *A. occidentalis* Dippel *A. rugosa* var. *occidentalis* (Dippel) Hitch. *A. tenuifolia* Nutt.	**thinleaf alder,** mountain alder	Yukon & Alaska S to W Montana & Oregon, in Sierra Nevada to central California, & E to Arizona & New Mexico
***A. maritima* (Marsh.) Muhl. ex Nutt.** *A. maritima* ssp. *metoporina* (.Furlow) E. Murr *A. metoporina* Furlow *Betula-alnus maritima* Marsh.	**seaside alder,** brook alder	Widely disjunct populations in Delaware, Maryland, & Oklahoma
***A. nepalensis* D. Don** *A. boshia* Buch.-Hamilt. ex D. Don *Clethropsis nepalensis* (D. Don) Spach.	**Nepal alder,** *utis, maibao*	Native of India & Burma; planted in Hawaii
***A. oblongifolia* Torr.**	**Arizona alder,** New Mexican alder, *aliso* (Mexico)	Scattered populations in high mtns of Arizona, New Mexico, & Mexico
***A. rhombifolia* Nutt.** *A. rhombifolia* var. *bernardina* Munz & Johnson	**white alder,** Sierra alder, California alder	Interior of S British Columbia, Washington, Oregon, & Idaho; Sierra Nevada & coastal ranges in California & N Baja California
***A. rubra* Bong.** *A. oregona* Nutt. *A. oregona* var. *pinnatisecta* Starker	**red alder,** Oregon alder, western alder, Pacific Coast alder	Pacific Coast region from SE Alaska to S California
***A. serrulata* (Ait.) Willd.** *A. incana* var. *serrulata* (Ait.) Boivin *A. novebroacensis* Britt. *A. rubra* (Marsh.) Tuckerman *A. rugosa* (Du Roi) Spreng. var. *serrulata* (Ait.) Winkler *A. serrulata* var. *subelliptica* Fern. *Betula serrulata* (Ait.)	**hazel alder,** smooth alder, black alder	SW Nova Scotia & central Maine W to Missouri & S to E Texas & Florida

hybrids of red alder with European or mountain alders (Chiba 1966; Hall and Maynard 1979; Ljunger 1959).

Flowering and fruiting. Species in the genus are typically monoecious, with clusters of separate male and female flowers in close proximity. Flower initiation probably occurs during late June or July for both red and European alders (Ager and others 1994; Brown 1986; McVean 1955). The male and female flowers develop into catkins that elongate in late winter or early spring and mature on the previous year's twigs (table 2). For red alders, peak pollen shedding precedes peak female receptivity by only 2 to 4 days (Stettler 1978). For a specific description of staminate and pistillate catkins, see Brayshaw (1976). The strobiles of most species are 10 to 15 mm long when mature (figure 1), but those of Nepal, red, and Sitka alders are larger, having lengths of 12 to 24 mm (Carlson and Bryan 1959; Funk 1990; Harrington 1990; Krstinic 1994; Townsend and Douglass 1994). They are produced in abundance before trees reach 10 years of age in at least 2 species. European alders can produce flowers by their second growing season, and individual red alder trees are sexually mature at 3 or 4 years. Most dominant trees in a red alder stand will produce seeds by age 6 to 8 years (Harrington and DeBell 1995; Stettler 1978). Although the majority of seeds produced are probably the result of outcrossing, both selfing and apomixis occur in red alder (Stettler 1978). Seed production resulting from selfing has been reported for European and mountain alders; however, in many cases self-fertilization results in

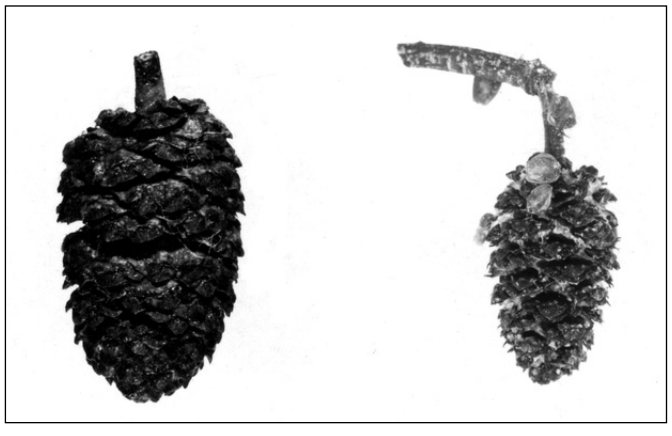
Table 1—*Alnus*, alder: nomenclature and occurrence (Continued)

Scientific name(s) & synonyms	Common name(s)	Occurrence
***A. viridis* (Vill.) Lam. & DC.** *A. ovata* (Schr.) Lodd. *Alnobetula* (Ehrh.) K. Koch *Betula viridis* Vill.	**Sitka alder**	S Arctic subarctic, and N mountainous regions of North America & Asia
***A. viridis* ssp. *crispa* (Ait.) Turrill** *A. crispa* (Ait.) Pursh *A. crispa* var. *elongata* Raup. *A. crispa* var. *harricanensiis* Lepage *A. crispa* var. *mollis* (Fern.) Fern. *A. crispa* var. *stragula* Fern. *A. mollis* Fern. *A. viridis* var. *crispa* (Michx.) House *A. alnobetula* var. *crispa* (Michx.) Winkler *Betula crispa* (Ait.)	**American green alder,** green alder, mountain alder	Labrador to Alberta, S to Minnesota & New England
A. viridis* ssp. *fruticosa* (Rupr.) Nyman *A. fruticosa* Rupr. *A. viridis* var. *fruticosa* (Rupr.) Reg.	**Siberian alder**	Alaska S to British Columbia & Alberta, disjunct populations in Washington, Oregon, & N California
***A. viridis* ssp. *sinuata* (Regel) A. Löve & D. Löve** *A. crispa* ssp. *sinuata* (Reg.) Hultén *A. sinuata* (Reg.) Rydb. *A. sitchensis* (Reg.) Sarg. *A. viridis* var. *sinuata* Reg.	**Sitka alder,** mountain alder, wavyleaf alder	Yukon & Alaska S to N California & W Montana; also in E Asia

Sources: Schopmeyer (1974), FNAEC (1997).

* In western North America, Siberian alder (*A. viridis* ssp. *fruticosa*) has long been mistaken for American green alder (*A. v.* ssp. *crispa*), which it closely resembles, or for Sitka alder (*A. v.* ssp. *sinuata*) (FNASEC 1997).

Figure 1—*Alnus*, alder: mature female catkins (strobiles) of *A. rhombifolia*, white alder (**left**); *A. serrulata*, hazel alder (**right**).



aborted ovules (Krstinic 1994). Information on the effects of management practices on reproductive processes is limited. In young red alder plantings in western Washington, flowering varied by half-sib family but overall was reduced in close spacings and by summer irrigation (Harrington and DeBell 1995). However, dry weather in spring reduced germination rates of European alder seeds, making irrigation early in the year desirable when precipitation is below normal (Hall and Nyong 1987).

Seed production varies from year to year, site to site, and tree to tree (Ager and others 1994; Brown 1985, 1986; Lewis 1985; Koski and Tallquist 1978; Krstinic 1994; McGee 1993), but good crops are borne at least once every 4 years (table 3). LaBastide and van Vredenburch (1970) reported that seed crops for European alder follow an annually alternating pattern. McVean (1955) concluded that seed crops of European alder could vary substantially from year to year, but that "boom-and-bust" patterns of seed production were not typical. Complete failure of a seedcrop is rare, but after a severe freeze in November 1955, almost no red alder seeds were produced in 1956 (Worthington 1965).

Seeds are small nuts ("nutlets") borne in pairs on the bracts of the strobiles. The nuts of red, Siberian, and Sitka alders have broad wings about as wide as or wider than the body of the nut. In the other species included here, the wings are reduced to a narrow border (figure 2) (Fernald 1950; Sargent 1965). Seeds are without endosperm and contain only small cotyledons (figure 3). For additional information on reproductive biology of red alders, see Ager and others (1994).

The factors regulating the timing of seed dispersal in alders have not been investigated, but they are probably similar to those regulating the release of seeds from the cones of conifers; that is, once strobiles are mature, disper-

Table 2—*Alnus,* alder: phenology of flowering and fruiting*

Species	Location	Flowering	Fruit ripening	Seed dispersal
A. glutinosa	E US	Mar–May	Sept	Sept or Oct–early spring
	S US & England	(can start Jan)	Feb–April	—
A. incana	Europe	Mar–May	Sept–Nov	Sept–Dec
ssp. *rugosa*	Canada, US	Mar-May	—	—
ssp. *tenuifolia*	Idaho, Montana, Oregon	Mar–Apr	Aug–Sept	—
A. nepalensis	Hawaii	—	Oct–Feb	Oct–Apr
A. rhombifolia	Oregon	Mar	Late Sept–early Oct	—
A. rubra	Washington, Oregon	Late winter–early spring	Aug–Oct	Sept–Dec
A. serrulata	—	Feb–May	Late Sept–early Oct	—
A. viridis				
ssp. *crispa*	E US, Alaska	Spring	Late Aug–mid-Oct	Soon after ripening
		Apr–June	Mid Sept–early Oct	Sept–early spring
ssp. *sinuata*	Alaska, W Canada, & NW US	Apr–June	Sept–Dec	—

Sources: Densmore (1979), Fernald (1950), Funk (1990), Harrington (1990), Hitchcock and others (1964), Lewis (1985), McDermott (1953), McGee (1988), McVean (1955), Schopmeyer (1974), White (1981).

* Flowering occurs during the period when leaves unfold.

Table 3—*Alnus,* alder: growth habit, height, seed-bearing age, and seedcrop frequency

Species	Growth habit	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yrs)	Years between large seedcrops
A. glutinosa	Tree	to 35	1866	6–7	—
A. incana	Tree	to 20	—	under 25	1–4
ssp. *rugosa*	Tree or shrub	to 8	—	—	—
ssp. *tenuifolia*	Tree or shrub	1–9	1880	—	—
A. nepalensis (Hawaii)	Tree	15–30	1916	10	—
A. rhombifolia	Tree	20–25	1885	—	—
A. rubra	Tree	12–27	1884	3–4	3–5
A. serrulata	Tree or shrub	to 8	1769	—	—
A. viridis					
ssp. *crispa*	Shrub	to 3	1782	—	—
ssp. *sinuata*	Tree or shrub	to 12	1903	—	—

Sources: Carlson and Bryan (1959), Fernald (1950), Funk (1990), Harrington (1990), Sargent (1965), Schopmeyer (1974).

sal is determined by the occurrence of weather that dries them, thus opening scales and allowing the seeds to be released (Harrington and others 1994). In general, wet weather following dry weather closes the strobiles, thus terminating a dispersal event. Nonetheless, heavy seedfall can occur during wet weather under certain conditions (Lewis 1985), but dispersal will not occur if ice freezes the seeds in the strobile. Although most seed dispersal occurs from September or October through February to April (table 2), some red alder seedfall has been observed in all months (Lewis 1985). American green alder strobiles do not release many seeds if the weather is wet during the autumn; substantial seed dispersal onto snow can occur throughout the winter (Densmore 1979). Alder seeds are very light, and when released they are dispersed long distances by wind, and in some species by water. Seeds of European alder have remained viable after floating for 12 months in still water (McVean 1955). In Alaska, seeds of thinleaf alder have corky, thick wings and float for long periods of time, whereas seeds of American green alder have thinner wings and sink rapidly (Densmore 1979). Birds or other animals also act as dispersal agents when moving through alder crowns and when extracting seeds from the strobiles (Harrington and others 1994).

Information on damaging agents is limited. Fungal diseases of alder catkins—caused by *Taphrina occidentalis* Ray and *T. alni* (Berk. & Broome) Gjaerum—cause enlargements of the bracts of female catkins (Mix 1949) and thus prevent or hinder normal fertilization and seed development. Jumping plant lice—*Psylla alni* (L.)—lay eggs in alder catkins in western North America (Furniss and Carolin 1977). Alder seeds are an important source of food for some

A

Figure 2—Alnus, alder: nuts (seeds); *A. viridis ssp. crispa*, American green alder (**top left**); *A. glutinosa*, European alder (**top right**); *A. nepalensis*, Nepal alder (**middle left**); *A. rhombifolia*, white alder (**middle center**); *A. rubra*, red alder (**middle right**); *A. serrulata*, hazel alder (**bottom left**);

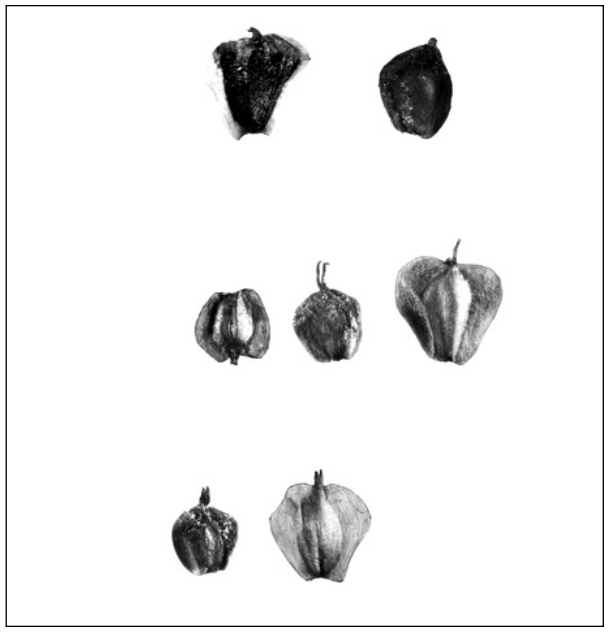
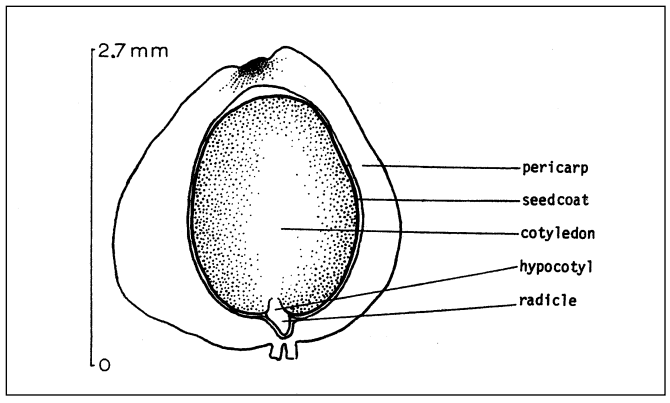


Figure 3—*Alnus rubra*, red alder: longitudinal section through a nut.



bird species (White and West 1977), and presumably seed predation by birds could have significant impacts when seedcrops are small.

Collection of fruits, extraction and cleaning, and storage of seeds. Seedcrops can be assessed in mid-summer by obtaining a count of mature strobiles and filled seeds (Ager and others 1994). Filled seed count should be determined from the upper third of the crown where viability is highest (Brown 1985). Seed quality can be assessed by cutting the strobile longitudinally and counting the filled seeds on one of the cut faces. Although the number of filled seeds on a cut face can vary from 0 to 20 or more in red alders, less than 3 or 4 seeds per cut face indicate a marginal crop (Ager and others 1994). Strobiles may be collected from standing or recently felled trees when the bracts (scales) start to separate on the most mature strobiles. In red alders, ripeness can be judged by twisting the cone along the long axis; if it twists easily and the scales part slightly, the seeds are sufficiently mature for collection (Hibbs and Ager 1989). Color is also a good indicator of maturity; immature cones are green whereas mature cones are mottled shades of green, yellow, gray, or brown (Hibbs and Ager 1989). Strobiles should be collected as soon as they are ripe, for the largest seeds with the best germinability are usually released first. Thus, both seed quality and seed yield are higher if collections are made in the fall rather than in the winter or spring (Lewis 1985; Krstinic 1994). Alder cones will open after being dried on screens or in fine mesh bags in a well-ventilated room for several weeks at ambient air temperature. They can be opened in a shorter time (2 to 7 days) by drying them in a kiln at 16 to 27 °C. Higher temperatures should not be used, as the strobiles will dry too quickly, harden and not open completely. Most of the seeds fall out of the strobiles during the drying process. The remainder, if needed, may be extracted by shaking or tumbling. Overall seed yields can be improved by either wetting cones again, placing them in a cooler for 24 hours, or spraying them with a fine water mist and then redrying (Ager and others 1994). Seeds may be cleaned by screening to remove large trash and further processing with an air column to remove small extraneous material.

Purity as high as 90% has been attained with European alder by fanning and screening seedlots. Quality, however, may be low because the light weight of alder seeds makes it difficult to separate and remove empty seeds (Ager and others 1994). Soundness in most cleaned seedlots has been between 30 and 70% (table 4). Number of seeds per weight ranges from 660,000 to 2,816,000/kg (or 300,000 to 1,277,000/lb) in lots of average quality (table 4). Except for seeds of American green alder, higher numbers may indicate a low percentage of filled seeds. Numbers ranging from 1,800,000 to 4,400,000 seeds/kg (800,000 to 2,000,000/lb) have been found in samples of Nepal, red, and thinleaf alders, but less than 5% of the seeds in these samples were full (Schopmeyer 1974). One red alder seedlot, however, was 70% sound and had 2,700,000 seeds/kg (1,224,000/lb). In a trial with red alder, the percentage of filled seeds determined by x-radiography was highly correlated ($r^2 = 0.91$)

Table 4—*Alnus*, alder: yield data and soundness

Species	Seed wt/ vol of strobiles		Cleaned seeds/ wt of strobiles		Cleaned seeds/ vol of strobiles		Cleaned seeds (x1,000)/wt of strobiles				Soundness	
							Range		Average			
	kg/hl	lb/bu	kg/100 kg	lb/100 bu	kg/hl	lb/bu	/kg	/lb	/kg	/lb	Samples	(%)
A. glutinosa												
Pennsylvania	—	—	—	—	1.5	1.2	565–882	257–401	706	321	7	—
Europe	—	—	—	—	—	—	635–1,406	289–639	774	352	86	39
A. incana												
Europe	21–30	16–23	8–10	8–10	—	—	961–1,980	437–900	1,470	668	123	51
A. incana												
ssp. *rugosa*	—	—	—	—	4.8	3.7	—	—	660	299	—	30–60
ssp. *tenuifolia*												
(fresh)*	14	11	7	7	1.3	1.0	—	—	—	—	—	—
(air dry)*	8	6	13	13	1.0	0.8	—	—	1,485	673	1	—
A. rhombifolia												
(fresh)*	23	18	5	5	1.3	1.0	—	—	—	—	—	—
(air dry)*	9	7	13	13	1.3	1.3	1,349–1,511	613–687	1,430	650	2	71
A. rubra	9	7	1.4–15	1.4–15	0.1–1.4	0. 1–1.1	1,843–2,700	350–1,400	1,712	776	5	70
A. viridis												
ssp. *crispa*	—	—	—	—	—	—	1,530–4,101	694–1,860	2,816	1,277	2	42–93
ssp. *sinuata*	—	—	—	—	—	—	—	—	2,200	998	1	70

Sources: Hibbs and Ager (1989), Liscinsky (1965), Mirov and Kraebel (1939), Schopmeyer (1974), Niemic and others (1995), USDA data on file at Olympia Forestry Sciences Laboratory.

* Yield data were determined on clusters of strobiles including stems.

with the actual germination percentage (Ager and others 1994).

Air-dried seeds have been stored in sealed containers at < – 2 °C. Under these conditions, viability has been maintained for 2 years in seeds of European alder (Holmes and Buszewicz 1958) and for 10 years in speckled alder (Heit 1967). For long-term storage, however, further drying of seeds to moisture content of less than 10% has been recommended for red alder (Ager and others 1994). This can be accomplished by kiln-drying or placing seeds in a room at 27 °C with less than 25% relative humidity. Red alder seeds can then be placed in moisture-proof containers and stored at < –12 °C for 10 to 20 years without substantial losses in viability (Ager and others 1994).

Pregermination treatments and germination tests. The degree of dormancy appears to vary among alder species and among provenances (geographic origins) within species. Thus, percentage germination of fresh seeds of white and thinleaf alders was equally good for stratified and nonstratified seed (Schopmeyer 1974). Fresh seeds of European and mountain alders also germinated promptly without stratification; but dried seeds, at a moisture of content of 8 to 9%, were dormant (table 5) (Schalin 1967). Germination capacity of the dried seeds, after stratification for 180 days at 5 °C was higher than that of fresh seeds. Maximum germination capacity, however, was obtained only when the stratification period was followed by 3 days at –20 °C (table 5) (Schalin 1967). A more recent study found that fresh mountain alder seeds initially exhibited some dormancy (that is, only about half of the filled seeds germinated in the incubator), but no dormancy was observed after one winter in the soil (Granstrom 1987). Dormancy also has been encountered in occasional seedlots of speckled (Heit 1968) and American green alders (Schopmeyer 1974). Stratification for 30 to 60 days at 1 to 5 °C has been recommended for these dormant lots (Schopmeyer 1974). Stratification for 30 to 90 days also has been recommended for Sitka alder (Emery 1988).

Although physiological seed dormancy is not widespread in red alder, it can exist (Elliot and Taylor 1981). Stratification at low temperature (0 to 5 °C) has little or no effect on the rate or completeness of germination of red alder seeds when tested at warm germination temperatures (Elliot and Taylor 1981; Radwan and DeBell 1981; Tanaka and others 1991).

Table 5—*Alnus*, alder: stratification and germination testing data

Species	Cold stratification period* (days)	Germination test conditions			Germination rate		Germination		Soundness (%)
		Temp (°C)			Amount (%)	Days	Avg (%)	Samples	
		Day	Night	Days					
A. glutinosa (Pennsylvania)	0	30	21	28	—	—	52	7	—
A. glutinosa (Finland)									
fresh seed	0	25	25	21	21	5	28	1	43
dried seed	0	25	25	21	9	*5*	13	1	43
dried seed	180	25	25	21	27	*5*	35	1	43
dried seed	180+3†	25	25	21	35	*5*	46	1	43
A. incana (Europe)	0	21	21	30	—	—	45	100	—
A. incana (Finland)									
fresh seeds	0	25	25	21	21	5	29	1	45
dried seeds	0	25	25	21	12	5	16	1	45
dried seeds	180	25	25	21	25	5	34	1	45
dried seeds	180+3†	25	25	21	38	*5*	49	1	45
A. i. ssp. *tenuifolia*									
fresh seeds	0	30	20	26	4	13	4	1	6
A. rhombifolia									
fresh seeds	0	30	20	30	59	14	59	1	65
A. rubra	0	24	16	7	56	7	56	4	—
dried seeds	0–60‡	30§	20	28	18	7	71	6	—
fresh seeds	0	30	20	28	21	7	75	6	87
fresh seeds	14	30	20	28	42	7	72	6	87
fresh seeds	28	30	20	28	49	7	72	6	87
fresh seeds	0	15	5	56	0	21	16	6	87
fresh seeds	14	15	5	56	17	21	63	6	87
fresh seeds	28	15	5	56	54	21	80	6	87
A. serrulata	||	27	23	10	27	2	36	1	—
A. viridis									
ssp. *crispa*	60	30	20	30–40	28	12	28	3	30–40
ssp. *sinuata*	14	30	20	21	*5*	7	14	1	—

Sources: ISTA (1993), McDermott (1953), Radwan and DeBell (1981), Schalin (1967), Schopmeyer (1974), Tanaka and others (1991), data on file at Olympia Forestry Sciences Laboratory.
Note: Day/night, 8 hrs/16 hours.
* Stratification, when used, was in a moist medium at 1 to 5 °C.
† 180 days at 5 °C, plus 3 days at 20 °C,
‡ No difference for 0, 30, or 60 days of stratification.
§ Light period was 10 housr/day at this temperature.
|| Seeds were stratified for an unspecified period.

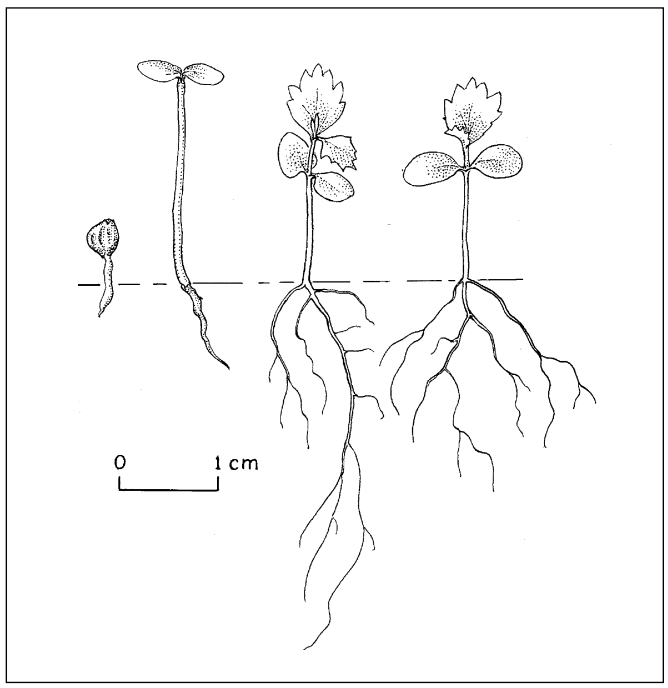
Under cool temperatures similar to those likely to prevail during outdoor sowings in early spring, however, 2 to 4 weeks of stratification substantially enhanced rate of germination and total germination (Tanaka and others 1991) and such a period is therefore recommended (Ager and others 1994). Thinleaf and American green alder seedlots collected near Fairbanks, Alaska, also germinated well without stratification at 25 °C but only germinated well at lower temperatures (10 to 15 °C) when combined with 72 days of stratification (Densmore 1979). Studies have also indicated the potential of 3 quick pregermination treatments for red alder seeds: gibberellin (Berry and Torrey 1985), 1% captan (Berry and Torrey 1985), and 30% hydrogen peroxide (Neal and others 1967). The results from these pregermination treatments, however, were obtained under warm germination conditions and need to be tested under the cooler conditions encountered in spring sowings. The captan and peroxide treatments may have a beneficial effect by reducing the amount of disease organisms present on seedcoats. Pretreatment with gibberellic acid improved greenhouse germination (21 °C day/13 °C night) of thinleaf alder seeds from 2 sources but did not affect germination of Arizona alder seeds from a single source (Dreesen and Harrington 1997).

For germination testing, both constant temperatures and diurnally alternating temperatures have been used (table 5). Official tests of the International Seed Testing Association (ISTA 1993) call for a 21-day test at alternating temperatures of 20/30 °C, with light during the 8 hours at 30 °C. Although seeds of European alder germinated as well in continuous darkness as under normal day length (McVean 1955), recent work indicates that seed germination of many alder species is markedly affected by light regime (Berry and Torrey 1985; Boojh and Ramakrishnan 1981; Bormann 1983; Densmore 1979; Khan and Tripathi 1989). Such effects in red alder are mediated by phytochrome: red light stimulates seed germination, far-red light inhibits it, and the effect of each light treatment can be reversed by the alternative treatment (Bormann 1983). Seeds of red alder are also sensitive to amount and quality of light under field conditions, and these factors—along with soil moisture—control germination success on disturbed sites (Haeussler and Tappeiner 1993; Haeussler and others 1995).

Nursery practice. Alder seedlings have been produced by bareroot nursery (open field or bedhouse) and container methods, as well as combinations thereof (Ahrens 1994; Ahrens and others 1992; Funk 1990; Radwan and others 1992). Successful stock types for red alder are grown in 1 year and include 1+0 open-bed bareroot, 1+0 bedhouse bareroot, 1+0 plug, and +0.5 (plug+transplant). Most nurseries sow in the spring when growing alder species (Ahrens and others 1992; Schopmeyer 1974), but fall-sowing is mentioned by Heit (1968). Spring-sowing is sometimes delayed until late spring to reduce seedling size. Sowing depths of 2 to 5 mm (.1 to .2 in) have been used for seeds of European alder and red alder (Schopmeyer 1974). In California, seeds of red alder have been mixed with 10 parts of vermiculite and drilled 1 cm (.4 in) deep (Schopmeyer 1974). In Oregon, seeds of red alder have also been sown on the soil surface and covered with peat. Seeds of Nepal alder have been mixed with sand and spread over the nursery beds. The number of plantable seedlings obtained from 1 kg (2.2 lb) of seed was 22,000 (10,000/lb) for European alder and 88,000 (40,000/lb) for hazel alder (Van Dersal 1938). Germination is epigeal (figure 4).

Alder seedlings, particularly those of red alder, grow rapidly and seedling densities should be lower than those used for conifers. Seedlings grown at open-bed densities of 60 to 180 seedlings/m^2 (5 to 15/ft^2) or in large containers result in much better outplanting performance than those grown at greater densities or in small Styroblocks® (Ahrens 1994). Inoculation of beds or container media with the nodulating actinomycete *Frankia* can improve establishment

Figure 4—*Alnus glutinosa*, European alder: seedling development at 1 and 7 days after germination (**left**); *Alnus incana* ssp. *tenuifolia*, thinleaf alder: 2 older seedlings (**right**).



and early growth in the nursery (Berry and Torrey 1985; Hilger and others 1991) and may enhance outplanting performance (McNeill and others 1990). Diluted suspensions of pure Frankia cultures and homogenates of crushed, fresh root nodules have been used for inoculation (Ahrens and others 1992; Perinet and others 1985). Detailed methods of preparation and application are available (Martin and others 1991; Molina and others 1994; Zasada and others 1991).

Development of nitrogen-fixing nodules is promoted by fertilization with low to moderate applications of nitrogen; phosphorus and lime are likely to be necessary for production of high-quality stock (Hughes and others 1968; Radwan 1987; Radwan and DeBell 1994). Although alder seedlings are produced operationally, optimum combinations of fertilizer source, amount, and timing of application have not been completely worked out; some combinations have had detrimental effects on alder seedlings or their root associates. Frequent irrigation may be necessary to prevent desiccation and heat damage of surface-sown seeds or germinants during germination and early establishment (Ahrens 1994).

Direct seeding in the field has been done successfully with 2 species. Speckled alder has been established in Pennsylvania by broadcast sowing on disked areas and on sod. Seeds collected in the fall were broadcast during the following February and March. Seeding rates were 0.28 liter/10 m^2 (or 0.5 pint/100 ft^2) on bare soil and 0.38 liter (0.7 pint) for the same area of sod (Liscinsky 1965). In England, better stocking was obtained on a shallow blanket bog with spot sowing of European alder than with broadcast sowing. About 15 viable seeds were sown in each spot and fertilized with about 60 g of rock phosphate (McVean 1959).

Seedling care. Information to guide lifting dates is very limited, even for red alder (Ahrens 1994; Ahrens and others 1992); current recommendations based on experience in southwest Washington are to lift seedlings in January. They are then stored at either +2 °C or –2 °C; the lower temperature is recommended because it prevents budbreak during storage (and possible *Botrytis* infection associated with budbreak during storage) and reduces the tendency for planted alders to break bud too soon after planting. Storage in sealed bags will prevent desiccation. Because alder stems are brittle and sensitive, seedlings must be handled carefully during storage, transport, and outplanting to avoid damage to stems, branches, and buds. At low elevations (< 300 m) in western Washington, it has been recommended that seedlings be planted between mid-March and mid-April. The spring planting period should begin when the probability of severe frost is low and end before there is appreciable soil drying (Dobkowski and others 1994).

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Asteraceae—Aster family

Ambrosia dumosa (Gray) Payne

bursage

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Synonyms. *Franseria dumosa* Gray

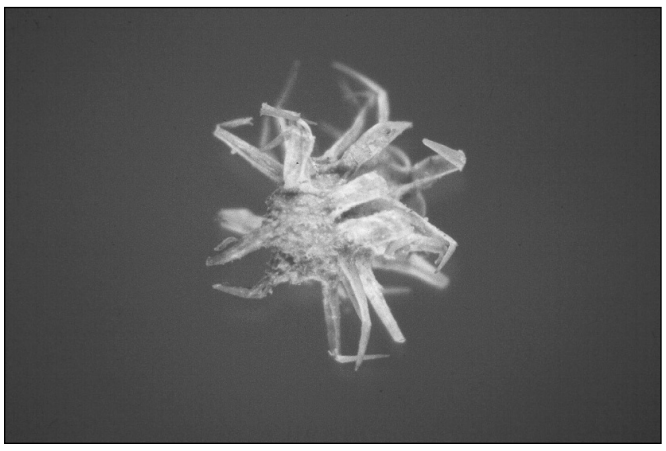
Other common names. white bursage, white burrobush, burrobush, burroweed, sandbur

Growth habit, occurrence, and use. Bursage is a low, intricately branched, rounded shrub abundant on well-drained soils through much of the Southwest. It is significant component in creosote bush scrub and Joshua tree woodland communities of the Mojave and Colorado Deserts of California, south and east to Utah, Arizona, Mexico, and lower California (Kay 1977). Bursage, like creosote, has a rhizomatous growth habit and is thus an extremely long-lived shrub (Muller 1953).

Flowering and fruiting. Bursage flowers are inconspicuous, with staminate and pistillate heads intermixed in the terminal and lateral spikes of the panicle (Bainbridge and Virginia 1989). Blooming occurs primarily from February to June, and occasionally during the fall or after rain (Kay 1977). Seeds resemble cockleburs (figure 1) and mature 3 to 4 months after flowering.

Collection, extraction, and storage. Seeds can be hand-stripped from the plants; collecting burs from the ground beneath the plants is impractical because the light burs are rapidly blown away (Bainbridge and Virginia 1989). Seed cleaning is difficult and rarely done due to the spiny burs. In long-term storage trials by Kay and others (1988), seeds were stored at room temperature, 4 °C, – 15 °C, and in warehouse conditions, with germination rates tested annually over a 14-year period. The results indicated that seed quality had been poor, even though seeds were collected numerous times. The sporadic germination under a variety of conditions reflected this. Kay recommended that seeding guidelines should specify seeding rates in seed weight of pure live seeds required for sowing an area (that is, kilograms per hectare or pounds per acre), and providing that extra seeds are planted to compensate for the low quality.

Figure 1—*Ambrosia dumosa*, bursage: mature seed.



Pregermination treatments. After overnight leaching/soaking, seeds begin germinating during the first and second weeks in moist paper towels or directly in a 50% vermiculite–50% soil mixture (CALR 1995). Optimal germination temperatures appear to be between 15 to 25 °C (table 1), as colder temperatures tend to inhibit germination (Kay 1975).

Germination tests. Tests using activated carbon and scarification both resulted in a slightly improved early germination rate (Graves and others 1975). Germination conditions tested at Joshua Tree National Park (JTNP) Native Plants Nursery include: (1) direct sowing to blotter paper, (2) overnight cold water soaking, and (3) initial cold water soaking followed by overnight leaching. All of these methods had moderate success, indicating that no treatment is necessary when sowing directly to moist toweling; average gemination ranges from 30 to 50% (CALR 1995). Other tri-

Table 1—*Ambrosia dumosa,* bursage: effect of temperature on germination

Temperature (°C)	2	5	10	15	20	25	30
Germination (%)	0	0	4	26	21	18	10

Source: Kay and others (1988).

als by Kay and others (1988) refer to initial germination of seeds using 4 replications of 100 seeds in damp paper toweling placed in a growth chamber at 15 °C. Test conditions were maintained for 28 days, with germination percentages recorded every 7 days; initial germination rate for bursage was 5%. Germination tests, conducted annually to test the effects of storage, were then averaged to a "best germination" of 9%. These annual tests consisted of 4 replications of 50 seeds using the same initial testing methods. Also tested were the effects of temperature on germination rates (table 1).

Nursery practice. Mature specimens have been transplanted with greater than 90% survival (Ruffner and others 1985). Graves (1976) transplanted 2-month-old stock in February 1973, with a survival rate 2 years later of 44 and 48% for 2 separate sites. Flowering occurred in 25% of the plants during first year's growth at one site, with no flowering or seed at other site. Initial mortality was due to cold transplanting temperatures. Spot-seeding, in comparison, was poor, with 18 burs/spot resulting in 16% germination and 0 to 4% stocking at the same sites. A one-time irrigation treatment did not improve results of either transplanting or spot-seeding. Seed germination may be induced from September–October rains (Went 1979).

At JTNP, 12-month-old plants grown from seed have been successfully outplanted using a 76-cm (30-in) tube "tall pot" with a 15-cm (6-in) diameter (CALR 1995). Other outplantings of bursage in the park include a restoration project at an abandoned surface mine. Three types of containers were used: 3.8-, 6.8-, and 9.2-liter (1-, 1.8-, and 2.6-gal) pots with an elongated design 35 to 43 cm (14 to 17 in) in height. Latest monitoring noted an overall survival rate of 80% (CALR 1995). Prior to outplanting, plants in smaller containers were between 4 and 5 months old and those in larger containers, between 6 and 7 months.

Seedling care. Seedlings grow quickly in greenhouse conditions, and new growth can be pruned back frequently to strengthen the sensitive root collar (CALR 1995). Both Graves (1976) and the JTNP Native Plants Nursery have noted seedling sensitivity to hardening-off in sub-freezing temperatures. Using plant bands, Graves (1976) recorded 80% mortality at 10 to –7 °C, with better survival after restarting and hardening-off at day-night temperatures of 14 and 4 °C. Stem pieces root easily from the field or greenhouse by dipping in rooting hormone powder and placing cuttings in vermiculite in a mist house until rooted (Wieland and others 1971).

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Rosaceae—Rose family

Amelanchier Medik.

serviceberry

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Growth habit, occurrence, and use. The serviceberries—the genus *Amelanchier*—include about 25 species of small deciduous trees and shrubs native to North America, Europe, and Asia. The distribution and chief uses of 6 species are listed in table 1. Most species provide browse and edible fruits for wildlife and many have attractive flowers. Saskatoon and common serviceberries have been used to a limited extent for shelterbelt and wildlife plantings and as a minor fruit crop, but other species also should be considered for these and other environmental uses. Native Americans have traditionally used most species of serviceberry for food and medicine (Meeker and others 1993; Moerman 1986). Common and Saskatoon serviceberries are tolerant of temperatures to –60 °C (Junttila and others 1983; Kaurin and others 1984; Lindstrom and Dirr 1989). Common serviceberry regenerates vegetatively and by seed after clearcutting and burning (Scheiner and others 1988). Geographic races of *Amelanchier* have not been identified, but they could occur in widely distributed species such as the Saskatoon and common serviceberries. Several natural hybrids are known (Campbell and others 1991; Cruise 1964; Flessner and others 1992).

Flowering and fruiting. The perfect white flowers of serviceberries appear in terminal and lateral clusters early in spring, before the leaves in some species (table 2). Fruits are berrylike pomes (figure 1) that turn dark purple or black when they ripen (table 3). Each fruit contains from 4 to 10 small seeds weighing from 1.1 to 6.9 mg, although some of these are usually abortive (St. Pierre and Steeves 1990). Gorchov (1985) reported that fruits containing more seeds develop quicker, suggesting asynchronous fruit development of the genus. Fertile seeds are dark brown with a leathery seedcoat (figure 2) and with the embryo filling the seed cavity (figure 3). Seeds are dispersed almost entirely by birds and animals; however, Turcek (1961) reported that seeds of some species are distributed by insects. Fruits usually are

Table 1—*Amelanchier,* serviceberry: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***A. alnifolia* (Nutt.) Nutt. ex M. Roemer** *Amelanchier carrii* Rydb. *Aronia alnifolia* Nutt.	**Saskatoon serviceberry,** juneberry, western shadbush	W Ontario to Yukon, S to Oregon & Utah, E to Utah, NW Iowa
***A. alnifolia* var. *semiintegrifolia* (Hook.) C.L. Hitchc.** *A. florida* Lindl.	**Pacific serviceberry,** western serviceberry	Pacific Coast region from Alaska S through W British Columbia, Washington, & NW California
***A. arborea* (Michx. f.) Fern.** *A. alabamensis* Britton *A. arborea* var. *alabamensis* (Britton) G. N. Jones	**common serviceberry,** downy serviceberry, shadblow, serviceberry	New Brunswick W to Ontario & Minnesota, S to Nebraska & Texas, E to Florida
***A. canadensis* (L.) Medik.** *A. lucida* Fern. *A. canadensis* var. *subintegra* Fern.	**Canadian serviceberry,** thicket shadblow, shadbush, thicket serviceberry	Maine to Pennsylvania & Georgia
***A. laevis* Wieg.** *A. arborea* var. *laevis* (Wieg.) Ahles	**Allegheny serviceberry,** juneberry, shadbush	Newfoundland & Quebec to Minnesota, S to Kansas, E to Ohio & Delaware, & in mtns to Georgia & Alabama
***A. sanguinea* (Pursh) DC.**	**roundleaf serviceberry,** roundleaf juneberry, shore mtns. shadbush, Huron serviceberry	Maine & S Quebec to Minnesota, S to Iowa & E to New Jersey, mtns.of North Carolina

A

Table 2—*Amelanchier,* serviceberry: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
A. alnifolia	—	May–June	July–Aug
var. *semiintegrifolia*	Oregon (520 m)	Apr	Aug
	Oregon (1,310 m)	May	—
		May	Aug
A. arborea	—	Mar–June	June–Aug
A. canadensis	Carolinas	Mar–April	May–June
		May	June
A. laevis	—	Mar–June	June–Aug
A. sanguinea	—	May–June	July–Sept

Sources: Fernald (1950), Jones (1946), Mowat (1969), Plummer and others (1968), Radford and others (1964), Rehder (1940), St. Pierre and Steeves (1990), Van Dersal (1938).

Figure 1—*Amelachier alnifolia* var. *semiintegrifolia*, Pacific serviceberry (**top**) and *A. laevis*, Allegheny serviceberry (**bottom**): pomes.

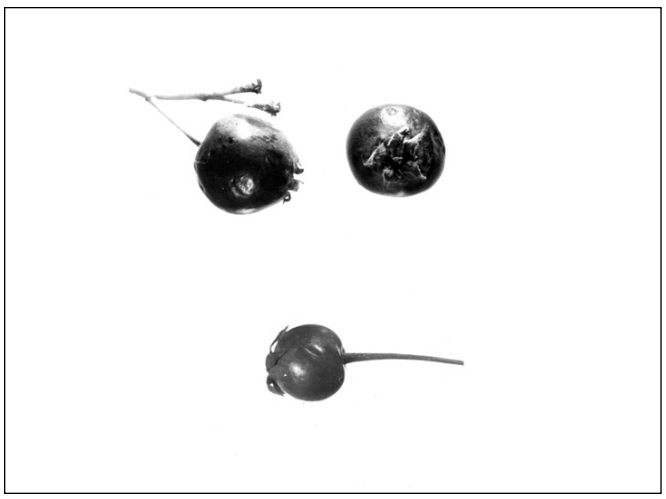


Figure 2—*Amelachier alnifolia,* Saskatoon serviceberry (**left**) and *A. alnifolia* var. *semiintegrifolia,* Pacific serviceberry (**right)**: seeds.

Table 3—*Amelanchier,* serviceberry: height and fruit ripeness criteria

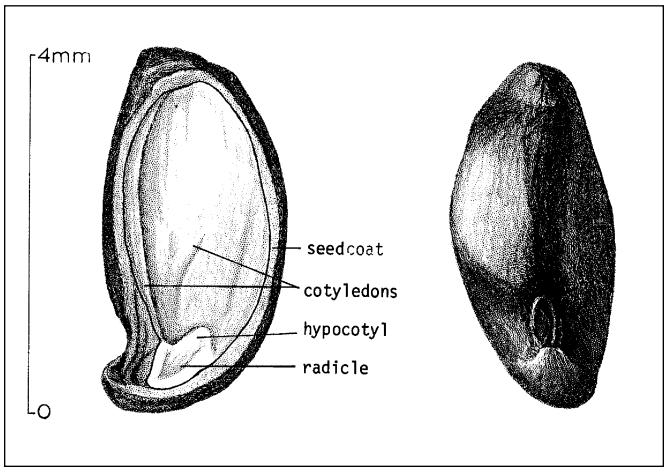
Species	Height at maturity (m)	Year first cultivated	Color of ripe fruit
A. alnifolia	5	1826	Blue purple
var. *semiintegrifolia*	12	1826	Purplish black
A. arborea	18	1623	Reddish purple
A. canadensis	8	1641	Nearly black (sweet)
A. laevis	9	1870	Dark purple
A. sanguinea	3	1824	Dark purple (sweet)

Sources: Fernald (1950), Jones (1946), Petrides (1958), Rehder (1940), Small (1933), Strausbaugh and Core (1953).

eaten by birds or animals as soon as they ripen. Fruit loss of Saskatoon serviceberry can be significant (up to 81% of the potential). These losses occurred because of insects and disease (54%) and frost (27%), with the remaining losses (19%) undetermined (St. Pierre 1989). Fruit loss can exceed 95% in some years and some locations (St. Pierre 1996).

Collection of fruits. To minimize losses to wildlife, fruits must be picked from the shrubs as soon as possible after ripening (table 2). Fruit color is the best way to judge maturity (table 3). Unless the seeds are to be extracted promptly, the fruits should be spread out in thin layers to dry. Loss of viability will result if the fruits are allowed to overheat.

Figure 3—*Amelachier sanguinea*, roundleaf serviceberry: longitudinal section through a seed (**left**) and exterior view (**right**).



Extraction and storage of seeds. Serviceberry seeds are usually extracted by macerating the fruits in water and washing them over screens (Heit 1967; Munson 1986; Peterson 1953), which removes most of the pulp. After this remainder is dried and rubbed through the screens, the seeds and remaining debris are run through a fanning mill to remove small, aborted seeds and bits of fruit (Brinkman 1974). Seed yield and weight data are listed in table 4. Few storage tests have been made of serviceberry seeds, but dry storage in sealed containers at 5 °C is usually recommended (Brinkman 1974; Crocker and Barton 1931). However, excessive drying of seeds may induce a deeper dormancy with consequential decrease in germination rate (St. Pierre 1996).

Pregermination treatments. Embryos of all species show dormancy that can be at least partially overcome by cold stratification (Crocker and Barton 1931), however, control of fungi during this period is critical (McTavish 1986). The seedcoat of some species also may retard germination. Scarification of Allegheny serviceberry in concentrated H_2SO_4 followed by stratification improved germination (Hilton and others 1965). Addition of a mixture of benzyladenine and thiourea enhanced seed germination of Saskatoon serviceberry (Weber and others 1982). The necessary time period of cold stratification varies, but most species require 2 to 6 months (Heit 1968) (table 5). Robinson (1986) reports improved germination from seeds of fruits consumed by cedar waxwings (*Bombycilla cedrorum*).

Germination tests. Germination of Saskatoon serviceberry appears to be genetically controlled and, to a limited extent, can be influenced by environmental fluctua-

Table 4—*Amelanchier*, serviceberry: seed yield data

Species	Place collected	Fruit wt/vol		Seed wt/fruit vol		Seed wt/fruit wt		Cleaned seeds (x1,000) /weight			
		kg/hl	lb/bu	kg/hl	lb/bu	kg/45 kg	lb/100 lb	Range /kg	Range /lb	Average /kg	Average /lb
A. alnifolia	—	—	—	—	—	0.9	2	80–251	36.3–113.8	181	82
var. *semiintegrifolia*	Oregon	118	42	2.8	1	0.9	2	—	—	119	54
A. arborea	—	—	—	—	—	0.5	1	110–178.6	50–81	176	80
A. sanguinea	Minnesota	—	—	—	—	—	—	—	—	185	84

Sources: Brinkman (1974), McKeever (1938), Mowat (1969).

tions (Acharya and others 1989). Germination of stratified seeds can be tested in sand or a sand–peat mixture. Constant temperatures of 21 °C or alternating day/night temperatures of 30 and 20 °C have been equally successful. Light does not appear to be necessary during tests (table 5).

Germination is epigeal (figure 4). Germination of Saskatoon serviceberry seeds often occurs during stratification (St. Pierre 1996). Previously stratified seeds of Saskatoon serviceberry showed 84 to 99% germination at 2 to 5 °C (McKeever 1938; McLean 1967). Under natural conditions, germination could begin in the early spring under snow or shortly after snowmelt.

Nursery practice. Serviceberry seeds may be either sown in the fall or stratified and sown in the spring (Bailey 1935). Many seeds do not germinate until the second spring. It is suggested that the seeds be sown as soon as possible after collection and that the beds be kept mulched until germination begins the following spring (Brinkman 1974). Seeds should be sown in drills at the rate of 80 sound seeds/m (25 seeds/ft) and covered with 6 mm ($^1/_4$ in) of soil. At least for Saskatoon serviceberry, half-shade during the first year apparently is beneficial.

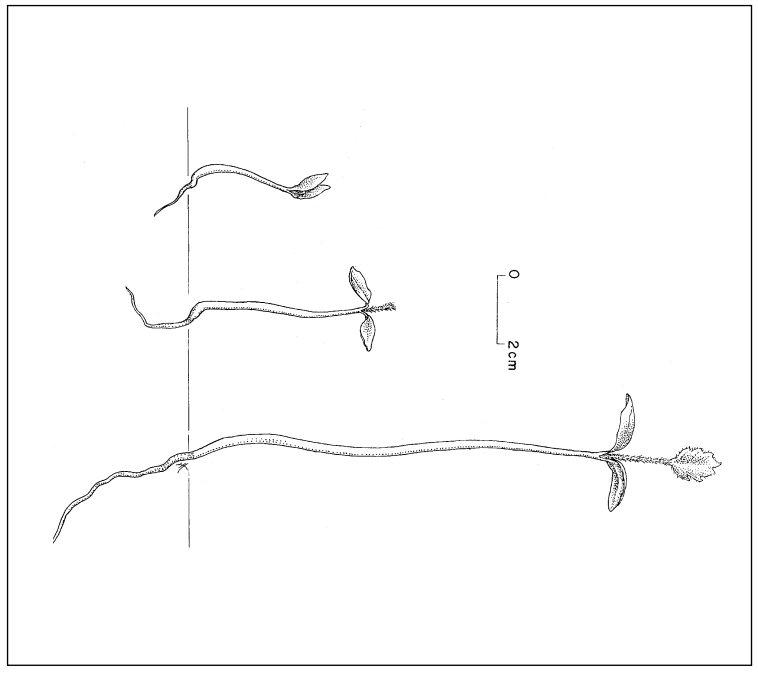


Figure 4—*Amelachier* spp.: seedling development at 3, 5, and 7 days after germination.

Table 5—*Amelanchier,* serviceberry: cold stratification period, germination test conditions, and results

Species	Cold stratification* (days)	Germination test conditions: Daily light (hrs)	Medium	Temp (°C): Day	Temp (°C): Night	Days	Germination rate: Amount (%)	Germination rate: Days	Germination percentage: Avg (%)	Germination percentage: Samples	Purity (%)
A. alnifolia	180+	16	Sand	30	20	30	—	—	—	70	2
	120	0	Sand or blotters	21	21	70	50	8	—	62	10
	98										
A. alnifolia var. *semiintegrifolia*†	30–90	6	Kimpack	30	20	31	—	—	10	2	—
A. arborea	90–120	16	Sand or sand & peat	30	20	—	—	—	54	2	93
A. canadensis	120	—	—	—	—	—	—	—	—	—	—
A. laevis‡	60+	—	Filter paper	20	20	6–7	—	—	61–74	4	—

Sources: Babb (1959), Brinkman (1974), Hilton and others (1965), McKeever (1938), Mclean (1967).

* Stratification was done in a moist medium at temperatures between 1 and 6 °C.

† In an additional test on excised embryos, germination was 82% (Brinkman 1974).

‡ In an additional test on excised embryos, germination was 95% (Hilton and others 1965)

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A

Fabaceae—Pea family

Amorpha L.

amorpha, indigobush

John C. Zasada and David Martineau

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Growth habit, occurrence, and use. In North America, the amorphas include about 15 species of deciduous shrubs or subshrubs (Wilbur 1975). Wilbur (1975) provides a thorough description of all species with range maps showing distribution. Four of the more common species and their ranges are listed in table 1. Leadplant and indigobush are the 2 most widely distributed and used species in the genus.

Leadplant is common in dry to wet–mesic prairie communities; in Wisconsin, its highest presence values are in the dry to dry–mesic communities (Curtis 1959; Henderson 1995; Johnson and Anderson 1985; Voigt and Mohlenbrock nd). Kotar and others (1988) list leadplant as a diagnostic species for the white oak–pin oak–leadplant habitat type that is transitional between prairie and forest in Wisconsin. Indigobush has a large range and within that range occurs on sites with fairly wet to dry moisture regimes and is relatively more common in riparian areas (Curtis 1959; Glad and Halse 1993). It can be an aggressive invader, as demonstrated by its spread along the Columbia and Snake Rivers in Oregon and Washington (Glad and Hulse 1993). Wilbur (1975) reported that indigobush is highly variable and that it is best described as a complex with variation due to both environmental and genetic factors. In North Dakota, plants from more southern seed sources grow more rapidly and are taller than those from North Dakota sources, but they are also more susceptible to winter damage (Lincoln Oakes Nurseries 1996).

Leadplant and indigobush are reported to hybridize, although hybrids are believed rare (Wilbur 1975). The hybrid has the greatest affinity with leadplant and differs in having a taller growth form as well as in several morphological traits (Wilbur 1975).

The growth form and stature of leadplant results from its tendency to die-back to varying degrees each year. Regrowth from basal stem and root collar buds maintains the above ground stems. Under some conditions, stems will be relatively longer-lived and attain heights of 1.5 to 2 m (table 2). Indigobush is taller than leadplant and its stem longevity is like that of a true shrub.

Leadplant is palatable to domestic livestock and under heavy grazing tends to disappear (Voigt and Mohlenbrock nd); however its palatability for whitetail deer (*Odocoileus virginiana*) was rated as low in a study in the Black Hills (Rosario 1988). A primary use, at present, is for landscaping, where low-maintenance, drought-resistant plants are desirable, and in restoration and reclamation projects (Brown and others 1983; Cox and Klett 1984; Dirr 1990;

Table 1—*Amorpha*, amorpha: nomenclature and occurrence

Scientific name & synonym	Common name(s)	Occurrence
***A. californica* Nutt.**	**mock locust,** false indigo, California amorpha	California Coast Range from Sonoma & Napa Cos. S to Riverside Co.
***A. canescens* Pursh**	**leadplant,** prairie shoestrings	Michigan to Saskatchewan, S to Indiana, W to Arkansas & New Mexico; prairies in region
***A. fruticosa* L.**	**indigobush,** false indigo	S Quebec to N Manitoba, S to Florida & Mexico; S California & Wyoming
***A. nana* Nutt.** *A. microphylla* Pursh	**dwarf indigobush,** fragrant false indigo	Manitoba and Saskatchewan S to Iowa & New Mexico

Sources: Brinkman (1974), Glad and Halsey (1993), Hickman (1993), Niering and Olmstead (1979), Rosario (1988), Voight and Mohlenbrock (nd), Wilbur (1975).

Table 2—*Amorpha,* amorpha: height and year of first cultivation

Species	Height at maturity (m)	Year first cultivated
A. canescens	1–3	1883
A. fruticosa	12–18	1724
A. nana	1–3	1811

Sources: Brinkman (1974), Dirr (1990) Niering and Olmstead (1979), Rehder (1940), Rosario (1988), Smith and Smith (1980), Vines (1960), Wilbur (1975).

Salac and others 1978). Indigobush is used in reclamation of strip-mined areas (Brown and others 1983; Weber and Wiesner 1980). Leadplant is an important prairie plant and is included in restoration projects (Salac and others 1978). All amorpha species are nitrogen-fixers and thus have the potential for improving soil nutrient status. In the traditional medicine of the Great Lakes Ojibwa, a decoction of the root of leadplant was used to treat stomach pain (Meeker and others 1993); leaves were used as a tobacco and for making tea (Niering and Olmstead 1979).

Flowering and fruiting. The irregular, perfect flowers of amorphas are blue to violet purple in color and are borne in the spring or summer (table 3). The inflorescence is a raceme; leadplant can have 200 to 300 flowers/raceme. The fruit is short, indehiscent, somewhat curved and often gland-dotted legume (pod) containing 1 (or sometimes 2) small glossy seed (figures 1 and 2). When ripe in mid to late summer, the legumes are light brown in color. Commercial seed usually consists of the dried legumes.

Good seedcrops of mock locust are borne every 2 years (Brinkman 1974), and similar frequencies probably are typical of the other species. Flowering in leadplant was stimulated by spring burning; periodic burning appears to stimulate both vegetative and reproductive growth (Richards and Landers 1973; Rosario 1988). Periodic, not annual, mowing may also improve seed production (Rosario 1988). Indigobush seed availability may be lowered significantly by seed beetles (Rogers and Garrison 1975). The majority of

Figure 1—*Amorpha*, amorpha: legume and seed of *A. fruticosa*, indigobush.

leadplant seeds are dispersed in September and October, but a few may may remain on the plant during winter.

Collection of fruits; extraction and storage of seeds. The ripe legumes can be stripped from the inflorescences and spread out in thin layers for a few days to permit drying.

Extraction of seeds is not essential for germination. The legumes are usually 1-seeded, thin walled, and soft enough so that germination does not appear to be reduced significantly if seeds are not removed from the legumes. However, the seeds may be extracted by gently beating or rubbing the legumes. Available data on seed and fruit weights are listed in table 4. Little is known about optimum storage conditions, but all evidence suggests that the seeds are orthodox in storage behavior. Seeds of leadplant stored for 22 months at 41 °C followed by 16 months at room temperature showed little loss in germination; sealed storage at continuous low temperature probably would prolong viability (Brinkman 1974). Seeds of indigobush have retained viabili-

Table 3—*Amorpha,* amorpha: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
A. californica	May–July	July–Sept	Aug–Sept
A. canescens	June–late July	Aug–Sept	Sept–Oct
A. fruticosa	May–June	Aug	Sept–Oct
A. nana	May–July	July	July

Sources: Brinkman (1974), Fernald (1950), Lincoln Oakes Nurseries (1996), Mirov and Kraebel (1939), Rehder (1940), Smith and Smith (1980), Van Dersal (1938).

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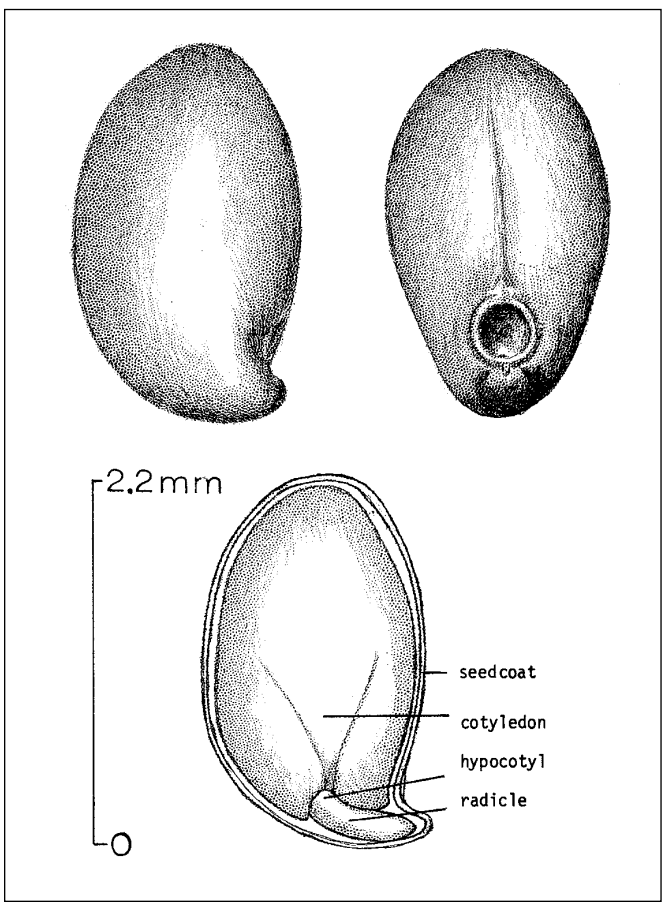
Figure 2—*Amorpha canescens,* leadplant: exterior views of seed and embryo (**top**) and interior of seed (**bottom**).



ty for 3 to 5 years at room temperature (Brinkman 1974); more recent experience indicates that seeds can be stored at 2 °C for at least several years with little loss in viability (Lincoln Oakes Nurseries 1996). The presence of leadplant in prairie soil seed banks also suggests that seeds may have relatively long lives without cold storage (Johnson and Anderson 1985).

Pregermination treatments and germination. The degree and type of dormancy appear to differ among species. As with many woody species, drying of seeds may induce seedcoat dormancy in seeds that would normally germinate without pretreatment (Dirr and Heuser 1987). Both mock locust and leadplant will germinate completely without treatment (Martineau 1996; Mirov and Kraebel 1939). Leadplant seeds obtained from commercial dealers following an unknown period of storage germinated without treatment, but stratification at 3 to 4 °C for 2 and 8 weeks increased the rate of germination; 30 minutes of scarification in sulfuric acid reduced germination by 50% (Cox and Klett 1984). Germination of some seed lots has been improved by soaking the seed in hot water for about 10 minutes. Cold stratification has been used in preparation for spring sowing in a nursery bed (Brinkman 1974). This cold treatment may reduce seedcoat impermeability. Dirr and Heuser (1987) indicate that fresh leadplant seeds germinate without pretreatment but that stored seeds may benefit from acid treatment.

Indigobush and dwarf indigobush appear to have seed coat dormancy. Light scarification of indigobush seeds and soaking seed of both this species and dwarf indigobush in sulfuric acid for 5 to 8 minutes have been used to stimulate germination (Brinkman 1974; Dirr and Heuser 1987). However, fall sowing with no pretreatment results in some, but not complete, germination (Brown and others 1983). Simulated acid rain with pH of less than 5 tended to reduce germination in indigobush, but significant germination occurred at pH 3 and 4 (Lee and Kim 1986). Total seedling dry weight of indigobush increased with decreasing pH of simulated acid rain (Lee and Kim 1986). Germination test conditions and results on pretreated seeds are in table 5. Germination is epigeal (figure 3).

Indigobush is the only species of amorpha that is listed in official seed testing rules. International Seed Testing Association (ISTA 1993) prescriptions call for a 28-day test at alternating temperatures of 20/30 °C on the top of moist

Table 4—*Amorpha,* amorpha or indigobush: fruit and seed data

	Ripe fruit (x1,000)/wt				Cleaned seed (x1,000)/wt			
	Range		Average		Range		Average	
Species	/kg	/lb	/kg	/lb	/kg	/lb	/kg	/lb
A. californica	—	—	—	—	43–146	19–66	84	38
A. canescens	194–233	88–106	211	96	598–651	272–296	624	284
*A. fruticosa**	81–205	37–93	114	52	158–180	72–82	170	77
A. nana	—	—	133	60	—	—	—	—

Sources: Brinkman (1974), Lincoln Oakes Nurseries (1996), Prairie Nursery (1996), Salac and others (1978).
* One hundred pounds of dried fruit will produce about 60 pounds of clean seeds (Swingle 1939).

germination paper. Light is required during the 8 hours at 30 °C, but no pretreatments are called for.

A procedure for tetrazolium testing of depodded seeds of indigobush has been developed (Weber and Wiesner 1980). Seeds are chipped at the distal end to avoid injury to the embryonic axis (the more rounded end in figure 1) and stained for 18 hours. Lactophenol clears the seed coat, making it possible to interpret seed viability without removing the seedcoat. The method distinguishes living from dead seeds (Weber and Wiesner 1980).

Nursery practice. Seedlings can be produced in containers or as bareroot stock. The need for pretreatment of seeds will be determined by species and condition of the seeds, for example, seeds may germinate faster if they are removed from the legume. Timing of sowing in container production is more flexible than in outdoor beds. Seed use may be more efficient in containers than in outdoor beds because temperature and water availability are more easily controlled in the greenhouse environment. Rock (1981) recommends inoculating seeds of leadplant with nitrogen-fixing bacteria before sowing. This recommendation is probably applicable to all amorpha species.

For container production of leadplant in a greenhouse, cleaned seeds (removed from the legumes, inoculated, and unstratified) may be sown at any time during the summer. Initial sowing is in small cells (about 2 to 3 cm^3); germination is completed in about 15 days. When seedlings are at the 3- to 5-leaf stage, they are transplanted to larger containers. Seedlings are kept in the greenhouse until established in the new containers and then moved outside. If seeds are sown in spring, seedlings can be transplanted to ~1 liter containers (~1 qt) in early to midsummer; seedlings will be ready for outplanting by fall (Martineau 1996).

For bareroot production of leadplant, cleaned, inoculated, unstratified seeds are sown in the spring, covered with a few millimeters of soil followed by a layer of sawdust. Seedbeds are lightly compacted and the beds are watered as needed. Germination will occur mostly in the first year with a small amount of carryover to the second growing season. Juvenile leaves (simple, round as in figure 3) are produced part way through the growing season with a transition to the characteristic pinnately compound leaves in mid to late summer. Seedlings will be about 30 to 50 cm (12 to 20 in) tall, with a taproot of equivalent length, after 2 growing seasons. Seedlings are lifted and sold after the second growing season or in the following spring while still dormant. Care should

Figure 3—*Amorpha canescens*, leadplant: seedling development at 1, 2, 8, 20, and 52 days after germination.

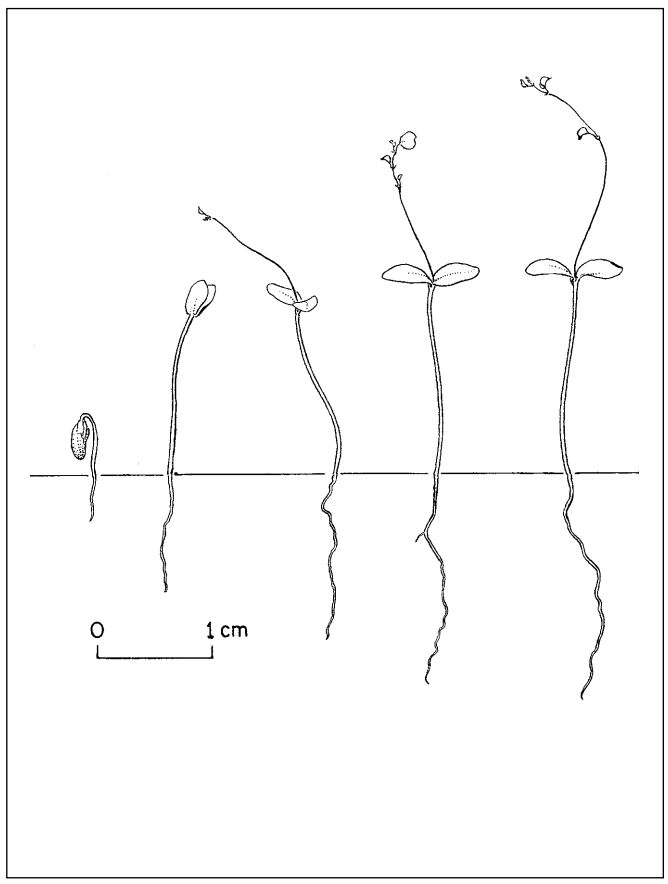


Table 5—*Amorpha.* amorpha: germination test conditions and results

Species	Day/night temp (°C)	Duration (days)	% Germination
A. californica	—	5	42
*A. canescens**	30/20	15–40	28
A. fruticosa	30/20	15–40	63
A. nana	30/20	30–40	70

Sources: Blake (1935), Brinkman (1974), Christiansen (1967), Hutton and Porter (1937), Kraebel (1939), Lincoln Oakes Nurseries (1996), Martineau (1996), Pammel and King (1928), Swingle (1939), Van Dersal (1938).
Note: Temperature is day/night regimen, photoperiod is 8 hours, based on Brinkman (1974).
* Germination of leadplant (*Amorpha canescens*) takes about 2 weeks when sown in nurserybeds in the spring (Lincoln Oakes Nurseries 1996; Martineau 1996).

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be taken when lifting, as the roots are split easily (Martineau 1996). Similar procedures are used for leadplant in North Dakota (Lincoln Oakes Nurseries 1996).

The following schedule for growing bareroot indigobush seedlings is reported by the Lincoln Oakes Nurseries (1996):

1. Legumes are hand-stripped from the plants in late September–late October.
2. Stem parts and impurities are removed, but the legumes are not removed.
3. Seeds are cold-stratified for 60 to 90 days in sand before sowing in the spring.
4. Seeds are sown in a single row of 80 to 100 seeds/m (25 to 35 seeds/ft) at a depth of 0.8 cm ($^1/_3$ in). Seedlings grow to heights of 25 to 35 cm (8 to 14 in) the first year and 0.6 to 1.2 m (2 to 4 ft) the second year.
5. Plants are harvested as 2+0 seedlings.

Seeds can also be sown in the fall to allow natural stratification to occur; this appears to partially eliminate the need for acid treatment in those species where it is recommended (Brown and others 1983; Dirr and Heuser 1987). For leadplant, 0.45 kg (1 lb) of commercial seed has produced about 22,000 usable plants; for indigobush, 1,000 to 5,600 plants (Brinkman 1974).

Amorpha species can be propagated from softwood and semi-hardwood cuttings. Untreated softwood cuttings root readily, but later-season cuttings may require treatment with a rooting compound (Bailey 1939; Dirr 1990; Dirr and Heuser 1987).

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Araliaceae—Ginseng family

Aralia L.

aralia

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Growth habit, occurrence, and uses. The genus *Aralia* comprises about 20 species of deciduous trees, shrubs, and herbs found in North America, Asia, Malayasia, and Australia (Blum 1974; Fernald 1950). The main species in North America include 3 subshrubs and a small tree (table 1)—the devil's-walkingstick—that is planted as an ornamental, as is the exotic Japanese angelica-tree—*A. elata* (Miq.) Seem. Animals utilize the vegetative growth and fruits to varying degrees. Two species were used for medicinal purposes by Native Americans. Underground parts are known for their aromatic qualities (Blum 1974; Braun 1961; Dirr 1990; Fernald 1950; Kenfield 1966; Krochmal and others 1969; MacKinnon and others 1992; Meeker and others 1993; Moore 1993; Stupka 1964; Tehon 1951; Voss 1985).

Within their respective ranges, the species occupy different types of sites. Devil's-walkingstick is intolerant of shade, occurring mostly on disturbed sites with no or light forest canopy. It develops best on rich, mesic soils but also occurs on a range of site conditions. Dense stands are formed by shoot production from rhizomes. The stem has prominent spines, hence the species' common name of devil's-walkingstick (Sullivan 1992).

Of the herbaceous perennials, wild sarsaparilla is the most widely distributed. It is a common understory species in a variety of forest types. In Wisconsin, for example, it occurs throughout the state but is most common in northern forests with dry-mesic to wet-mesic moisture regimes (Curtis 1959); it occupies similar sites in Newfoundland, Michigan, and British Columbia (MacKinnon and others 1992; Meades and Moores 1994; Voss 1985). Compound leaves develop annually from a well-developed rhizome system. Clones may be 10 m or more in diameter (Bawa and others 1982; Edwards 1984). The age of the perennial shoot-bearing portion of the rhizome can be determined from leaf scars and frequency of flowering from inflorescence scars (Bawa and others 1982).

Spikenard and bristly aralia are less widespread than wild sarsaparilla. Spikenard occurs on relatively richer sites and is described as one of the largest herbaceous plants in the flora of Michigan (Voss 1985).

Bristly aralia occurs on drier sites. Small clones are formed by development of the rhizome system and consist of vegetative and reproductive ramets (Thomson and Barrett

Table 1—*Aralia,* aralia: nomenclature, occurrence, growth habit, and height

Scientific name	Common name(s)	Occurrence	Year first cultivated	Growth habit	Height at maturity (m)
***A. hispida* Vent.**	**bristly aralia,** wild-alder, bristly sarsaparilla, dwarf-elder	Newfoundland to North Carolina & W to Minnesota & Indiana	1788	Subshrub or perennial herb	0.3–0.9
***A. nudicaulis* L.**	**wild sarsaparilla,** small spikenard	Newfoundland to North Carolina & W to Manitoba & Missouri	1731	Subshrub or perennial herb	0.2–0.4
***A. spinosa* L.**	**devil's-walkingstick,** angelica-tree, Hercules-club, prickly-ash	Pennsylvania to Florida, W to SW Iowa & W Texas; range extended by planting in Massachusetts, Oregon, Washington, & W Europe	1688	Tree	7.7–9.2
***A. racemosa* L.**	**spikenard,** petty morrel, life-of-man	Quebec to Manitoba, Great Lakes region, New England, & SE US	—	Subshrub or perennial herb	0.5–3.0

Source: Blum (1974).

1981). A distinguishing characteristic is the presence of spines on the stem (Curtis 1959; Voss 1985).

Flowering and fruiting. The flowers of *Aralia* are polygamous, white or green, and occur in umbels or panicles (Fernald 1950; Harrar and George 1962). Wild sarsaparilla has 3 to 4 umbels/inflorescence (figure 1) and bristly aralia has approximately 9 umbels/ramet. Flowering occurs from May to September depending on species; fruits mature in late summer or fall (figure 2) (Blum 1974; Fernald 1950). Flowers of wild sarsaparilla develop on a separate stalk that is overtopped by the associated vegetative stalk. In the other species, flowers are terminal and axillary or a combination of the two (Fernald 1950). Fruits are light green when immature, changing to bluish or purplish black when mature (Dirr 1990; Mackinnon and others 1992; Meades and Moores 1994; Soper and Heimberger 1982; Voss 1985). Male flowers retained in bristly aralia umbels with both male and hermaphrodite flowers turn red, making the fruit more conspicuous than if only the fruits were present (Thomson and Barrett 1981).

In bristly aralia, umbels contain male-only and hermaphrodite flowers. During the early stages of flowering, all flowers function as males; the female portion of the hermaphrodite flowers is receptive after the male parts have ceased to function. The number of flowers per umbel ranges from 30 to 40. Twenty-seven to 35% of the flowers are

Figure 1—*Aralia nudicaulis*, wild sarsaparilla: male inflorescence with 3 umbels, stamens just beginning to appear; the larger vertical stem in the background is the leaf-bearing vegetative shoot.

Figure 2—*Aralia nudicaulis*, wild sarsaparilla: developing fruits with stigmas still attached; additional blurred umbels are part of the same inflorescence.

hermaphrodites and more than 90% of these produced fruits (Thomson and Barrett 1981).

Wild sarsaparilla is dioecious with complete flowers uncommon (Bawa and others 1982). The sex ratio tends to be male-dominated but varies among sites and with time during the period of flowering, as male and female ramets do not flower synchronously (Barrett and Helenrum 1981). Infloresences on female plants contain on average 55 to 125 flowers. About 68% of the flowers produced fruits. Controlled pollinations produced 90 to 100% fruit set; flowers remain receptive for about 6 days. Some of the main differences between male and female clones are that males have more flowers per inflorescence, greater frequency of flowering, and occur in higher densities and greater numbers of ramets than do females (Barrett and Helenrum 1981; Barrett and Thomson 1982; Bawa and others 1982).

Insects are the major means of pollination in the genus (Bawa and others 1982; Barrett and Helenrum 1981; Thaler and Plowright 1980; Thomson and Barrett 1981; Thomson and others 1982). In areas treated to control spruce budworm, 71% of flowers produced fruits in sprayed and 49% in unsprayed sites, respectively (Thaler and Plowright 1980).

The fruit is a small, berry-like drupe containing 2 to 5 compressed, crustaceous, light reddish brown nutlets that are round, oblong, or egg-shaped. Each nutlet contains 1 compressed, light brown seed with a thin coat that adheres closely to the fleshy endosperm (Sargent 1965; Thomson and Barrett 1981) (figures 2 and 3).

Collection, extraction, and storage. Aralia fruits may be collected when they begin to fall from the plants in autumn (table 2). The seeds are ripe when the endocarps of the nutlets become hard and brittle, and this ripening may occur somewhat later than the ripening of pulp. The fruits should be run through a macerator, with water, immediately after collection. This will prevent fermentation and enable

the pulp and empty seeds to float off or be screened out. Small samples can be pulped by rubbing, with water, between 6.35-mm (#16) screens. Purity of seeds cleaned by the macerator technique was 98% (Blum 1974), but soundness in some lots has been only 30 to 60% (Heit 1968). Seed size and weight of cleaned seeds is indicated in figures 3 and 4 and table 3. Refrigerated storage of cleaned seed in sealed containers is recommended (Dirr and Heuser 1987; Heit 1967a), but the duration of viability under these conditions is not known.

Seeds of early successional aralia species from temperate and tropical regions elsewhere in the world have been found in soil seedbanks (Cheke and others 1979; Hirabuki 1988). Seedbanks in beech–birch–maple forests in New England had a minor amount of spikenard, bristly aralia, and wild sarsaparilla (Graber and Thompson 1978). No information was found on buried seeds of devil's-walkingstick, a plant that better fits the ecological characteristics—that is, early successional, intolerant species—of the aralia species found to occupy seedbanks in other parts of the world (Cheke and others 1979; Hirabuki 1988). The longevity of aralia seeds in the forest floor environment is not known.

Germination. Aralia seeds have dormant embryos, and some species, notably bristly aralia, appear to have impermeable endocarps (hardseededness) (Heit 1967b). There may be a combination of both hardseededness and embryo dormancy, requiring either mechanical or chemical scarification of the seedcoat in addition to a prechilling treatment (Heit 1967b). Seed dormancy in devil's-walkingstick can be overcome satisfactorily by 3 months of stratification at low temperatures (Blum 1974; Dirr and Heuser 1987). Hartmann and others (1990) also suggest that 30 minutes of soaking in sulfuric acid in addition to stratification improves germination. Dirr and Heuser (1987) reported 1% germination without stratification and 55% following 3 months of cold treatment. Although pretreatment with sulfuric acid and stratification at low temperatures will partially overcome hardseededness and embryo dormancy, other complications such as immature embryos further hinder germination (Heit 1968). In a study by Nichols (1934), seeds of wild sarsaparilla had 34% germination in 21 to 35 days after pretreating for 71 days at low winter temperatures in a cold frame. However, in this same study, seeds of bristly aralia had only 8% germination after exposure to low temperatures for 83 days. Seeds not exposed to low temperatures, on the other hand, had only 3% germination. Seeds of bristly aralia

Figure 3—*Aralia spinosa*, devil's-walkingstick: nutlets (seeds).

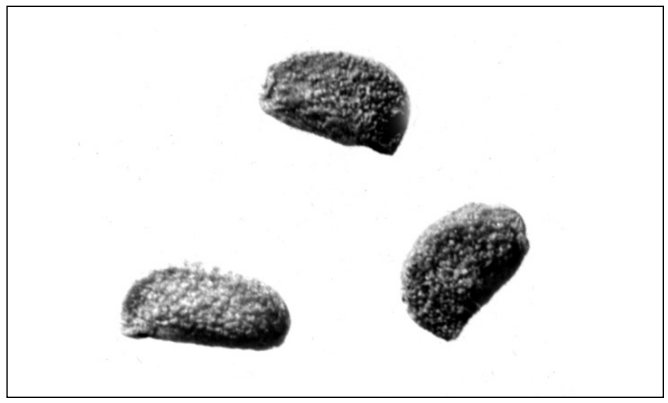


Table 2—*Aralia,* aralia: phenology of flowering and fruiting

Species	Flowering Dates	Fruit Ripening Dates	Seed Dispersal Dates
A. hispida	June–July	A	
A. nudicaulis	May–June	A	
A. spinosa	July–Aug	S	

Source: Blum (1974).

Table 3—*Aralia,* aralia: seed data

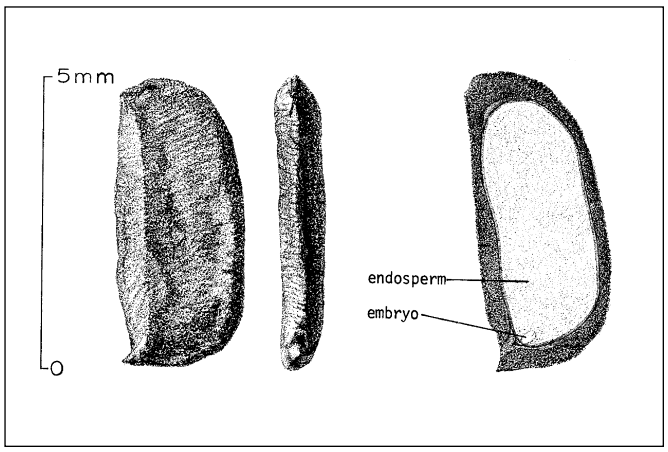
	Cleaned seeds/weight				
	Range		Average		
Species	/kg	/lb	/kg	/lb	Samples
A. hispida	207,740–218,790	94,000–99,000	203,320	92,000	2
A. nudicaulis	185,640–245,310	84,000–111,000	218,300	99,000	3
*A. spinosa**	232,050–346,970	105,000–157,000	288,850	131,000	2

Source: Blum (1974).

* 100 pounds of fruit have yielded 11 pounds of seed.

A

Figure 4—*Aralia nudicaulis*, wild sarsaparilla: exterior views of nutlets in 2 planes and longitudinal section.



were shown to benefit from after-ripening at temperatures ranging between 1 to 10 °C; optimum 5 °C for 90 to 120 days before planting in a greenhouse (Crocker 1948).

Japanese angelica-tree may benefit from 3 months of warm followed by 3 months of cold treatment; however, 70% germination has been reported following cold treatment only (Dirr and Heuser 1987).

Warm plus cold stratification of wild sarsaparilla brought about germination of 24% (with a potential germination of 66 to 92%). The seeds were stratified for 60 days at 20 °C (night) to 30 °C (day), plus 60 days at 5 °C, plus 60 more days at 20 to 30 °C, plus 60 more days at 5 °C. Similar treatment brought about only 0.5% germination of bristly aralia (Blum 1974). Obviously, this species still needs further study before fully satisfactory seed treatments can be developed (Heit 1967a).

Nursery practice. Heit (1968) recommends treating small lots of aralia seeds with sulfuric acid for 30 to 40 minutes and broadcast sowing in September. The aralias also may be propagated vegetatively. Root and rhizome cuttings offer the best method of vegetative propagation (Dirr and Heuser 1987).

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Araucariaceae—Araucaria family

Araucaria Juss.

araucaria

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Growth habit, occurrence, and use. The araucarias are 15 species of evergreen coniferous trees that are generally confined to the Southern Hemisphere. They are found in South America, Australia, New Guinea, New Caledonia, the New Hebrides Islands, and Norfolk Island under tropical, subtropical, and temperate climates (Dallimore and Jackson 1954; Howcroft 1978a&b; Ntima 1968; Record and Hess 1943; Veblen and Delmastro 1976; Webb and others 1984). They are noted for their long, straight, clear boles and symmetrical crowns; many are useful for timber and some are cultivated as ornamental trees and houseplants (Streets 1962).

Several species have been introduced to California, Oregon, Washington, Florida, Hawaii, Puerto Rico, the U.S. Virgin Islands, Guam, American Samoa, and other U.S. territories in the South Pacific region (table 1) (Francis 1988; Walters 1974). Araucaria species are generally found on sites at elevations from sea level to 2,100 m, with 1,200 to 2,400 mm of rainfall and well-drained soils. Cook-pine and Norfolk-Island-pine have been widely planted in Hawaii (Menninger 1964; Walters 1974). The botanical identities of these 2 species are often confused, and no one (not even visiting foresters from Australia) is absolutely sure which species is which! Recipients of araucaria seeds shipped out of Hawaii should be made aware of this confusion. All data on phenology and methods reported here are based on information obtained from the areas of natural occurrence. Norfolk-Island-pine is also a very common ornamental tree in Florida, California, Puerto Rico, and the U.S. Virgin Islands.

Flowering and fruiting. Araucarias generally begin to flower and set seeds between the age of 15 to 20 years. Most hoop-pine trees begin producing female flowers and fruits when they are between 10 and 12 years old and 6 to 10 m tall. Flowering and fruiting is very intermittent from year to year, and pollen production begins when trees are 22

Table 1—*Araucaria,* araucaria: nomenclature, occurrence, and heights attained

Scientific name & synonym(s)	Common name(s)	Occurrence		Maximum height (m)
		Native	US	
***A. angustifolia* (Bertol.) Kuntz**	**parana-pine,** candelabra tree, Brazilian-pine	Brazil, Argentina, & Paraguay	Hawaii & Puerto Rico	36
***A. araucana* (Molina.) K. Koch.** *A. imbracata* Par.	**monkey-puzzle tree,** monkey-puzzle, Arauco-pine, Chilean-pine	Chile & Argentina	California, Oregon, & Washington	50
***A. bidwillii* Hook.**	**bunya-pine,** bunya-bunya	Australia	California, Florida, Hawaii, & Puerto Rico	43
***A. columnaris* (Forster) Hook.** *A. excelsea* (Lamb.) R. Br.	**Cook-pine,** columnar araucaria	New Caledonia	Hawaii, Florida, & Puerto Rico	60
***A. cunninghamii* Aiton ex D. Don)**	**hoop-pine,** Moreton-Bay-pine	New Guinea & Australia	California, Hawaii, & Puerto Rico	60
A. heterophylla (Salisb.) Franko	**Norfolk-Island-pine,** Australian-pine	Norfolk Island	California, Florida, Hawaii, & Puerto Rico	60
A. hunsteinii K. Schum. & Hollrung *A. schummaniana* Warb. *A. klinkii* Laut.	**klinki-pine**	New Guinea	Hawaii & Puerto Rico	80

Sources: Dallimore and Jackson (1954), LHBH (1976), Walters (1974).

to 27 years old and are about 20 m tall (Haines and Nikles 1987). Male and female flowers are generally found on different parts of the same tree. Male flowers usually appear at the base of the crown in young trees and the female flowers at the top. As the tree grows older, the male and female flowers come closer to each other. Bisexual flowers are also found. After pollination, the female flowers develop slowly, with the cones maturing in about 2 years (Ntima 1968). The mature cones are ovoid or almost spherical, ranging in size from 10 by 5 cm for hoop-pine to 30 by 20 cm for bunya-pine (Ntima 1968). In natural stands, seedlots collected from hoop-pines are rarely more than 65% viable (Haines and Nikles 1987).

Upon maturing, cones turn from green to brown (Ntima 1968; Walters 1974). Cones disintegrate on the tree or fall to the ground and disintegrate. The brown seeds are kite-shaped and have papery wings on either side (figures 1 and 2) or are thick and heavy with much endosperm. Araucaria seeds may be carried a short distance from the mother tree by wind, but generally the seeds fall within the periphery of the crown (Ntima 1968). Animals and birds that prey on the seeds are the most effective natural dispersers of the heavy seeds. The time of flowering, seed development, and seed dispersal, as well as seedcrop intervals are listed for 5 species in table 2.

Collection, cleaning, and storage. Most of the seeds of hoop-pine collected for planting are grown in seed orchards (Haines and Nikles 1987). Collection of cones should begin when the first trace of brownness is observed on the cone. In natural stands, the second-year cones are generally picked by climbing or felling trees (Howcroft 1978; Ntima 1968; Walters 1974). Cone collection must be timed correctly to get the highest proportion of mature and fertile seeds. A method for timing cone matureness is to pick a cone and measure the time it takes to disintegrate; ripe cones spontaneously disintegrate within 7 days. Collected cones should be spread on shelves in single layers for drying and turned daily. The cones normally will begin to disintegrate within a few days. Cones that fail to disintegrate within 10 days should be discarded, as they are considered too immature (Ntima 1968; Walters 1974). The average number of seeds per weight ranges from 77/kg (35/lb) for bunya-pine to 4,400/kg (1,995/lb) for hoop-pine (table 3) (Howcroft 1986; Walters 1974).

Most araucaria are recalcitrant (that is, intolerant of desiccation). Their seeds have short viability under atmospheric conditions and normally should be sown within a month of collection (Ntima 1968). If the seeds cannot be sown immediately, they should be stored under cold, moist, and airtight conditions at a temperature of 3 °C (Ntima 1968; Walters 1974). Klinki-pine seeds can be stored for at least 6 months with 32% moisture at a temperature of 3.5 °C (Willan 1991). Damp storage at 4 to 7 °C was best for monkey-puzzle-tree seeds. After 3 months of storage, these seeds began to germinate after 21 days at 25 to 30 °C and reached 70 to 90% germination after 7 days (Swindells 1980). Hoop-pine seeds appear to be orthodox (that is, tolerant of dessication); air-dried seeds stored at temperatures ranging from 1.7 to –15 °C showed little reduction in germination percentage for 17 months of storage (46 to 50% germination), but

Figure 1—*Araucaria,* araucaria: seeds of *A. columnaris*, Cook-pine (**left**) and *A. heterophylla,* Norfolk-Island-pine (**right**).

Figure 2—*Araucaria heterophylla*, Norfolk-Island-pine: longitudinal section through a seed.

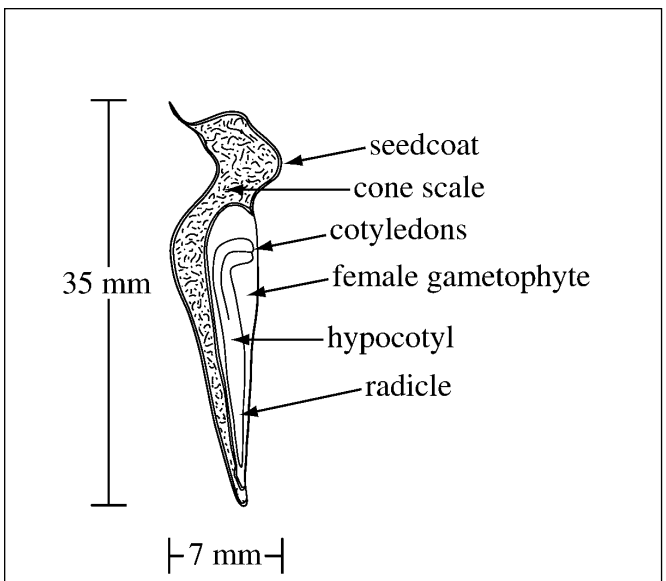

Table 2—*Araucaria,* araucaria: phenology of flowering, seed development and dispersal, and seedcrop intervals

Species	Flowering	Seed ripening	Seed dispersal	Crop intervals (yrs)
A. angustifolia	—	Apr–May	May–Aug	1
A. bidwillii	Sept–Oct	Jan–Feb	Jan–Feb	1–2
A. columnaris	Dec–Jan	Dec–Feb	Dec–Feb	3–4
A. cunninghamii				
Early-flowering races	Dec–Jan	Dec	Dec	4–5
Late-flowering races	Apr–May	—	—	—
A. heterophylla	Sept	Apr	Apr–May	3–4

Source: Walters (1974).
Note: Information for all species is based on their natural ranges.

Table 3—*Araucaria,* araucaria: seed data

	Cleaned seeds/weight			
	Range		Average	
Species	/kg	/lb	/kg	/lb
A. angustifolia	—	—	108	50
A. bidwillii	66–88	30–40	77	35
A. columnaris	1,980–2,640	900–1,200	2,200	1,000
A. cunninghamii	3,300–6,600	1,500–3,000	4,400	2,000
A. heterophylla	550–620	250–280	573	260
A. hunsteinii	2,000–2,500	900–1,100	—	—

Sources: Howcroft (1986b), Walters (1974).

decreased significantly between 17 and 100 months of storage. However, after 100 months of storage, germination still ranged from 25 to 44% (Shea and Armstrong 1978). Tompsett (1984) found that seeds of monkey-puzzle-tree, parana-pine, klinki-pine, and bunya-pine could not be safely dried below 25 to 40% moisture content; seeds of cook-pine and 2 other araucarias (*A. nemorosa* de Laubenfels and *A. scopulorum* de Laubenfels) cannot be dried below 12%; and seeds of hoop-pine could be dried to 2% without damage. Seeds in the second 2 groups dried to moisture contents just above the critical levels can be stored at –18 °C and thus appear to be orthodox. Parana-pine, monkey-puzzle-tree, and bunya-pine seeds are classified as recalcitrant (Farrant and others 1989; Ramos and others 1988). Plastic bags are good containers (Ntima 1968). Seeds of hoop-pine can be stored up to 8 years (Shea and Armstrong 1978).

Germination. No pregermination treatments are needed for araucaria seed (Ntima 1968; Walters 1974). Under suitable moisture and temperature (21 to 30 °C) conditions, germination (which is cryptogeal in this genus) may begin about 10 days after sowing. Germination is delayed by cooler temperatures, sometimes taking 50 days or more (Ntima 1968). Seed quality varies from year to year; if sufficient pollen is available to the parent trees, seed quality is generally good (Walters 1974).

Twenty-nine and 45% of a large number of hoop-pine and klinki-pine seeds germinated within 9 weeks in a germination test (Thong 1974). Klinki-pine seeds are pregerminated (incubated until the radicle begins to show) before sowing into containers. In a test with 3 replications of 1,200 seeds each, germination averaged 85% in 22 days. Of those seeds not germinating, 54% were dead, 30% were rotten, and 16% had not germinated yet. Survival of seedlings in containers to outplanting size was 88%. Broadcasting seeds on the surface of wet sawdust with a second shadecloth a few centimeters above the bed gave better germination than covering seeds with sawdust or germinating them without the second shadecloth covering (Howcroft 1974). Tompsett (1984) obtained 80 to 100% germination of 6 species tested when seed moisture contents were optimal.

Nursery practice. Araucarias can be grown under high shade or low shade. For both types of shade, seeds are sown during spring. Norfolk-Island-pine seeds are placed on a bed of sand–soil–peat mix to germinate with the pointed end of the seed slightly embedded. About 70% of fresh seedlots germinate in 4 to 12 days (Logsdon 1973). Seeds

should be treated with a fungicide to prevent damping-off. Fungi pathogenic to seedlings can be isolated from seed collected from the ground and even from seeds extracted from cones collected from trees (El-Lakany and others 1981). *Rhizoctonia solani* Kühn—the fungal species causing most of the cases of pre- and post-emergence damping-off—was one of the most commonly isolated fungi from *Araucaria* seeds (Kamara and others 1981). Control of seedborne and soilborne fungi should be undertaken before planting. With high shade, the seeds of all species except bunya-pine are sown in flat-bottomed drills about 1.25 cm ($^1/_2$ in) deep and then covered with the same amount of softwood sawdust (fungicide-treated hardwood sawdust may also be suitable).

Bunya-pine seeds are sown in drills 7 to 10 cm (3 to 4 in) deep or on shaded, moist media. A few months after sowing, fusiform radicles, called "tubers," are formed. The seedbeds are re-dug, and these tubers are collected and then either planted directly into containers or stored at room temperature until required for planting. Exposure of the tubers to sunlight before re-planting breaks their dormancy, and the plants begin to grow. Almost every seed produces a tuber and all of these develop into plants (Walters 1974).

With low shade, the seeds are broadcast on well-prepared nursery beds and covered with about 2 cm ($^3/_4$ in) of sawdust. The aim in both types of sowing is to have a stocking of 130 to 180 plants/m^2 (12 to 17/ft^2) (Ntima 1968; Walters 1974).

Newly sown beds should be given full overhead shade within several days of sowing. Best shoot development occurs when the seedbeds are given 75% shade for the first few months and 5% shade for the next 3 months (except for hoop-pine). Shading should be removed in 2 steps after this shading treatment to give full exposure 2 weeks before transplanting to containers. Full light is not admitted until nearly 1 year after sowing hoop-pine. When 75% of the seedlings are 15 to 22 cm (6 to 9 in) tall, the seedlings should be transplanted. Lifting and planting need to be done carefully to minimize damage to the roots. Transplanting should be done about 5 months before field planting. The seedlings should be spaced 5 by 20 cm (2 to 8 in) apart (stem to stem) and given full shade. The shade should be gradually removed to give full sunlight to the seedlings for at least a month before transferring them to the planting site (Ntima 1968). About 50 to 60% of the seeds will develop into plantable seedlings. Seedlings are generally outplanted when 2 years old (Ntima 1968). Norfolk-Island-pine seedlings grown in nursery beds or containers will be 15 to 20 cm (6 to 8 in) tall in 1 year and 60 to 76 cm (24 to 30 in) tall in 2 years (Logsdon 1973).

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Ericaceae—Heath family

Arbutus menziesii Pursh

Pacific madrone

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Other common names. madrone, arbutus, madroño.

Occurrence and growth habit. Pacific madrone—*Arbutus menziesii* Pursh—is 1 of 3 species of *Arbutus* native to the western United States (Little 1979). It is an evergreen tree that occurs in coastal mountains from southwestern British Columbia to southern California, and also in the Sierra Nevada of north central California. It often is found as a single tree or in groves, only rarely occupying extensive areas (McDonald and Tappeiner 1990; McDonald and others 1983). Seldom does Pacific madrone form pure stands; usually it is found in mixture with several conifer and hardwood species. It also competes successfully in both overstory and understory canopies (Sawyer and others 1977). Although some trees originate from seed, most begin life as root crown sprouts. Tree height and form vary widely: height from 8 to 38 m, and form from straight to crooked (Sudworth 1908). Stand density is a prime determinant of form and also affects tree height. In general, the more dense the stand, the better the form and the greater the height. On good sites with well-stocked stands, plentiful moisture, and some shade, the tree grows straight and tall with a narrow crown. On poorer sites with lower stocking and inadequate soil moisture, the tree becomes short and crooked, with a relatively wide crown. Clumps of trees are prevalent and increase as stands become more open. The species seems to be phototropic and trees are often observed leaning into gaps in the canopy. Asymmetric bole development is common. Over the entire range, the majority of Pacific madrone trees have some lean and some crook. Forking also is common.

Use. The strong, smooth, fine-grained wood has been utilized for many purposes, ranging from lumber, veneer, and fuelwood to furniture, flooring, interior trim, and paneling (EDA 1968; Overholser 1968). In the past, the wood of Pacific madrone was prized for making charcoal for gunpowder (Koch 1973) and was found to be without peer when made into bobbins and spools. This species was first cultivated in 1827 and has been planted occasionally as an ornamental tree in Europe and the United States (McMinn and Maino 1959).

Flowering and fruiting. Flowers, which bloom from March to June, are formed on a panicle 12 to 15 cm long. The 8-mm flowers consist of 5 sepals fused at the base with 5 fused urn-shaped petals and 10 stamens. The anthers split open when ripe, the awns are elongate, and the superior ovary is rough and bumpy with 5 chambers (Hickman 1993). The fruit is a berry, also rough and bumpy, less than 12 mm in diameter (figure 1). The generic name derives from *arboise*, a Celtic word for "rough fruit" (Roy 1974). The thin-skinned berry has rather dry, mealy flesh and generally is 5-celled (figures 1 and 2). McDonald (1978) found that, in northern California, the number of seeds per berry ranged from 2 to 37, with an average of 20. The berries ripen in September through November but often remain on the trees through December. Fully ripe berries are bright red

Figure 1—*Arbutus menziesii*, Pacific madrone: exterior view of the fruit (**left**) and transverse section of fruit showing its 5 carpels (**right**).

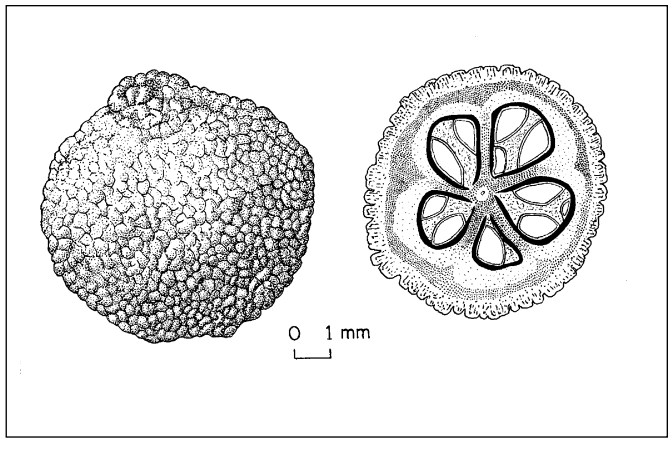

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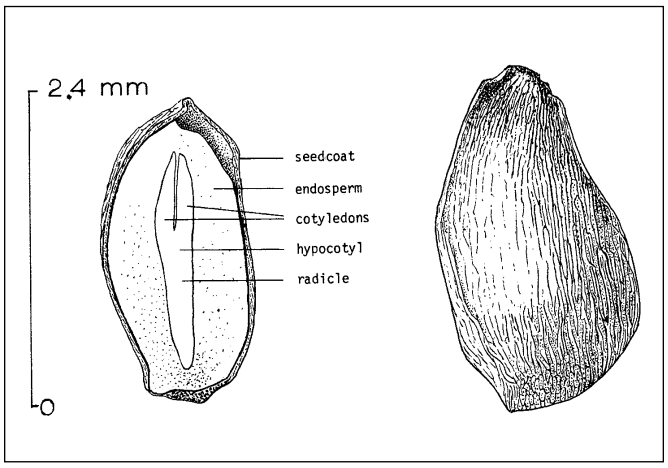
Figure 2—*Arbutus menziesii*, Pacific madrone: longitudinal section through a seed (**left**) and exterior view of a seed (**right**).



or bright reddish orange (Peattie 1953). However, the smaller numbers of yellowish orange or yellowish green berries that are usually present at the same time also furnish viable seeds (McDonald 1978).

The minimum seed-bearing age (from root crown sprouts) is 4 years but more commonly at least 8 years. Older trees have tremendous capability to produce seeds. On a good site in northern California, the number of berries produced during a light seed year for 3 representative trees that were 23, 36, and 41 cm in dbh ranged from 13,320 to more than 107,000/tree and related best to amount of living crown (McDonald 1978). On this same site, annual records showed that during a 24-year period (1958–1981), Pacific madrone produced 2 medium to heavy and 10 very light to light seedcrops (McDonald 1992). In years when the overall seedcrop is poor or nonexistent, madrone trees may be stimulated to produce heavy crops by logging and thinning. Apparently, the reduced stand density provides additional water and nutrients that become manifest in reproductive material.

A recent phenomenon that has greatly reduced seed production (Thornburgh 1994) is dieback and death of Pacific madrone trees infected by the madrone canker—*Botryosphaeria dothidea Moug.:Fr.*) Ces. & De Not.—which is virulent in northern California (McDonald and Tappeiner 1990).

Collection, extraction, and storage. Berries of Pacific madrone can be collected during the ripening period, dried thoroughly, and stored at room temperature for 1 or 2 years (Mirov and Kraebel 1939). Separating the seeds from the pulp after soaking and maceration of the berries probably is best (McDonald 1978). Only dry seeds should be stored, probably in sealed containers at temperatures just above freezing (Roy 1974). Fresh berries picked in the northern Sierra Nevada numbered 1,390 to 2,490/kg (630 to 1,130/lb), and the yield of cleaned seeds was 1.6 to 2.0 kg/45 kg (3.6 to 4.4 lb/100 lb) of fruit. The number of seeds ranged from 434,310 to 705,470/kg or 197,000 to 320,000/lb (McDonald 1978). Dried berries from an unknown source numbered 900/kg (2,000/lb) (Mirov and Kraebel 1939).

Pregermination treatments. Because the seeds exhibit strong embryo dormancy, stratification is critical. McDonald (1978) found that only 1 of 400 sound seeds germinated without stratification. For stratification, much evidence shows that storage in a plastic bag containing a small amount of moist paper or peat moss at temperatures just above freezing for 35 to 45 days is all that is needed to break dormancy (McDonald 1978; Roy 1974). With this treatment, 78 to 90% of a seedlot will have germinated in 10 days.

Germination tests. Only sound seeds should be used in germination trials. For red berries, darker color and slight rounding at the pointed end proved diagnostic for separating sound from unsound seeds; for yellowish berries, only seed size was a worthwhile indicator—larger seeds were more likely to be sound than small ones (McDonald 1978). Extensive trials in laboratory and field have shown the perils of germinating seeds in berries. If berries were present, so were virulent fungi and consumers. Indeed, in a field trial, snaptraps baited with a single red madrone berry caught more white-footed deer mice (*Peromyscus maniculatus*) than those baited with peanut butter and wheatflakes.

Nursery practice. Pacific madrone can be propagated by germinating seeds in flats and transplanting the seedlings to individual containers. Losses from damping-off fungi, however, can be huge. Hundreds of seedlings die overnight and the number available for planting often is small. Van Dersal (1938) noted that a yield of about 450 usable plants/kg of seeds (1,000/lb) was the best that could be expected. Although this species has been propagated vegetatively by grafting, layering, and rooting of cuttings (Roy 1974), no operational application of these techniques is known.

Seedling care. The problem of fungi does not end after the germinants become seedlings. Even after transfer to peat pots or other containers, the seedlings need to be protected from fungi. And even after great care, survival and growth in a conventional (sunlit) plantation is poor. In a trial on a high site in the northern Sierra Nevada, survival of seedlings in large containers (plugs) on competition-free ground was 33% after 6 years (McDonald 1978). All

seedlings died back at least once, developed multiple stems of poor form, and grew poorly. Natural seedlings developing in the wild also have a dismal establishment record, with first-year survival rates of 0 to 6%. Damping-off fungi, drought, predation by invertebrates, and litterfall, often interacting together, seriously limit the reproductive efforts of Pacific madrone (McDonald 1978; Pelton 1962; Tappeiner and others 1986). Based on this evidence, the best environment for establishment of both natural and planted seedlings is bare mineral soil and moderate shade (McDonald and Tappeiner 1990). However, the rate of seedling growth and its consistency in this environment is unknown.

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A

Ericaceae—Heath family

Arctostaphylos Adans.

manzanita

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Growth habit, occurrence, and uses. The shrub genus *Arctostaphylos,* or manzanita, comprises about 50 species, 90% of which are endemic to California and adjacent areas (Munz and Keck 1959). Three species—greenleaf manzanita, Mexican manzanita, and rosybract manzanita—are widely distributed in the southwestern United States and Mexico. One species—bearberry or kinnickinnick—is circumboreal in distribution (table 1). The manzanita habit varies from mat-forming (bearberry) to nearly arborescent (bigberry manzanita). About a quarter of the species have subterranean burls that generate new sprouts both after fire and throughout the long life of the plant (Keeley 1992; Wells 1969). The leaves of manzanitas are leathery, entire, and evergreen. They are major components of chaparral and are also common understory species in montane coniferous forest types, especially ponderosa (*Pinus ponderosa* Dougl. ex Laws.) and Jeffrey (*P. jeffreyi* Grev. & Balf.) pines. They are most abundant in the fire-prone vegetation of regions with dry summers.

The manzanitas are moderately important as winter browse plants for wild ungulates but are less important for domestic livestock (Berg 1974). They are used principally after fire, when new shoots or seedlings are produced in abundance. The fruits are eaten by bears (*Ursus* spp.), grouse (*Dendragapus* spp.), and coyotes (*Canis latrans*) (Belcher 1985; Kauffmann and Martin 1991) and the seeds by various rodents (Keeley and Hays 1976). The sprouting species are particularly important for watershed protection after fire, and many species could be used in revegetation for erosion control. Manzanitas also have great potential for use as ornamentals. Their smooth red bark; interesting, twisted growth forms; and bright evergreen leaves make them attractive year-round. Bearberry has found wide

Table 1—*Arctostaphylos,* manzanita: habitat requirements and geographic distribution

Scientific name	Common name(s)	Habit	Habitat	Distribution
***A. canescens* Eastw.**	**hoary manzanita**	Shrubby, without burl	Ponderosa pine forest, chaparral	N California to Oregon
***A. glandulosa* Eastw.**	**Eastwood manzanita**	Shrubby, with burl	Ponderosa pine forest, chaparral	California to Oregon
***A. glauca* Lindl.**	**bigberry manzanita**	Shrubby or treelike, without burl	Chaparral, joshua tree woodland	S California to Baja California
***A. patula* Greene**	**greenleaf manzanita**	Shrubby, with burl	Ponderosa pine forest	California to Oregon, Arizona, & Colorado
***A. pungens* Kunth**	**Mexican manzanita,** pointleaf manzanita	Shrubby, without burl	Ponderosa pine forest, chaparral, pinyon-juniper woodland	S California, E to Utah & Texas & S into Mexico
***A. pringlei* Parry**	**rosybract manzanita,** Pringle manzanita	Shrubby, without burl	Ponderosa pine forest, chaparral, mixed warm desert shrubland	S California, S to Baja California & E to Arizona & SW Utah
***A. uva-ursi* (L.) Spreng.**	**bearberry,** kinnickinnick	Mat forming, without burl	Coniferous forest mostly at high elevation	Circumboreal, S to California, New Mexico, Illinois, & Georgia

Source: Munz and Keck (1959).

acceptance as a versatile groundcover (Dirr 1983) and has also been used medicinally (Belcher 1985).

Flowering and fruiting. Small urn-shaped white to pink perfect flowers appear on the plants from early winter through spring. The bud primordia are formed the previous year, and flowering and fruiting intensity is positively correlated with the previous year's precipitation (Keeley 1977). The flowers are pollinated by insects, principally bees and flies (Fulton and Carpenter 1979). Obligately seeding species (that is, those unable to sprout after fire) may have a higher investment in pollinator attraction than sprouting species, as evidenced as higher flower density and nectar production (Fulton and Carpenter 1979). They may also be more likely to be self-fertile and to have higher seed-set overall as measured by the incidence of inviable or unfilled seeds (Keeley and Zedler 1978). Many of the sprouting species are tetraploids, and Kelly and Parker (1991) report that lower seed set may be associated with polyploidy rather than the sprouting habit per se.

Fruits ripen about 2 months after full-flowering, generally from June to September, depending on elevation. The fruits are drupe-like, with a hard, bony endocarp enclosing multiple seeds, a mealy mesocarp, and a thin exocarp (figure 1). Each seed is borne in a nutlet-like section. Ripe fruits may persist on the plant for several months but eventually fall. They may be dispersed by birds or mammals, especially coyotes (*Canis latrans)* (Kauffman and Martin 1991). The nutlets themselves may be dispersed by scatter-hoarding rodents, but rodents most often consume the seeds *in situ* and thus act solely as seed predators (Keeley 1977).

The nutlets may break apart at maturity or remain variously fused. In some species (for example, bigberry manzanita) the nutlets are completely coalesced, whereas in most species, including Eastwood and greenleaf manzanitas, the stone breaks irregularly into 1- to several-seeded-segments. The endocarp wall surrounding each seed is usually thick, hard, resinous, and impervious (figure 2). The wall has a channel (periole) at the basal or micropylar end. This channel is plugged with tissue that is not as hard as the endocarp itself. When the seed germinates, the radicle and hypocotyl are forced out through this periole (Berg 1974). The endocarp wall is thought to have a protective function, especially with regard to heat damage during fire. Seeds surrounded by very thick endocarps or contained within fused nutlets are apparently more likely to survive fire than those borne singly or with thinner endocarps (Keeley 1977). The testa itself is thin and membranous, and the well-developed straight or curved embryo is embedded in abundant endosperm (Berg 1974).

Seed collection, cleaning and storage. Good seed crops are produced on average every 2 to 3 years, usually the year following a year of high precipitation (Keeley 1977). The fruits range from pink or red to black when ripe, depending on species. They may be hand-stripped or picked up off the ground. Seed fill is often low, and considerable insect damage may be evident (Keeley and Hays 1976). Fill

Figure 1—*Arctostaphylos*, manzanita: *A. glauca*, bigberry manzanita bottom (**left**) and top (**right**) views of a drupe; *A. glandulosa*, Eastwood manzanita: drupe (**left**) and coalesced nutlets (**right**); *A. patula*, greenleaf manzanita, drupe (**left**) and partially coalesced nutlets plus 2 separated nutlets (**right**).

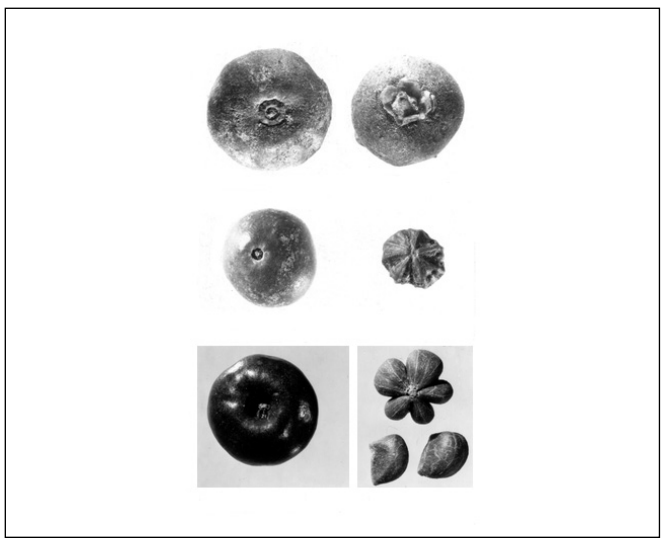
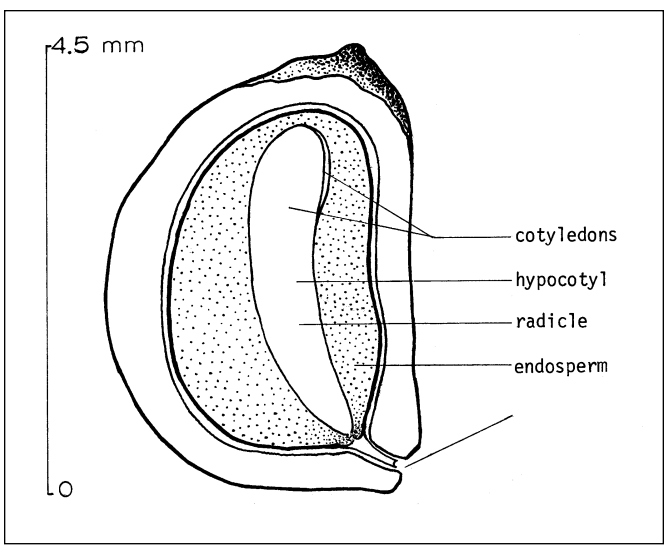


Figure 2—*Arctostaphylos uva-ursi*, bearberry: longitudinal section through a nutlet.



may be checked in the field by cutting the fruits transversely, preferably before the endocarp hardens (Berg 1974). Kelly and Parker (1991) reported a mean set (percentage of ovules forming seeds) of 62% for 14 California species, with a range from 50 to 80%.

To clean manzanita seeds, the fruits should be soaked in water, then macerated by hand or in a macerator to separate the pulp from the stones. The pulp may be removed by flotation, or the material may be dried, after which nutlets may be separated from the dried pulp using screens or a fanning mill (Berg 1974). Seedlots may be cleaned to high purity (Belcher 1985). Representative seed unit weights are given in table 2. Seed unit weights are highly variable even within a seedlot because a seed unit may be single or multiple-seeded, depending on the degree of coalescence of the nutlets.

Manzanita seeds form persistent seed banks and are apparently long-lived under field conditions (Kelly and Parker 1990). There is little information on longevity in warehouse storage, but it is probable that seedlots would maintain viability over periods of 10 years or more.

Germination and seed testing. In natural stands, new seedlings (figure 3) of most species of manzanita grow only after fire, and the seeds of these species are considered to be refractory, that is, germinating only in response to fire-related environmental cues (Keeley 1991, 1995). But unlike the refractory seeds of most chaparral shrubs, manzanita seeds apparently do not become germinable through heat shock (Kauffman and Martin 1991; Keeley 1987a). There is evidence that charate leached from incompletely burned wood can trigger germination in manzanita seeds, but the maximum percentages attained using recently collected seeds were not high (13% for Eastwood manzanita and 19% for greenleaf manzanita (Keeley 1987a, 1991). It is probable that, under field conditions, the seeds change in some way following dispersal (perhaps through dry after-ripening at the embryo level) that renders them more responsive to the charate stimulus. Parker and Kelly (1989) report that hoary manzanita seeds retrieved from the soil seedbank germinated readily in response to charate, whereas hand-harvested seeds less than 1 year old did not. In spite of the massive endocarp, manzanita nutlets are permeable to water, and the enclosed seeds are capable of imbibition without any pretreatment, at least in greenleaf manzanita (Meyer 1997). This explains how charate rather than heat shock could trigger germination. Presumably the charate stimulus enters the seed through the periole.

Even though manzanitas form persistent seedbanks, there is evidence that these seedbanks turn over fairly quickly, as there was no net gain in size of the seedbank in the absence of fire over 10 years for 2 chaparral species (bigberry and Eastwood manzanitas), even in the face of massive inputs (Keeley 1987b). Most of the seed loss appears to be due to rodent predation rather than germination or loss of

Figure 3—*Arctostaphylos patula,* greenleaf manzanita: seedling at 1 month.

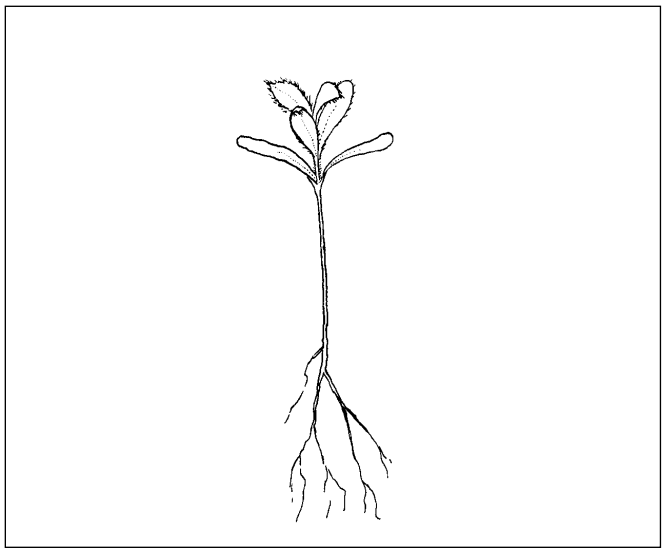


Table 2—*Arctostaphylos,* manzanita: seed weights and filled seed percentages

Species	Seed unit	Seeds/weight /kg	Seeds/weight /lb	Filled seeds (%)	Sample
A. glandulosa	1–2 seeded	66,150–97,020	30,000–44,000	—	2
A. glandulosa	1–3 seeded	55,125	25,000	58	2
A. glauca	Entire stone	990–1,760	450–800	83	5
A. patula	Variable	36,690–55,125	18,000–25,000	—	1+
A. patula	1-seeded	44,100	20,000	85	1
A. uva-ursi	1-seeded	59,535–90,405	27,000–41,000	—	3+

Sources: Belcher (1985), Berg (1974), Keeley (1977, 1991), Keeley and Hayes (1976), Meyer (1997).

viability (Keeley and Hays 1976). This suggests that the seeds available for seedling recruitment after fire probably belong mostly to recently produced cohorts.

Even though manzanita nutlets are water-permeable, most reports on germination describe the seeds as hard-seeded, and the traditional pretreatment is sulfuric acid scarification for 3 to 15 hours (Belcher 1985; Berg 1974; Carlson and Sharp 1975; Emery 1988). Because the periole is much weaker than the endocarp wall, acid can enter there and damage the embryo long before the endocarp wall is stripped away, so care must be taken to remove the seeds before this damage occurs (Belcher 1985; Berg 1974). Coalesced nutlets generally require more time in acid than solitary nutlets, perhaps because the perioles, which are on the inner face of each nutlet, are better-protected when the nutlets are coalesced. Chaparral species such as bigberry and Eastwood manzanitas may be rendered immediately germinable by acid scarification, although reported percentages are low—3 to 8% (Berg 1974). Populations of greenleaf manzanita required both acid scarification (2 to 4 hours) and subsequent chilling for 60 days (Berg 1974) and 90 days (Carlson and Sharp 1975). Final germination percentages were 20 to 50%. Bearberry has been reported to respond to warm plus cold stratification following a 3- to 6-hour acid treatment—60 to 120 days at 25 °C, followed by 60 to 90 days at 5 °C (Berg 1974). Final germination percentages ranged from 30 to 60%. Belcher (1985) reported that warm plus cold stratification of bearberry resulted in 40 to 60% germination without acid scarification, but that acid scarification for 3 hours could be substituted for warm stratification. In bearberry, even excised embryos were dormant prior to chilling (Giersbach 1937).

Emery (1988) reported that a fire treatment (burning 3 to 4 inches of pine straw or excelsior over the planted seeds) in fall resulted in some emergence the following spring for many species of manzanitas, but the mechanism of dormancy loss under these conditions was not further explored. Charate could have been the stimulus responsible for this effect. It would be worth experimenting with charate as a germination stimulant in a nursery propagation setting.

Formal seed quality evaluation in manzanita is rendered difficult by the lack of reliable germination tests and by the thick endocarp. Tetrazolium staining requires excision of the seed from the endocarp by twisting it open along the suture or by cutting the nutlet off-center longitudinally, procedures difficult to carry out without damage (Belcher 1985). A seed unit may contain multiple seeds, only 1 of which has to be viable for the seed unit to be considered viable. For seedlots that have not been incorrectly handled (for example, stored at high moisture content) or stored for long periods, a cut test to determine fill is probably the best way to get a quick idea of total viability.

Field seeding and nursery practice. It will probably continue to be very difficult to obtain manzanita from direct seeding until there is a much better understanding of factors controlling release from dormancy. The absence of manzanita seedlings in unburned chaparral (Keeley 1992) coupled with the regular appearance of thousands of manzanita seedlings per hectare following fire, as reported by Keeley (1977), strongly suggests that a successful seeding prescription would include a seed pretreatment simulating fire-related germination cues. The sulfuric acid–stratification treatments described above and the fire treatment of Emery (1988) are currently the only published procedures for nursery seed propagation. The mazanitas are much more easily propagated from cuttings than from seeds, and in practice most nursery propagation is probably accomplished in this way (Berg 1974; Emery 1988).

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Rosaceae—Rose family

Aronia Medik
chokeberry

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Growth habit, occurrence, and uses. The chokeberries—genus *Aronia*—discussed here are 2 closely related species (red and black chokeberries) and 1 hybrid deciduous shrub (purple chokeberry) (table 1). Black chokeberry is small, only 0.5 to 1 m tall. Red chokeberry and purple chokeberry are medium sized, 3 to 4 m tall. Red and black chokeberries hybridize readily and may be difficult to distinguish. Red and purple chokeberries are practically identical ecologically (Van Dersal 1938), and the only satisfactory way to distinguish between them is by the color of their ripe fruit. Both have pubescence on younger branches, leaf stems, and lower leaf surfaces. In contrast, black chokeberry is smooth or has only a few scattered hairs on these parts (Gleason 1963). The combined ranges of these 3 include most of the eastern United States and southern parts of adjacent Canadian provinces (table 1). All are moderately tolerant of shading and prefer moist soils, which usually are acidic. The most likely habitats are bogs and swamps, low woods, clearings, and damp pine barrens. However, each species will tolerate drier conditions, and black chokeberry is better adapted than the others to growth in drier thickets or clearings on bluffs or cliffs (Fernald 1950; Gleason 1963). All are valuable as food sources for wildlife in fall and winter (Hosely 1938). Their handsome foliage, flowers, and fruits also make them attractive as ornamentals, but none has been cultivated extensively. Red and black chokeberries were first cultivated about 270 years ago (Rehder 1940).

Flowering and fruiting. The white, bisexual flowers bloom for 2 to 3 months during March to July, the local flowering period depending on latitude and elevation. Fruit ripening dates are similarly dependent and range from August to November (table 2). Fruits drop from the plants shortly after ripening and may continue through the winter and spring. The fruits are rather dry, berrylike pomes (figure 1) containing 1 to 5 seeds (figure 2), some of which may be empty (aborted). Natural seed dispersal is chiefly by animals. Black chokeberry fruits shrivel soon after ripening,

Table 1—*Aronia,* chokeberry: nomenclature, occurrence, and height at maturity

Scientific name & synonym(s)	Common name	Occurrence	Height (m)
***A. arbutifolia* (L.) Pers.** *A. arbutifolia* var. *glabra* Ell. *Pyrus arbutifolia* (L.) L. f. *Sorbus arbutifolia* (L.) Heynh.	**red chokeberry**	Nova Scotia to S Ontario & S to Florida & E Texas	1–4
***A. melanocarpa* (Michx.) Ell.** *A. nigra* (Willd.) Koehne *Pyrus melanocarpa* (Michx.) Willd. *Pyrus melanocarpa* (Michx.) Heynh. *Sorbus melanocarpa* (Michx.) Heynh.	**black chokeberry,** *gueles noires*	Newfoundland to Minnesota & S to Tennessee & South Carolina	0.5–1
***A. x prunifolia* (Marsh.) Rehd. (pro sp.)** *A. arbutifolia* var. *atropurpurea* (Britt.) Seymour *A. atropurpurea* Britt.; *A. floribunda* (Lindl.) Spach *Pyrus arbutifolia* var. *atropurpurea* (Britt.) B.L. Robins. *Pyrus floribunda* Lindl. *Sorbus arbutifolia* var. *atropurpurea* (Britt.) Schneid.	**purple chokeberry,** hybrid chokeberry	Newfoundland to Ontario & S to Indiana & Virginia	1–4

Source: Gill and Pogge (1974).

A

Table 2—*Aronia,* chokeberry: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
A. arbutifolia	Texas	Mar–Apr	Oct–Nov
	West Virginia	Mar–May	Sept–Oct
	North	Apr–July	Sept–Nov
A. melanocarpa	South	Mar–June	Aug
	North	Apr–July	Aug–Oct
	West Virginia	June	Sept–Oct
A. x *prunifolia*	—	Apr–July	Aug–Oct

Sources: Ammons (1975), Fernald (1950), McDonald (1960), Mahlstede and Maber (1957), Van Dersal (1938).

Figure 1—*Aronia arbutifolia*, red chokeberry: leaf and cluster of fruits (pomes).

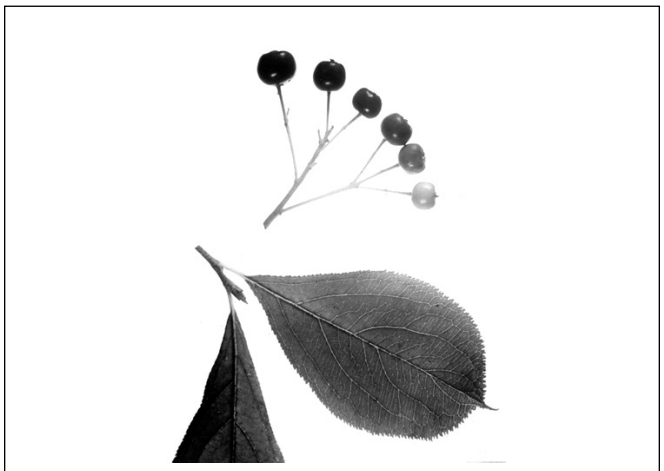
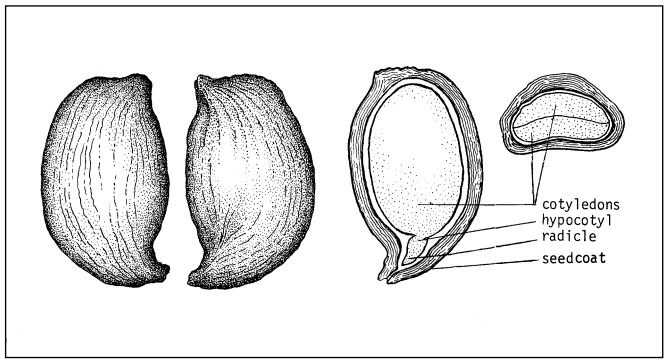


Figure 2—*Aronia melanocarpa*, black chokeberry: exterior views of seed, as well as longitudinal and transverse



and most of them drop. Purple chokeberry fruits shrivel at the beginning of winter, whereas fruits of red chokeberry remain plump and bright into the winter. Red chokeberry may yield fruit first at 2 years of age (Spinner and Ostrum 1945) and produces good seedcrops almost every year. Black chokeberry yields a good crop about every second year (Gill and Pogge 1974).

Collection of fruits; extraction and storage of seeds. If loss to birds is a hazard, fruits should be handpicked as soon as they ripen. Otherwise, they should be picked within a month or so. The delay should be least with black chokeberries and can be longest with red chokeberry. Fruits of the latter species collected in January and cleaned and sown right away will germinate in 2 weeks (Dirr and Heuser 1987). Commercial seeds usually consist of the dried pomes or "dried berries" as usually listed in seed catalogs. There are about 16,220 dried pomes/kg (7,355/lb) of red choke berry (Swingle 1939). Although seed extraction and cleaning may be impractical on a large scale, small lots of seeds can be extracted by rubbing fresh fruits over screens and floating off the debris. If the fruits have dried, they can be soaked in water until the pulp is soft enough to come off (Mahlstede and Maber 1957). A kitchen blender can be useful for extracting seeds from small lots of several kinds of small berries and other soft fruits, including chokeberries (Morrow and others 1954; Munson 1986). Cleaned seeds per weight average about 564,480/kg (256,000/lb) for red chokeberry and 608,580/kg (276,000/lb) for black chokeberry (Gill and Pogge 1974; Swingle 1939). No data were found on longevity of seeds, but drying before storage is recommended (Chadwick 1935), so they are undoubtedly orthodox in storage behavior.

Pregermination treatments and germination tests. Chokeberry seeds have an internal dormancy that can be overcome by stratification in a moist medium at temperatures of 1 to 5 °C. A higher stratification temperature 10 °C also was effective on seeds of purple chokeberry (Crocker and Barton 1931). Optimum duration of stratification may be 60 to 120 days and varies with the species (table 3).

Table 3—*Aronia,* chokeberry: cold stratification periods, germination test conditions and results

Species	Cold stratification period (days)	Germination test conditions: Temp (°C) Day	Germination test conditions: Temp (°C) Night	Germination test conditions: Days	Germinative capacity: Amount (%)	Germinative capacity: Samples
A. arbutifolia	90	20	20	30	94	4
A. melanocarpa	90–120	30	20	30	22	4
A. x prunifolia	60	20	20	30	96	2

Sources: Crocker and Barton (1931), Gill and Pogge (1974).

There are no official test prescriptions for chokeberries, but tests of stratified seeds can be done on paper or in soil, sand, or peat for 28 days, at diurnally alternating temperatures of 30 (day) and 20 °C (night) or at a constant 20 °C. Gemination starts after about 8 days and may be virtually complete in 20 to 30 days (Crocker and Barton 1931). Germination of seeds stratified as recommended here was mostly in the 90 to 100% range (table 3). Germination of unstratified seed was quite low, 0 to 15%, in tests that extended into a second year (Adams 1927). Germination is epigeal.

Nursery practice. In some nurseries, the dried fruits are soaked in water for a few days and mashed and then the whole mass is stratified until spring. Limiting the stratification period to 60 days for purple, 90 days for red, and 120 days for black chokeberry may increase germination in the nursery. Fall planting is done by some growers (Dirr and Heuser 1987). The recommended sowing depth is about 10 mm ($^1/_3$ in) (Sheat 1948). Germination mostly takes place within a few days after sowing. As a rule of thumb, 0.45 kg (1 lb) of cleaned seed may yield about 10,000 usable plants (Van Dersal 1938). Outplanting may be done with 2-year-old seedlings (Sheat 1948).

Vegetative propagation is possible with red chokeberry (and perhaps the others). Softwood cuttings taken in July and treated with 4,000 ppm of indole-butyric acid solution root very well. Cuttings taken in December or January will root also (Dirr and Heuser 1987). Irrigation of the mother plant a few days before the cuttings are taken will help rooting (Dehgan and others 1989).

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A

Asteraceae—Aster family

Artemisia L.

sagebrush

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Growth habit, occurrence, and use. Sagebrush—*Artemisia* L.—species are probably the most common shrubs in western North America. Big sagebrush alone occupies an estimated 60 million ha as a landscape dominant or codominant in the semiarid interior, and related species of the subgenus Tridentatae are estimated to occupy an additional 50 million ha (Beetle 1960; McArthur and Stevens in press). Sagebrush-dominated vegetation occurs mostly under semiarid climatic regimes characterized by cold winters and predominantly winter precipitation. The genus is circumboreal in distribution and consists of about 400 species of mostly evergreen shrubs, subshrubs, and herbaceous perennials.

The 20 or so shrubby sagebrush species in the United States differ widely in their growth form, ecology, distribution, and abundance (table 1). Big, black, silver, and low sagebrushes are widely distributed, polymorphic species of relatively broad ecological amplitude, whereas most of the remaining species are either more geographically restricted or more specialized in their habitat requirements. The subshrub fringed sagebrush, common and widespread in both the Old and New Worlds, may be the most widely distributed sagebrush taxon. Sand sagebrush is an important species on sandy soils on the Great Plains and in the Southwest, whereas the summer-deciduous subshrub budsage is the principal sagebrush species of salt desert shrub vegetation in the Great Basin.

Because of their status as regional dominants, sagebrush species—especially those of the subgenus *Tridentatae*—have been the object of a great deal of study (McArthur and Welch 1986). Many have long been regarded as undesirable plants by the ranching industry because of their perceived low palatability to livestock and propensity for increase under conditions of abusive grazing. However, they provide a principal source of browse on winter ranges for both wild and domestic ungulates, and undoubtedly are central to the habitat requirements of many other wildlife species.

Most sagebrush species rely on seeds for regeneration and have neither the ability to resprout following burning—with notable exceptions (McArthur and others 2004)—nor a long-lived soil seedbank (Young and Evans 1975, 1989; Meyer 1990). Invasion by exotic annual grasses and the associated increase in fire frequency has resulted in loss of big sagebrush over vast acreages of its former area of dominance (Billings 1990; D'Antonio and Vitousek 1992). This loss has led to a realization of the importance of the shrub overstory for maintaining the integrity of the ecosystem and also to a renewed interest in seed propagation of sagebrush species (Meyer 1994). Sagebrush has been seeded as part of big-game winter-range rehabilitation and mined-land reclamation efforts for over 30 years, so there is a considerable fount of knowledge to draw upon (Plummer and others 1968).

Subspecies and ecotypes. The more complex sagebrush species are made up of series of subspecies that are morphologically and ecologically distinct. In addition, many sagebrush taxa have been shown through common garden studies to be made up of numerous ecotypes that result from adaptation to local conditions through the process of natural selection (McArthur and others 1979). Such site-specific adaptation may be reflected in traits such as frost or drought hardiness, growth rate, competitive ability, flowering time, and seed germination regulation (McArthur and Welch 1982; Meyer and Monsen 1990). This means that the use of seed from locally adapted or at least habitat-matched populations is important to successful long-term restoration of these species.

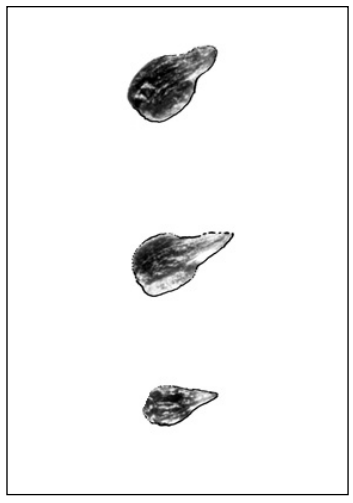
An alternative to using adaptedness as the principal criterion for ecotype selection has been to identify native germplasms with desirable traits such as high winter-forage-quality for wild ungulates (for example, Welch and others 1986). Their use is recommended in artificial seedings with specific management objectives on sites that fall within their range of adaptation.

Table 1—*Artemisia,* sagebrush: distribution and ecology of principal shrubby species in the United States

Scentific name	Common names(s)	Distribution	Habitat
SUBGENUS *TRIDENTATAE*			
***A. arbuscula* Nutt.**	**low sagebrush**	Widely distributed, mostly intermountain	Shallow, rocky soils in mtns
***A. bigelovii* Gray**	**Bigelow sagebrush,** rimrock sagebrush	SW deserts	Shallow rocky soils at middle to low elevations bottoms or
***A. cana* Pursh**	**silver sagebrush**	NW Great Plains, N intermountain region & N Sierras	Deep sandy soils in valley snow catchment basins in mtns
***A. nova* A. Nels.**	**black sagebrush**	Widely distributed, mostly intermountain	Shallow soils over bedrock at middle to low elevations region
***A. pygmaea* Gray**	**pygmy sagebrush**	Utah & adjacent parts of Nevada & Colorado	Fine-textured calcareous soils at low elevations
***A. rigida* (Nutt.) Gray**	**stiff sagebrush,** scabland sagebrush	Columbia Plateau, E Washington & Oregon	Shallow rocky soils over basalt at low elevations
***A. tridentata* Nutt.**	**big sagebrush**	Widely distributed, W North America	Wide ecological amplitude
***A.t.* ssp. *tridentata* Nutt.**	**basin big sagebrush**	See species	Mostly on deep well-drained soils of valley bottoms
***A.t.* ssp. *vaseyana* (Rydb.) Beetle**	**mountain big sagebrush,** Vasey sagebrush	See species	Mostly on coarse soils at middle to high elevations benchlands
***A.t.* ssp. *wyomingensis* Beetle & Young**	**Wyoming big sagebrush**	See species	On coarse to fine soils of at middle to low elevation
***A. tripartita* Rydb.**	**threetip sagebrush**	Columbia Plateau E into Wyoming	Deep to shallow mostly volcanic soils at low elevations
OTHER SUBGENERA			
***A. filifolia* Torr.**	**sand sagebrush,** old man sagebrush	W Great Plains & SW deserts	Sandy soils at low to middle elevations
***A. frigida* Willd.**	**fringed sagebrush**	W North America to central Asia	Very wide ecological amplitude
***A. spinescens* D.C. Eat.** *Picrothamnus desertorum* Nutt.	**budsage**	Widely distributed, mostly N intermountain region	Semiarid bottoms, benches, & foothills, salt desert shrublands

Flowering and fruiting. Most North American sagebrush species flower in late summer or autumn and ripen fruit from September through December. Seeds of high-elevation populations generally ripen earlier than those of low-elevation populations. Budsage, which flowers in March or April and sets seed in May or June before entering summer dormancy, is a major exception. The tiny yellowish or brownish flowers are wind-pollinated and are borne in groups of about 2 to 70 (depending on species) in small heads enclosed in overlapping bracts with thin, dry margins. The numerous heads are arranged in spikelike or open panicles that occur terminally on the branches of current-season growth. Each fertile floret within a head may develop into a small, 1-seeded fruit (achene) that lacks any special appendages for dispersal (figure 1). The pericarp of the achene is papery and membranous, whereas the seedcoat of the enclosed seed is firmer and somewhat shiny. The endosperm is reduced to a membrane fused to the inner wall of the seedcoat, whereas the embryo is well-developed and fills the interior of the seed. Mucilaginous nerves on

Figure 1—*Artemisia*, sagebrush: achenes (cleaned seeds) of *A. arbuscula*, low sagebrush (**top**); *A. nova*, black sagebrush (**middle**); and *A. tridentata*, big sagebrush (**bottom**).



the exterior of the pericarp may aid in adhesion to the soil surface during radicle penetration (Walton and others 1986). The hypocotyl hairs that develop as a first manifestation of germination have been shown to have a similar function (Young and Martens 1991).

The fruits fall or are shaken from the plant by wind within a few weeks of maturation. The potential yearly seed production of a single plant of big sagebrush is prodigious, on the order of hundreds of thousands of seeds (Welch and others 1990). However, many factors operate to restrict seed production in wildland stands, including excessive browsing (Fairchild 1991; Wagstaff and Welch 1991), intraspecific competition (Fairchild 1991; Young and others 1989), insect and disease attack (Welch and Nelson 1995), and cycles of dry years (Young and others 1989). Sagebrush in field cultivation for seed production yields harvestable crops within 2 years of establishment and generally produces high yields yearly (Welch and others 1990). Wildland stands vary in the consistency and quality of their seedcrops, depending on the factors listed above and also on the taxon under consideration and on site quality factors. An alternative to field cultivation for needed ecotypes that produce minimal numbers of seeds in the wild is management of wildland stands through thinning or protection from browsing to maximize seed production.

Seed collection, cleaning, and storage. Sagebrush seeds (actually, the 1-seeded achenes) are collected by beating or stripping them into shoulder hoppers, baskets, or bags. They are much more easily harvested by beating when dry than wet. Usually there is considerable among-bush variation in ripening date within a population. Harvesting too late may result in a high proportion of half-filled and aborted fruits.

Purity on a dry-weight basis before cleaning is often 10% or less. Passage through a barley de-bearder serves to break up the inflorescences to release the seeds; hammermilling is less desirable, as it tends to make the material ball-up and may damage the seeds (McArthur and others 2004). Screening and fanning can then be used to remove sticks and other debris, resulting in lot purities of 50% or more. This cleaning procedure may strip many of the seeds of their membranous pericarps, but this has no effect on viability or storage life, although it may reduce seed dormancy or light requirement somewhat (Meyer and others 1990; Welch 1995). Sagebrush seeds are not easily damaged in cleaning equipment because of their small size (Welch 1995). Advantages to cleaning to relatively high purities include improved accuracy in quality evaluation; reduced shipping, handling, and storage costs; better regulation of moisture content during storage; and better metered flow through seeding devices (Welch 1995). On the other hand, sagebrush seeds are so small that lots at high purity must be diluted with a carrier in order to achieve realistic seeding rates. Seed size varies substantially among species and also among populations within species (table 2). Seeding rates should take seed size and therefore seed number per unit weight into account.

Sagebrush seeds are not long-lived in warehouse storage. Seedlots commonly hold full viability for 2 or 3 years (Stevens and others 1981). Seedlots of initial low quality lose viability more quickly than high-quality lots. Careful attention to moisture content (6 to 8% is optimal) and storage at relatively low temperatures (<10 °C) can extend storage life to 5 years and possibly longer. Because of late ripening dates, almost all sagebrush seed is held at least 1 year (until the following autumn) before planting.

Germination. We have good information on seed germination patterns for only a few species of sagebrush, but evidence indicates that this information may be broadly applicable to other species (Meyer and Monsen 1991, 1992; Meyer and others 1990). Variation in germination response is generally related to climatic variation at collection sitse rather than to specific or subspecific identity. Timing mechanisms are keyed to a pattern of winter or early spring germination and early spring emergence for all species examined so far. Sagebrush seeds are characterized by relatively low levels of dormancy at dispersal but may be more or less strongly light-requiring or slow to germinate. Both dormancy and light requirement are removed through moist chilling (stratification), so that most seeds become germinable during winter. After-ripening in storage also tends to reduce dormancy or light requirement. In the studies of big sagebrush germination ecophysiology cited above, patterns of variation in dormancy, light requirement, and germination rate were shown to be linked to collection site habitat. Seeds of populations from montane habitats with long, snowy winters tend to be dormant, light-requiring, or slow to germinate at autumn temperatures. These traits protect them from autumn germination, a risk for seeds dispersed in early autumn into relatively mesic environments. Seeds of populations from habitats with short, mild winters and hot, dry springs are dispersed later. They tend to be nondormant, not light-requiring, and quick to germinate, which facilitates germination during winter, when conditions are most favorable on warm desert fringe sites.

Germination under winter snowcover conditions is also keyed to habitat. Seeds of montane populations may take 20 weeks or more to germinate under conditions simulating

snowcover in the field, whereas those of warm desert fringe populations may do so in as little as 1 week. Seeds of montane populations can also sense and respond with increased germination rates to the shift from dark to light in the cold that results from thinning snow cover in the early spring. These habitat-correlated patterns apparently hold for black, silver, and low sagebrushes as well as for big sagebrush, based on preliminary data (table 3). Germination under snowcover seems to be a common pattern for sagebrush, ensuring emergence in very early spring just as the snow is melting (Meyer 1990; Meyer and Monsen 1990; Monsen and Meyer 1990).

Most big sagebrush seeds germinate during the winter and spring following the autumn of their production. They have no apparent mechanisms for seed bank carryover from year to year, and studies on *in situ* seed banks have failed to detect any substantial carryover (Young and Evans 1975, 1989). The tiny fraction of seeds that sometimes carries over (Hassan and West 1986) is probably made up of buried seeds whose light requirement has not yet been overcome because of inadequate chilling (Meyer and others 1990).

The observation that sagebrush seeds germinate over a broad range of temperatures (see for example, Bai and Romo 1994; McDonough and Harniss 1974; Weldon and

Table 2— *Artemisia,* sagebrush: seed data (pure live seeds)

Species	Cleaned seeds (million)/weight			
	Mean		Range	
	/kg	/lb	/kg	/lb
A. arbuscula	1.81	0.82	1.13–2.15	0.15–0.98
A. bigelovii	5.54	2.52	—	—
A. cana	2.87	1.30	1.81–4.90	0.82–2.23
A. nova	2.03	0.92	2.00–2.12	0.91–0.96
A. pygmaea	1.04	0.47	—	—
A. rigida	1.10	0.50	—	—
A. tridentata				
spp. *tridentata*	5.26*	2.38*	4.25–5.67*	1.93–2.58*
spp. *vaseyana*	4.30	1.95	4.23–4.36	1.92–1.98
spp. *wyomingensis*	4.72	2.14	4.00–5.42	1.82–2.46
A. tripartita	4.87	2.21	—	—
A. filifolia	3.20	1.45	—	—
A. frigida	10.0	4.55	—	—
A. spinescens	3.06	1.39	2.25–3.70	1.02–1.68

Sources: Belcher (1985), Deitschman (1974), McArthur and others 2004, Meyer (1990).
* Subspecies not distinguished.

Table 3—*Artemisia,* sagebrush: germination data

Species	Germination percentage* on day 14 at 15 °C				Days to 50% germination at 1 °C (light)		
	Mean		Range				
	Light	Dark	Light	Dark	Mean	Range	Lots #
A. arbuscula	100	—	—	—	38.2	38	1
A. bigelovii	100	—	—	—	—	—	1
A. cana,	100	81.5	100	75–88	56.0	54–58	2
A. nova	92.3	21.2	75–100	3–57	47.6	17–80	5
A. tridentata							
ssp. *tridentata*	94.6	18.6	84–100	0–46	54.0	27–95	5
ssp. *vaseyatia*	85	12.2	64–94	0–24	49.2	16–98	5
ssp. *wyomingensis*	98.4	13.4	94–100	2–46	55.2	18–98	5
A. filifolia	100	—	—	—	—	—	1
A. spinescens	92.7	72.6	87–98	52–93	45.5	38–53	2

Sources: All data from Meyer (1990) except for *A. tridentata* lots stored 4 months (Meyer and others 1990).
* Expressed as percentage of viable seeds.

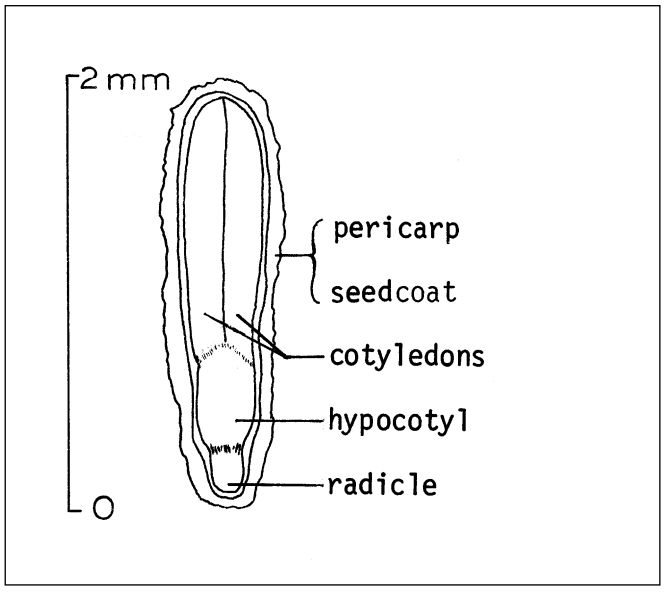
others 1959; Wilson 1982) probably stems from the fact that sagebrush seeds have no need for protection from germination at summer temperature, as they almost never encounter summer regimes. Budsage, a species with seeds that ripen in early summer but do not germinate until the following early spring, shows strong germination suppression at summer temperatures (Meyer and Kitchen 1997).

Germination testing for sagebrush species is a relatively straightforward process. We recommend a 21-day test at 15 or 20 °C with light as the standard for big sagebrush and black sagebrush, with a 2-week chill (stratification) for more dormant lots (AOSA 1993; Meyer and others 1988a, 1988b). Because many dormant sagebrush seeds will not germinate in response to a short chilling, the viability of ungerminated seeds should be evaluated with tetrazolium.

Tetrazolium staining also represents an alternative to the germination test for evaluating the viability of sagebrush seeds. The fruits are pierced with a needle through the center of the cotyledon region of the embryo (figure 2) and immersed in buffered 1% tetrazolium chloride solution for 6 hours at 25 °C. The pericarp and seedcoat are then slit with a needle at the cotyledon end, and the embryos are squeezed out. Embryos stained a uniform bright red may be classed as viable.

The principal source of inconsistent results in sagebrush seed testing comes from decisions made during the purity evaluation. The inclusion of non-viable half-filled and aborted fruits in the pure seed fraction has little effect on the value for percentage purity but can affect the viability percentage considerably. In research, we routinely exclude such fruits and only occasionally encounter recently collected or properly stored lots whose viability is less than 90%. The seed analyst has a more difficult problem and we hope that the advent of better cleaning procedures for sagebrush seeds will help to make these difficulties unnecessary.

Figure 2—*Artemisia nova*, black sagebrush: longitudinal section through an achene.



Nursery and field practice. Many species of sagebrush have been successfully grown both as container and as bareroot stock (Long 1986; McArthur and others 2004; Welch and others 1986). In addition, the practice of transplanting wildlings has been particularly successful with sagebrush (McArthur and others 2004). Planting is best carried out in early spring, when moisture conditions are favorable. Container stock requires careful hardening (Long 1986).

Sagebrush species are among the few native shrubs that can be reliably established by direct seeding. Seedling recruitment is regularly observed on small-scale disturbances in wildland stands where competition from adult plants and from weedy understory species is not too severe. Artificial seeding should mimic natural processes of dispersal. Seeding in late fall or onto snow in winter is most successful; spring-seeding is not recommended. Seeding rates that result in an average of 50 to 100 seeds/m^2 (5 to 9/ft^2) usually result in adequate stands. This corresponds to a rate of 0.1 to 0.2 kg/ha (1.5 to 3 oz/ac) on a pure live seed (PLS) basis for a lot that averages 4 million seeds/kg (113,400/oz). The seeds should be planted at or near the surface of a firm but not compacted seedbed. Because of their small size, drilling or broadcasting seeds into a loose, sloughing seedbed may bury them too deeply for successful emergence (Jacobsen and Welch 1987; Monsen and Meyer 1990).

Sagebrush plants are generally quite long-lived, and successful recruitment from seeds every year is not necessary for perpetuation of the stand. On drier sites, winter snowfall may be inadequate for successful emergence and establishment in a typical year, especially on the bare, windswept surfaces of artificial seedings. Small-scale use of snow-fencing has been shown to enhance sagebrush stand establishment under such marginal conditions (Monsen and others 1992). Once nuclear stands are established, the shrubs themselves may act as both seed sources and living snow entrapment structures. It is common to see newly establishing seedlings spread out on the leeward side of an adult plant, where drifting snow accumulates.

Sagebrush species have been successfully seeded onto drastic disturbance sites such as mine- waste rock dumps, but adding topsoil (even minimally) often greatly enhances

success, perhaps through re-inoculation with essential symbionts such as mycorrhizae (Monsen and Richardson 1984). Fertilization per se usually favors herbaceous competitors over the shrub seedlings and is not generally recommended.

Reports on seedling competitiveness in sagebrush are somewhat contradictory. In the era of sagebrush control on rangelands, managers often remarked on the ability of sagebrush to reestablish in perennial forage grass plantings (Pechanec and others 1944). Follow-up moisture in the summer appears to facilitate shrub seedling survival in competition with perennial grasses. Success in mixed seedings may be enhanced by separating the seeds spatially, for example, in separate drop boxes on the seeding implement, or by interseeding into scalps (McArthur and others 2004).

Sagebrush seedings in the presence of strong exotic annual grass competition have almost universally been failures (Monsen 1995). It may be that, in order to restore big sagebrush–bunchgrass communities on many sites now dominated by exotic annuals like cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* (L.) Nevski), seeding and establishment of the native perennial understory is a necessary prerequisite to successful establishment of sagebrush. More-expensive weed-control measures are often not an option on the large acreages involved.

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Annonaceae—Custard-apple family

Asimina Adans.

pawpaw

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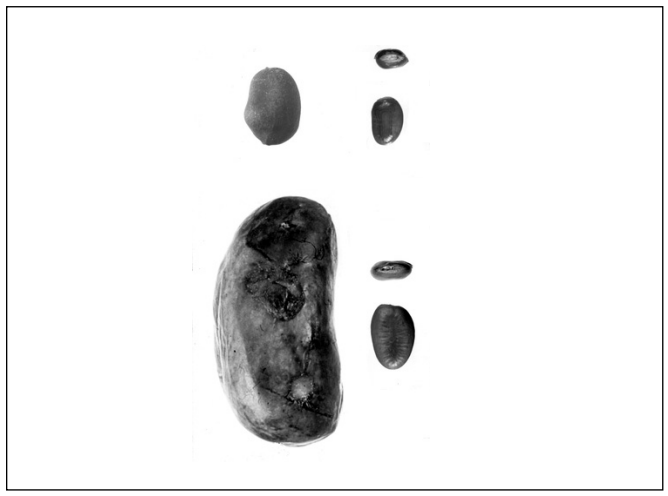
Growth habit and use. Of the 9 species of the genus *Asimina*, seed data are available only for small-flower pawpaw and pawpaw (table 1). Both form shrubs or small deciduous trees (Vines 1960). Their fruits provide food for wildlife and are also eaten by humans. There is some interest in commercial fruit production of pawpaw, and cultivar selections have been made since the early part of the century (Peterson 1990).

Flowering and fruiting. Flowers of the pawpaw genus are solitary, perfect, and greenish purple. They appear in the spring during March to May, about the same time as the leaves. In natural stands of pawpaw, pollination and seed set are very poor (Norman and others 1992; Willson and Schemske 1980), conditions that discourage commercial productions. In central Illinois, pawpaw averaged 3.5 to 10.5 seeds/fruit (Willson and Schemeske 1980). Pawpaw fruits are 5 to 17 cm long, whereas those of small-flower pawpaw are 5 to 12 cm long (Halls 1973). Pawpaw fruits are greenish yellow before maturity and turn brown to black as they ripen in July to August and fall to the ground in August and September. Seeds of small-flower pawpaw mature while the fruit coat is still green (Norman and others 1992). The fruits are fleshy berries that contain several dark brown, shiny seeds (figure 1). The fleshy part of the fruit is considered edible, but there appear to be 2 different fruit types. Those with white flesh are barely edible, whereas others are larger and have a yellowish or orange flesh with a much better taste (Bonner and Halls 1974). The seeds themselves are oblong, rounded, flat, and bony (figures 1 and 2).

Figure 1— *Asimina*, pawpaw: fruits and seeds of *A. parviflora*, small-flower pawpaw (**top**) and *A. triloba*, pawpaw (**bottom**).



Collection and extraction. Pawpaw fruits should be picked or shaken from the trees as soon as the flesh is soft. The seeds may be extracted by macerating the fruits in water and floating off the pulp, but the entire fruit may be sown (Bonner and Halls 1974). Seed yield, purity, and

Table 1— *Asmina,* pawpaw: nomenclature, occurrence, and size

Scientific name	Common name(s)	Occurrence	Height at maturity (m)
***A. parviflora* (Michx.) Dunal**	**small-flower pawpaw,** small-fruited pawpaw, small custard-apple, dwarf pawpaw	Texas E to Florida; N to Virginia	3.5
***A. triloba* (L.) Dunal**	**pawpaw,** custard-apple common pawpaw	Texas & Arkansas E to Florida; N to New York, Michigan, & Nebraska	12

Source: Vines (1960).

soundness are as follows (Bonner and Halls 1974; Vines 1960):

	small-flower pawpaw	pawpaw
Cleaned seeds/wt	2,860/kg (1,300/lb)	1,540/kg per (700/lb)
Purity (%)	98	100
Sound seeds (%)	94	96

There is no storage information available on these species.

Germination. Germination is usually very slow because seeds have dormant embryos, and seedcoats are slowly permeable. Moist stratification for 60 days at 5 °C resulted in germination of 50, 62, and 82% for 3 samples of pawpaw seeds (Bonner and Halls 1974). Stratification for 100 days has been recommended, but germination still may be slow and irregular. Fall-sowing of untreated seeds does not improve results (Bonner and Halls 1974). No specific test conditions have been reported, but alternating temperatures of 20 °C during the day and 30 °C at night on a moist medium have been satisfactory for most species of the northern temperate zone.

Nursery practice. Pawpaw seeds may be sown in the fall without pretreatment, or stratified and sown in the spring. Seeds should be covered about 20 mm ($^3/_4$ in) deep. Some shade is helpful to germinating seedlings (figure 3). Another method is to plant fresh seeds, before they dry, in pots of sand and then to keep them in a cool cellar or similar place. As the seeds sprout, they can be picked out and transplanted into nursery beds. Pawpaws can also be propagated by layering and root cuttings (Bonner and Halls 1974) but apparently not by stem cuttings (Dirr and Heuser 1987).

Figure 2—*Asimina parviflora*, small-flower pawpaw: longitudinal section through a seed.

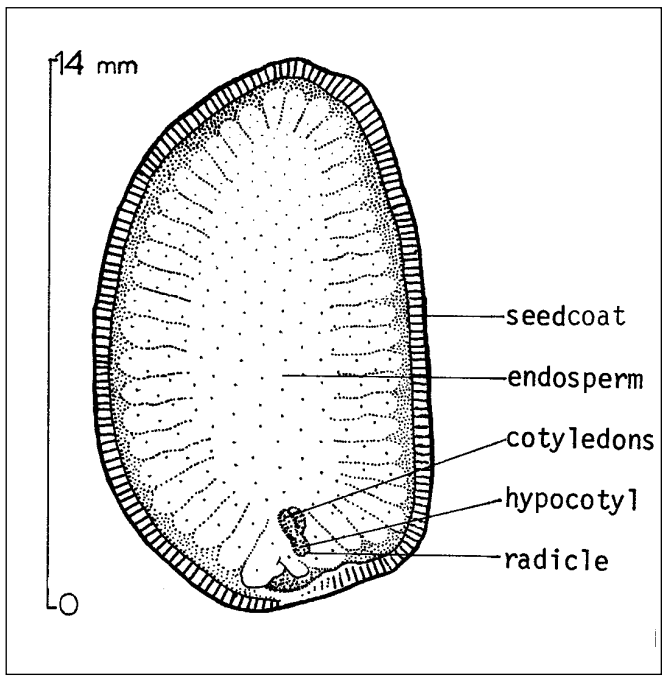
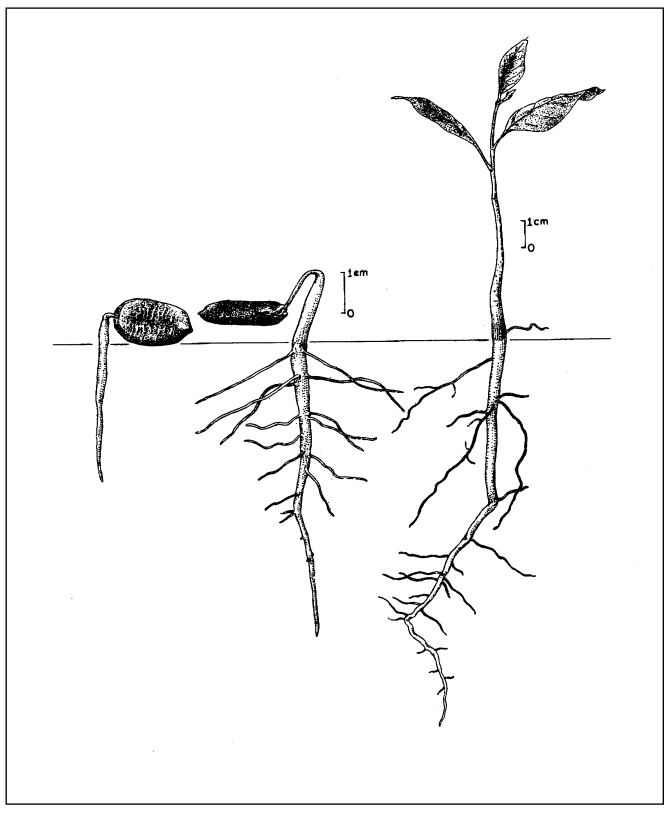


Figure 3—*Asimina triloba*, pawpaw: seedling development at 2, 9, and 20 days after germination.



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Chenopodiaceae—Goosefoot family

Atriplex L.

saltbush

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Growth habit, occurrence, and use. The genus *Atriplex* L.—saltbush—is cosmopolitan in distribution and comprises about 250 species of annual and perennial herbs, subshrubs, and shrubs (McArthur and Sanderson 1984). Most species are halophytic (at least to some degree) and occupy salt desert, coastal strand, or saltmarsh habitats. Shrubby species are important in arid and semiarid regions throughout the world, with centers of diversity in south central Asia, Australia, temperate South America, and western North America. Western North America is an area of particularly high genetic diversity, with more than 20 principal species of shrubs and subshrubs as well as countless hybrids and variants; 12 of these species are described here (table 1). The genus is in a state of active evolution in the Intermountain region (Stutz 1978, 1984). The drying up of Pleistocene lakes 10,000 or so years ago opened up vast areas of unexploited salt-desert habitat. Shrubby saltbush species migrated in rapidly from several directions and hybridized freely, giving rise to the rich complex of forms in the region today.

In terms of areal extent, the most important species are probably shadscale and Gardner saltbushes (Blauer and others 1976). These species are regional dominants over millions of hectares in the Intermountain and northwestern Great Plains regions, respectively. Shadscale saltbush mostly occurs with winterfat (*Krascheninnikovia lanata* (Pursh) Guldenstaedt.); budsage (*Artemesia spinescens* D.C. Eaton); and other salt-desert shrubs, whereas Gardner saltbush is able to maintain codominance with perennial grasses (Stutz 1978). In the Mojave Desert, desert-holly is an upland landscape dominant, particularly in the Death Valley region, whereas allscale saltbush is a dominant species on playa fringes. Fourwing saltbush is the most widely distributed shrubby saltbush in North America and is often an important component of grassland communities, especially in the Chihuahuan Desert and western Great Plains. Sickle and basin saltbushes are inconspicuous but common components of northern Intermountain salt-desert vegetation.

Shrubby saltbush species are extremely important as forage plants for livestock and wildlife in arid and semiarid regions worldwide (Goodall 1982). They provide palatable and nutritious feed on a year-round basis and are especially important on winter ranges. As a consequence, they have been studied and used in range rehabilitation far more extensively than most other shrubs (Jones 1970; McArthur and Monsen in press; Osmond and others 1980; Tiedemann and others 1984). There is also considerable interest in utilizing saltbush species as irrigated forage crops on marginal, salinized agricultural land (Glenn and others 1992; Watson and O'Leary 1993). Some shrubby saltbush species are also used extensively for the stabilization of drastically disturbed land because of their ability to establish and grow on harsh sites.

Geographic races and hybrids. An important feature of infraspecific variation in many saltbush species is the presence of series of races at different ploidy levels (Sanderson and others 1990; Stutz 1978; Stutz and Sanderson 1979). Polyploid races often show dwarfing and adaptation to extremely harsh environments. The tendency to evolve polyploid races has also been important in facilitating the formation and stabilization of interspecific hybrids. Saltbush species possess a wealth of genetic variability, both within and among ploidy levels for numerous traits that may be important for survival both of local populations in nature and of the products of artificial seedings. Hybrid forms, even those that have not yet formed stabilized populations in nature, may possess attributes that make them useful in specific disturbed land rehabilitation applications (Stutz 1995).

Common garden studies with fourwing saltbush have demonstrated ecotypic variation in growth form, growth rate, winter-greenness, drought and cold hardiness, palatability, nutrient status, seed size, and seed germination and establishment traits (McArthur and others 1983; Springfield 1970; Van Epps 1975; Welch and Monsen 1981, 1984). It is

Table 1—*Atriplex,* saltbush: ecology and distribution

Scientific name	Common name(s)	Geographic distribution	Ecology
***A. canescens* (Pursh) Nutt.**	**fourwing saltbush,** chamisa	Widely distributed in W North America	Wide ecological amplitude; mostly in sandy uplands & gravelly washes
***A. confertifolia* (Torr. & Frem.) S. Wats.**	**shadscale saltbush,** spiny saltbush, sheepfat	Widely distributed in W North America	Wide ecological amplitude; mostly on silt or clay soils of low to moderate salinity
***A. corrugata* S. Wats.**	**mat saltbush**	Colorado Plateau N to Red Desert of Wyoming	Restricted to heavy saline clays on shale outcrops
***A. cuneata* A. Nels.**	**Castle Valley saltbush**	Colorado Plateau	Restricted to heavy saline clays on shale outcrops
***A. falcata* (M.E. Jones) Standl.**	**sickle saltbush,** falcate saltbush, Nuttall saltbush	N Great Basin	Subsaline soils of benches & alluvial fans
***A. gardneri* (Moq.) D. Dietr.**	**Gardner saltbush**	NW Great Plains, Wyoming, & Montana	Mostly on saline or subsaline clay soils
***A. hymenelytra* (Torr.) S. Wats.**	**desert-holly**	Mojave Desert	Clay flats & gravelly fans under extreme aridity
***A. lentiformis* (Torr.) S. Wats.**	**big saltbush,** quailbush, lensscale	Mojave Desert; cismontane & coastal California	Mostly around saline springs & seeps
***A. obovata* Moq.**	**mound saltbush,** broadscale saltbush	Chihuahuan Desert	Saline flats
***A. polycarpa* (Torr.) S. Wats.**	**allscale saltbush,** cattle saltbush, desert saltbush	Mojave Desert; Central Valley of California	Saline & subsaline slopes & flats
***A. semibaccata* R. Br.**	**Australian saltbush,** trailing saltbush	Introduced from Australia	Along roadsides & in saline disturbances
***A. tridentata* Kuntze**	**basin saltbush,** trident saltbush	NE Great Basin, & Uinta Basin of Utah	Saline flats

Sources: Ansley and Abernathy (1985), Meyer (1996), Mikhail and others (1992), Young and others (1980).

likely that other widely distributed saltbush species possess similar ecotypic differentiation. Many researchers who have studied saltbush establishment from artificial seedings emphasize the importance of using not just adapted species, but locally adapted ecotypes of these species (Bleak and others 1965; McArthur and others 2004; Nord and others 1971; Plummer and others 1968; Springfield 1970).

Cultivar development for saltbush has also emphasized ecotypic adaptation. The 3 released cultivars of fourwing saltbush were developed for warm winter ('Marana'), intermountain cold desert ('Rincon'), and northwestern Great Plains ('Wytana') planting applications (Carlson 1984). 'Wytana' was developed from a fourwing saltbush × Gardner saltbush hybrid entity known as *Atriplex aptera* A. Nels.

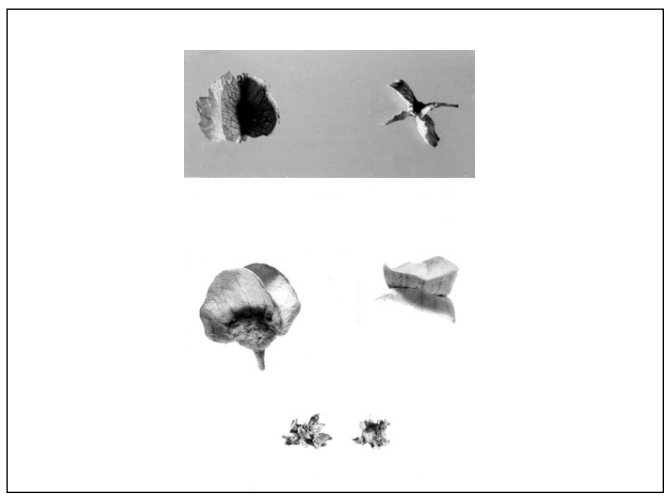
Flowering and fruiting. The flowers of saltbush are yellowish or brownish, inconspicuous, and unisexual, and are borne in the axils of the upper leaves or in terminal spikes. The male flowers consist of groups of stamens within a shallow 5-toothed calyx; petals are absent. Both petals and calyx are absent in the female flowers. The naked 1-seeded ovary is borne instead between 2 leaflike bracteoles.

Most native shrubby saltbush species are dioecious, that is, the sexes are borne on separate plants. Fourwing saltbush possesses a unique gender system known as trioecy, with genetically male plants, genetically female plants, and a third category that can switch sexes depending on environmental conditions (McArthur and others 1992). Australian saltbush is monoecious, that is, the flowers are unisexual and both sexes are present on the same plant.

Saltbush species flower in early to late summer, and fruits ripen from early fall to winter. The flowers are wind-pollinated. The leaflike bracteoles stay green and photosynthetically active until quite late in the ripening process and probably provide resources directly to the ripening ovule within. The fruits often persist on the bushes at least until spring, and it is not uncommon to find 2 generations of fruits on a plant simultaneously. Harvestable seedcrops of fourwing saltbush are produced on average 3 of every 5 years, whereas some of the more xerophytic species, such as mat saltbush, produce good seedcrops only occasionally.

The terminology describing the fruits of saltbush has been a source of confusion. The family Chenopodiaceae as a whole is characterized by a fruit type known as a utricle, which is defined as a small, bladdery 1-seeded fruit with a thin, membranous pericarp (Munz 1974). The utricle in saltbush is contained within the bracteoles, which enlarge in size and become more or less sealed, forming a false-fruit, which will hereafter be referred to simply as "the fruit"

Figure 1—*Atriplex*, saltbush: bract-enclosed utricles ("fruits") of; *A. canescens*, fourwing saltbush (**top**), *A. confertifolia*, shadscale saltbush (**middle**); and *A. falcata*, sickle saltbush (**bottom**).



(figure 1). The bracteoles are not fused to the utricle, but in native species they usually enclose it so completely that threshing is not possible. In Australian saltbush, the bracteoles are not fused across the top and the utricles may be threshed free (figure 2) (Foiles 1974).

The saltbush seed itself is contained within the utricle and is generally not separable from it (figure 3). The disk-shaped seed has a curved embryo on its outer perimeter and a scanty provision of storage tissue (in this case perisperm) in the center. In most native species, the ovule (and thus the seed) is inverted within the fruit, meaning that the radicle end points upward. This facilitates radicle emergence from between the bracteoles, which often have their only opening or weakest point at the tip. The degree of woody thickening of the bracteole walls varies among and within species and may be linked to the persistent seed dormancy often encountered.

Seed collection, cleaning and storage. Saltbush seeds are harvested by stripping or beating the ripe fruits into shoulder hoppers, boxes, or bags, or onto tarps spread under the bushes. Vacuum or reel-type harvesters may also be used (McArthur and others 2004). In field cultivation, 'Wytana' fourwing and Gardner saltbushes have been cut and windrowed with a hay-swather and then combine-harvested. Seeds shattered during combining were salvaged using a vacuum harvester (Carlson and others 1984).

Seed collections of fourwing and shadscale saltbushes are commonly hammermilled to remove the bracteole wings (McArthur and others 2004). This reduces bulk by half and facilitates cleaning, handling, and seeding through conventional drills. Hammermilling has little effect on dormancy of

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Figure 2—*Atriplex semibaccata*, Australian saltbush: bract-enclosed utricle

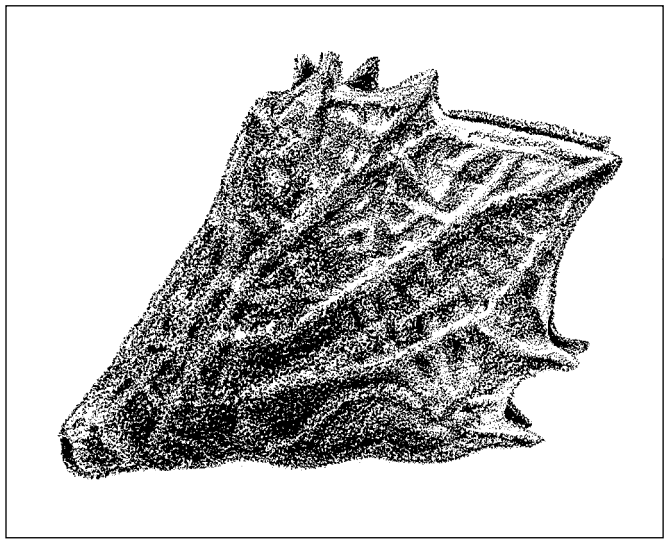
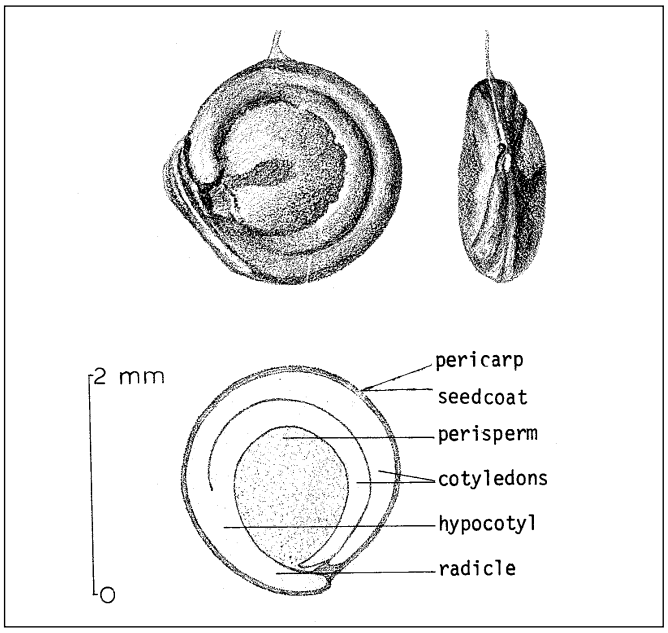


Figure 3—*Atriplex semibaccata*, Australian saltbush: exterior views in 2 planes of utricles removed from their bracts and a longitudinal section through a utricle.



fourwing saltbush but may speed the germination of nondormant seeds somewhat (Gerard 1978; Springfield 1970). Collections of wingless small-fruited species such as Gardner, sickle, and mat saltbushes do not require hammermilling. Seed collections of all species may be cleaned by screening and blowing in a fanning mill (McArthur and others 2004).

Even relatively high-quality seedlots of saltbush may average only 50% fill. A cut test to determine fill is often carried out before harvest. Fills of 40% or less are usually considered substandard. Such a seedlot would not normally be worth the expense of harvesting, cleaning, and transporting. Field-grown saltbush seedlots often have higher fill than wild-collected lots (Briggs 1984; Carlson and others 1984; McArthur and others 1978; Stroh and Thornberg 1969). Most of the weight of a saltbush fruit is in the bracteole walls, even after de-winging. Filled and unfilled fruits thus have similar density, making it impossible to remove unfilled fruits by fanning. Also, the variation in fruit size within a lot is not highly correlated with fill, so that screening to improve fill is not feasible.

Fruit size varies considerably among and within lots, especially for fourwing and shadscale saltbushes (table 2). Polyploid races often have smaller fruits. This variation in fruit size makes it essential to explicitly consider number of fruits per unit weight as well as fill percentage when planning seeding rates.

Seeds of most saltbush species are long-lived in dry storage and can be stored in an open warehouse for at least 5 to 10 years with little or no loss of viability (Springfield 1970; Stevens and others 1981). Controlled storage presents little advantage over open warehouse storage for these species. Attack by seed-destroying insects such as dermestid beetles (*Dermestes* spp.) during storage has been reported (Haws and others 1984)

Germination. Seeds of saltbush species as a group are characterized by high levels of dormancy and complex multiple dormancy mechanisms. The most universal characteristic seems to be the tendency to lose dormancy, or after-ripen, under dry conditions. For less-dormant species and lots this is manifested as an increase through time in the fraction of seeds germinable without pretreatment, or in the fraction of seeds able to germinate under non-optimum conditions, for example, osmotic stress. For more dormant species, after-ripening is manifested as an increase through time in storage in the response to dormancy-breaking treatments such as chilling (table 3).

In general, species and populations from warm desert and California cis-montane habitats produce seeds that are relatively nondormant, after-ripen quickly, and do not require chilling (Cornelius and Hylton 1969; Edgar and Springfield 1977; Kay and others 1977a&b; Mikhiel and others 1992; Springfield 1970; Warren and Kay 1984; Young and others 1980) (tables 1 and 3). Seeds of species and populations from cold desert, foothill, and northern plains habitats often require chilling for germination even after an after-ripening period (Ansley and Abernethy 1985; Meyer and others 1998) (tables 1 and 3). Shadscale saltbush seeds

Table 2—*Atriplex,* saltbush: fruit yield data

Species	Fruit (x1,000) /weight			
	Range		Average	
	/kg	/lb	/kg	/lb
A. canescens				
intact	17–120	8–55	68	31
de-winged	29–326	13–148	118	54
A. confertifolia	65–277	30–126	142	65
A. corrugata	—	—	174	79
A. cuneata	—	—	180	82
A. falcata	—	—	434	197
A. gardneri	210–262	95–119	233	106
A. hymenelytra	—	—	477	217
A. lentiformis	900–2,000	409–909	1,957	890
A. obovata	—	—	457	208
A. polycarpa	785–1,370	357–623	1,078	490
A. semibaccata	165–317	75–144	—	—
A. tridentata	120–370	55–168	280	128

Sources: Belcher (1985), Foiles (1974), McArthur and others 2004).

Table 3—*Atriplex,* saltbush: germination data

Species	Storage (months)	Incubation treatment	Germination (%)		Samples
			Mean	Range	
A. canescens	3	15 °C	32	4–96	23
	24	15 °C	54	10–100	23
	3	4 wk @ 1–15 °C	41	4–93	23
	24	4 wk @ 1–15 °C	69	21–100	23
A. confertifolia	3	5/15 °C	0	0–1	15
	36	5/15 °C	2	0–6	15
	3	16 wk @ 1–5/15 °C	16	0–47	15
	36	16 wk @ 1–5/15 °C	46	4–83	15
A. gardneri	3	Mean multiple treatments	26	—	1
	15	Mean multiple treatments	48	—	1
A. hymenelytra	8	5/15 °C	33	—	1
A. lentiformis	8	10/20 °C	56	29–71	3
	24	Mean multiple treatments	39	39–40	2
	24	Best treatment 10/25 %C	68	—	1
A. obovata	8	10/20 °C & 0.05 M NaCl	42	—	1
A. polycarpa	8	10/20 °C	53	11–94	2
	8	20/30 °C	50	21–79	2
A. semibaccata	24	Mean multiple treatments	41	37–46	3
	24	Best treatment 10/25 °C	69	—	1

Sources: Ansley and Abernathy (1985), Meyer (unpublished data), Mikhail and others (1992), Young and others (1980).
Note: Germination period is 28 days and germination is expressed as percentage of filled fruits, except for *A. gardneri* data, where germination is 14 days, and for *A. lentiformis* and *A. semibaccata* data, where germination is expressed as percentage of total fruits.

rarely become germinable without chilling, regardless of their habitat of origin (Mikhiel and others 1992) (table 3).

Other treatments that have sometimes been found to remove dormancy include scarification and leaching (Ansley and Abernethy 1985; Graves and others 1975; Nord and Whitacre 1957; Sabo and others 1979; Twitchell 1955; Young and others 1980). Scarification apparently acts by weakening the bracteole walls. Actual rupture of the membranous utricle wall is usually damaging to the seed (Sabo and others 1979). After-ripening may also act on the bracteole walls, as evidenced by work with a seedlot of the South American species *A. repanda* Phil., for which optimum time for sulfuric acid scarification decreased from 7 to 2 hours during 5 years in dry storage (Fernandez 1978). The bracte-

ole walls may also be weakened by the action of saprophytic fungi under field conditions (Vest 1952). Hand-removal of the bracteoles promotes increased germination in many species but does not necessarily remove dormancy completely, suggesting that either the utricle wall or the testa interacts with the embryo to impose dormancy even in excised fruits. The failure of excised fruits to germinate suggests a chilling requirement. Sanderson and others (1990) found that excised fruits of warm-winter populations of shadscale saltbush were more likely to germinate without chilling than those of cold winter populations.

Leaching probably promotes germination by removing some inhibitor from the fruit, either inorganic salts such as sodium chloride (Beadle 1952) or an organic inhibitor such as saponin (Nord and Van Atta 1960). It is important to remove excess water after soaking, as germination can be inhibited by inadequate aeration (Beadle 1952; Young and others 1980). Rates of leaching under field conditions are probably controlled by the osmotic potential of the seedbed. In the highly saline litter underneath bushes of many species, the salts in the bracteole walls would make only a minor contribution.

The complex dormancy mechanisms shown by many saltbush species function both to time germination appropriately within a given year and to ensure carryover of a persistent seedbank between years (Garvin and others 1996). Seed pretreatments to circumvent these mechanisms have limited application in field plantings but may be useful in seed quality evaluation and in nursery propagation.

Seed quality evaluation in saltbush is complicated by dormancy problems. Seedlots are usually cleaned to high purity, making the purity analysis quite simple. For fourwing saltbush, we proposed a 21-day germination test at 15 °C, a recommendation that was subsequently accepted as the official testing procedure (Meyer and others 1986). The most important determinant of viability is the fill percentage, that is, the proportion of fruits that contain an undamaged seed with a well-developed embryo. Post-test viability determination is essential in fourwing saltbush. Germination percentage may vary as a function of after-ripening status, or the test temperature may not be optimum for a particular lot. Post-test evaluation is even more essential for species of saltbush with less-known germination requirements.

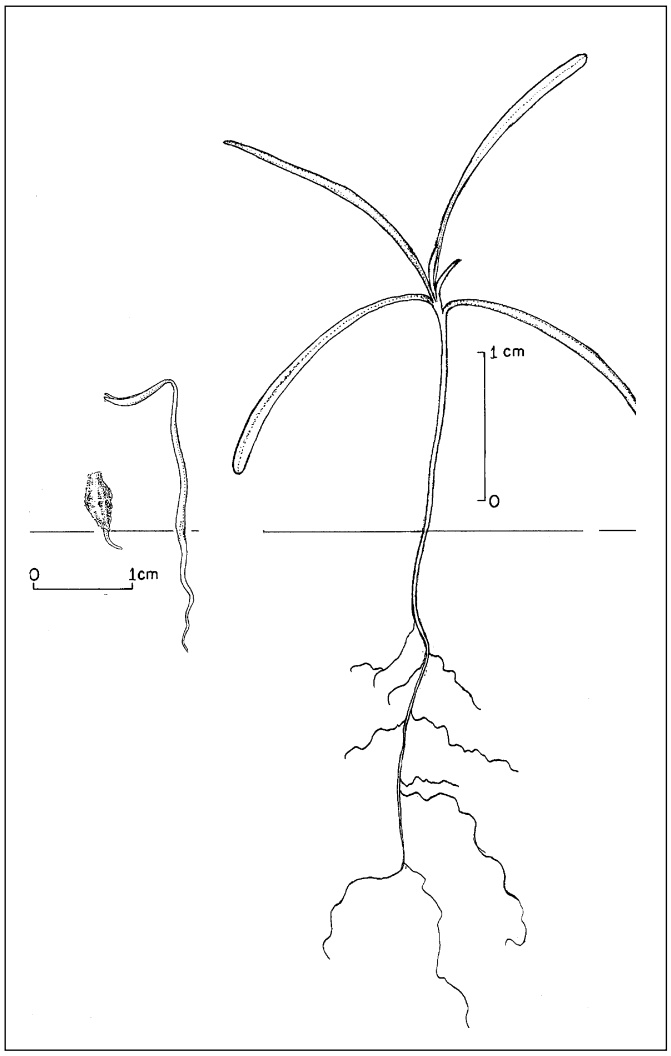
In practice, few seedlots of saltbush are evaluated using a germination test. Because of dormancy problems, the tetrazolium test has become the standard method. The general method is to soak the intact (bracteoled) fruit for several hours or overnight and extract the utricle by either prying open the bracts, clipping at the stem end, or off-center longitudinal bisection (Belcher 1985). The utricles are then pierced in the center and placed in 1% tetrazolium solution for several hours, and the staining patterns on the linear embryos are evaluated. Saltbush seed quality is somewhat difficult to evaluate using tetrazolium. Staining is often weak and incomplete for embryos that are germinable, resulting in viability estimates that tend to be low (Ansley and Abernethy 1984; Springfield 1970).

Nursery and field practice. Saltbush species have been successfully propagated in the nursery, both as container stock (Ferguson 1980) and as bareroot stock (Shaw and Monsen 1984). Most of the information available is for fourwing saltbush, but it is probably broadly applicable to other species. Propagation may be from seeds or from stem cuttings (McArthur and others 1984; Richardson and others 1979). The latter are advantageous for obtaining clonal material of known sex for the establishment of seed orchards with optimal sex ratios (McArthur and others 1978). When high-quality seedlings of an adapted ecotype are outplanted during periods of optimal moisture, survival can be high (Foiles 1974; McArthur and others 2004). Wildlings of fourwing saltbush have also been used as transplant stock.

Saltbush species may also be direct-seeded successfully, although results have been inconsistent (McArthur and others 2004). Pitfalls include poor choice of species or ecotypes; using poor-quality seeds (low fill); planting too deep; planting at the wrong season; excessive competition from weeds or seeded grasses; interactions with pathogenic fungi such as damping-off diseases; and seedling predation by grasshoppers, rabbits, or other animals. Fourwing saltbush fruits are apparently not particularly attractive to granivorous rodents (Everett and others 1978), possibly because of the saponin content of the bracts (Sanderson and others 1986), so pre-emergence seeds predation is rarely a problem. Seeding rates of 4 to 8 kg/ha (3.5 to 7 lb/ac) have been recommended for de-winged lots of fourwing saltbush. This corresponds to about 200 to 530 live seeds/m^2 (25 to 50/ft^2) for a seedlot of average fruit size (122,000/kg) and fill (50%). In regions of low and unpredictable precipitation, saltbush seedlings may fail to emerge or survive in dry years even when all planting guidelines are followed. As annual recruitment is not necessary for the perpetuation of natural stands, this poses a problem only in artificial revegetation. Once seedlings establish, however, young plants grow rapidly (figure 4) and may become reproductively mature in their second growing season.

The large fruits may create the impression that saltbush should be drill-seeded at considerable depth, but seed reserves are small, as bracteole tissue is not nutritive. Most

Figure 4—*Atriplex canescens*, fourwing saltbush: seedling development at 1 and 2 days after germination, and at a later time.



authors recommend drilling at depths of 0.5 to 1 cm. Broadcast seeding followed by chaining has produced good stands of fourwing saltbush (Plummer and others 1966). Most species probably need shallow coverage. Young and others (1980) reported that surface seeding prevented emergence of quailbush and reduced that of Australian saltbush by half, even under conditions of unlimited moisture.

Optimal season for planting varies according to precipitation patterns. In winter precipitation zones such as the Intermountain area and the Mojave Desert, fall or early winter planting has been most successful (Kay and others 1977a&b; McArthur and others 2004; Plummer and others 1968). In summer precipitation zones such as the southern Great Plains and Chihuahuan Desert, spring and midsummer plantings are more likely to succeed (Springfield 1970). Northern Great Plains species with a chill requirement, such as Gardner saltbush, are probably best fall-seeded, whereas fourwing saltbush could be fall- or spring-seeded in the northern Great Plains area.

The expectation that highly dormant seedlots will emerge during the first year after planting is possibly the major source of disappointment in saltbush seedings. Knowledge of after-ripening patterns in the genus suggests that the best way to circumvent this problem is to use seedlots that have been given ample opportunity to after-ripen in dry storage prior to planting.

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Asteraceae—Aster family

Baccharis L.
baccharis

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Growth habit, occurrence, and use. The genus *Baccharis* is composed of more than 400 species native to tropical and subtropical America (Barkley 1986; Correl and Johnson 1970). Some species are used as ornamentals, some for erosion control, and some for medicinal purposes (Olson 1974). There are 21 species native to the United States (table 1); 14 of which are found in the far western United States. Baccharis plants are of poor forage value and some are poisonous to livestock and can cause contact dermatitis in humans. On the positive side, baccharis species have metabolites that have antitumor, antimicrobial, and insecticidal properties (Kuti and others 1990). Coyotebrush has a special use in southern California as a fire protection plant (Olson 1974). Desertbroom has been found suitable for copper mine reclamation in Arizona (Day and Ludeke 1980). Eastern baccharis is reported to be an important flower for beekeepers in Queensland, Australia (Westman and others 1975). Many species have good salt tolerance, and saltwater falsewillow and eastern baccharis are known for good growth in soil conditions that range from pure sand to pure clay (Dirr and Heuser 1987).

Growth habit varies considerably among the different species; a few examples follow. Saltwater falsewillow is a small evergreen shrub to 2.4 m high; eastern baccharis is deciduous to 3.6 m in height; Rooseveltweed is also deciduous, growing to 2.7 m or more; coyotebrush is a low evergreen shrub, 15 to 30 cm high, spreading out as much as 3 m; mulefat baccharis is an evergreen shrub to 3.6 m (LHBH 1976). Desertbroom is a shrub to 3.6 m (Sundberg 1993).

Flowering and fruiting. The white or yellowish male and female flowers, borne separately on different plants, are in heads that occur in clusters. In eastern baccharis, the male flowers are yellow and the female are white (Westman and others 1975). The female flowers develop into compressed, usually 10-ribbed achenes, tipped by a pappus of bristly hairs 13 mm long or less (figures 1 and 2). Achenes are dispersed by wind soon after ripening (table 2). Seedcrops are borne annually.

Quantities of seeds produced on an individual plant can be very high in full sunlight. A single plant of eastern baccharis has been estimated to produce over 1 million seeds (Westman and others 1975). Dense shade (3% of full sunlight) reduced seed production dramatically but did not totally eliminate it (Westman and others 1975).

Collection of fruits; extraction and storage of seeds. The ripe fruits of baccharis are either collected by hand or brushed onto cloth or plastic sheets spread beneath the shrubs. The fruits should be spread out to dry in a warm well-ventilated room or in the sun, protected from the wind. When dried, the fruits may be rubbed between the hands or treated in bulk to remove the pappus. Alternatively, full inflorescences can be fed into a brush machine, where the fruit is threshed from the stems and the pappus removed. The seeds can then be cleaned with air, screens, or other equipment described in the seed handling chapter. Sometimes the entire fruits are used without removing the pappus. The number of fruits per weight for coyotebrush is about 180,800/kg (82,000/lb) (1 sample); for mulefat baccharis, about 110,250/kg (50,000/lb) (1 sample) (Olson 1974). Cleaned seeds of baccharis species can be stored dry at 1.7 to 4.5 °C in airtight containers (McBride 1964). Data published by Westman and others (1975) indicate that seeds of eastern baccharis could be stored for 1 to 4 months at room temperature. After 4 months of room temperature storage, the final germination was actually slightly higher than with seeds stored for only 1 month. Panetta (1979) found that seeds stored in an atmosphere of 33% relative humidity maintained their germination of 98% for 12 months at 20 °C but that their percentage germination had dropped to 67% by 24 months. For seeds stored in the laboratory in a constant 70% relative humidity, germination began to drop at 6

Table 1—*Baccharis*, baccharis: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***B. angustifolia* Michx.**	**saltwater falsewillow,** narrowleaf baccharis	North Carolina S to Florida, W to Louisiana
***B. bigelovii* Gray**	**Bigelow falsewillow**	Arizona, New Mexico, & Texas
***B. brachyphylla* Gray**	**shortleaf baccharis**	Arizona, California, Nevada, New Mexico, & Texas
***B. dioica* Vahl**	**broombush falsewillow**	Florida, Puerto Rico, & the Virgin Islands
***B. douglasii* DC**	**saltmarsh baccharis**	California & Oregon
***B. emoryi* Gray**	**Emory baccharis**	Arizona, California, Nevada, Texas, & Utah
***B. glomeruliflora* Pers.**	**silverling**	North Carolina to Florida, also Mississippi
***B. halimifolia* L.** *B. halimifolia* var. *angustior* DC.	**eastern baccharis**	Connecticut to Maryland, North Carolina to Florida & W to Mississippi, Arkansas
***B. havardii* Gray**	**Harvard falsewillow**	Texas
***B. myrsinites* (Lam.) Pers.**	**Santo Domingo falsewillow**	Puerto Rico
***B. neglecta* Britt.**	**Rooseveltweed**	Arizona, New Mexico, & Oregon
***B. pilularis* DC.** *B. pilularis* ssp. *consanguinea* (DC.) C.B. Wolf *B. pilularis* var. *consanguinea* (DC.) Kuntze	**coyotebrush,** kidneywort baccharis	California, New Mexico, & Oregon
***B. plummerae* Gray**	**Plummer baccharis**	California
***B. pteronioides* DC.**	**yerba de pasmo**	Arizona, New Mexico, & Texas
***B. salicifolia* (Ruiz & Pavon) Pers.** *B. viminea* DC. *Molina salicifolia* Ruiz & Pavon *B. glutiosa* Pers.	**mulefat baccharis**	California E to Texas & Utah
***B. sarothroides* Gray**	**desertbroom**	Arizona, California, Nevada, & Utah
***B. sergiloides* Gray**	**squaw waterweed baccharis**	Arizona, California, Nevada, & Utah
***B. texana* (Torr. & Gray) Gray** *Linosyris texana* Torr. & Gray	**prairie falsewillow**	New Mexico, Oklahoma, & Texas
***B. thesioides* Kunth**	**Arizona baccharis**	Arizona & New Mexico
***B. vanessae* Beauchamp** *B. glutinosa*	**Encinitis falsewillow**	California
***B. wrightii* Gray**	**Wright baccharis**	Arizona & Utah, E to Kansas, Oklahoma, & Texas

Sources: BONAP (1996), Olson (1974).

months. By contrast, seeds buried in the soil in the field at a depth of 5 cm maintained their germination rate at 99% for 2 years. Numbers of cleaned seeds per weight (determined from 1 sample, except for coyotobrush, which was determined from 2) for 4 species are as follows (McBride 1964; Mirov and Kraebel 1939; Olson 1974; Panetta 1979):

Species	seeds/kg	seeds/lb
saltwater falsewillow	4,989,600	2,268,000
eastern baccharis	10,000,000	4,500,000
coyotebrush	8,316,000	3,780,000
mulefat baccharis	11,000,000	5,000,000

Germination tests. Tests have been completed in 15 to 30 days at diurnally alternating temperatures of 30/20 °C (table 3). When comparing germination at constant 10, 15, 20, 25, 30, and 35 °C, Westman and others (1975) found that eastern baccharis germinated most quickly above 20 °C but germinated at higher numbers between 15 and 20 °C. Light was necessary for germination of eastern baccharis and mulefat baccharis. Without light, no or minimal germination was obtained. In another experiment with eastern baccharis (Panetta 1979), alternating temperatures of 19/22 °C partially compensated for the lack of light. However, in this same experiment, it was shown that an 8-hour photoperiod produced twice as much germination as constant light. Alternating temperatures were used and the effective range was from 19/22 °C to 19/24 °C. The ratio of red to far red light was also examined by Panetta (1979), but it was found to be important only when constant light was used. Therefore, either incandescent or fluorescent light for 8 hours each day would give good germination results for eastern baccharis. No pregermination treatments are needed (Emery 1964; McBride 1964; Mirov and Kraebel 1939), although prechilling at 5 °C for 1 week gave higher germi-

Figure 1—*Baccharis angustifolia,* saltwater falsewillow: achene with pappus (**top**); achenes with pappus removed (**bottom**).

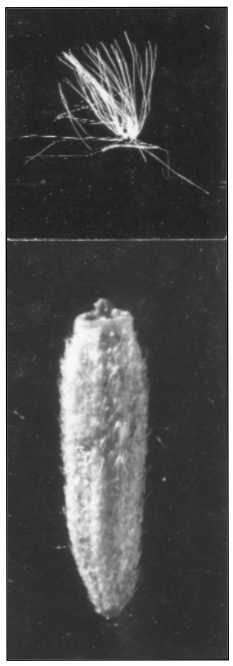
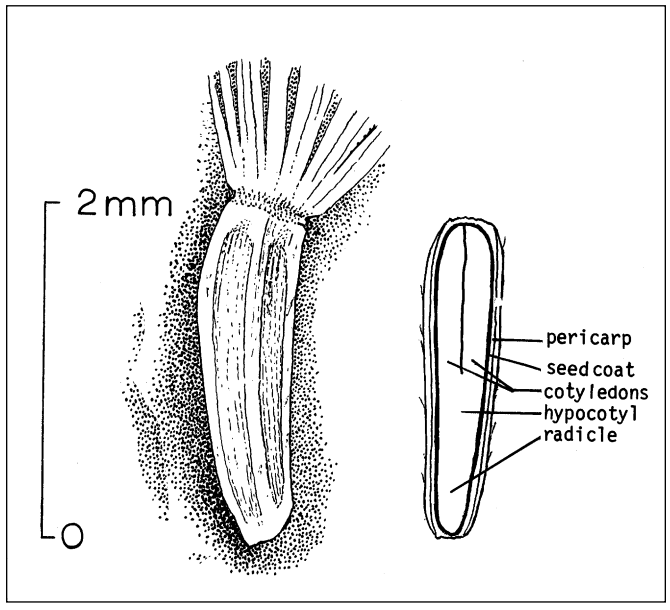


Figure 2—*Baccharis viminea,* mulefat baccharis: achene with pappus (**left**) and longitudinal section through an achene (**right**).



nation than no prechilling or prechilling at 0 °C when eastern baccharis was germinated at 10, 15, or 20 °C with continuous light. In a greenhouse test of eastern baccharis, there was no apparent reduction in germination under 56.7, 23.6, or 17.4% of full sunlight (Panetta 1990). Embryo excision was found to speed embryo germination in both Encinitis falsewillow and eastern baccharis (Kuti and others 1990), demonstrating that there is some inhibitory effect from the seedcoat.

Nursery practice. Seeds may be sown in the fall or early spring in flats or seedbeds using a sandy soil mixture, or one of the vermiculite, perlite, or sphagnum moss seeding media (Everett 1957). Seeds usually germinate within 7 to 15 days. Plants large enough for 10-cm (4-in) pots can be taken from outside seedbeds within 4 months (Everett 1957) (figure 3). Rooseveltweed seeds sown in 15-cm-deep (6-in-deep) pots germinated slowly, requiring 1 month to establish seedlings (Van Auken and Bush 1990).

Figure 3—*Baccharis pilularis,* coyotebrush: seedling development 60 days after germination.

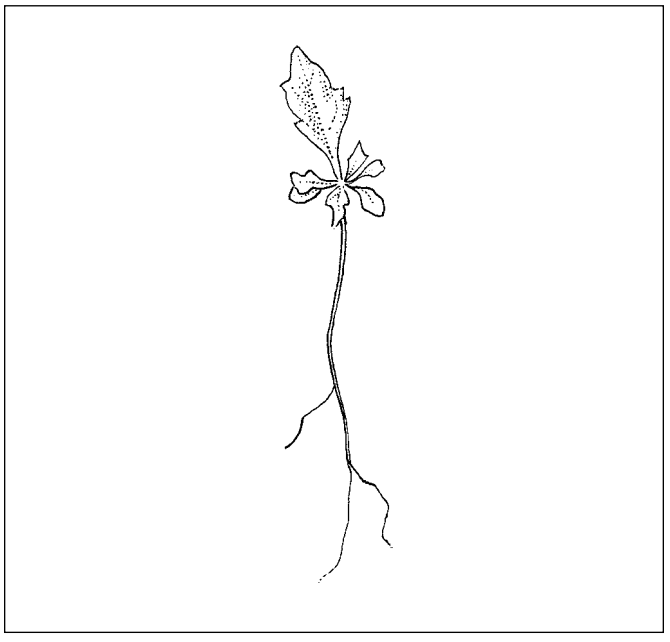


Table 2—*Baccharis,* baccharis: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
B. angustifolia	Sept–Oct	Sept–Oct	Oct
B. pilularis	July–Oct	Sept–Dec	Fall
B. salicifolia	May–July	May–July	May–July

Sources: McBride (1964), Mirov and Kraebel (1939), Olson (1974), Radford and others (1964).

Table 3 —*Baccharis,* baccharis: germination test conditions and resulting germination

Species	Medium	Germination test condition: Temp (°C) Day	Germination test condition: Temp (°C) Night	Germination test condition: Days	Germination: Average (%)	Germination: Samples
B. angustifolia	Kimpak	15.6	15.6	55	21	2
B. halimifolia	—	23	19	10	92	1
B. pilularis	Moist paper	22–24	19	10	93	1
	Moist paper	30	17.3	15–30	92	1
	Moist paper	15–25	7.2–25	30	40–54	28
B. salicifolia	—	30	20	15–30	75–82	3

Sources: McBride (1964, 1969), Mirov and Kraebel (1939), Olson (1974), Panetta (1979).

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Fabaceae—Pea family

Bauhinia L.

bauhinia

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Growth habit, occurrence, and use. There are about 600 species of the bauhinia genus found in the tropical regions of the world (Larson 1974). The genus includes trees, vines, and shrubs that are frequently planted for their showy flowers and ornamental foliage (Bailey 1941; Neal 1965). Practical usage of the bark of orchidtree as an astringent in tanning and dyeing and of the leaves and flower buds as a vegetable has been reported (Bailey 1941). Seeds of some bauhinia species have served as a human food source (malucreeper, *B. vahlii* Wight & Arn.) (Ramasastri and Shenolikar 1974); a source of vitamin A (butterfly bauhinia) (Essien and Fetuga 1989); and as a possible pest control agent (malucreeper) (Freedman and others 1979). Butterfly bauhinia is used for fuelwood on Puerto Rico and for fences on Jamaica (Little and Wadsworth 1964), but it is considered a weed on Guam (McConnell and Muniappan 1991). Four species, all small evergreen or deciduous trees, have been planted in the continental United States (table 1). Hawaii has 13 species of introduced bauhinias (Neal 1965), whereas Puerto Rico has at least 5 (Francis and Liogier 1991).

Flowering and fruiting. The large 5-petaled orchid-like flowers of bauhinias occur in racemes and range in color from white to deep purple and yellow. The fruits (figure 1) are flat and dark, and dehiscent or indehiscent legumes (pods) varying in length from 8 to 60 cm (Bailey 1941). Flowers of butterfly bauhinias have only 1 fertile

Figure 1—*Bauhinia variegata,* orchidtree: flowers and legumes (from Little and others 1974).

Table 1—*Bauhinia,* bauhinia: nomenclature, occurrence, and uses

Scientific name & synonym(s)	Common name(s)	Occurrence
***B. megalandra* Griseb.** *B. multinervia* (Kunth) DC.	**bauhinia** petite flambouyant	Carribean basin
***B. monandra* Kurz** *B. kappleri* Sagot *Caspareopsis monandra* (Kurz) Britt. & Rose	**butterfly bauhinia,** pink bauhinia, pink orchidtree	Native of SE Asia; planted in Hawaii, escaped & naturalized in Puerto Rico & throughout the West Indies
***B. purpurea* L.** *Phanera purpurea* (L.) Benth. *Caspareopsis purpurea* (L.) Pittier	**purple bauhinia**	Native of SE Asia from India to China; planted in Florida, Hawaii, Puerto Rico, the Virgin Islands, & elsewhere in tropical America
***B. variegata* L.**	**orchidtree,** poor-man's-orchid, mountain-ebony	Native from India to China; planted in Florida & Hawaii; escaped & naturalized in Puerto Rico & the Virgin Islands

Sources: Francis and Liogier (1991), Little and others (1974), Neal (1965).

Table 2—*Bauhinia,* bauhinia: flower and fruit morphology

Species	Flowering time	Petal color	Fertile stamens/flower	Legume
B. monandra	All year	Pink with red dots	1	15–30 cm long, pointed at apex, twists as opens
B. purpurea	Autumn & winter	Deep pink to purple	3–4	15–30 cm long, black, thin, twists as opens
B. variegata	Autumn to spring	Purple variegated with red & yellow	5–6	13–30 cm long, thin, pointed on both ends

stamen per flower and a calyx splitting along one side (Little and Wadsworth 1964; table 2). Flowers of purple bauhinias have 3 to 4 fertile stamens and a 2-parted calyx, whereas those of orchidtrees have 5 to 6 fertile stamens/flower and a calyx that splits on one side (Little and others 1974; Neal 1965). Information on pollinators is scarce, but Heithaus and others (1982) report that *B. ungulata* L. is pollinated by bats and that 59.4% of flowers examined show evidence of herbivory.

Butterfly bauhinia seeds are elliptic, flat, and 1 cm long; fruits are present throughout the year (Little and Wadsworth 1964). Purple bauhinia seeds are shiny-brown, rounded, flat, and range in length from 1.3 to 1.6 cm; flowering and fruiting occur in autumn and winter months (Little and others 1974). Orchidtree seeds are fairly large, about 1.3 cm in diameter, and the fruits mature in late spring or early summer. *Bauhinia megalandra* seeds are shown in figure 2 and 3. Rugenstein and Lersten (1981) report the presence of stomata on the seeds and pods of purple bauhinias and orchidtrees. In general, bauhinia seeds contain high amounts of linoleic and oleic fatty acids and low amounts of myristic and linolenic fatty acids (Balogun and Fetuga 1985; Ramasastri and Shenolikar 1974; Sherwani and others 1982; Zaka and others 1983).

Collection, storage, and germination. Seeds may be stripped from unopened legumes (pods). Some and others (1990) reported satisfactory germination after 52 weeks when seeds of *Bauhinia rufescens* Lam. were scarified using 97% sulfuric acid (H_2SO_4), washed, dried, sealed into containers, and stored at 4 °C. Another study determined that seeds of orchidtree had a higher germination percentage when stored after cleaning; however, viability was lost within 3 years (Athaya 1985). Because *Bauhinia* is a hard-seeded Fabaceae, dry seeds should store well for many years. Loss of viability after 3 years could be attributable to high moisture content or mechanical damage. Germination studies of orchidtree using excised embryos produced results comparable to experiments using intact seeds (Babeley and Kandya 1986). Francis and Rodrıguez (1993) reported excellent germination of bauhinia without scarification (table 3).

Nursery practices. Bauhinias species grow easily from seeds and bloom within 3 to 4 years (Bailey 1941). Some species can be propagated from suckers but rarely from cuttings.

Figure 2—*Bauhinia megalandra,* bauhinia: seed.

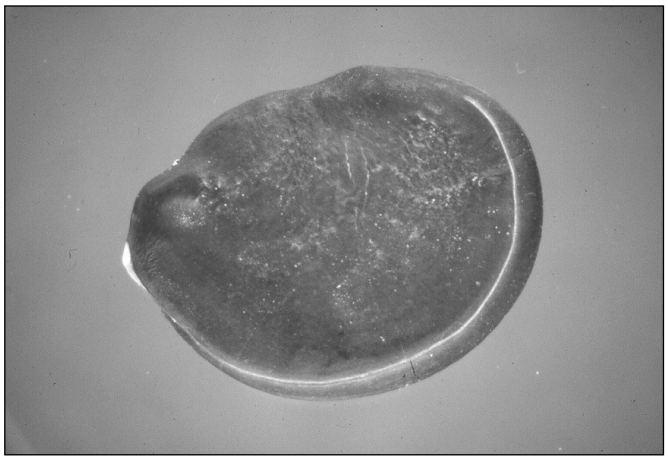

Figure 3—*Bauhinia megalandra,* bauhinia: longitudal drawing of seed section.

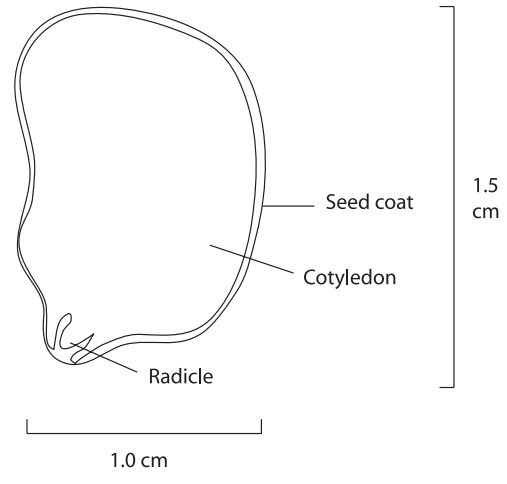

Table 3—*Bauhinia,* bauhinia: seed and germination data

Species	Seeds/wt /kg	Seeds/wt /lb	Germination * Period (days)	Germination * Percentage
B. monandra	5,680	2,576	4	100
B. purpurea	4,670	2,118	4	99
B. variegata	4,950	2,245	4	77

Source: Francis and Rodríguez (1993).

* Sample size = 100; germinated on filter paper; germination recorded when radicle emerged from seed

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B

Berberidaceae—Barberry family

Berberis L.

barberry

Don Minore and Paul O. Rudolf

Dr. Minore retired from USDA Forest Service's Pacific Northwest Research Station;
Dr. Rudolf (deceased) retired from the USDA Forest Service's North Central Forest Experiment Station

Growth habit, occurrence, and use. The barberries include about 500 species of spiny or unarmed, evergreen or deciduous shrubs (rarely small trees) native to Asia, Europe, North Africa, and to North, Central, and South America (Ahrendt 1961). Some authorities consider that the genus *Mahonia*, consisting of about 100 species that closely resemble the barberries, should be a section of *Berberis* (Hitchcock and others 1964), whereas others consider *Mahonia* to be a separate genus (Ahrendt 1961). The USDA plant nomenclature system (USDA NRCS 1999) separates them into 2 separate genera, and that is the authority used for this manual (table 1). Thus, *Mahonia* is treated separately in a later chapter. The barberry genus is essentially diploid, with 2n = 28 (Cadic 1992). Many interspecific hybrids are known, such as those between Japanese and common barberries (*B.* × *ottawensis* Scheid.), and Japanese barberry and Julian berberis (Rehder 1940). There are more than 60 crosses within *Berberis*, 6 in *Mahonia,* and 4 "mahoberberis" hybrids (Ahrendt 1961).

Several barberry species are grown as ornamentals because of their handsome foliage and often attractive flowers or fruits (Bailey 1939; Rehder 1940; Schlosser and others 1992). Barberries also are of value for wildlife food (Decker and others 1991), cover, and erosion-control planting. However, Japanese and common barberries, as "invasive aliens," are considered by many to be noxious weeds (Mack 1991). The names, heights, habits, and ripe fruit colors of some common species are listed in table 1.

A yellow dye can be extracted from barberry roots, and the plants contain many alkaloids (Hussain and others 1984;

Table 1—*Berberis,* barberry: nomenclature, height, growth habit, and color of ripe fruit

Scientific name & synonym	Common name(s)	Height at maturity (m)	Growth habit	Color of ripe fruits
***B. buxifolia* Lam.**	**boxleaf barberry**	0.6–2.1	Deciduous	Pruinose blue
***B. candidula* (C.K. Schneid.) C.K. Schneid.**	**paleleaf barberry**	0.6–1.2	Evergreen	Purplish, bloomy
***B. circumserrata* (C.K. Schneid.) C.K. Schneid.**	**cutleaf barberry**	0.6–0.9	Deciduous	Pale red
***B. darwinii* Hook.**	**Darwin barberry**	1.5–2.4	Evergreen	Pruinose blue
***B. gagnepainii* C.K. Schneid.**	**black barberry**	0.9–1.8	Evergreen	Pruinose blue
***B. gilgiana* Fedde**	**wildfire barberry**	1.8–2.4	Deciduous	Reddish
***B. julianiae* Schneid.**	**Julian barberry,** wintergreen barberry	1.8–3.0	Evergreen	Bluish-black
***B. koreana* Palibin.**	**Korean barberry**	1.2–1.8	Deciduous	Bright red
***B. sargentiana* C.K. Schneid.**	**Sargent barberry**	1.8–2.7	Evergreen	Black
***B. thunbergii* DC.** *B. trifoliata* Moric.	**Japanese barberry**	0.9–1.8	Deciduous	Bright red
***B. tricanthophora* Fedde**	**threespine barberry**	0.9–1.5	Evergreen	Bluish-black
***B. vernae* C.K. Schneid.**	**Verna barberry**	0.9–1.2	Deciduous	Pale red
***B. verruculosa* Hensl. & E.H. Wilson**	**warty barberry**	0.9–1.8	Evergreen	Violet-black
***B. vulgaris* L.**	**common barberry,** European barberry	1.8–3.0	Deciduous	Scarlet or purple

Sources: Ahrendt (1961), Dirr (1990), Dirr and Heuser (1987), Garrett (1969), Hitchcock and others (1964), McMinn (1951), Rehder (1940), Rudolf (1974), Vines (1960).

Ikram 1975; Kostalova and others 1986; Pitea and others 1972). Some of those alkaloids (for example, berberine and jatrorrhizine) are used for medicinal purposes (Ikram 1975; Liu and others 1991). Other barberry extracts may significantly reduce infection with fireblight—*Erwinia amylovora* (Burrill) Winslow et al.—infection when applied as bactericides (Mosch and Zeller 1989). Three species that have been used for conservation planting but are now often considered invasive are listed in table 2. Many of the barberries are alternate hosts for the black stem rust—*Puccinia graminis* Pers:Pers.—of grains, but common barberry is the most susceptible species (LHBH 1976). Some species (for example, Korean barberry and Japanese barberry) are resistant (Rehder 1940).

Flowering and fruiting. Perfect yellow flowers are borne in the spring in racemes, panicles, umbels, fascicles, or individually, depending on the species (Ahrendt 1961). Stamens are contact-sensitive, and they respond to a tactile stimulus by snapping toward the stigma (Fleurat-Lessard and Millet 1984; Lebuhn and Anderson 1994; Millet 1976, 1977). Fruit set and fruit weight are improved by spraying with 200 ppm gibberellic acid (GA_3) at full bloom and again 15 and 30 days later (Malasi and others 1989). The fruit is a berry with one to several seeds (figure 1). Late-fruiting plants often contain more seeds per berry than early-fruiting plants in common barberry; and late-fruiting, large-berried plants may disperse seeds more efficiently than early-fruiting plants with smaller berries (Obeso 1989). Predation by fly larvae (diptera: Tripetidae) tends to increase with increasing number of seeds in the fruit, however, and individual developing seeds have a greater average probability of escaping predation when they occur singly in fruits (Herrera 1984). Fruits having the least number of seeds contain the highest amounts of edible pericarp (Malasi and Paliwal 1984). Starch is not present, but polyfructans are characteristic of barberry fruits (Srepel and Mijatovic 1975). Soluble sugar and anthocyan levels increase while those of chlorophyll and berberine decrease during the ripening of those fruits (Chandra and Todaria 1983).

Good fruit crops are borne almost annually. They ripen in the summer and autumn (table 2). In New Zealand, the proportion of mature flowers that survive to produce ripe fruit and the proportion of ripe fruit taken by birds may be higher in introduced, naturalized barberry species than in most other species with similar reproductive ecology that are growing within their natural range (Allen and Wilson 1992). As a result, establishment of seedlings of Darwin barberry may exceed that of native shrub and tree species in New Zealand (Allen 1991). The presence of a waxy bloom does

Figure 1—*Berberis thunbergii*, Japanese barberry: longitudinal section through 2 seeds in a berry.

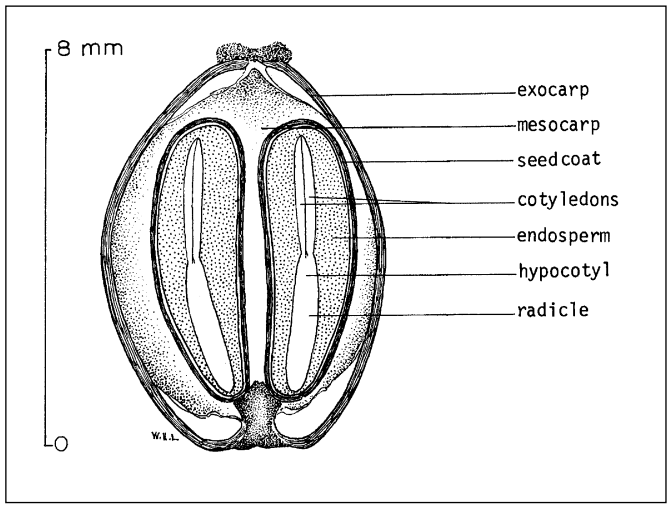

Figure 2—*Berberis thunbergii,* Japanese barberry: seedling development at 1 and 16 days after germination.

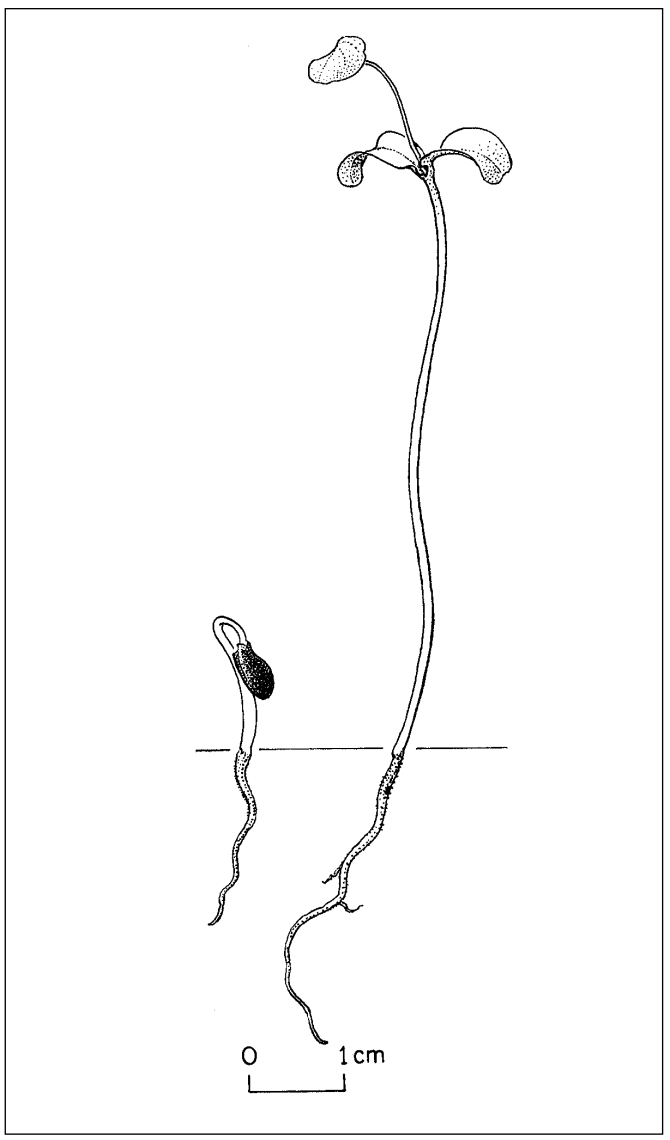

Table 2—*Berberis*, barberry: phenology of flowering and fruiting for 3 species

Species	Origin	Location	Flowering	Fruit ripening
B. koreana	Korea	NE US & Carver Co., Minnesota	May–early June	Sept–Oct
B. thunbergii	Japan	Japan	Apr–June	Oct
		SE US	Mar–Apr	May–Sept
		NE US & Germany	May–June	Sept–Nov
B. vulgaris	Europe †	NE US & W Europe	Apr–June	Sept–Oct

Sources: Bailey (1939), Loiseau (1945), McMinn (1951), Mirov and Kraebel (1939), NBV (1946), Ohwi (1965), Plummer and others (1965), Radford and others (1964), Rudolf (1974), Van Dersal (1938), Vines (1960), Wappes (1982), Wyman (1947).

* Fruits of these 3 species often remain on bushes over winter.

† To 1,525 m in the Alps.

not increase fruit attractiveness, but physical alteration of the fruit surface reduces fruit selection by birds (Allen and Lee 1992). Seed dispersal by both birds and mammals is widespread (Rudolf 1974; Vines 1960).

Collection of fruit; extraction and storage of seeds. Ripe barberry fruits may be picked by using protective gloves, or they may be flailed onto cloths or receptacles spread beneath the bushes. The ripe fruits may be run through a macerator or blender with water and the pulp then screened out or floated off. The seeds should then be dried superficially and either sown immediately or stored in sealed containers at temperatures slightly above freezing (Heit 1967a; NBV 1946; Rudolf 1974). Seed purity and soundness for the species included here have been as high as 90 to 99% (Davis 1927; Rafn and Son nd; Rudolf 1974). Seeds of Japanese and common barberries remained viable for at least 4 years when held at 1 to 3 °C in sealed containers (Heit 1967b), which indicates that these species are orthodox in storage behavior. Fruit yields, seed yields, and numbers of seeds per weight for 3 species are listed in table 3.

Pregermination treatments. Seeds of some barberry species have embryo dormancy that requires cold stratification to provide prompt germination. Dirr and Heuser (1987) recommend 1 to 2 months for wildfire and Japanese barberries, and 2 to 3 months for boxleaf, paleleaf, cutleaf, Darwin, Julian, and Korean barberries. Germination data for 3 species are found in table 4. However, a simple cold stratification is not always successful. Immature or improperly developed embryos may be present in some barberry seeds, and maximum germination may require warm incubation, followed by cold stratification as in the closely related *Mahonia* genus (Dirr and Heuser 1987; McLean 1967). Under natural conditions, barberry seeds germinate in the spring following seed dispersal (Kern 1921).

Germination tests. Germination of seeds from several barberry species has been tested in sand-filled flats, in petri dishes, on paper or blotters, or in standard germinators. Day temperatures of 16 to 30 °C, night temperatures of 13 to 21 °C, and germination periods of 20 to 95 days have been used. Results are summarized in table 4. For Japanese and common barberries, the Association of Official Seed Analysts (AOSA 1993) recommends germination of excised embryos in covered petri dishes at temperatures of 18 to 22 °C for 10 to 14 days. This method may be satisfactory for other barberry species.

Nursery practice. Whole berries or (preferably) cleaned seeds may be sown in the fall, or stratified seeds may be sown in the spring. Injury from molds is more likely if whole berries are used (Chadwick 1936). Fall-sown beds should be mulched until germination begins (NBV 1946). The seeds should be covered with 0.3 to 1.3 cm ($^1/_8$ to $^1/_2$ in) of soil plus 0.6 cm ($^1/_4$ in) of sand (Rudolf 1974). Germination is epigeal (Terabayashi 1987), and seedlings develop rapidly (figure 2). In a sowing of common barberry, 22% of the seeds survived to produce shrubs (Swingle 1939). Barberries may be field-planted as 2+0 stock (Rudolf 1974).

The barberries can be propagated from rooted stem cuttings. Several deciduous species are best rooted when propagated from softwood cuttings collected in the summer, but many of the evergreen species root better when hardwood cuttings are collected in the autumn or winter (Dirr and Heuser 1987). Both should be treated with indole butyric acid (IBA) rooting hormone in talc or in solution.

Table 3—*Berberis*, barberry: seed yield data

Species	Place collected	Fruit wt/fruit vol kg/hl	Fruit wt/fruit vol lb/bu	Seed wt/fruit vol kg/hl	Seed wt/fruit vol lb/bu	Cleaned seeds(x 1,000)/weight Range /kg	Range /lb	Average /kg	Average /lb	Samples
B. koreana	Carver Co., MN	39	30	4	3	—	—	84	38	2
B. thunbergii	US	9–15	16–25	—	—	55–82	25–37	64	29	5+
B. vulgaris	US	—	—	—	—	75–90	34–41	84	38	2

Source: Rudolf (1974).

Table 4—*Berberis*, barberry: stratification periods, germination test conditions, and results for 3 species

Species	Cold stratification* (days)	Daily light (hrs)	Germination test conditions Medium	Temp (°C) Day	Temp (°C) Night	Days	Germination rate Amount (%)	Days	% germination Avg (%)	Samples	Purity (%)	Soundness (%)
B. koreana	60	16	Sand or perlite	16	16	20	64	6	88	1	97	95
B. thunbergii	90	—	Wet paper or sand	24†	13†	40	—	—	90	4	93	95
B. vulgaris	40	—	Wet paper or sand	24†	13†	40	—	—	91	2+5	—	96

Sources: Davis (1927), Heit (1968a,b), McLean (1967), Mirov and Kraebel (1939), Morinaga (1926), Plummer and others (1968), Rafn and son (nd), Rudolf (1974), Swingle (1939), Vines (1960).

* Cold stratification temperatures ranged from -1 to 5 °C.

† Twenty-one to 27 °C during the day and 10 to 16 °C during the night.

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Betulaceae—Birch family

Betula L.

birch

Robert P. Karrfalt

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Growth habit, occurrence, and use. The birch-genus—*Betula*—consists of about 40 to 50 species of deciduous trees and shrubs occurring in the cooler parts of the Northern Hemisphere (Weaver 1978). Several species produce valuable lumber. Other species are useful for ornamental plantings because of their attractive growth habit, foliage, and bark. Nearly all species provide food and cover for wildlife, and some are valuable because they seed-in promptly on harvested or burned lands. The 14 species native to the Unites States are listed in table 1, along with several species that are introduced or are referenced in the seed literature.

Flowering and fruiting. The flowers are monoecious and borne in catkins. Staminate catkins are formed in late summer or autumn, remain naked during winter, and open after considerable elongation in the spring (table 2). The pistillate catkins, which are cone-like with closely overlapping scales, are born terminally on short, spur-like lateral branches and appear with the leaves (table 2). When the female catkins (strobiles) ripen in late summer or autumn (table 2), they become brown and woody and are either erect or pendulous (figure 1). Each scale may bear a single small, winged nut (seed) (figures 2 and 3) that is oval, with 2 persistent stigmas at the apex. The seeds turn from greenish tan to light brown or tan when mature (Brinkman 1974). Seeds disperse from late fall until the following spring (Houle and Payette 1990; Matlack 1989). Although seeds can begin to disperse in late summer, these early-shed seeds may be of poor quality. Seeds of yellow birch shed in August were found to not be viable. Viable seeds were not released in meaningful amounts until September, with the maximum of good seeds being released in October (Houle and Payette 1990). After seedfall, the strobiles slowly disintegrate on the trees, with the axes persisting on the branchlets.

Seed production. Birch tends to flower at the relatively young age of 10 to 15 years (Lepisto 1973) (table 3). Some individuals are precocious in flowering and this appears to be under genetic control (Huhtinen and Yahyaoglu 1974). Clausen (1980) reported on a progeny test of 147 open-pollinated yellow birch families from 21 stands. He found that some female-flowering began at 6 years from seed, but this occurred in only 1% of the trees. By age 9, 14% of the trees were producing seeds. Male-flowering commenced 1 year later than female-flowering. Seedlings from northern sources tended to flower earlier than those from southern sources. In greenhouse conditions with irrigation, fertilization, and CO_2-enriched air, European white birch seedlings have produced male catkins as early as 9 months and commercial quantities of seed at 5 years (Lepisto 1973).

Birches are known to hybridize readily. These hybrids appear to be at least partially fertile, allowing for the production of second generation hybrids and backcrossing to the parent species (Barnes and others 1974).

The holartic lygaeid—*Kleidocerys resedae* (Panzer)—feeds on the seeds of European white birch and cause premature drop of catkins and seed failure. The feeding does not affect the vigor of the parent plant, even though the insects can be quite numerous and visible (Wheeler 1976).

Seed production is usually regular and abundant. Bjorkbom and others (1965) reported that paper birch produced a higher proportion of viable seeds in good seed years than it did during poor seed years. The percentage of viable birch seeds can be estimated by examining the seeds on a light table (Patterson and Bruce 1931). The seeds are primarily dispersed by wind as they are shed from the catkins. Wind can also blow seeds along the surface of the snow up to 80 m from the mother tree. This secondary dispersal may be the more effective method; it has been predicted to increase sweet birch seed dispersal by a factor of 3.3 over that of aerial dispersal alone (Matlack 1989). Ford and others (1983) trapped about 5% of the total seed-fall from round-leaf birch at nearly 100 m from the parent tree.

Table 1—*Betula,* birch: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***B. alleghaniensis* Britt.** *B. lutea* Michx. F.	**yellow birch**	Newfoundland to SE Manitoba, S to NE Iowa N Illinois & Delaware; mtns to Tennessee
***B. borealis* Spach**	**northern birch**	Massachusetts, New Hampshire, Vermont, Maine, N to Nova Scotia, Newfoundland, Quebec, & Labrador
***B. davurica* Pall.**	**Dahurian birch**	Temperate China, Japan, & Russian Federation
***B. ermanii* Cham.**	**Erman birch**	NE China, Japan, Korea, Russian Federation in Chita, Kamchatka, Sakhalin, Yakutia-Sakha, & Bryansk
***B. lenta* L.**	**sweet birch,** black birch, cherry birch	S Maine to S Ontario, S to E Ohio & Delaware; mtns to N Alabama & Georgia
***B. mandshurica* var. *japonica* (Miq.) Rehder** *B. alba* var. *japonica* Miq. *B. japonica* Siebold ex H.J.P. Winkl. *B. japonica* var. *Kamtschatica* (Regel) H.J.P. Winkl. *B. platyphylla* var. *japonica* (Miq.) H. Hara *B. platyphylla* var. *kamtschatica* (Regel) H. Hara	**Japanese white birch,** Asian white birch	Japanese islands of Hokkaido & Honshu; Russian Siberia in Kamchatka, Magadan, & Sakhalin
***B. maximowicziana* Regel**	**monarch birch**	Japanese islands of Hokkaido & Honshu; Kurile Islands, Russia
***B. minor* (Tuckerman) Fern.** *B. saxophila* Lepage *B. papyrifera* var. *minor* (Tuckerman) S. Wats. & Coult.	**dwarf white birch**	New York, New Hampshire, Maine, New Brunswick, N to Ontario, Quebec, Newfoundland, & Labrador
***B. murrayana* Barnes & Dancik**	**Murray birch**	Michigan
***B. nana* L.** *B. gladulosa* Michx. *B. exilis* Sukatschev *B. michauxii* Sarg. *B. glandulosa* var. *hallii* (T.J. Howell) C.L. Hitchc. *B. glandulosa* var. *sibirica* (Ledeb.) Schneid. *B. nana* ssp. *exilis* (Sukaczev) Hutten *B. nana* var. *sibirica* Ledeb.	**bog birch,** swamp birch, dwarf birch	Newfoundland to Alaska, S to higher mtns of California, Colorado, & Maine
***B. neoalaskana* Sarg.** *B. papyrifera* var. *neoalaskana* (Sarg.) Raup	**Alaska birch**	Alaska, Alberta, N British Columbia, Manitoba, W Northwest Territory, NW Ontario, Saskatchewan, & Yukon Territory
***B. nigra* L.**	**river birch,** black birch, water birch	Connecticut to E Iowa & SE Kansas, S to E Texas, E to N Florida
***B. occidentalis* Hook.** *B. beeniana* A. Nels *B. fontinalis* Sarg. *B. papyrifera* Marsh. ssp. *occidentalis* (Hook.) Hulten *B. occidentalis* var. *inopina* (Jepson) C.L. Hitchc. *B. papyrifera* var. *occidentalis* (Hook.) Sarg.	**water birch**	Alaska, Canada, W US, E to the Dakotas, Nebraska, Colorado, & New Mexico
***B. papyrifera* Marsh.** *B. cordifolia* Regel *B. alba* var. *cordifolia* (Regel) Regel	**paper birch,** canoe birch, silver birch, white birch	Newfoundland to Canada, S to Washington & E to North Dakota, NE Iowa & New England; locally in other states in N
***B. pendula* Roth** *B. verrucosa* Ehrh.	**European white birch**	Europe to Japan
***B. populifolia* Marsh.**	**gray birch,** white birch, wire birch	Nova Scotia to S Ontario, S to N Ohio, Pennsylvania, & Delaware

Table 1—*Betula,* birch: nomenclature and occurrence (Continued)

Scientific name & synonym(s)	Common name	Occurrence
***B. pubescens* Ehrh.** *B. alba* L. *B. tortusa* Ledeb.	**downy birch**	N & central Europe to E Siberia
***B. pumila* L.** *B. pumila* var. *glandulifera* Regel (Gleason) *B. glandulifera* (Regel) Butler *B. nana* var. *glandulifera* (Regel) Boivin *B. glandulosa* var. *glandulifera* (Regel) Gleason	**swamp birch**, glandulose birch, bog birch, swamp birch	W Quebec to British Columbia, S to Montana, E to North Dakota & N New York
***B. uber* (Ashe) Fern.**	**roundleaf birch**	Smyth Co., Virginia
***Betula x utahensis* Britt. (pro sp.)** *B. andrewsii* A. Nels. *B. piperi* Britt.; *B. (commixta* Sarg. *B. occidentalis* var. *fecunda* Fern. *B. papyrifera* var. *subcordata* (Rydb.) Sarg.	**northwestern paper birch**	Yukon Territory, S through British Columbia, Alberta, Saskatchewan, Washington, Idaho, Montana, Oregon, Wyoming, & Utah

Source: Brinkman (1974)

Table 2—*Betula,* birch: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
B. alleghaniensis	Mid-range	Apr–May	Aug–Oct	Sept–Spring
B. davurica	Japan	May	Oct	—
B. lenta	Mid-range	Apr–May	Aug–Sept	Sept–Nov
B. nana	Mid-range	June–Aug	Aug–Oct	Sept–Mar
B. nigra	N part of range	Apr–May	May–June	May–June
B. papyrifera	Mid-range	Apr–June	Aug–Sept	Aug–Spring
B. pendula	Russia & Finland	Apr–June	July–Aug	July–Sept
B. populifolia	Mid-range	Apr–May	Sept–Oct	Oct to mid-winter
B. pubescens	Germany & Finland	May–June	Aug–Sept	Fall–Winter
B. pumlia	Mid-range	May–June	Sept–Oct	Oct–Mar

Sources: Ahlgren (1957), Brinkman (1974), Damberg (1915), Fernald (1950), NBV (1946), Sarvas (1952), Van Dersal (1938), Wappes (1932).

Although an abundance of seeds can be found in the forest soil, these seeds are short-lived. Most seeds are nonviable after the second or third year (Granstrom 1987; Granstrom and Fries 1985; Johnson 1975; Moore and Wein 1977; Perala and Alm 1989; Steijlen and Zackrisson 1986). The abundance of seeds in the forest soil is, therefore, likely supported by regular replenishment from new crops (Komarova 1986). A rare case of excessive seed production has been observed to lead to crown deterioration and reduced growth of the parent trees (Gross 1972).

Seed collection. Birch seeds are collected by picking or stripping the strobiles from standing trees or shrubs or from trees recently felled in logging operations. This is best done while strobiles are still green enough to hold together. Because ripe strobiles shatter readily, they are usually put directly into bags rather than allowed to fall onto the ground or tarps, which can result in loss of the seeds. However, seeds can also be collected from paved surfaces in urban areas.

Seed extraction. Freshly collected strobiles can be subject to heating because they usually are at least somewhat green. They should be spread out to dry for several weeks until they begin to disintegrate. Low relative humidity is the most important factor in drying the strobiles. Matlack (1989) found that sweet birch strobiles released their seeds at low humidity anywhere in the temperature range of –14 to 16 °C. Once the strobiles begin to fall apart, they can be shattered by rubbing or shaking, and the seeds can be separated from most of the scales and debris by screening and fanning. Round-hole screens of the following sizes have

Figure 1—*Betula*, birch: ripe female strobiles; *B. pendula*, European white birch (**top right**); *B. populifolia*, gray birch (**bottom left**); *B. papyrifera*, paper birch (**bottom middle**); and *B. lenta*, sweet birch (**bottom right**).

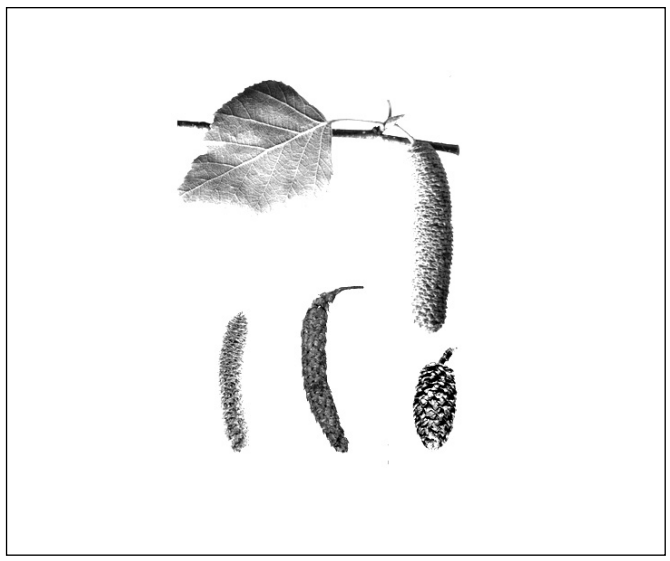
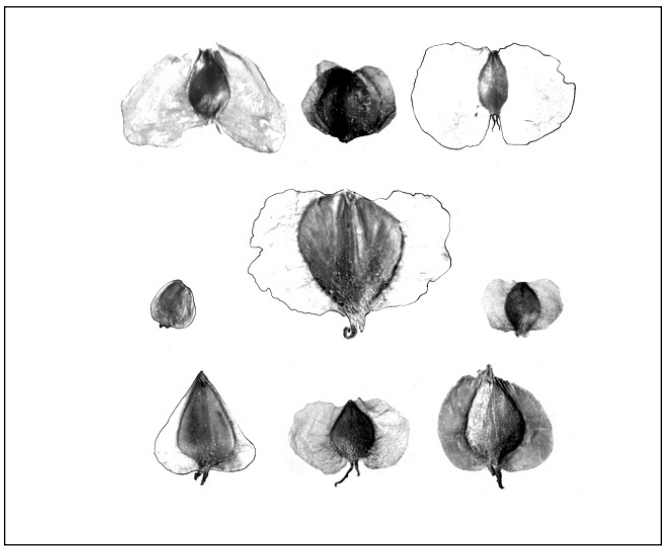
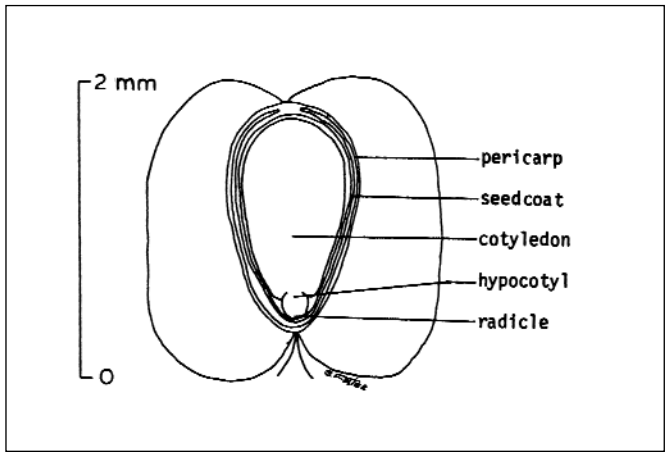


Figure 2—*Betula*, birch: winged nuts of *B. pendula*, European white birch (**top left**); *B. pumila*, low birch (**top center**); *B. populifolia*, gray birch (**top right**); *B. nana,* bog birch (**middle**); *B. nigra*, river birch (**middle center**); *B. pubescens,* hairy birch (**middle right**); *B. lenta*, sweet birch (**bottom left**); *B. papyrifer*a, paper birch (**bottom center**); and *B. alleghaniensis*, yellow birch (**bottom right**), enlarged.



proved satisfactory for the following species: glandulose birch, 2.38 mm (#6); yellow birch, 3.2 mm (#8); river birch, 4 mm (#10); paper birch, 3.2 mm (#8); European white and downy birches, 2.6 mm (~#7). The remaining scales can be removed by fanning (Brinkman 1974). Any stems can be removed with an indent cylinder. Very careful adjustment

Figure 3—*Betula nigra*, river birch: longitudinal section through a nut (seed).



with a column blower or a specific gravity table can upgrade the seedlot. Birch seeds are very small and light, with the number per weight and yield per volume varying considerably among species (table 4).

Seed storage. Heit (1967) reported that birch seeds apparently stored best at 1 to 3% moisture content and temperatures of 2.2 to 3.3 °C. Other tests with sweet, paper, and gray birches are in basic agreement with this position, thus indicating that birch seeds are orthodox in storage behavior. Seeds of these 3 species were found to keep for 1 $^1/_2$ to 2 years at room temperature if the moisture content was between 1 and 5%. If the moisture content was much higher, germination dropped even though the seeds were stored at 1.7 to 4.4 °C (Brinkman 1974). Slightly higher moisture content seems possible if freezer storage is used. One lot each of yellow, sweet, and paper birch seeds was successfully stored in the USDA Forest Service's National Tree Seed Laboratory seed bank for about 15 years with moisture contents between 5 to 9% at –8 °C (table 5). A lower moisture content would probably have been better, because the paper birch seeds began to deteriorate at 15 years and were discarded at 17 years. Liquid nitrogen storage also appears to be an option for the birch seeds (Iriondo and others 1992).

Pregermination treatment. It has been known for over 50 years that prechilling (that is, stratification) improved germination of birch seeds (Brinkman 1974). Several sources (Brinkman 1974; Heit 1967; ISTA 1996) state that light during germination is able to reduce or replace the need for prechilling to obtain complete germination. The barriers to germination in European white birch are removed by light or stratification (Black 1956; Black and Wareing 1954, 1955). However, prechilling can still be an important procedure. For example, Vanhatalo and others

Table 3—*Betula,* birch: height, seed-bearing age, and seed crop frequency

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yr)	Years between large seedcrops
B. allenghaniensis	30	1800	40	2
B. davurica	19.5	1883	—	2
B. lenta	24	1759	40	1–2
B. nana	1.8	1880	—	—
B. nigra	30	1736	—	—
B. papyrifera	21	1750	15	2
B. pendula	19.5	Long	15	2–3
B. populifolia	12	1750	8	1
B. pubescens	19.5	1789	15	2–3
B. pumila	3	1762	—	1–2

Sources: Brinkman (1974), Wappes (1932), Yelenosky (1961).

Table 4—*Betula,* birch: seed yield data

Species	Seeds/fruit vol		Cleaned seeds (1,000)/weight				
			Range		Average		
	kg/hl	lb/bu	/kg	/lb	/kg	/lb	Samples
B. alleghaniensis	1.3–4.5	1.0–3.5*	612–1,995	278–907	990	450	24
B. davurica	—	—	1,518–1,672	690–760	1,595	725	2+
B. lenta	—	—	975–2053	443–933	1,421	646	13
B. nana	—	—	6,547–11,253	2,976–5,115	8,446	3,839	3
B. nigra	—	—	631–1,206	287–548	825	375	13
B. papyrifera	2.6–9.4	2.0–3.4*	1,342–9,064	610–4,120	3,036	1,380	28
B. pendula							
(de-winged)	—	—	3,332–11,088	1,510–5,040	5,317	2,417	154+
(winged)	—	—	1,606–1,892	730–860	1,749	795	10
B. populifolia	—	—	7,878–10,846	3,581–4,930	9,363	4,256	2
B. pubescens	—	—	1,650–9,900	750–4,500	3,784	1,720	45
B. pumila	—	—	3,072–7,634	1,396–3,470	5,328	2,422	4

Sources: Brinkman (1974), NBV (1946), Rafn & son (1928).
* De-winged seeds.

(1996) found that not only did prechilling result in faster and higher germination, but it also improved the ability to germinate at temperatures below the optimum.

Furthermore, the birch genus is divided into 2 groups in regards to prechilling: those that will germinate in the dark with adequate prechilling and those that require light. For example, European white birch (Black and Wareing 1955, Vaartaja 1956) and paper birch (Bevinton and Hoyle 1981) can germinate in the dark, whereas monarch and Japanese white birches and Erman birch require light regardless of prechilling (Nagata and Black 1977; Nagata and Tsuda 1975; Odani and Anma 1986). Giberellic acid (GA_3) in concentrations of 50 to 100 ppm could substitute for the light with Erman birch (Odani and Anma 1986). However, in the light-obligatory group, the sensitivity to light is markedly increased by providing prechilling (Nagada and Black 1977). Therefore, prechilling can reduce the requirement for light when growing plants under artificial conditions. This might provide some cost savings during the germination phase by reducing lighting expense. Reducing the light requirement might also allow birch to be germinated in a greenhouse with other plants that had low light requirements. On the other hand, if there is not time for pregermination chilling, then light sufficient to keep dark periods less than about 6 hours may fully replace the need for prechilling.

It is important to know a seedlot's characteristics well when making the refined manipulations of light and prechilling suggested above, for prechilling beyond 3 weeks can lead to increased dormancy and obligatory use of light

Table 5—*Betula,* birch: germination of 3 seedlots stored for 8 years at the USDA Forest Service's National Tree Seed Laboratory, Dry Branch, Georgia

Species	Moisture content (%)	Prechilling (days)	Percent germination
B. alleghaniensis			
1974	—	—	—
1977	5.0	0	45
1983	—	63	70
1988	7.0	63	67
1991	—	0	32
1992	—	0	56
1992	—	21	58
B. lenta			
1974	—	30	54
1977	—	—	
1983	—	63	72
1988	7.9	63	67
1991	—	—	—
1992	—	0	45
1992	—	63	37
B. papyrifera			
1974	—	—	—
1977	7.0	0	76
1977		63	82
1983	—	63	87
1988	8.9	—	—
1991	—	0	4
1991	—	63	16
1992	—	0	18

in some sources of paper birch (Bevington 1986; Bevington and Hoyle 1981). Although light use was obligatory in these sources of paper birch, the seeds were well sensitized to the light and germination was prompt and complete. Bevington (1986) further found that seeds from different sources varied in the range of temperatures at which they would germinate. Seeds from northern sources were able to germinate over a wider range of temperatures than those from southern sources, mostly because they could germinate at cooler temperatures. Sensitivity to light did not seem to be related to geographic source but was universally enhanced in proportion to the length of prechilling, at least up to 6 weeks as demonstrated by faster and higher germination (Bevington 1986).

Prechilling temperatures need to be close to 2 or 3 °C. A rise in temperature to even 5 °C can increase the time needed to effectively overcome the dormancy (Bevington and Hoyle 1981; Vanhatalo and others 1996).

Germination tests. The use of light during the test can reduce or eliminate the need for prechilling. However, because some seedlots may benefit from prechilling, a test with and a test without prechilling are frequently recommended (AOSA 1998; ISTA 1996). Tests should be made on germination paper or sand at alternating temperatures of 30 °C for 8 hours and 20 °C for 16 hours with light supplied during the 30 °C period. Testing by AOSA rules requires planting 4 dishes of 100 seeds each. Should the seedlot be less than 98% pure, then a partial purity analysis must be done to acquire the needed pure seeds for the germination test. Because catkin bracts are not removed from many seedlots, the seedlots have low purity and ISTA prescribes testing by weighed replicate. In the weighed replicate test, 0.10 g of seed are planted in each of the 4 replicates. The number of normal seedlings per weight of seeds is then reported instead of a germination percentage. The results of some published test data are presented in table 6.

Nursery practice. Birch seeds can be sown after collection in the late summer or fall, or in the spring after prechilling for 4 to 8 weeks. Seeds are broadcast and covered as lightly as possible, with about 3 mm ($^1/_{16}$ to $^3/_{16}$ in) of soil. The seeds can be sown without covering (Brinkman 1974) if adequate irrigation can be supplied, which provides more light to the seed. Germination is epigeal (figure 4) and usually complete in 4 to 6 weeks after spring-sowing. Birch seedlings require light shade for 2 to 3 months during the first summer. Tree percent is low; only 15 to 20% of European white birch and downy birch seeds will produce 1+0 seedlings (Deasy 1954; Wappes 1932). A seedling density of 278 to 500/m^2 (25 to 45/ft^2) is desirable (Heit 1964). Stock usually is field planted as 1+0 or 2+0 seedlings. Birch seeds have shown marked sensitivity to herbicides and insecticides (Weinberger and others 1978; Weinberger and Vladut 1981).

In a study of open-pollinated families of yellow birch (Wearstler and Barnes 1977), heavier seeds produced taller seedlings immediately after germination. Seeds from mountain and more northern sources germinated earlier, but the seedlings tended to be shorter. The shorter seedlings and faster germination were generally associated with shorter growing season.

Cherry leaf roll virus is known to be transmitted through seeds. Transmission of this pathogen is highly variable and not generally strong. Two generations were estimated to be enough for the disease to be lost from a population of European white birch (Cooper and others 1984).

Germination on adverse sites. Environmental disturbances caused by mining operations and air pollution create conditions that have been suspected of interferring with normal seed germination for birch. The germination of European white and downy birches was found to be inhibited by high zinc concentrations (Brown and Wilkins 1986). Such heavy metal concentrations were thought to be a major reason for lack of colonization of these 2 species on mine

Table 6—*Betula,* birch: germination and purity test data

Species	Prechill period (days)	Daily light (hr)	Germination conditions			Germination			Purity (%)
			Medium	Temp (°C) Day	Night	Days	Avg (%)	Samples	
B. alleghaniensis	30–0	8+	Sand	32	15	30–40	27	22	56
	None	8+	—	30	20	14–28	59	3	60
B. davurica	None	8+	—	30	20	14–8	18	4	—
B. lenta	40–70	8+	Sand	32	15	30	43	13	72
B. nana	(over winter)	—	Sand	30	20	30	24	1	—
	None	20	Perlite	24	18	30	3	5	—
B. nigra	30–60	8+	Sand	30	20	30	34	13	42
	None	20	Perlite	24	18	30	73	35	—
B. papyrifera	60–75	8+	Sand	32	15	30–40	—	—	24
	None	8+	Paper pads	—	—	40	47	6	—
B. pendula	30–40	8+	Sand	—		—	30	10+	68
	None	8+	—	30	20	30–40	36	143	—
B. populifera	60–90	8+	Sand	30	20	40	64	3	—
B. pubescens	30–60	8+	—	30	20	30	40	44	69
	None	8+	—	25	15	30	87	17	—
B. pumila var. glandulifera	None	20	Perlite	24	18	30	31	4	38

Sources: Black and Waring (1954, 1955), Brinkman (1974), Heit (1968), Gorshenin (1941), Yelenosky (1961).

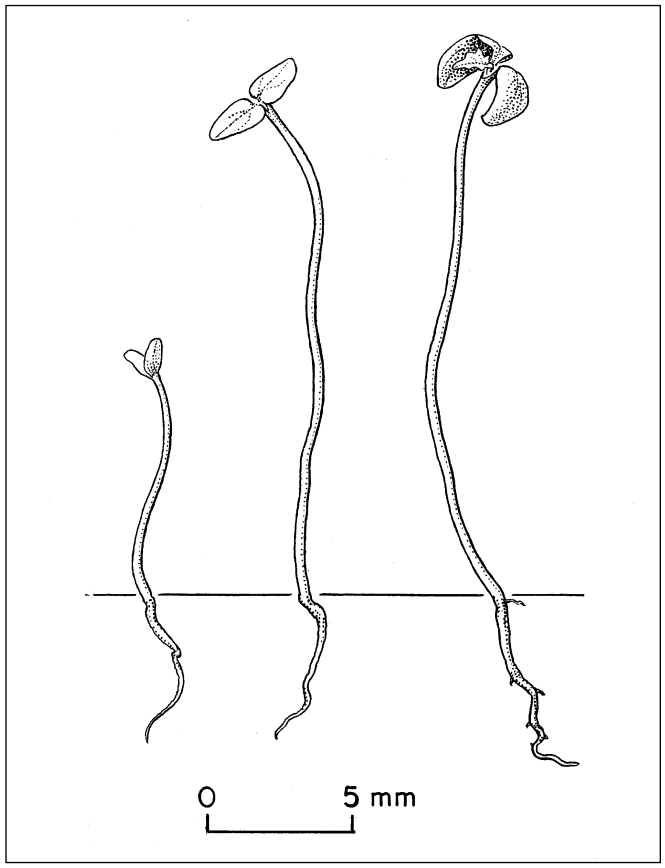


Figure 4—*Betula populifoliaa*, gray birch: seedling development at 1, 10, and 40 days after germination.

spoil in Wales. On the other hand, Scherbatskoy and others (1987) found that heavy metals and low pH did not reduce germination of yellow or paper birch seed samples taken in Vermont. Reduced regeneration of these 2 species had been associated with low soil pH and increasing concentrations of heavy metals believed to be caused by air pollution. In fact, pH of 3 produced germinations higher than controls or pH values of 4 or 5. Growth of gray birch on coal mine spoils in Pennsylvania is likely to be inhibited by the high temperatures of the soil surface(Pratt 1986).

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Verbenaceae—Verbena family

Callicarpa americana L.

American beautyberry

Franklin T. Bonner

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Other common names. French-mulberry, Spanish-mulberry, sour-bush, sow-berry.

Growth habit, occurrence, and uses. American beautyberry—*Callicarpa americana* L.—is a small, woody shrub of the pine forests in the southern coastal plain. It seldom grows taller than 2 or 3 m. The shrub is common underneath the pine overstory and along roads and forest edges, where it grows best. It is found from Virginia to Florida and west to Texas and Oklahoma; it also occurs in the West Indies (Vines 1960). American beautyberry is an important food plant for wildlife, especially birds and eastern white-tailed deer *(Odocoileus virginianus)* (Blair and Epps 1969; Grelen and Duvall 1966; Halls 1973). The shrub's well-branched root system and drought resistance make it desired for erosion control in some areas (Brown 1945), and it is frequently grown as an ornamental because of the colorful fruits (Dirr and Heuser 1987).

Flowering and fruiting. The small, inconspicuous flowers are borne in axillary, dichotomous cymes about 8 to 36 mm long. Flowering starts in early June and may continue into the fall months, even as the fruits mature in August to November (Dirr and Heuser 1987; Vines 1960). The fruit is a berrylike, globose drupe, about 3 to 6 mm in diameter, that is borne in conspicuous axillary clusters on the current season's growth. The rose to purple, or sometimes white (Brown 1945), fruit color gives this plant its ornamental value. A single fruit cluster may contain as many as 300 fruits, although about 100 is typical. Each fruit usually contains 4 small flattened seeds that are light brown in color and about 1 to 1.5 mm in length (Grelen and Duvall 1966; Vines 1960) (figures 1 and 2). Plants begin to bear fruit as early as 2 years of age, and mature plants may yield over $^1/_2$ kg (about 1 lb) annually (Halls 1973).

Collection of fruits; extraction and storage of seeds. Fruits can be easily collected by hand in autumn, when their rose to purple color indicates maturity. The soft fruits quickly disintegrate when they are macerated with water. Filled

Figure 1—*Callicarpa americana*, American beautyberry: seeds.

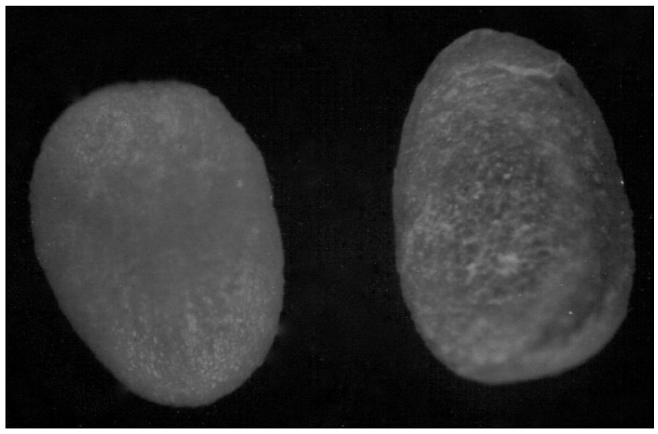
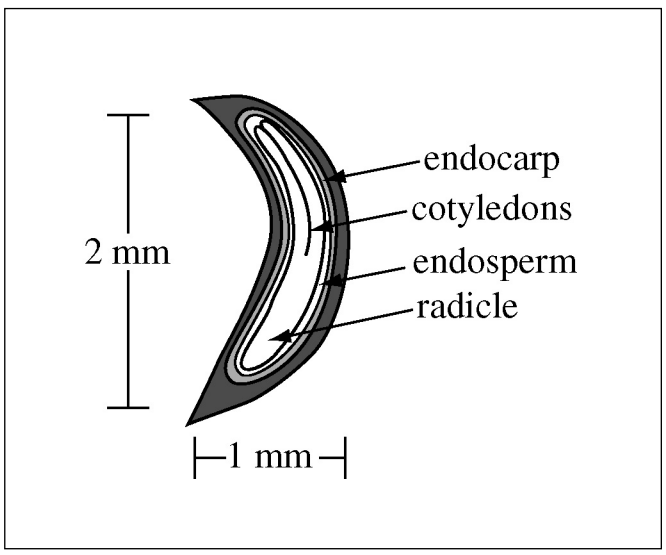


Figure 2—*Callicarpa americana*, American beautyberry: longitudinal section through a seed.



seeds sink in water, and the pulp can be floated off. Any type of macerator should work, even laboratory or kitchen blenders for small lots. There are about 600 seeds/g (17,000/oz), and good cleaning should yield a purity of practically 100%. There are no known storage data for this species, but soil seed bank studies show that the seeds will survive for at least 1 year buried in the soil. This fact, plus the hard seedcoat, suggest that these seeds are orthodox in storage behavior. Long-term storage at temperatures near or below freezing should be successful with seeds that are dried to below 10% moisture content.

Pregermination treatments and germination tests. The seeds have a hard seedcoat, and germination is relatively slow. One sample stratified for 30 days yielded only 22% germination in 90 days when tested at an alternating temperature of 20 °C at night and 30 °C in the light. Untreated seeds sown in the fall, however, were reported to give excellent germination in the spring (Dirr and Heuser 1987). There are no official test prescriptions for American beautyberry.

Nursery practice. No details of nursery practices for American beautyberry are available, except the successful fall-sowing mentioned above. The small seed size suggests that soil or mulch covers after sowing must be very light. Vegetative propagation is not difficult with this species. Softwood cuttings taken anytime from June to September root well if treated with IBA (1,000 ppm) and placed in a mist bed (Dirr and Heuser 1987).

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Cupressaceae—Cypress family

Calocedrus decurrens (Torr.) Florin

incense-cedar

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Synonyms. *Libocedrus decurrens* Torr., *Heyderia decurrens* (Torr.) K. Koch.

Other common names. California incense-cedar, pencil cedar, pecky cedar.

Growth habit, occurrence, and uses. Incense-cedar was once classified as the only species in the genus *Libocedrus* native to the United States (Harlow and others 1979; Little 1979), but recent taxonomic changes have included it as 1 of 3 species in the genus *Calocedrus* Kurz. Regional genetic variation within incense-cedar is small, but 12-year growth of trees from southern California was less than that of trees from more northerly regions (Rogers and others 1994). Recognized cultivars under the former classification include *L. decurrens* cv. *aureovariegata* Beissner, *L. decurrens* cv. *columnaris* Beissner, *L. decurrens* cv. *compacta* Beissner, and *L. decurrens* cv. *glauca* Beissner (Harrison and Dallimore 1966; Rehder 1940).

Mature trees of this evergreen conifer vary in height from 15 to 46 m and from 0.3 to 2.13 m in diameter (Jepson 1910; Sargent 1961; Sudworth 1908). A maximum circumference of 12.9 m (van Pelt 2001) and a maximum height of 68.6 m have been reported (Stein 1974). Young trees generally have dense pyramidal to columnar crowns; older trees are characterized by more open, irregular crowns; rapidly tapering trunks with buttressed bases; and deeply furrowed and ridged bark.

The range of incense-cedar spans about 15 degrees of latitude, from the southeastern slopes of Mount Hood in Oregon southward within and adjacent to the Cascade, Siskiyou, coastal, and Sierra Nevada ranges to the Sierra de San Pedro Martír in northwestern Mexico (Griffin and Critchfield 1976; Sudworth 1908). It extends eastward from the coastal fog belt to arid inland parts of central Oregon, northern California, and westernmost Nevada. In elevation, incense-cedar is found from 50 to 2,010 m in the north and from 910 to 2,960 m in the south (Peattie 1953; Powers and Oliver 1990; Sudworth 1908). Incense-cedar grows on many kinds of soil and is one of the most prominent conifers on serpentine soils. Typically, it is a component of mixed conifer forest and may make up as much as 50% of the total stand (Powers and Oliver 1990).

Trees are harvested primarily for lumber and for round or split wood products. The wood is variable in color, durable, light, moderately soft, uniformly textured, easy to split and whittle, and finishes well. Incense-cedar is also used as a pulp additive and for making a variety of specialty items, the best known being the wooden pencil (Betts 1955; Panshin and others 1964). Boughs, particularly those bearing staminate cones, are harvested commercially for decorations (Schlosser and others 1991), and young trees are a minor component of the Christmas tree trade.

First cultivated in 1853, ornamental specimens with shapely crowns have grown well in many places outside of their native range in the Pacific Northwest—in New England and in the mid-Atlantic region of the United States and western, central, and southern Europe (Edlin 1968; Harrison and Dallimore 1966; Jelaska and Libby 1987; Sargent 1961). Within its native range, incense-cedar is commonly planted for highway landscaping, screenings, and home-site improvement.

Young incense-cedars are sometimes browsed extensively (Stark 1965), but in general, the species rates low to moderate in value as wildlife browse (Longhurst and others 1952; Sampson and Jespersen 1963; Van Dersal 1938). Its seeds are eaten by small mammals (Martin and others 1951) but are not a preferred food of chipmunks (Tevis 1953). Dense understory incense-cedars provide an important source of cover and food for overwintering birds in the western Sierra Nevada (Morrison and others 1989).

Flowering and fruiting. Yellowish green staminate flowers develop terminally on twigs as early as September even before the current year's cones on the same twigs have opened (Stein 1974). These flowers, 5 to 7 mm long, are prominently present "...tingeing the tree with gold during

the winter and early spring..." (Sargent 1961). The inconspicuous pale yellow ovulate flowers also develop singly at tips of twigs. Flowering has been reported to occur as early as December and as late as May (Britton 1908; Hitchcock and others 1969; Mitchell 1918; Peattie 1953; Sargent 1961; Sudworth 1908), but it is not clear how well observers distinguished between flower appearance and actual pollen dissemination. Unopened staminate flowers and open or nearly open ovulate flowers were present on branches collected in the first week of April west of Klamath Falls, Oregon (Stein 1974).

Individual cones (figure 1), each containing up to 4 seeds, are scattered throughout the crown, and mature in a single growing season. As they ripen, their color changes from a medium green to a yellowish green or yellow tinged with various amounts and shades of brown. During opening, the cone becomes reddish brown and acquires a purplish cast. Insect-attacked cones are among the first to change color. Generally, cones of many color shades are found on a tree as opening commences.

Seed dispersal may extend over a lengthy period, from late August through November or later (Fowells and Schubert 1956; McDonald 1992; Mitchell 1918; Powers and Oliver 1990; Sudworth 1908). For example, in 1937 and 1940, respectively, 11 and 32% of the seed had fallen by early October at 1 or 2 California locations, yet 47 and 66% of the total fell after November 11 (Fowells and Schubert 1956). Cutting tests have shown that 14 to 65% of the naturally dispersed seeds appear sound, with higher values coincident with heavy crops (Fowells and Schubert 1956).

The oft-repeated generalization that incense-cedars bear some seeds every year and abundant crops frequently (Betts 1955; Mitchell 1918; Sudworth 1908; Van Dersal 1938) has not been confirmed by systematic observations made in 3 locations. During a 35-year period on the Stanislaus National Forest in California, incense-cedars bore a heavy or very heavy crop in 7 of those years, a medium crop in 11 years, and a light crop in 17 years (Schubert and Adams 1971). On the Challenge Experimental Forest in central northern California, there were 1 medium to heavy and 9 light to very light crops in 24 years (McDonald 1992). During 15 years on the South Umpqua Experimental Forest in southwest Oregon, there were 2 abundant crops, 1 medium crop, and 12 years with light or no crops (Stein 1974). Generalized statewide reports for California and Oregon show that incense-cedar cone crops are often light and that there is wide geographic variability in crop abundance (Schubert and Adams 1971). During years when crops are reported as light or a failure, scattered cones, even an occasional heavily loaded tree, may be found somewhere.

Figure 1—*Calocedrus decurrens*, incense-cedar: cones hang singly from branch tips well-dispersed over the crown and contain up to 4 seeds each.

Flowers and young cones may be damaged or killed occasionally by adverse climatic factors, and squirrels cut some mature cones (Fowells and Schubert 1956). Losses are also caused by sawflies (*Augomonoctenus libocedrii* Rohw.), juniper scale (*Carulaspis juniperi* Bouche*)*, and leaf-footed bugs (*Leptoglossus occidentalis* Heidemann) that feed on developing cones and seeds (Furniss and Carolin 1977; Koerber 1963).

Collection of cones. Cones are generally hand-picked from standing or felled trees. Stripping cones or using a cone rake will expedite collection because cones hang dispersed over the crown. The ideal time for collection is the short period when cleavages appear between the scales of many cones on a tree. If large quantities of seeds are needed, both collecting them from plastic sheets spread beneath or enclosing the tree and vacuum-harvesting seeds from the ground merit consideration. Dispersed seeds should be collected promptly to minimize heat damage. To facilitate later seed cleaning, foliage intermixed with cones or seeds should be removed during collection or shortly afterward, before it dries and crumbles.

Cones are normally handled and transported in partly filled open-mesh sacks that facilitate cone expansion and air exchange. Good aeration should be provided around each sack to keep the cones from overheating during storage.

Extraction and storage of seeds. To maintain high seed viability, cones should not be exposed to high temperatures. Under warm, dry conditions, cones will air-dry outdoors or indoors in 3 to 7 days if layered thinly in trays or on sheeting or tarps. Turning or stirring layered cones will

facilitate drying and opening. They may also be kiln-dried at 27 °C or lower (Lippitt 1995).

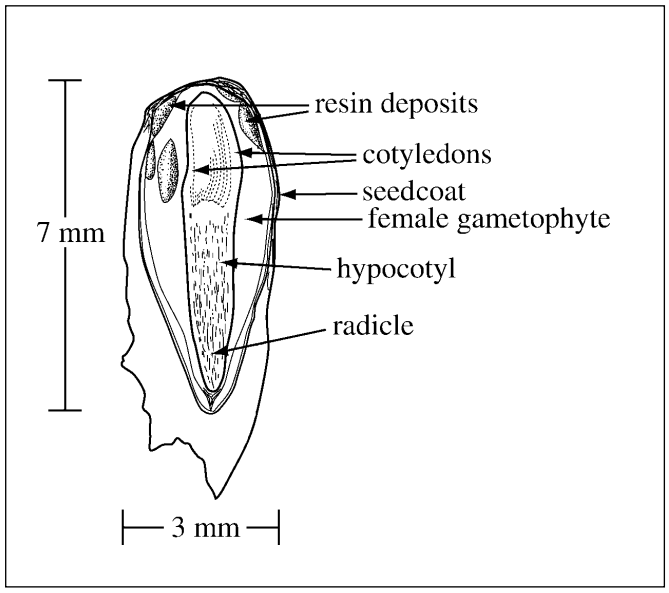
Seeds separate readily from well-opened cones; moderate tumbling or shaking is helpful. Whether done by improvised methods or in commercial machines, tumbling or shaking should be done gently, preferably at less than 27 °C, because seedcoats of incense-cedar are thin and easily broken.

The winged seeds are about 2.5 cm long and nearly one-third as wide (figure 2). Although appearing to have only 1 wing, each seed actually has 2 wings—a long, wide wing extending lengthwise beyond the seed on one side and a narrow, much shorter wing barely merging alongside the first from the opposite side. The wings are persistent and project past the narrow radicle end of the seed rather than from the cotyledon end as in many other conifers (figure 3).

The persistent wings should be left intact. When seeds are run through mechanical de-wingers, the narrow radicle ends may break off along with the wings. This type of damage was the probable cause of the very low viability observed in some lots of de-winged seeds. Damaging effects should be evaluated before using any proposed hand or mechanical de-winging technique.

Figure 2—*Calocedrus decurrens*, incense-cedar: each seed has 2 wings, a long, wide wing on one side (**right**) and a narrow, much shorter one on the other side (**left**).

Figure 3—*Calocedrus decurrens*, incense-cedar: longitudinal section showing the radicle located at the narrow end of the seed.



Small particles of debris can be removed from among winged seeds by screening. Sensitive adjustment of an air stream or gravity separator will permit further cleaning and adequate separation of empty from full seeds with wings intact. Purities of 85 to 98% or more have been obtained (Lanquist 1946; Lippitt 1995; Rafn 1915; Toumey and Korstian 1942).

Thirty-five liters (1 bu) of cones weigh 18 to 23 kg (40 to 50 lbs) and yield from 0.45 to 1.36 kg (1 to 3 lb) of seeds (CDF 1969; Tillotson 1925; Toumey and Korstian 1942). A minimum of 14,110 and a maximum of 63,930 seeds/kg (6,400 and 29,000 seeds/lb) were found among 55 samples from northern California weighed by Show in 1918. More recent collections indicate that seeds per weight values differ by seed zone (Lippitt 1995):

	Average		Range		
Region & seed zone series no.	**/kg**	**/lb**	**/kg**	**/lb**	**Samples**
Siskiyou Mtns. & inland north coastal range (SZ #300)	27,270	12,368	24,820–29,960	11,260–13,588	41
Sierra Nevada (SZ #500)	31,820	14,433	21,540–45,330	9,768–20,562	36
Southern California & Central Valley (SZ #900)	33,420	15,160	24,120–38,760	10,940–17,583	5

Reported averages representing collections made largely in northern and central parts of the species' range vary from 27,270 to 44,450 seeds/kg (12,368 to 20,160 seeds/lb) (CDF 1969; Lanquist 1946; Lippitt 1995; Mitchell 1918; Rafn 1915; Show 1918; Stein 1963; Sudworth 1900; Tillotson 1925; Toumey and Korstian 1942). The smaller averages are probably the most realistic, for samples weighed by several investigators contained only 60 to 67% full seeds either winged or wingless (Lanquist 1946; Show 1918).

Incense-cedar seeds do not keep well in dry storage at room temperature (Shaw 1918), but high viability can be maintained for several years in cool storage. In limited tests, 2 seedlots retained 98% and 74% viability after storage in closed metal containers at 5 °C for 2 and 3 years, respectively, but lost all viability after 8 years (Schubert 1954). It is now common practice to store incense-cedar seeds dried to low moisture content near –18 °C in cloth or plastic bags or in plastic-lined fiberboard containers. Mature, undamaged seedlots have retained viability in cold storage for 10 years at 5 to 9% moisture content (Lippitt 1995); maximum duration before such lots begin losing viability has not been determined.

Pregermination treatments and germination tests. Standard procedures prescribed by the Association of Official Seed Analysts (1999) for testing incense-cedar seeds include chilling them for 30 days at 2 to 5 °C before germination. Comparison tests showed that prechilling markedly improved total germination and rate of germination of some but not all lots (Stein 1974). Short of making a paired test, there is no way to identify which lots benefit from prechilling and which ones do not. To prepare them for prechilling, seed samples are either (1) placed on a moist substratum in a closed dish; (2) placed in a loosely woven bag or screen surrounded by moist peat, sand, or vermiculite; or (3) allowed to soak for 24 hours in tap water at room temperature, drained, and then placed in a glass or plastic container.

Following prechilling, germination of incense-cedar is determined by subjecting seeds for 28 days to alternating temperatures—16 hours at 20 °C and 8 hours at 30 °C with 750 to 1250 lux (75 to 125 foot-candles) exposure to cool-white fluorescent illumination at least during the high-temperature period (AOSA 1999). Tests should be carried out on cellulose paper wadding or blotters in closed germination boxes. Germination for 85 lots now in storage at one nursery has averaged 72% following 8 weeks of naked stratification (Lippitt 1995).

The viability of incense-cedar seeds can also be determined by a tetrazolium test (AOSA 2000). The preparation sequence involves removal of wings from dry seeds followed by soaking in water at room temperature for 6 to 18 hours (overnight). Shallow longitudinal cuts are then made on both ends of the seed to expose the embryo. Cut seeds are immersed in a 1% tetrazolium solution and kept in darkness for 6 to 18 hours at 30 to 35 °C. Seeds having a completely stained embryo and a completely stained endosperm are considered viable. Viability determined by the tetrazolium test reveals the seeds' maximum potential and generally is somewhat higher than indicated by a germination test.

Nursery practice and seedling development. Soil fumigation of outdoor beds to combat damping-off and other diseases may or may not be necessary before sowing incense-cedar seeds. Maintenance or replacement of endomycorrhizal fungi is of concern if beds are fumigated. Spring-sowing is now most common even though fall-sown seeds germinated earlier and more uniformly than those sown in the spring and resulting seedlings grew larger in the first season if they escaped damage by late spring frosts (Show 1930). An intermediate approach is to prepare seedbeds in the fall to facilitate early sowing in February or March. Before sowing, seeds are usually stratified naked or in a moist medium at 2 to 5 °C for 30 to 60 days (Lippitt 1995). Well-timed spring-sowings of unstratified seeds have produced satisfactory crops (Show 1930; Stein 1974), but results are less certain. Some spring-sown seeds may hold over to produce seedlings the following spring (Show 1930).

The winged seeds are usually hand-sown in rows. They should be covered about 6 to 12 mm ($^1/_4$ to $^1/_2$ in) deep (Show 1930). Burlap mulch proved satisfactory to keep seedbeds moist (Show 1930); sawdust or other mulch material and frequent sprinkler irrigation are currently used.

Incense-cedar can readily be grown in containers to plantable size in one season. Containers about 15 cm (6 in) deep with a volume of 165 to 215 cm^3 (10 to 13 in^3) are recommended. The seedlings may be started about February in a greenhouse and moved outdoors after 4 to 8 weeks or they may be germinated and grown entirely outdoors.

Germination is epigeal and the radical emerges from the narrow winged end of the seed (figure 4). Young seeds usually have 2, rarely 3, cotyledons (Harlow and others 1979). Leaves about 1.2 cm (0.5 in) long develop along the epicotyl (figure 5). On the first branches, awl-shaped transitional leaves grade into the normal scalelike leaves (Jepson 1910). Seedlings grow 5 to 20 cm (2 to 8 in) tall in the first season and develop a well-branched root system. Young seedlings are fairly resistant to frost and drought (Fowells and Stark 1965; Pharis 1966; Stone 1957). They are preferentially attacked by cutworms, however, and need protection from damping-off (Fowells 1940; Fowells and Stark 1965; Show

Figure 4—*Calocedrus decurrens*, incense-cedar: germinating seed with radicle and hypocotyl emerging from the winged end.

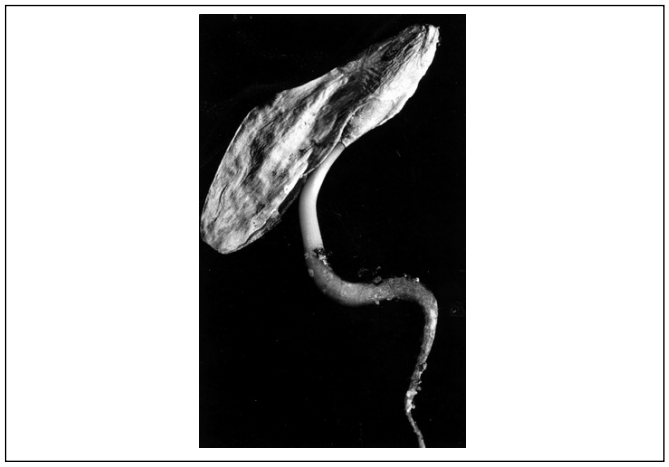
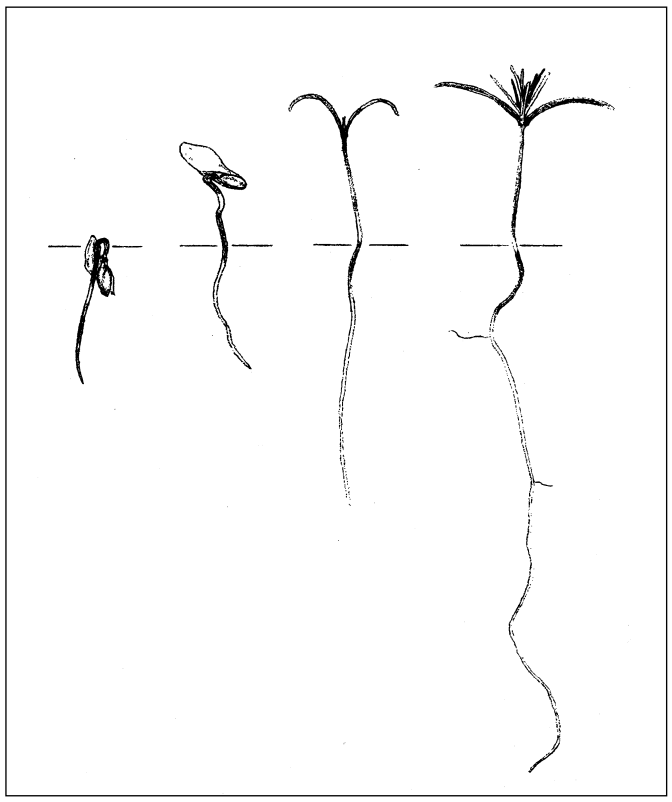


Figure 5—*Calocedrus decurrens*, incense-cedar: seedling development 4, 7, 10, and 17 days after germination.



1930; Stein 1963). In the north-central Sierra of California, they grew about as well unshaded as with one-fourth shade (Show 1930). In current practice, both bareroot and container seedlings are grown without shade. They should be watered regularly but not to excess. Beds may be weeded entirely by hand or with mechanical and chemical assistance.

Seedbed densities of 270 to 325 seedlings/m^2 (25 to 30/ft^2) are satisfactory for producing 1+0 stock. Densities of 160 to 215 seedlings/m^2 (15 to 20/ft^2) are used for 2+0 stock. Tree percents range from 20 to 75 (Show 1930; Stein 1974). Generally, 2+0 bareroot seedling stock is used for outplanting, but 1+0, 1+1, 2+1, and 1+2 transplants have also been used. Some of the target sizes now used for producing stock include 1+0 (stem caliper 3 mm and top length 13 cm), 2+0 (stem caliper 3.5 cm and top length 20 cm), and 1+1 (stem caliper 4 mm and top length 25 cm). Outplanting in the spring proved best in long-ago tests (Show 1930) and continues to be favored.

Incense-cedar also can be reproduced from cuttings started in November (Nicholson 1984), and responds better than most conifers to cell and tissue culture (Jelaska and Libby 1987).

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Bignoniaceae—Trumpet-creeper family

Campsis radicans (L.) Seem. ex Bureau

common trumpet-creeper

Franklin T. Bonner

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Synonyms. *Bignonia radicans* L., *Tecoma radicans* (L.) Juss.

Other common names. trumpetvine, cowitch vine, trumpet-flower.

Growth habit, occurrence, and uses. Common trumpet-creeper—*Campsis radicans* (L.) Seem. ex Bureau, a deciduous vine—is native from Texas to Florida and north to Missouri, Pennsylvania, and New Jersey (Vines 1960). It has also been introduced into New England (Bonner 1974). The vine is sometimes used in erosion control and as an ornamental, but its greatest value is for wildlife food. Hummingbirds are common visitors to trumpet-creeper flowers.

Flowering and fruiting. The large, orange-to-scarlet, perfect flowers are 5 to 9 cm long and appear from May through September (Bonner 1974; Vines 1960). This species is largely self-sterile, but pollinates well when self and cross pollen are mixed (Bertin and Sullivan 1988). The fruit is a 2-celled, flattened capsule about 5 to 15 cm long (figure 1) that matures from September to November (Vines 1960). The capsules turn from green to gray brown as they mature, and the small, flat, winged seeds (figures 1 and 2) are dispersed chiefly by wind as the mature capsules split open on the vine from October through December (Bonner 1974; Vines 1960). Good seed crops are borne annually.

Collection and extraction. Ripe capsules should be gathered when they turn grayish brown in the fall before splitting open. Seeds can be extracted by hand-flailing. There are approximately 300,000 cleaned seeds/kg (136,000/lb) (Bertin 1990; Bonner 1974). One sample had a purity of 98%, with 52% sound seeds (Bonner 1974). The longevity of common trumpet-creeper seeds in storage is not known, but if the seeds are dried to about 10% moisture content, they should store as well as other orthodox seeds.

Germination and nursery practice. The seeds exhibit some embryo dormancy. Pretreatment is not necessary for germination, but cold, moist stratification for 60 days at 5 to

Figure 1—*Campsis radicans*, common trumpet-creeper: fruit (**top**) and seed (**bottom**).

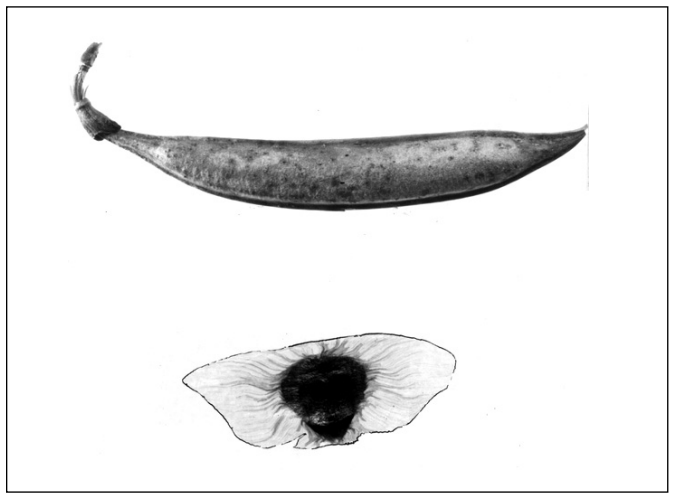
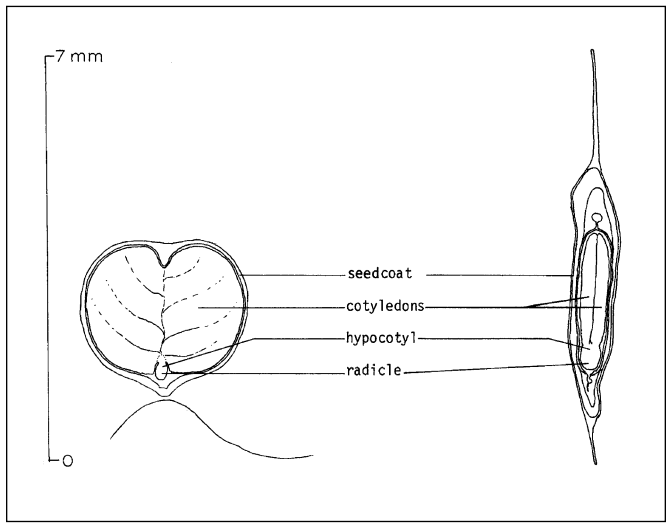
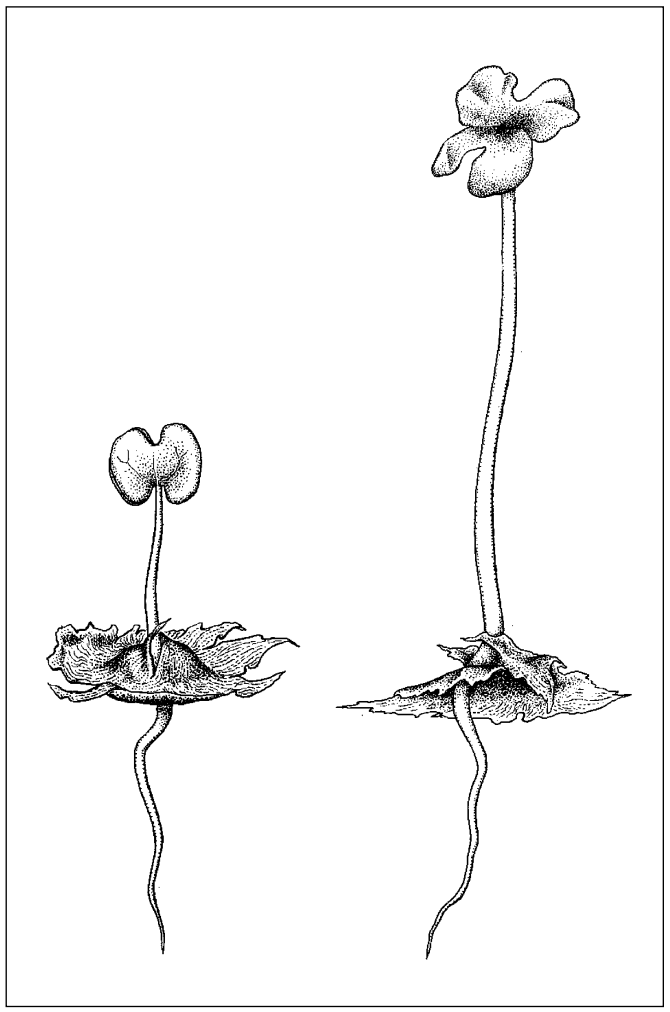


Figure 2—*Campsis radicans*, common trumpet-creeper: longitudinal section through a seed.



10 °C is recommended for quick and uniform germination (Bonner 1974; Dirr and Heuser 1987). Germination tests in sand have been run for 30 days at 20 °C night and 30 °C day temperatures. Four tests with stratified seeds averaged 66% germination, and germination rate was 51% in 19 days (Vines 1960). Germination is epigeal (figure 3). Seedlings can be grown in nurserybeds from either untreated seeds sown in the fall or from stratified seeds sown in the spring. Some horticultural cultivars are propagated by stem and root cuttings and layering. Softwood cuttings taken in June to September are easily rooted without hormone treatments (Dirr and Heuser 1987).

Figure 3—*Campsis radicans*, common trumpet-creeper: seedling development at 1 and 9 days after germination.



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Fabaceae—Pea family

Caragana arborescens Lam.

Siberian peashrub

Donald R. Dietz, Paul E. Slabaugh, and Franklin T. Bonner

Drs. Dietz and Slabaugh (deceased) retired from the USDA Forest Service's Rocky Mountain Forest and Range Experiment Station; Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi

Synonym. *Caragana caragana* Karst.

Other common names. caragana, pea-tree.

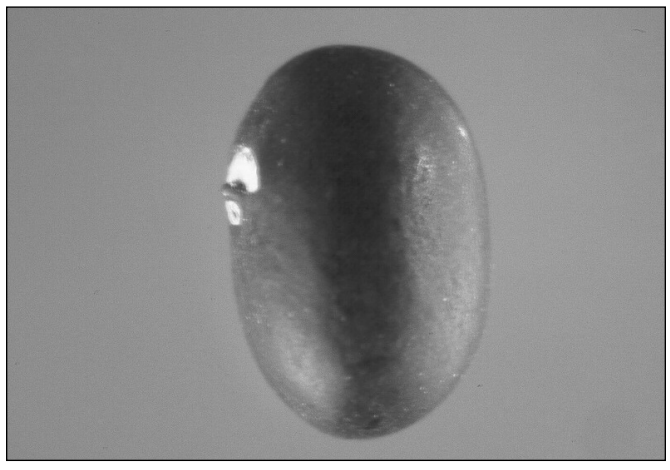
Growth habit, occurrence, and use. Siberian peashrub—*Caragana arborescens* Lam.—is one of the most hardy small deciduous trees or shrubs planted on the northern Great Plains (George 1953; Rehder 1940). Introduced into North America in 1752 (Rehder 1940), Siberian peashrub is native to Siberia and Manchuria and occurs from southern Russia to China *(Graham 1941)*. Varieties include the dwarf (*C. a. nana* Jaeg.) and Lorberg (*C. a. pendula* Carr.) peashrubs (Kelsey and Dayton 1942). The species readily adapts to sandy, alkaline soil and open, unshaded sites on the northern Great Plains, where it grows to heights of 7 m. It has been planted extensively for shrub buffer strips and windbreaks on farmlands and for hedges and outdoor screening in many towns and cities of the upper mid-West (Dietz and Slabaugh 1974; George 1953). It was also planted for wildlife and erosion control in the Great Lakes region (Graham 1941) and for deer-range revegetation programs in the Black Hills of South Dakota (Dietz and Slabaugh 1974). It is now considered invasive.

Flowering and fruiting. The yellow bisexual flowers appear from April to June. The fruit is a legume (pod) that measures 2.5 to 5 cm (figure 1) and contains about 6 reddish-brown, oblong to spherical seeds 2.5 to 4.0 mm in diameter (Lindquist and Cram 1967; Ross 1931) (figures 2 and 3). Fruits change in color to amber or brown as they ripen from June to July (Rehder 1940). Seed dispersal is usually completed by mid-August in most areas on the Great Plains. Shrubs take about 3 to 5 years to reach commercial seed-bearing age, and good crops occur nearly every year (Dietz and Slabaugh 1974).

Collection of fruits. The optimum seed collection period for Siberian peashrub is less than 2 weeks—usually in July or early August. Because the fruits begin to split open and disperse the seeds as soon as they are ripe, the legumes should be gathered from the shrubs by hand as soon as the first ones begin to open (Dietz and Slabaugh 1974).

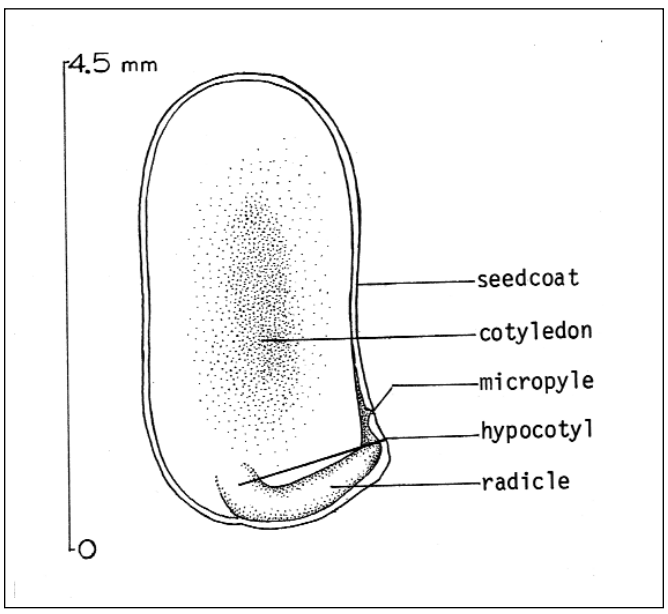
Figure 1—*Caragana arborsecens*, Siberian peashrub: legume.

Figure 2—*Caragana arborsecens*, Siberian peashrub: seed.



Extraction and storage of seeds. The legumes should be spread out to dry in a protected area until they pop open. The seeds can then be extracted easily by light maceration or beating. Legume fragments and other trash can be removed with aspirators, air-screen cleaners, or fanning mills. The average number of cleaned seeds per weight ranges from 28,700 to 48,500/kg (13,000 to 22,000/lb), with a purity of 97 to 100% (Dietz and Slabaugh 1974). A yield

Figure 3—*Caragana arborsecens*, Siberian peashrub: longitudinal section through a seed.



of 13 to 20 kg of seeds/100 kg (13 to 220 lb/100 lb) of fresh legumes has also been reported.

Seeds of Siberian peashrub, like those of other legumes, are orthodox in storage behavior. Studies in Canada have shown that the seeds remain viable for at least 5 years when stored dry at room temperatures. Germination of seedlots stored this way was 94% after 1 and 2 years and 93% after 5 years (Cram 1956). For the best long-term storage, seeds should be stored dry in polyethylene bags (or other sealed containers) at –18 to 4 °C, with a moisture content between 9.6 and 13.5% (Lindquist and Cram 1967).

Pregermination treatments and germination testing. For a leguminous species, Siberian peashrub does not have a very impermeable seedcoat. Untreated seeds will germinate in 15 days after sowing, but the best germination (87 to 100% in 5 days) can be obtained by soaking seeds for 24 hours in cold or hot (85 °C) water (Dirr and Heuser 1987). Successful germination has also been reported after acid scarification, cold stratification for 2 weeks, or fall planting (Dietz and Slabaugh 1974; Dirr and Heuser 1987; Hamm and Lindquist 1968; Lindquist 1960). Certain pesticides, such as captan and thiram, can apparently increase germination, possibly by inhibiting seed-borne disease (Cram 1969). The official testing prescription for Siberian peashrub seeds calls for clipping or filing through the seedcoat on the cotyledon end, soaking these seeds in water for 3 hours, then germinating them for 21 days at alternating temperatures of 20/30 °C (ISTA 1993). Germination tests have also been carried out in flats of sand or perlite and in Jacobsen germinators for 14 to 60 days at the same alternating temperatures (Dietz and Slabaugh 1974; Hamm and Lindquist 1968). Germination after 25 to 41 days averaged 45 to 72%, and 55 to 100% after 60 days (Dietz and Slabaugh 1974).

Nursery practice. Seeds of Siberian peashrub may be drilled or broadcast in late summer or spring. In a North Dakota nursery, Siberian peashrub is seeded during the last week in July or the first week in August. A cover crop of oats is seeded between the tree rows early enough to give winter protection. The shrubs are large enough to dig the following fall (Dietz and Slabaugh 1974). Many nurseries recommend drilling 80 to 160 seeds/m (25 to 50/ft) at 6, 9, or 12 mm ($^1/_4$ to $^1/_2$ in) depth; percentages of seeds growing into seedlings have varied from 35 to 50 (Dietz and Slabaugh 1974; Lindquist and Cram 1964).

Grading seeds for size has greatly increased the percentage of plantable seedlings. To be plantable, seedlings should be 30 cm (12 in) or more in height at the time of lifting. Only 87% of the seedlings grown from seeds measuring 2.5 mm in diameter were plantable, whereas 77% of seeds measuring 4.0 mm in diameter were plantable (Lindquist and Cram 1967). Inoculation of seeds with *Rhizobium* ssp. before sowing has been recommended (Wright 1947), but other workers report no significant effect on 1+0 seedlings (Cram and others 1964). Commercial nurseries have recommended anywhere from 1+0 to 3+0 stock for outplanting (Dietz and Slabaugh 1974).

Spraying to control insects in the nursery may be necessary. Grasshoppers are especially destructive to Siberian peashrub, sometimes completely defoliating the plants (Kennedy 1968). Plants have also been extensively damaged by deer browsing.

Vegetative propagation of Siberian peashrub is also possible. Untreated cuttings taken in late July rooted 80% in sand, whereas cuttings taken earlier (May to June) responded well to indole-butyric acid (IBA) in talc (Dirr and Heuser 1987).

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C

Cactaceae Cactus family

Carnegiea gigantea (Engelm.) Britton & Rose

saguaro or giant cactus

Susan E. Meyer

Dr. Meyer is a research ecologist at the USDA Forest Service's Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, Utah

Growth habit, occurrence, and use. Saguaro—*Carnegiea gigantea* (Engelm.) Britton & Rose—has the northernmost distribution of any of the large, columnar cacti of the tropical and subtropical Americas. Formerly regarded as a member of the genus *Cereus,* it is now considered the single species of its own genus, *Carnegiea*. It is a principal indicator species of the Sonoran Desert and is found at elevations below 1,200 m from extreme southeastern California east to south central Arizona and south into northern Sonora (Kearney and Peebles 1960; Munz 1964). Saguaro is an arborescent, sometimes branched, stem succulent that reaches 10 m in height. It is found primarily in desert upland communities with coarse, gravelly, well-drained soils.

Saguaro is an important component of the communities where it occurs, providing food and shelter to a host of desert animals. Its wood has been used for fence and hogan construction by indigenous people of the area, and its fruits provided one of their most reliable wild food sources. The sweet, fleshy fruit pulp can be eaten raw or used to make confections or jams. The nectar is reported to be a source of excellent honey (Alcorn and Martin 1974). In addition, saguaro is one of the most well-known and beloved plants in the country, recognizable at a glance by most Americans.

Flowering and fruiting. Saguaro plants normally produce fruit on a yearly basis, even if the winter has been dry (Steenbergh and Lowe 1977). They have sufficient water and energy reserves in their succulent stems to buffer fruit production from the yearly vagaries of water availability. Even plants that have been severed at the base are capable of fruit production for 2 subsequent years. Plants in the wild reach reproductive maturity at a height of about 2 m and an age of about 40 years (Steenbergh and Lowe 1983). Flowering occurs from March through May, depending on latitude and elevation, with later flowering on cooler sites. The fruit crop may be damaged or destroyed by frost during flowering. The large, fragrant, epigynous flowers are borne at the stem apices. They open in the evening, and each lasts only until midday the following day. The flowers produce copious pollen and nectar and are pollinated primarily by nectar-feeding bats, although many other visitors take advantage of the rich resource (Hevly 1979; Steenbergh and Lowe 1977).

Fruits ripen from June through August. A single fruit contains 2,000 to 2,500 seeds. The succulent fruits usually split open while still attached to the plant, exposing the tiny seeds (figures 1 and 2) to removal by rain, but the fruits eventually fall to the ground. Many animals utilize the fruits and seeds. Larger mammals such as coyotes (*Canis latrans*) may act as dispersers, but most users, especially harvester ants (*Pogonomyrmex* spp.) and doves (*Zenaida* spp.), are consumers only. Most of the seeds are consumed before the beginning of summer rains, especially in years when fruits ripen early or initiation of the summer rainy season is delayed (Steenbergh and Lowe 1977).

Figure 1—*Carnegiea giganteus*, saguaro: seeds.

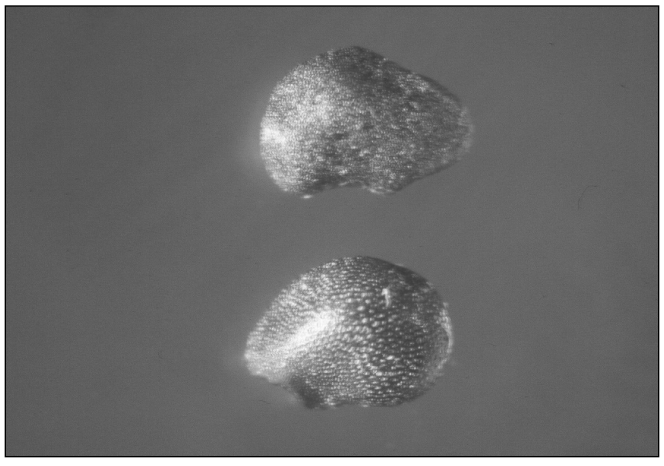
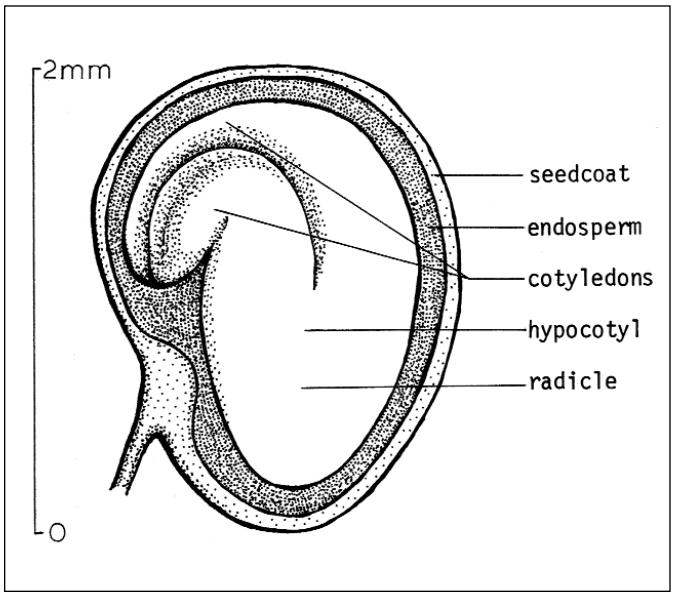


Figure 2—*Carnegiea giganteus*, saguaro: longitudinal section through a seed.



Seed collection, cleaning and storage. Ripe fruits turn from green to purple and can be collected by cutting with long-handled knives prior to dehiscence on the plant. The seeds can be removed from the fruits using standard procedures for fleshy fruited species, such as maceration in a macerator; forcing the fruits through an appropriately sized sieve; removing the pulp by flotation; drying the seeds and cleaning them in a fanning mill or aspirator. Extra care must be taken because of the small size of the seeds. The average number of seeds per weight is 990/g (450,000/lb) (Alcorn and Martin 1974). The seeds are usually of high quality (>95% germination of seedlots). Seeds apparently may be stored at room temperature for several years without much loss of viability, and germination values as high as 51% have been recorded, even after 10 years (Alcorn and Martin 1974).

Germination. Saguaro seeds are readily germinable when the fruits are ripe. Their germination is suppressed by the fruit pulp, but once they are washed free of the pulp they germinate freely, as long as temperatures are high (25 °C is optimum) and the seeds are exposed to light (Alcorn and Martin 1974; Steenburgh and Lowe 1977). Official testing calls for germination on moist blotter paper for 20 days at alternating temperatures of 20/30 °C, with light during the 8 hours at the higher temperature; no pretreatment is needed (AOSA 1993). In the field, seeds germinate soon after dispersal in response to adequate summer storms. Time to 50% germination of initially air-dried seeds is about 72 hours. If seedlots are first exposed to high-humidity air (without condensation) for 24 hours, they can reach 50% germination in 48 hours, an apparent adaptation for speeding germination during closely spaced summer storms (Steenbergh and Lowe 1977). Saguaro seeds do not form persistent seed banks; all viable seeds germinate soon after dispersal.

Because of apparently poor recruitment in natural stands, factors affecting survival of saguaro seedlings and young plants have been studied in some detail (Despain 1974; Nobel 1980; Steenbergh and Lowe 1969, 1976, 1977, 1983). New seedlings are highly susceptible to drought and herbivore damage, and young plants are at risk both of overheating in summer and freezing in winter. Nurse plants and other sheltering objects such as rocks greatly decrease these risks.

Nursery practice. Cleaned saguaro seeds may be surface-sown on coarse potting medium. The seedlings are highly susceptible to fungal pathogens, and care must be taken to provide good drainage and avoid overwatering (Alcorn and Martin 1974). They must be protected from freezing and also from full sunlight. Shade is probably beneficial for plants up to a meter (39 in) in height. The seedlings grow very slowly at first—only a few millimeters a year for the first several years.

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C

Hydrangeaceae—Hydrangea family

Carpenteria californica Torr.

carpenteria

Donald L. Neal

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Growth habit. Carpenteria (bush-anemone or tree-anemone)—*Carpenteria californica* Torr.—is an erect evergreen shrub that is 1 to 3 (sometimes 4 m) tall with large showy white flowers. Plants are usually multi-stemmed and about as wide as tall. The leaves are oblong–lanceolate on short petioles and placed opposite. The leaves are leathery and in response to moisture stress, they turn yellow and twist and their edges roll under. They return to normal appearance and color when moisture is available (Kottcamp 1983; Sanwo 1997).

Occurrence. The range of carpenteria is extremely limited, occurring only between 300 and 1,500 m on the west slope of the Sierra Nevada, between the San Joaquin and Kings Rivers in eastern Fresno County, California. The shrub is found in scattered stands over an area 20 by 30 km or about 60,000 ha. The total number of plants has been estimated to less than 5,000 (Clines 1995).

Most stands are in small drainages on dry rocky slopes, mixed with Digger pine (*Pinus sabiniana* Dougl. ex Dougl.), interior live oak (*Quercus wislizeni A*. DC.), chaparral whitethorn (*Ceanothus leucodermis* Greene), and other representatives of the foothill woodlands at the lower elevational limits of its range. At their upper elevational limit, carpenteria plants can be found growing with ponderosa pine (*Pinus ponderosa* P. & C. Lawson), interior live oak, and other species of the lower yellow pine zone.

About two-thirds of the existing plants occur on lands of the USDA Forest Service's Sierra National Forest, and carpenteria is classified as a sensitive plant by the Forest Service. It receives some protection on 2 areas set aside by the Sierra National Forest and 1 owned by The Nature Conservancy. Carpenteria is a threatened species under the California Endangered Species Act, and in October of 1994 it was proposed for listing as endangered under the Federal Endangered Species Act (Federal Register 1994).

Natural reproduction. Until recently, all observed natural reproduction was by stump-sprouting after fire (Stebbins 1988; Wickenheiser 1989). However, after a large wildfire in 1989, an abundance of naturally occurring seedlings were found where mineral soil was exposed (Clines 1994) and many of them later had become established plants. In one study, hand-seeding in mineral soil after a fire produced abundant seedlings (Clines 1994). Stem layering and adventitious rooting have also been observed (Clines 1994).

Use. Carpenteria was first collected by the John C. Fremont expedition of 1845. It drew the attention of horticulturalists early and was found in gardens in the United States, England, and Europe by the early 1880s (Cheatham 1974). It is raised commercially for the garden in several California nurseries (Laclergue 1995).

Flowering and fruiting. Flowers are large (3 to 7 cm in diameter) and appear in May and June in a terminal cyme. The calyx is 5 (or 6) parted and there are 5 to 8 large white petals. The ovary is incompletely 5 (2 to 8)–celled. Up to 1,500 (2,000) ovules are attached to axile placentas that protrude into the locule (Clines 1994). The style has 5 to 7 closely grouped branches topped with numerous spreading yellow stamens. Pollination seems to be mostly outcrossing by insects but geitonogamy also produces viable seeds (Clines 1994).

Extraction and cleaning. Capsules (figure 1) can be collected by hand in July and August from native or commercially grown stands. The capsules are hard and must be cut open when collected intact. They can be found partially open on the shrubs later in the season. Each capsule may contain over 1,000 viable seeds (figure 2). Germination occurs easily without treatment and ranges from 70 to 100% (Mirov and Kraebel 1939; Clines 1994). There are 33 to 47.2 million seeds/kg (15.0 to 21.5 million/lb) (Mirov and Kraebel 1939).

Nursery practice. Carpenteria is grown in commercial nurseries both from seeds and cuttings. One common practice involves direct seeding into flats of well-drained soil. Damping-off is a problem and top dressing with perlite reduces but does not eliminate this problem. Cuttings root readily, especially those taken from the terminal few inches of the branches and treated with rooting compound.

Figure 1—*Carpenteria californica*, carpenteria: exterior view of fruit (**upper left**), cross section of fruit (**upper right**), exterior view of seeds in 2 planes (**bottom**).

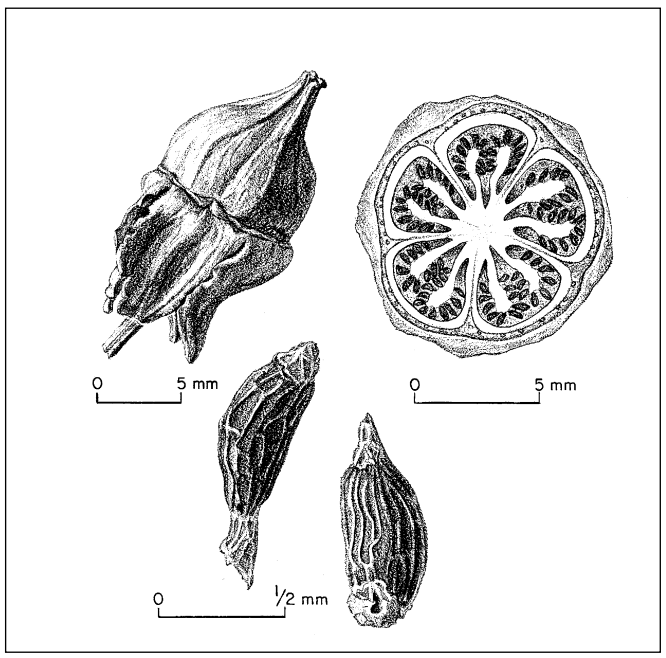
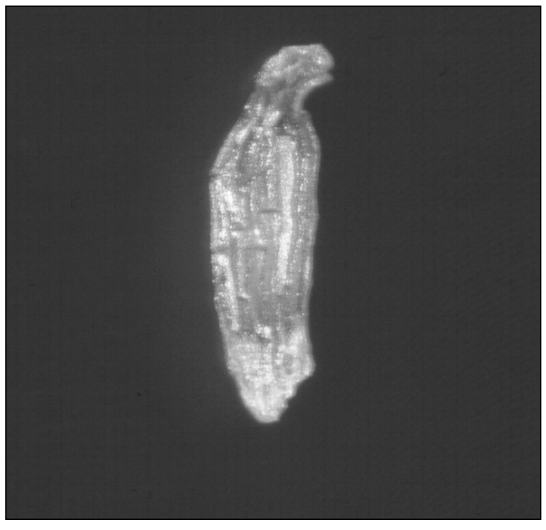


Figure 2—*Carpenteria californica*, carpenteria: seed.



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C

Betulaceae—Birch family

Carpinus L.

hornbeam or ironwood

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Growth habit, occurrence, and use. The hornbeam genus—*Carpinus* L.—includes about 35 species of deciduous, monoecious, small to large trees, that are native to the Northern Hemisphere from Europe to eastern Asia, south to the Himalayas, and in North and Central America (Furlow 1990; Hillier 1991; Krüssmann 1984; LHBH 1976; Suszka and others 1996). Five species are considered here (table 1). Hornbeams occur mainly as understory trees in rich, moist soils on bottomlands and on protected slopes (Metzger 1990; Rudolf and Phipps 1974). European hornbeam is an important forest tree species throughout Europe (Furlow 1990). In Mexico and Central America, *Carpinus tropicalis* (J.D. Sm.) Lundell forms a dominant canopy component (Furlow 1990). American hornbeams, which are native to the eastern United States and Canada, are smaller trees that grow in the mixed hardwood forest understory (Furlow 1990; Metzger 1990). Several geographic races of American hornbeam exist in North America (Fernald 1935; Furlow 1990). The races are morphologically variable and difficult to distinguish on the basis of independent characters. Furlow (1987a), using multivariate analysis, analyzed this geographical variation. The northern American hornbeam species is divided into the subsp. *caroliniana* from along the Atlantic and Gulf Coastal Plains of the southeastern United States and the subsp. *virginiana* of the Appalachian Mountains and northern interior regions to the West (Furlow 1987b). The Latin American *C. tropicalis* is divided into subsp. *tropicalis* of the highlands of southern Mexico and north Central America and subsp. *mexicana* of the mountains in northeastern Mexico and the trans-Mexican volcanic belt (Furlow 1987b).

The wood of hornbeams is extremely hard—hence the common name "ironwood"—and is used for making tool handles and mallet heads. It is also used to produce the high-quality charcoal used in gunpowder manufacture (Bugala 1993; Furlow 1990). Species of ornamental interest in the United States are listed in table 1. Most of the information presented in this chapter deals with European and American hornbeams, unless noted otherwise.

European hornbeam is a slow-growing tree (about 3 m over 10 years) that is pyramidal in youth but oval-rounded to rounded at maturity (Dirr 1990; Suszka and others 1996). This species is planted in the landscape as single specimen trees or as screens or hedges. It tolerates a wide range of soil and light conditions but grows and develops best in full sun on rich, moist sites with good drainage (Dirr 1990; Metzger 1990). Several cultivars produce excellent color, form, and texture. The cultivar 'Fastigiata' is the most common one in cultivation, with foliage more uniformly distributed along the branches than on other cultivars (Dirr 1990; Hillier

Table 1—*Carpinus,* hornbeam: nomenclature, occurrence, height at maturity, and date of first cultivation

Scientific name	Common name(s)	Occurrence	Height at maturity (m)	Year first cultivated
***C. betulus* L.**	**European hornbeam**	Europe, Asia Minor, & SE England	12–21	1800s
***C. caroliniana* Walt.**	**American hornbeam,** musclewood, blue beech, ironwood	Nova Scotia S to Florida, W to Texas, & N to Minnesota & Ontario; also in central & S Mexico & Central America	6–9	1812
***C. cordata* Blume**	**heartleaf hornbeam**	Japan, NE Asia, & China	6–15	1879
***C. japonica* Blume**	**Japanese hornbeam**	Japan	6–9	1895
***C. orientalis* Mill.**	**Oriental hornbeam**	SE Europe & SW Asia	6–8	1739

Sources: Dirr (1990), Hillier (1991), Krüssmann (1984), LHBH (1976), Metzger (1990).

1991; Krüssmann 1984). This cultivar is used primarily as a screen hedge because of its dense, compact, ascending branches (Dirr 1990). The bark on older trees is gray and beautifully fluted.

American hornbeam is a small, multi-stemmed, bushy shrub or single-stemmed tree with a wide-spreading, flat or round-topped crown, that grows slowly; averaging 2.5 to 3 m over a 10-year period (Dirr 1990; Metzger 1990). This species has considerable fall color variation, from yellow to orange-red, and is planted in the landscape in groups or as an understory tree (Beckett 1994; Dirr 1990). The bark on older trees is slate gray, smooth, and irregularly fluted; the overall appearance is comparable to the flexed bicep and forearm muscles—hence another common name, "musclewood" (Dirr 1990).

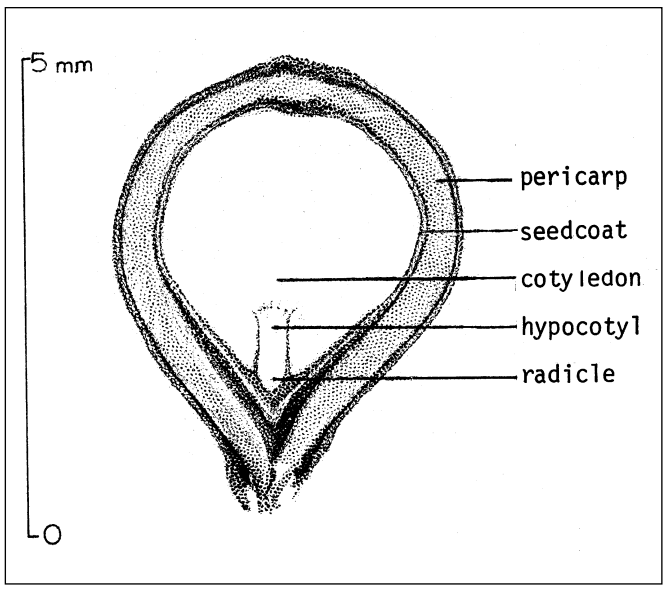
Heartleaf hornbeam is a small tree of rounded habit with leaves that are large with deeply heart-shaped bases, and with large, rich brown winter buds (Dirr 1990; Hillier 1991; Krüssmann 1984). The bark is slightly furrowed and scaly (Dirr 1990). The fruits are borne in cigar-shaped catkins (Dirr 1990). Japanese hornbeam is a wide-spreading small tree or large shrub with prominently corrugated leaves and with branches that radiate like the ribs on a fan (Dirr 1990; Hillier 1991). Oriental hornbeam grows as a large shrub or small tree with an overall U-shaped branching pattern (Dirr 1990). The bracts of this species are unlobed, differentiating it from European and American hornbeams (Dirr 1990). The main branches and stems are twisted, giving this species an interesting winter appearance (Dirr 1990).

Flowering and fruiting. In most species, the staminate and pistillate catkins appear in the spring concurrently as the trees are leafing out (Dirr 1990; Furlow 1990; Metzger 1990; Suszka and others 1996). The fruits are ovoid, ribbed, single-seeded nutlets (figures 1 and 2), each borne at the base of a distinctive 3-lobed involucre (bract) (Metzger 1990; Rudolf and Phipps 1974). The fruits ripen from late summer to fall. They are dispersed from fall to spring and are carried only a short distance by the wind or may be dispersed farther by birds (Rudolf and Phipps 1974). Details of flowering and seeding habits for European and American hornbeams are described in tables 2 and 3.

Collection of fruits; extraction, cleaning, and storage of seeds. Fruits harvested while they are still green (when the wings are turning yellow and are still soft and pliable) can be fall-sown for germination the following spring (Bugala 1993; Dirr 1990; Hartmann and others 1990). These seeds should not be allowed to dry out, as a hard seedcoat will develop, and they should be checked before sowing for the presence of well-developed embryos (Bugala 1993;

Figure 1—*Carpinus caroliniana*, American hornbeam: nutlet with involucre removed

Figure 2—*Carpinus caroliniana*, American hornbeam: longitudinal section through a nutlet.



Leiss 1985). Green seeds can also be stratified for 3 to 4 months over winter and sown the following spring (Hartmann and others 1990).

Mature seeds (with hardened seedcoats) should be collected, spread out in thin layers in a cool, well-aerated room or shed, and allowed to dry superficially (Macdonald 1986; Rudolf and Phipps 1974; Suszka and others 1996). The bracts do not need to be removed if the seeds are to be broadcast (Macdonald 1986). They should be removed, however, from large quantities of seeds (to aid in mechanical sowing) by placing the seeds in a de-winging machine or beating the seeds in bags (Rudolf and Phipps 1974; Suszka

Table 2—*Carpinus,* carpinus: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
C. betulus	Europe & NE US	Apr–May	Aug–Nov	Nov–spring
C. caroliniana	NE US	Mar–June	Aug–Oct	Nov–spring

Source: Rudolf and Phipps (1974).

Table 3—*Carpinus,* hornbeam: seed-bearing age, seedcrop frequency, seed weight, and fruit ripeness criteria

Species	Minimum seed-bearing age (yrs)	Years between large seedcrops	Average no. cleaned seeds /kg	Average no. cleaned seeds /lb	Preripe color	Ripe color
C. betulus	10–30	1–2	28,660	13,000	Green	Brown
C. caroliniana	15	3–5	66,138	30,000	Green	Greenish brown

Sources: Allen (1995), Rudolf and Phipps (1974).

and others 1966). The debris can be removed from seedlots by screening and fanning (Macdonald 1986). European hornbeam seeds with bracts weigh 15 to 18 kg/0.35 hl (33 to 40 lb/bu). Fruits weighing 45 kg (100 lb) yield about 23 kg (50 lb) of cleaned seed (Rudolf and Phipps 1974). The average numbers of cleaned seeds per weight of European and American hornbeam are listed in table 3.

Hornbeam seeds stratified immediately after extraction can be stored up to 2 years (Rudolf and Phipps 1974). European hornbeam seeds in nuts partially dried to 8 to 10% moisture content can be stored in sealed containers at a temperature of –3 °C for at least 5 years (Bugala 1993). Seeds of this species stored at 10% moisture content in sealed containers at 3 °C lost no viability after 14 months (Suszka and others 1969).

Pregermination treatments. Hornbeam seeds that are allowed to mature and become dry will develop a hard seedcoat. Dormancy, caused by conditions in the embryo and endosperm, may be overcome by stratification treatments (a warm period followed by a cold period). In general, 1 to 2 months of warm stratification followed by 2 to 3 months of cold stratification are necessary to break dormancy of the European hornbeam. The International Seed Testing Association (1993) prescribes 1 month of moist incubation at 20 °C, followed by 4 months at 3 to 5 °C, for laboratory testing of European hornbeam. Results of stratification treatments vary for different species of hornbeam, so several are presented in table 4. Bretzloff and Pellet (1979) reported that gibberellic acid treatment at 0.025, 0.1, and 0.5 g/liter (25, 100, and 500 ppm) generally increased germination of American hornbeam seeds stratified at 4 °C for 6, 12, or 18 weeks, compared to stratification alone. Scarification of the seedcoat plus gibberellic acid also improved germination (Bretzloff and Pellet 1979). Gordon and others (1991) and Suszka and others (1996) provide extensive information on the sampling, seed pretreatment, purity, viability, and germination testing, seedling evaluation, and storage of forest tree and shrub seeds. Specific procedures are presented for a number of species.

Germination tests. Germination percentage of stratified seeds is low, usually less than 60% and occasionally as low as 1 to 5% (Metzger 1990). Germination tests may be made on pretreated seeds in germinators, or in flats of sand, or sand plus peat (Rudolf and Phipps 1974). Viability of European and American hornbeams is best determined by using the tetrazolium test for viability (Chavagnat 1978; Gordon and others 1991; ISTA 1993; Suszka and others 1996). Details of germination test results are shown in table 5. Germination of hornbeam seeds is epigeal.

Nursery practice and seedling care. The optimum seedbed is continuously moist, rich loamy soil protected from extreme atmospheric changes (Rudolf and Phipps 1974; Suszka and others 1966). Germination of many naturally disseminated seeds is delayed until the second spring after seed dispersal (Rudolf and Phipps 1974). If germination is expected the first spring, seeds should be collected while they are still green (the wings turning yellow and still soft and pliable) and sown in the fall, or stratified immediately and sown the following spring (Bugala 1993; Dirr 1990; Hartmann and others 1990; Rudolf and Phipps 1974). Macdonald (1986) suggested collecting European hornbeam seeds in the fall, followed by extraction, stratification for 8

Table 4—*Carpinus,* hornbeam: stratification treatments for breaking embryo dormancy

Species	Warm period Temp (°C)	Warm period Days	Cold period Temp (°C)	Cold period Days	Percentage germination
C. betulus	20	28	3–5	90–112	NS
	20	14	5	210	65
	20	30	4	120	65
C. caroliniana	20–30	60	5	60	10
	—	—	4.5	126	58
C. orientalis	20	60	5	90–120	NS

Sources: Allen (1995), Blomme and Degeyter (1977), Bretzloff and Pellet (1979), Bugala (1993), Rudolf and Phipps (1974), Suszka and others (1996).
NS = not stated.

Table 5—*Carpinus,* hornbeam: germination test conditions and results with stratified seed

Species	Test conditions* Temp (°C) Day	Night	Days	Germination rate %	Days	% Germination Avg	Samples	Purity (%)	Soundness (%)
C. betulus	20	20	70	30	7	18–90	50	97	60
C. caroliniana	27	16	60	2	12	1–5	2	96	62

Source: Rudolf and Phipps (1974).
* Tests were made in sand or soil.

weeks at 18 to 21 °C and then for 8 to 12 weeks at 0.5 to 1 °C, and then spring-sowing. Seeds collected later should be partially dried, stratified, and sown the next fall or the following spring to avoid having seedbeds with germination spread out over 2 years (Rudolf and Phipps 1974). Seeds should be sown in well-prepared beds at a rate of 323 to 431/m^2 (30 to 40/ft^2) and covered with 0.6 to 1.3 cm ($^1/_8$ to $^1/_4$ in) of soil (Rudolf and Phipps 1974). Macdonald (1986) suggested sowing seeds at a rate of 250/m^2 (23/ft^2) for lining-out stock and 150 to 250/m^2 (14 to 23/ft^2) for rootstocks. Fall-sown beds should be mulched with burlap, pine straw, or other material until after the last frost in spring (Rudolf and Phipps 1974). The soil surface should be kept moist until after germination, and beds should shaded lightly for the first year (Rudolf and Phipps 1974). Davies (1987, 1988) demonstrated that growth of European hornbeam transplants was greatly increased by using a chemical for weed control and various synthetic sheet mulches. Black polythene sheets (125 m thick) gave the best results for controlling weeds and aiding in tree establishment (Davies 1988).

Cultivars of hornbeam may be grafted (side whip or basal whip) or budded onto seedlings of the same species (Hartmann and others 1990; Macdonald 1986; MacMillan-Browse 1974). Hornbeam can also be propagated by cuttings, but with variable success. Stem cuttings of European hornbeam 'Fastigiata' rooted when treated with 2% (20,000 ppm) indole-3-butyric acid (IBA); American hornbeam 'Pyramidalis' with 1 and 1.6% IBA; heartleaf hornbeam (var. *chinensis*) with 1.6 and 3% IBA–talc; and Japanese hornbeam with 3 g/liter (3,000 ppm) IBA–talc plus thiram (Cesarini 1971; Dirr 1990; Dirr and Heuser 1987; Obdrzalek 1987). After rooting, the cuttings require a dormancy period (Dirr 1990). Placing cuttings at a temperature of 0 °C during the winter months satisfies the dormancy requirements (Dirr 1990). Stock plant etiolation and stem banding have been shown to improve the rooting of hornbeam (Bassuk and others 1985; Maynard and Bassuk 1987, 1991, 1992, 1996). Chalupa (1990) reported the successful micropropagation of European hornbeam by using nodal segments and shoot tips as initial explants. Oriental hornbeam has been established in bonsai culture (Vrgoc 1994).

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Juglandaceae—Walnut family

Carya Nutt.

hickory

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Growth habit, occurrence, and use. Of the dozen or so species of hickories native to the United States, 9 are valuable for timber and the food they provide for wildlife (table 1). All are deciduous trees. Pecan and its many horticultural varieties and hybrids are widely cultivated for nuts in large plantations in the southern and southwestern United States, as well as in many other countries. The first known selections were made in 1846, and many cultivars were available by the late 19th century (Madden and Malstrom 1975). Budding and grafting have been the primary means of improvement, but new provenance studies (Grauke and others 1990) and advanced research on the reproductive biology and genetics of pecan (Graves and others 1989; McCarthy and Quinn 1990; Yates and Reilly 1990; Yates and Sparks 1990) demonstrate the promise for future improvements in nut production and disease resistance. Shellbark and shagbark hickories have also been planted for nut production.

Flowering and Fruiting. Hickories are monoecious and flower in the spring (table 2). The staminate catkins develop from axils of leaves of the previous season or from inner scales of the terminal buds at the base of the current

Table 1—*Carya,* hickory: nomenclature and occurrence

Scientific name & synonym(s)	Common name	Occurrence
***C. alba* (L.) Nutt. ex Ell.** *C. tomentosa* (Lam. ex Poir.) Nutt. *Hicoria tomentosa* (Lam. ex Poir.) Raf.	**mockernut hickory,** bullnut, white hickory, whiteheart hickory, hognut, mockernut	S New Hampshire to S Michigan, S to E Texas & N Florida Valley to Illinois
***C. aquatica* (Mich f.) Nutt.** *Hicoria aquatica* (Michx. f.) Britt.	**water hickory,** bitter pecan swamp hickory	Coastal plain from Virginia to S Florida & E Texas; N in Mississippi Valley to Illimois
***C. cordiformis* (Wangenh.) K. Koch.** *Hicoria cordiformis* (Wagenh.) Britt.	**bitternut hickory,** bitternut, swamp hickory, pignut	New Hampshire to Minnesota, S to E Texas & Georgia
***C. glabra* (P. Mill.) Sweet** *Hicoria glabra* (Mill.) Britt. *C. microcarpa* (Nutt.) Britt.	**pignut hickory,** sweet pignut, pignut, swamp hickory	New Hampshire to NE Kansas, S to Arkansas & NW Florida
***C. illinoensis* (Wangenh.) K. Koch** *Hicoria pecan* (Marsh.) Britt. *C. oliviformis* (Michx. f.) Nutt. *C. pecan* (Marsh.) Engl & Graebn.	**pecan,** sweet pecan, *nuez encarcelada*	S Indiana to SE Iowa; S to Texas & E to Mississippi & W Tennessee; local to Ohio, Kentucky, & Alabama
C. laciniosa (Michx. f.) G. Don *Hicoria laciniosa* (Michx. f.) Sarg.	**shellbark hickory,** bigleaf shagbark hickory, big shellbark, kingnut, bottom shellbark, big shagbark hickory	Ohio & Mississippi Valleys; W New York to E Kansas, E to Georgia & Virginia; local in Louisiana, Alabama, & Virginia
***C. myristiciformis* (Michx. f.) Nutt.** *Hicoria myristicaeformis* (Michx. f.) Britt.	**nutmeg hickory,** bitter water hickory, swamp hickory	Mississippi W to SE Oklahoma, S to E Texas & Louisiana; also E South Carolina & central Alabama
***C. ovata* (P. Mill.) K. Koch** *Hicoria alba* Britt. p.p.; *H. ovata* (P. Mill.) Britt.	**shagbark hickory,** scalybark hickory, shagbark, shellbark hickory	Maine to SE Minnesota, S to E Texas & Georgia
***C. pallida* (Ashe) Engl. & Graebn.** *Hicoria pallida* Ashe	**sand hickory,** pale hickory, pallid hickory	New Jersey & Illinois, S to Florida & SE Louisiana

Sources: Little (1979), Sargent (1965).

Table 2—*Carya,* hickory: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
C. alba	Apr–May	Sept–Oct	Sept–Oct
C. aquatica	Mar–May	Sept–Nov	Oct–Dec
C. cordiformis	Apr–May	Sept–Oct	Sept–Dec
C. glabra	Apr–May	Sept–Oct	Sept–Oct
C. illinoensis	Mar–May	Sept–Oct	Sept–Oct
C. laciniosa	Apr–June	Sept–Nov	Sept–Oct
C. myristiciformis	Apr–May	Sept–Oct	Sept–Oct
C. ovata	Apr–June	Sept–Oct	Sept–Oct
C. pallida	Mar–Apr	Sept–Oct	Sept–Oct

Source: Bonner and Maisenhelder (1974).

growth. The pistillate flowers appear in short spikes on peduncles terminating in shoots of the current year. Hickory fruits are ovoid, globose, or pear-shaped nuts enclosed in husks developed from the floral involucre (figure 1). Husks are green prior to maturity and then turn brown to brownish black as they ripen (Bonner and Maisenhelder 1974). The husks become dry at maturity in the fall (table 2) and split away from the nut into 4 valves along sutures. Husks of mockernut, nutmeg, shagbark, and shellbark hickories, as well as those of pecan, split to the base at maturity, usually releasing the nuts. Husks of pignut, bitternut, sand, and water hickories split only to the middle or slightly beyond and generally cling to the nuts. The nut is 4-celled at the base and 2-celled at the apex. The edible portion of the embryonic plant is mainly cotyledonary tissue (figure 2) and has a very high lipid content (Bonner 1971; Bonner 1974; Short and Epps 1976).

Figure 1—*Carya*, hickory: nuts with husks attached and removed (the size and shape of individual nuts varies greatly within a species and may differ from the examples shown here); *C. aquatica*, water hickory (**first row left**) and *C. cordiformis*, bitternut hickory (**first row right**); *C. glabra*, pignut hickory (**second row left**) and *C. myristiciformis*, nutmeg hickory (**second row right**); *C. illinoensis*, pecan (**third row left**) and *C. laciniosa*, shellbark hickory (**third row right**); *C. ovata*, shagbark hickory (**fourth row left**) and *C. alba*, mockernut hickory (**fourth row right**).

Collection, extraction, and storage. Hickory nuts can be collected from the ground after natural seedfall or after shaking the trees or flailing the limbs. Persistent husks may be removed by hand, by trampling, or by running the fruits through a macerator or a corn sheller. Several studies have shown that the larger nuts of pecan make larger seedlings (Adams and Thielges 1977; Herrera and Martinez 1983), so sizing of nuts may be beneficial. Shagbark and shellbark hickory trees have been known to produce 0.5 to 0.75 hl ($1^1/_2$ to 2 bu) and 0.75 to 1.1 hl (2 to 3 bu) of nuts, respectively (Bonner and Maisenhelder 1974). Good crops of all species are produced at intervals of 1 to 3 years (table 3). Some typical yield data are presented in table 4.

Figure 2—*Carya ovata*, shagbark hickory: longitudinal section through the embryo of a nut with husk removed.

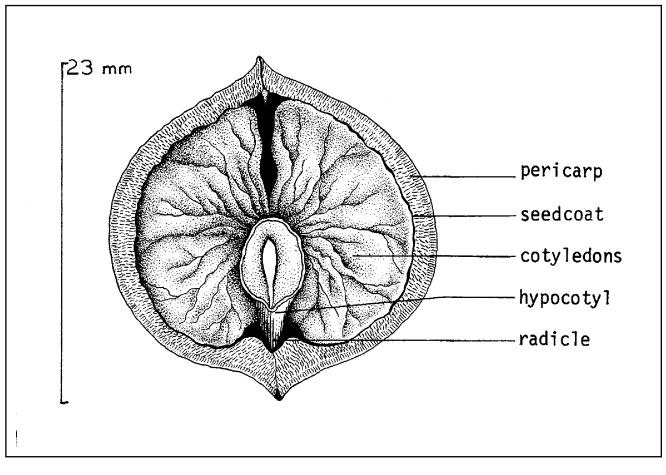

Table 3—*Carya,* hickory: height, seed-bearing age, seedcrop frequency, and year first cultivated

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yrs)	Years between seedcrops
C. alba	30	1766	25	2–3
C. aquatica	30	1800	20	1–2
C. cordiformis	15–30	1689	30	3–5
C. glabra	24–27	1750	30	1–2
C. illinoensis	34–43	1766	10–20	1–2
C. laciniosa	37	1800	40	1–2
C. myristiciformis	24–30	—	30	2–3
C. ovata	21–30	1911	40	1–3
C. pallida	12-30	—	—	2–3

Source: Bonner and Maisenhelder (1974).

Table 4—*Carya,* hickory: seed data

Species	Place collected	Fruits/vol /hl	Fruits/vol /bu	Seed wt/fruit vol kg/hl	Seed wt/fruit vol lb/bu	Cleaned seeds/weight Range /kg	Range /lb	Average /kg	Average /lb
C. alba	—	—	—	—	—	75–249	34–113	200	90
	Mississippi	5,040	1,776	57	44	71–106	32–48	79	36
C. aquatica	Mississippi	—	—	—	—	305–419	138–140	360	164
C. cordiformis	—	—	—	51	40	275–408	125–185	344	156
C. glabra	—	—	—	51	40	386–496	175–225	441	200
	Mississippi	10,100	3,552	—	—	—	—	143	65
C. illinoensis	—	—	—	—	—	121–353	55–160	220	100
	Mississippi	20,800	7,330	—	—	333–384	151–174	357	162
	Texas	—	—	—	—	—	—	311	141
C. laciniosa	—	—	—	—	—	55–77	25–35	66	30
C. myristiciformis	Mississippi & Arkansas	14,500	5,110	—	—	207–375	94–170	273	124
C. ovata	—	17,600	6,200	38–49	30–38	176–331	80–150	220	100
	Wisconsin	—	—	—	—	—	—	291	32
	Mississippi	12,100	4,264	—	—	—	—	207	94

Source: Bonner and Maisenhelder (1974).

Storage tests with pecan and shagbark hickory have demonstrated that the hickories are orthodox in storage behavior, that is, they should be dried to low moisture contents and refrigerated. Seedlots of nuts of both species dried to below 10% moisture and stored at 3 °C in sealed containers retained viability well for 2 years before losing half to two-thirds of their initial viability after 4 years (Bonner 1976b). The poor results after 4 years are probably due to the high lipid levels in these seeds, which places them in the sub-orthodox storage category (Bonner 1990). There are no storage data for other species of hickory, but it is reasonable to think that they can be stored in a similar fashion.

Pregermination treatments. Hickories are generally considered to exhibit embryo dormancy, although work with pecan suggests that mechanical restriction by the shell is the reason for delayed germination in that species (van Staden and Dimalla 1976). Other research with pecan has shown that there is a clinal gradient in stratification requirement. Seedlots from southern sources are practically nondormant, whereas those from northern sources require treatment for prompt germination (Madden and Malstrom 1975). The common treatment is to stratify the nuts in a moist medium at 1 to 4 °C for 30 to 150 days (table 5). Stratification of

imbibed nuts in plastic bags without medium is suitable for most species (Bonner and Maisenhelder 1974), and good results have been reported for pecans from southern sources by soaking the nuts at 20 °C for 64 hours (Goff and others 1992). There are indications that stratification should be shortened for stored nuts; this was the case in one storage test on pecan and shagbark hickory (Bonner 1976b). If cold storage facilities are not available, stratification in a pit with a covering of about 0.5 m of compost, leaves, or soil to prevent freezing will suffice. Prior to any cold stratification, nuts should be soaked in water at room temperature for 2 to 4 days with 1 or 2 water changes each day to ensure full imbibition (Eliason 1965). There is evidence that germination of pecan can be increased by treatment with gibberellins (Bonner 1976a; Dimalla and van Staden 1977), but practical applications have not been developed.

Germination tests. Official testing rules for North America (AOSA 1993) prescribe testing pecan and shagbark hickory at alternating temperatures of 20 °C (dark) for 16 hours and 30 °C (light) for 8 hours on thick creped paper for 28 days. Stratification for 60 days as described above is also recommended. Adequate germination tests can also be made on stratified nuts in flats of sand, peat, or soil at the same temperature regime (table 5). Quick tests with tetrazolium salts can also be used with hickories (Eliason 1965).

Nursery practice. Either fall-sowing with untreated seed or spring-sowing with stratified seed may be used. Excellent results with fall-sowing have been reported for shagbark hickory, but good mulching is necessary (Heit 1942). Drilling in rows 20 to 30 cm (8 to 12 in) apart and 2 to 4 cm ($^3/_4$ to 1 $^1/_2$ in) deep with 20 to 26 nuts/m (6 to 8/ft) is recommended; about 100 seedlings/m^2 (10/ft^2) is a good density (Williams and Hanks 1976). Mulch should remain until germination is complete. Shading is generally not necessary, but shellbark hickory may profit from shade. Protection from rodents may be required for fall-sowings.

Table 5—*Carya, hickory:* stratification period, germination test conditions, and results

Species	Cold stratification (days)	Germination test conditions				Germination		Germination %	
			Temp (°C)			Rate		Avg	
		Medium	Day	Night	Days	(%)	Days	(%)	Samples
C. alba	90–150	Sand, peat, soil	30	20	93	54	64	66	4
C. aquatica	30–90	Soil	27–32	21	63	76	28	92	1
C. cordiformis	90	Sand, peat, soil	30	20	250	40	30	55	3
	90	Soil	27	21	50	60	50	60	1
C. glabra	90–120	Sand, peat, soil	30	20	30–45	—	—	85	2
C. illinoensis	30–90	Sand, peat	30	20	45–60	—	—	50	9
	30–90	Kimpak	30*	20	60	80	33	91	6
	30	Soil	32	21	35–97	—	—	75	2
C. laciniosa	90–120	Sand, peat, soil	30	20	45–60	—	—	—	—
C. myristiciformis	60–120	Kimpak	30*	20	60	53	50	60	2
C. ovata	90–150	Sand, peat	30	20	45–60	75	40	80	6
	60–120	Kimpak	30*	20	60	65	35	73	2

Source: Bonner and Maisenhelder (1974).

* Daily light period was 8 hours.

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C

Fagaceae—Beech family

Castanea P. Mill.

chestnut

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Growth habit, occurrence, and use. The genus *Castanea*—the chestnuts—comprises 11 species of small to medium-sized deciduous trees found in southwestern and eastern Asia, southern Europe, northern Africa, and the eastern United States. Five species are covered in this chapter; only 2 are native to the United States (table 1). American chestnut formerly ranked as one of the most valuable timber species in the Appalachian region, and the nuts were an important wildlife food as well as being extensively marketed for human consumption. In the years since the chestnut blight—*Cryphonectria parasitica* (Murr.) Barr—was discovered in New York in 1904, the disease has spread throughout the range of the American chestnut and completely destroyed it as a commercial species. Many rootstocks still survive and send up multiple sprouts that grow to the size of a small tree (table 2) before dying. Some of these sprouts occasionally produce a few seeds, but they usually do not live long enough for significant production (Sander 1974).

Japanese, Chinese, and European chestnuts (table 1) were introduced into the United States in the 18th and 19th centuries (Anagnostakis 1990; Sander 1974). The Asian species demonstrated good resistance to the chestnut blight, and breeding programs were started as early as the 1890s to transfer the resistance to American chestnut (Jaynes 1975). Chinese chestnut, the most promising of these introductions, has been widely planted throughout the eastern United States, mostly in orchards for nut production. Allegheny chinkapin is somewhat resistant to the blight and might be useful as a rootstock in grafting; its other good features are small size, precocity of fruiting, and heavy seedcrops (Payne and others 1994). Breeding for resistance has not been highly successful, but advances in tissue culture offer new promise (Dirr and Heuser 1987).

Flowering and fruiting. Chestnuts are monoecious, but some trees produce bisexual catkins also (Sander 1974). Unisexual male catkins, 15 to 20 cm long, appear near the base of the flowering branches. The pistillate flowers occur singly or in clusters of 2 to 3, near the end of the branches (Brown and Kirkman 1990; Sander 1974), with the female catkins at the base of the shoot (Payne and others 1994). Flowering begins in April or May in the Southeast (Hardy 1948) and in June in the Northeast (Sander 1974).

Chestnut fruits are spiny, globose burs, from 2.5 to 7.5 cm in diameter, borne singly or in spikelike clusters (Sander 1974; Vines 1960). The fruits each contain from 1 to 3 seeds (nuts); Allegheny chinkapins have 1 seed and American chestnuts (figure 1) have 3 seeds/fruit (Brown and Kirkman 1990; Sander 1974). The nuts are flattened on one side and range from light to dark brown or black in color (Brown and Kirkman 1990; Rehder 1940). Nuts of American chestnut are 12 to 25 mm wide and about 25 mm long. The exotic chestnuts bear larger nuts that are 19 to 38

Table 1—*Castanea,* chestnut: nomenclature and occurrence

Scientific name	Common name(s)	Occurrence
***C. crenata* Siebold & Zucc.**	**Japanese chestnut**	Japan
***C. dentata* (Marsh.) Borkh.**	**American chestnut**	S Maine to Michigan; S to S Mississippi & Georgia
***C. mollissima* Blume**	**Chinese chestnut**	China & Korea
***C. pumila* (L.) P. Mill.**	**Allegheny chinkapin**	Pennsylvania S to central Florida & W to E Texas & Oklahoma
***C. sativa* P. Mill.**	**European chestnut,** Spanish chestnut	S Europe, W Asia, & N Africa

Sources: Little (1979), Sander (1974).

Table 2—*Castanea,* chestnut: height, year first cultivated, and seed weights

Species	Height at maturity (m)	Year first cultivated in US	Cleaned seeds/weight /kg	Cleaned seeds/weight /lb
C. crenata	10	1876	33	15
C. dentata	20–25*	1800	220–360	100–162
C. mollissima†	21	1853	50–220	23–100
C. pumilla	15	—	300	136
C. sativa	21	Pre 1880	33	15

Sources: Payne and others (1994), Sander (1974).
* Height refers to sprouts from living rootstocks of trees killed by the blight; before the blight this species obtained heights of 21 to 30 m.
† Bears large crops annually in orchards beginning at about 8 years of age.

Figure 1—*Castanea dentata*, American chestnut: fruit (bur) and nut.

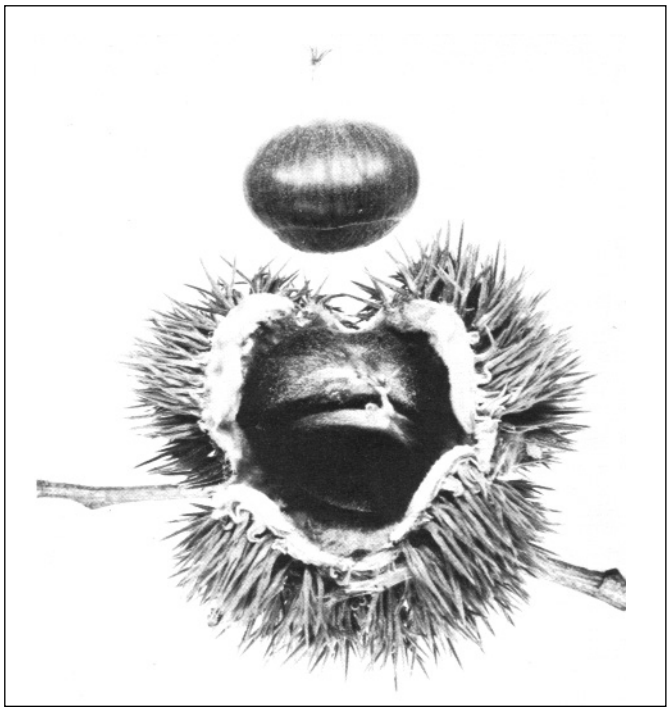
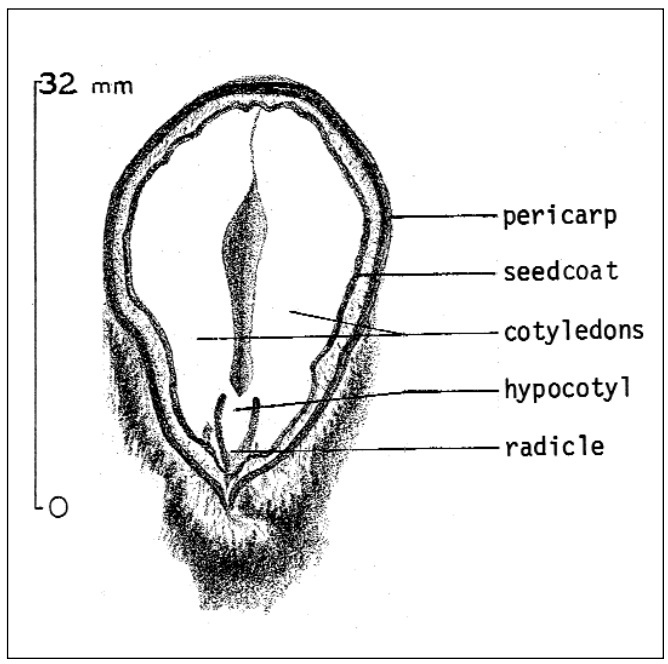


Figure 2—*Castanea dentata,* American chestnut: longitudinal section through a nut.



mm wide (Sander 1974). Food reserves, primarily starch, are stored in the large cotyledons (figure 2). Fresh nuts are 40 to 45% starch by weight, with very little lipid content (Jaynes 1975; Payne and others 1994; Wainio and Forbes 1941). Seeds ripen in August to October, depending on species and location (Hardy 1948; Sander 1974). Seed weights are listed in table 2.

Superior strains and hybrids. There are no identified superior strains of native chestnuts, but many cultivars and hybrids have been developed with the exotic chestnuts, primarily in Europe. The search for blight-resistant American chestnuts continues, however, with breeding, tissue culture, and innovative budding and grafting techniques (Ackerman and Jayne 1980; ACF 2002).

Collection of fruits. Chestnuts can be picked from the trees, collected from the ground by hand, or shaken from the trees onto ground cloths. Burs of Allegheny chinkapin do not open widely, and the seeds are difficult to shake out. Some remain on the trees throughout winter (Payne and others 1994). Harvesting should begin as soon as the burs begin to split open. The nuts are intolerant of desiccation (recalcitrant) (Aldous 1972; Pritchard and Manger 1990), so collections from the ground should be done very soon after dissemination to prevent excessive drying. Frequent collection

is especially important if the weather is hot and dry, as nuts can lose viability within a week on the ground (USDA 1951). If the weather is wet, Allegheny chinkapin nuts will sometimes germinate on the trees (Payne and others 1994).

Storage of seeds. Because of their recalcitrant nature, chestnuts are normally stored no longer than 6 months (overwinter). With good care, however, storage for 18 months is not difficult, and some have been successfully stored for 3.5 years (Jaynes 1975). Immediately after collection, the nuts should be floated in water to remove trash and immature and damaged nuts. If collected from the ground in a dry condition, they should be left in water overnight to restore their naturally high moisture content. Upon removal from water, the nuts should be spread to dry in a cool, well-ventilated place to remove all surface moisture. The nuts should be placed in containers that inhibit drying, such as polyethylene bags, and stored at 1 to 3 °C; however, the containers should not be airtight so that some gas exchange between nuts and the storage atmosphere is possible. Moisture content of the nuts should be about 40 to 45% during storage (Sander 1974). Too much moisture can result in loss of seeds to microorganisms (Woodruff 1963).

Pregermination treatments. Chestnut seeds are dormant and require a period of cold, moist stratification for prompt germination. In normal nursery practice, overwinter storage of fully imbibed nuts at 1 to 3 °C will satisfy the chilling requirement to overcome dormancy. For nuts that have not been stored moist, or if a deeper dormancy than usual is suspected, then stratification should be used; 1 to 3 months is the recommended period for American and Chinese chestnuts (Dirr and Heuser 1987; Jaynes 1975). If nuts are planted in the fall, stratification is not necessary, but the nuts should be kept in cold storage until planted (Sander 1974).

Chestnuts are commonly infested with the larvae of the seed weevils *Curculio sayi* Gyllenhall and *C. caryatrypes* Bohemon (Gibson 1985). A simple method to kill the larvae is to submerge the nuts for 20 to 40 minutes in water at 49 °C (Payne and Wells 1978).

Germination tests. The standard laboratory testing procedure for European chestnut is to (1) soak the seeds in water for 24 hours; (2) cut off a third of the seed at the cup-scar end; (3) remove the testa; and (4) germinate the seeds for 21 days in or on top of sand at the standard test regime of alternating 20 and 30 °C (ISTA 1993). If only constant temperatures are available, 28 °C is recommended for this species, which also has no specific light requirement of germination (Pritchard and Manger 1990). Data are lacking on other chestnut species with this procedure, but it quite likely will work for any of them. There are alternate procedures for whole nuts. Stratified nuts of Chinese chestnut have been germinated in a moist medium at 15 to 21 °C; germination reached 100% in 42 days (Berry 1960).

Nursery practice. Chestnuts may be planted in autumn or spring. Nuts that have been kept in cold storage from the time they are harvested should be planted in September or October (Sander 1974). Fall-sown beds should be mulched and protected as much as possible against rodents (Williams and Hanks 1976). Nuts for spring-planting should be stratified for 2 to 3 months.

In both fall- and spring-plantings, nuts should be sown 2 to 4 cm ($^3/_4$ to 1 $^1/_2$ in) deep and spaced 7.5 to 10 cm (3 to 4 in) apart in rows 7.5 to 15 cm (3 to 6 in) apart in the nursery beds. Nuts can be either sown or drilled by hand, or broadcast mechanically (Sander 1974; Williams and Hanks 1976). Some growers recommend planting by hand so that the nuts can be placed on their sides to promote better seedling form (Jaynes 1975). European chestnuts are normally broadcast at a density of 100 nuts/m^2 (9 to 10/ft^2) (Aldous 1972). One should expect 75 to 80% germination in beds with good seeds (Aldous 1972; Sander 1974). A study with Chinese chestnuts found that grading nuts by size had no influence on time of emergence, although larger seeds did tend to produce larger seedlings (Shepard and others 1989).

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C

Casuarinaceae—Casuarina family

Casuarina Rumph. ex L.

casuarina

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Growth habit, occurrence, and use. The genus *Casuarina*—the only genus in the Casuarina family—comprises about 50 species, chiefly Australian, with a few having native ranges extending from Bangladesh to Polynesia. Casuarina trees are evergreen angiosperms, resembling conifers, with thin crowns of drooping branches and leaves reduced to scales (Little 1949; Little and Wadsworth 1964). Three species of this genus have been introduced successfully into continental United States, Hawaii, and Puerto Rico (table 1) (Bailey 1949; Rockwood and others 1990). Beach she-oak, especially, is planted as a windbreak throughout its native and introduced ranges and as an ornamental in parks and gardens (Parrotta 1993; Rockwood and others 1990). It was first introduced into Hawaii in 1882 (Neal 1965). The bark has been used in tanning, in medicine, and for the extraction of dye (Parrotta 1993). The fruits are made into novelties and Christmas decorations (Little and Wadsworth 1964). The wood is hard and heavy and is difficult to work, hence the common name "ironwood." It was once heavily used for building poles and firewood but now is seldom used commercially in the United States (Parrotta 1993). Beach and gray she-oaks are considered invasive pests in southern Florida and gray she-oak in Hawaii.

Flowering and fruiting. Casuarinas are monoecious or dioecious. Minute male flowers are crowded in rings among grayish scales. Female flowers lack sepals but have pistils with small ovaries and threadlike dark red styles (Little and Wadsworth 1964). The multiple fruit is conelike, about 8 to 20 mm in diameter (figure 1), and composed of numerous individual fruits. Each fruit is surrounded by 2 bracteoles and a bract that splits apart at maturity and releases a 1-winged light brown samara (figures 2 and 3). The immature fruits of the genus are green to gray-green, becoming brown to reddish brown when ripe (Neal 1965). In warm climates, flowering and fruiting occur throughout the year. Consequently, time of seed collection varies from place to place (Little and Wadsworth 1964; Olson and Petteys 1974). In Hawaii, Florida, and Puerto Rico, the peak of the flowering period appears to be April through June, with fruiting from September through December (Magini and Tulstrup 1955; Neal 1965; Olson and Petteys 1974; Rockwood and others 1990). Minimum seed-bearing age is 2 to 5 years, and good seedcrops occur annually (Magini and Tulstrup 1955; Olson and Petteys 1974; Parrotta 1993).

Collection, extraction, and storage. The multiple fruits may be picked from the trees or shaken onto canvas or

Table 1—*Casuarina,* casuarina: nomenclature, occurrence, and uses

Scientific name(s) & synonym	Common name(s)	Occurrence (native & introduced)
***C. cunninghamiana* Miq.** *C. tenuissima* Hort.	**river she-oak,** river-oak casuarina, Cunningham beefwood, ironwood	Australia & New Caledonia; Hawaii, S US, & California
***C. equisetifolia* L.** *C. litorea* L.	**beach she-oak,** Australian pine, horsetail casuarina, horsetail beefwood	Burma through Australia & Polynesia; Hawaii, Florida, & Puerto Rico
***Casuarina glauca* Sieb. ex Spreng.**	**gray she-oak,** longleaf casuarina, longleaf ironwood	Australia; Hawaii

Sources: Olson and Petteys (1974), Parrotta (1993).

Figure 1—*Casuarina cunninghamiana*, river she-oak: multiple fruit.

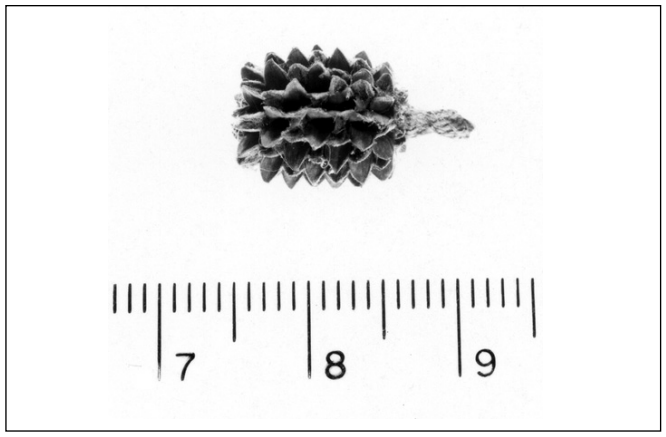
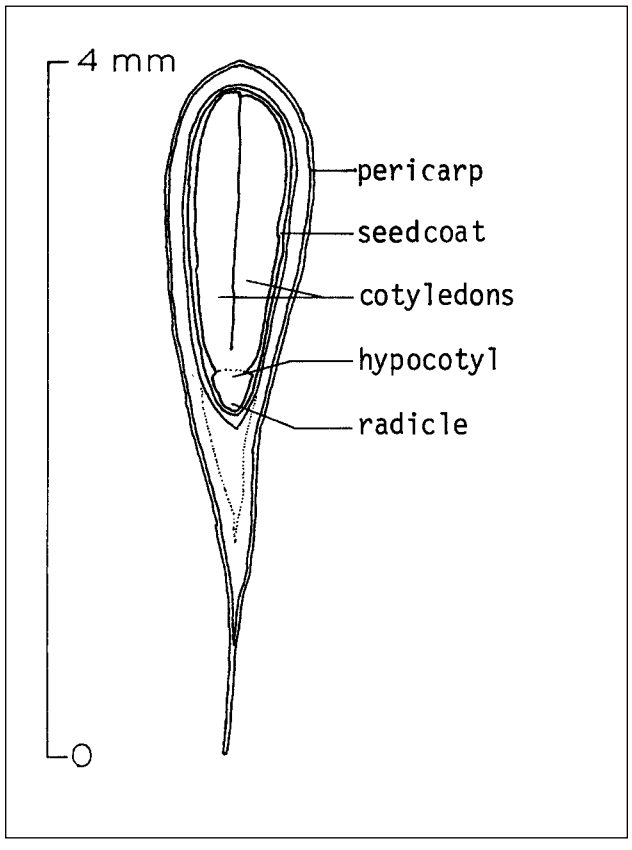
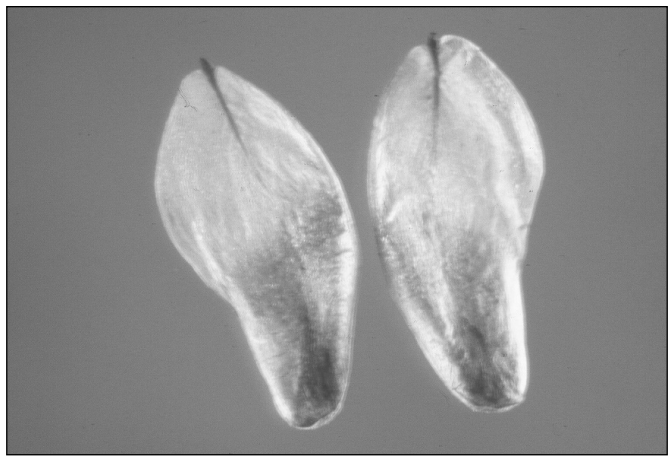


Figure 2—*Casuarina cunninghamiana*, river she-oak: longitudinal section through a seed.



plastic sheets. Seeds reach maximum weight and germinability 18 weeks after anthesis, or when cones change in color from green to brown (Rai 1990). The samaras, which are used as seeds, may be separated from the fruits by shaking and screening (Olson and Petteys 1974). Cones placed in trays, covered by a thin cloth, and dried under full sunlight will soon begin to release their seeds, usually within 3

Figure 3—*Casuarina cunninghamiana*, river she-oak: winged seeds.



days (Kondas 1990). A kilogram of fruits (about 250 cones) yields between 20 and 60 g of seeds (1 lb of cones yields 1.5 to 2.4 oz of seeds). There are about 650 to 760 seeds/g (300,000 to 350,000 seeds/lb) (Kondas 1990; Turnbull and Markensz 1990). The application of an insect repellant effective against ant predation is advisable during the drying process (Kondas 1990). Seeds do not retain their viability for more than 3 months at ambient temperatures (Kondas 1990), but appear to be orthodox in storage behavior (Jones 1967). Seeds stored at subfreezing (–7 °C) or close to freezing (3 °C) temperatures, with moisture contents ranging from 6 to 16%, retain viability for up to 2 years (Turnbull and Markensz 1990). In Hawaii, seeds have been successfully stored in sealed polyethylene bags at 1 °C (Olson and Petteys 1974).

Germination. Germination in beach she-oak is epigeal; it takes place 4 to 22 days after sowing and is optimal at 30 °C under well-lighted conditions (Parrotta 1993). Casuarina seeds are usually sown without pretreatment (Magini and Tulstrup 1955; Olson and Petteys 1974), although soaking seeds for 36 hours in a 1.5% solution of potassium nitrate reportedly enhances germination (Rai 1990). Germination ranges from 40 to 90% for fresh seeds and from 5 to 25% for seeds stored in airtight containers at 4 °C for 1 year (Parrotta 1993). Official test prescriptions for casuarina species call for a 14-day test at alternating temperatures of 20/30 °C on the top of moist blotter paper (AOSA 1993). In the Philippines, germination of seedlots collected from different trees within a single plantation ranged from 33 to 75% for fresh seeds (Halos 1983). A significant positive relationship between cone size and seed germination rate was also noted in this study.

Nursery practice. In the nursery, seeds are generally germinated in trays under full sunlight at an optimal density of 1,000 to 7,500 seeds (weighing 2 to 10 g) /m^2 (93 to 700 seeds/ft^2), covered with about 0.5 cm of soil (Olson and Petteys 1974; Parrotta 1993). In South Africa, seedling yield averages are 18,000 plants/kg (8,200/lb) of river she-oak seeds (Magini and Tulstrup 1955). Nursery soils should be light textured, optimally sandy loams or a mixture of sand and peat moss. Seedlings are transferred from germination trays to containers when they reach a height of 10 to 15 cm (4 to 6 in), usually within 6 to 10 weeks after germination. Seedling containers measuring about 15 cm (6 in) in diameter and 20 cm (8 in) in depth are recommended. Seedlings may also be transplanted to new beds at densities of 100 to 400 seedlings/m^2 (9 to 37/ft^2) to obtain bareroot planting stock. Seedlings should be kept under partial shade until shortly before outplanting. Seedlings reach plantable size of 20 to 50 cm (8 to 20 in) in height in 4 to 8 months (Parrotta 1993). It is recommended that seedlings be inoculated in the nursery with pure cultures of effective strains of *Frankia* (a nitrogen-fixing actinomycete) or an inoculum from a nodule suspension prepared from fresh, healthy nodules collected in the field. Roots can be inoculated by dipping them into the suspension or by directly applying the suspension to the soil. Alternatively, crushed, fresh nodules, leaf litter, or soils from the vicinity of effectively inoculated trees may be incorporated directly into the nursery potting mix (Parrotta 1993).

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Bignoniaceae—Trumpet-creeper family

Catalpa Scop.

catalpa

Franklin T. Bonner and David L. Graney

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Growth habit, occurrence, and use. The catalpas include about 10 species of deciduous or rarely evergreen trees native to North America, the West Indies, and eastern Asia (Rehder 1940). Two deciduous species, southern catalpa and northern catalpa (table 1), are native to the continental United States and have been planted quite widely outside their native range, especially northern catalpa. Mature trees of both species attain heights of 9 to 18 m (Little and Delisle 1962; Sargent 1965). Both have been grown to some extent in Europe. Catalpas are used in shelterbelts and ornamental planting and have minor value as timber trees, mainly for posts and small poles. Haitian catalpa, or yokewood, a native of the West Indies, has also been widely planted for forestry and ornamental purposes (table 1).

Flowering and fruiting. Attractive clusters of showy, white perfect flowers with purplish and orange blotches and stripes in the throat are borne in May and June on southern and northern catalpas (Brown and Kirkman 1990; Sargent 1965). Fruits of these species ripen in October, and good crops are borne every 2 to 3 years beginning at about age 20 (Bonner and Graney 1974; Sargent 1965; Vines 1960). Haitian catalpa flowers, which vary from white to solid rose in color, appear irregularly throughout the year. Even 6-month-old seedlings flower, and abundant seed crops are borne by the age of 18 months (Francis 1993). Mature fruits are round, brown, 2-celled capsules, 15 to 75 cm long (figure 1). In late winter or early spring, the capsules of northern and southern catalpas split into halves to disperse the seeds (Sargent 1965). Each capsule contains numerous oblong, thin, papery, winged seeds 1 to 5 cm long and about 1 to 6 mm wide (figure 2). Removal of the papery outer seedcoat reveals an embryo with flat, round cotyledons (figure 3). Southern and northern catalpas are separate from each other. The most consistent identification feature is the relative thickness of the fruit walls. Northern catalpa fruit walls are considerably thicker than those of southern catalpa (Brown and Kirkman 1990).

Collection, extraction, and storage. Fruits should be collected only after they have become brown and dry. When dry enough, the seeds can be separated by light beating and shaking. Pods of northern catalpa collected in February and March had seeds of higher quality than those collected in

Table 1—*Catalpa,* catalpa: nomenclature and occurence

Scientific name & synonym(s)	Common name(s)	Occurrence	Year first cultivated
***C. bignonioides* Walt.** *C. catalpa* (L.) Karst.	**southern catalpa,** common catalpa, Indian-bean, catawba, cigar-tree	SW Georgia & Florida to Louisiana; naturalized to New England, Ohio, Michigan, & Texas	1726
***C. longissima* (Jacq.) Dum.-Cours.**	**Haitian catalpa,** yokewood, *roble de olor, chenn*	Hispaniola & Jamaica; naturalized in Martinique, Guadeloupe, & the Grenadines; planted in Florida, Hawaii, & the West Indies	—
***C. speciosa* (Warder) Warder ex Engelm.**	**northern catalpa,** hardy catalpa, western catalpa, western Catawba-tree, Indian-bean, catawba	SW Indiana & Illinois to NE Arkansas & W Tennessee; widely naturalized in NE & SE US	1754

Sources: Bonner and Graney (1974), Francis (1990), Little (1979).

Figure 1—*Catalpa bignonioides*, southern catalpa: capsule and leaf.

Figure 2—*Catalpa speciosa,* northern catalpa: seed.

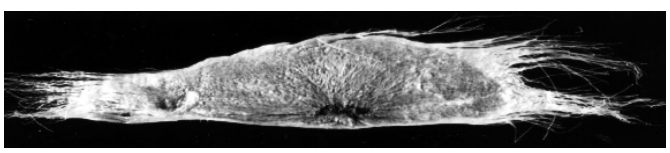
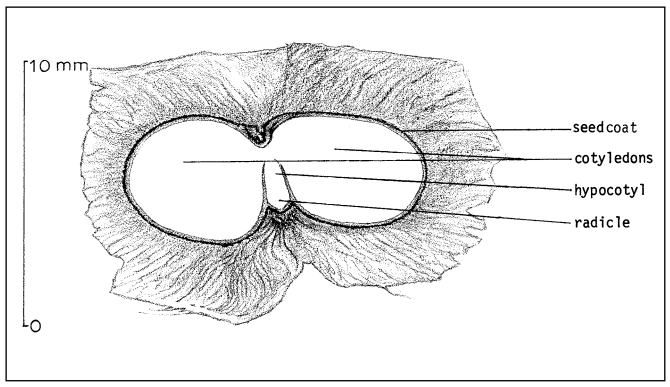


Figure 3—*Catalpa speciosa*, northern catalpa: longitudinal section through a seed.



the fall (Bonner and Graney 1974). In terms of size, seeds of northern catalpa are slightly smaller than seeds of southern catalpa, and seeds of Haitian catalpa are by far the smallest of these three (table 2). Seeds of all 3 species dried to about 10% moisture content can be stored under refrigerated conditions. Successful storage for 2 years has been reported for southern catalpa (Bonner and Graney 1974) and 1 year for Haitian catalpa (Francis 1990). Long-term storage has not been studied, but this genus appears to be orthodox in storage behavior and capable of extended storage at low moisture contents and temperatures.

Germination tests. Seeds of all 3 species germinate promptly without pretreatment. Tests should be made on wet germination paper for 21 days with 20 °C night and 30 °C day temperatures. Other moist media also are satisfactory. Although northern catalpa is known to be photosensitive (Fosket and Briggs 1970), light is not necessary for germination tests (AOSA 1993). Germination in excess of 90% (25+ samples) has been obtained in about 12 days with good quality seeds of southern and northern catalpas (Bonner and Graney 1974). Francis (1993) has reported 40% germination of Haitian catalpa in 8 days on potting mix. Germination is epigeal, and the emerging 2-lobed cotyledons look like 4 leaves (figure 4).

Nursery practice. Catalpa seeds should be sown in late spring in drills at the rate of about 100/linear m (30/ft), and covered lightly with 4 mm ($^1/_8$ in) of soil or sown on the surface. A target bed density of 108 to 215 seedlings/m^2 (10 to 20/ft^2) is recommended (Williams and Hanks 1990). Stratification or other pretreatment is not needed. A pine needle mulch has been recommended for southern catalpa (Bonner and Graney 1974). In Louisiana, this species starts germination about 12 days after March sowing and germination is about 80%. In Puerto Rico, Haitian catalpa seeds can be spread thinly on a shaded bed of moist, sterile soil or

Figure 4—*Catalpa bignonioides*, southern catalpa: seedling development at 1, 5, 8, and 20 days after germination.

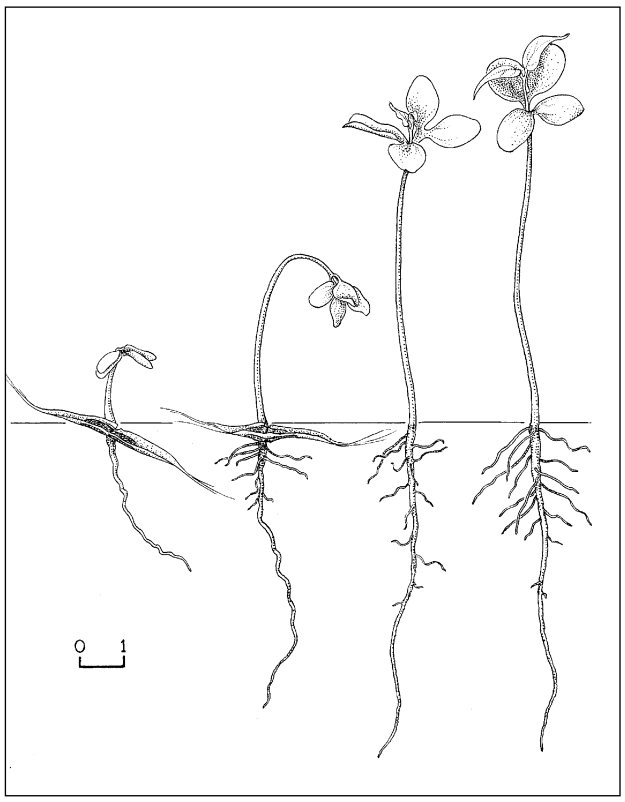


Table 2—*Catalpa,* catalpa: seed data

Species	Place collected	Wt yield of seeds/ 100wt fruit	Cleaned seeds/weight			
			Range		Average	
			/kg	/lb	/kg	/lb
C. bignonioides	Florida	—	32,600–40,10	14,800–18,200	36,400	16,500
		35	30,900–81,600	14,000–37,000	44,100	20,000
C. longissima	Puerto Rico	—	572,000–618,000	259,460–280,325	600,000	272,160
C. speciosa	Minnesota	—	29,450–48,300	13,359–21,910	—	—
	Prairie states	10–25	30,000–80,700	13,600–36,600	—	—
		25–35	35,300–66,150	16,000–30,000	46,300	21,000

Sources: Bonner and Graney (1974), Francis (1990).

sand and covered lightly with sand (Francis 1990). This species can also be sown directly into containers; germination begins in about 10 days. Nematodes, powdery mildews, and the catalpa sphinx—*Ceratonia catalpae* (Boisduval)—may give trouble in the nursery. Southern and northern catalpas are normally planted as 1+0 stock (Bonner and Graney 1974). Haitian catalpa seedlings should be ready for planting 10 to 14 weeks after sowing in containers. Untreated woody cuttings can also be used for vegetative propagation of Haitian catalpa (Francis 1990).

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C

Rhamnaceae—Buckthorn family

Ceanothus L.

ceanothus

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Growth habit, occurrence, and use. Van Rensslaer and McMinn (1942) recognized 55 species of ceanothus, 25 varieties, and 11 named natural hybrids, all restricted to the North American continent. Most of them are found along the Pacific Coast of the United States, and only 2 are found east of the Mississippi River (Hitchcock and others 1961; Kearney and Peebles 1951; Munz and Keck 1968; Rowntree 1948; Sampson and Jesperson 1963; Schmidt 1993; Van Rensslaer and McMinn 1942). Forty-three species and 21 varieties are described in the most recent flora of California, which does not recognize hybrid forms (Schmidt 1993). Although hybridization appears to be common in nature, there are few named hybrids (Lentz and Dourley 1981; Schmidt 1993). Ceanothus species are mainly evergreen or deciduous shrubs, some of which may attain the height of small trees. In the West, they occur in a diversity of habitats, ranging from interior desert chaparral to moist redwood forest along the Pacific Coast (table 1). Ceanothus species are important as wildlife food and shelter, for erosion control, as hedges and shelterbelts, and in soil development and soil nitrogen regimes (Conard and others 1985; Graham and Wood 1991). Deerbrush ceanothus is rated as one of the most important summer browse species in California for deer and cattle (Sampson and Jesperson 1963), and redstem ceanothus is a key winter browse plant for deer (*Odocoileu* spp.) and elk (*Cervus cervus*) in parts of Idaho, Washington, and Oregon (Hickey and Leege 1970). All species that have been investigated bear root nodules containing a nitrogen-fixing *Frankia* symbiont (for example, Delwiche and others 1965); species from both forest and chaparral systems have been associated with accretion of soil nitrogen over time (Binkley and Husted 1983; Binkley and others 1982; Conard and others 1985; Hellmers and Kelleher 1959; Youngberg and Wollum 1976; Youngberg and others 1979; Zavitkovski and Newton 1968; Zinke 1969).

On forest sites, ceanothus species have alternately been considered a problem because they compete with commercial conifers and a benefit because of their nitrogen-fixing ability and their wildlife value (Conard and others 1985). Although there was early experimentation with planting ceanothus species for erosion control on chaparral sites (DFFW 1985) and there has been some interest in ceanothus establishment for browse or general site improvement in forest sites (Hickey and Leege 1970; Radwan and Crouch 1977), the dominant horticultural uses have continued to be for domestic, commercial, and right-of-way landscaping—particularly in California and the Pacific Northwest. Ceanothus species are valued particularly for their showy flowers (they are sometimes called "California lilacs"), relatively rapid early growth, drought adaptation, and ability to tolerate landscape watering. Some species have been cultivated for many years (table 2), and the potential for hybridization has led to the development of numerous cultivars, many of which are available from commercial native plant nurseries (for example, Lentz and Dourley 1981; Perry 1992). Distribution and uses of some of the more common species are described in table 1.

Flowering and fruiting. Flowers are small, bisexual, and regular, and are borne in racemes, panicles, or umbels. The 5 sepals are somewhat petal-like, united at the base with a glandular disk in which the ovary is immersed. The 5 petals are distinct, hooded, and clawed; the 5 stamens are opposite the petals, with elongated filaments. Petals and sepals can be blue, white purple, lavender, or pink. The ovary is 3-celled and 3-lobed, with a short 3-cleft style. Fruits are drupaceous or viscid at first but soon dry up into 3-lobed capsules (figure 1) that separate when ripe into 3 parts. Seeds are smooth, varied in size among species (figures 2 and 3; table 3), and convex on one side.

Flowering and fruiting dates for several species are listed in table 2. Feltleaf ceanothus is reported to begin bearing seeds at 1 year (Van Rensslaer and McMinn 1942), deerbrush ceanothus at 3 years (McDonald and others 1998),

Table 1—*Ceanothus,* ceanothus: nomenclature and occurrence

Scientific name & synonym(s)	Common name	Occurrence
***C. americanus* L.**	**New-Jersey-tea,** Jersey-tea,	Dry woods, Ontario to Manitoba, Maine to North Dakota, S to Florida & Texas
***C. arboreus* Greene** *C. arboreus* var. *glabra* Jepson	**feltleaf ceanothus,** island myrtle, Catalina ceanothus	Larger islands of Santa Barbara Channel, California (up to 300 m on dry slopes & chaparral)
***C. cordulatus* Kellogg**	**mountain whitethorn,** snowbush, whitethorn ceanothus	Baja California & mtns of S California, N to SW Oregon, E to Nevada (900–2,900 m on rocky ridges & ponderosa pine to red fir forests)
***C. crassifolius* Torr.**	**hoaryleaf ceanothus**	Cis-montane southern California & Baja California (to 1,100 m on dry slopes & ridges, chaparral)
***C. cuneatus* (Hook.) Nutt.**	**buckbrush ceanothus,** wedgeleaf ceanothus, hornbrush, buckbrush	Inner Coast Range & Sierra Nevada foothills, California into Oregon, S to Baja California (100–1,800 m in chaparral & ponderosa pine forests)
***C. cuneatus* var. *rigidus* (Nutt.) Hoover** *C. rigidus* Nutt.	**Monterey ceanothus**	San Luis Obispo Co., N through Mendocino Co., California (up to 200 m on coastal bluffs, in closed-cone pine forests)
C. diversifolius Kellogg	**trailing ceanothus,** pinemat, Calistoga ceanothus	Westside Sierra Nevada, spotty in northern Coast Range, California (900–1,800 m, under oaks & pines)
***C. fendleri* Gray**	**Fendler ceanothus,** buckbrush	South Dakota to New Mexico, Arizona, & Mexico (1,500 to 3,000 m, in ponderosa pine to dry Douglas-fir forests)
***C. greggii* Gray**	**desert ceanothus,** mountain buckbrush	W Texas to S California, Utah, & N Mexico (300–2,300 m, chaparral & desert chaparral)
***C. impressus* Trel.**	**Santa Barbara ceanothus**	Coastal areas in Santa Barbara & San Luis Obispo Cos., California (to 200 m in dry, sandy flats & slopes)
***C. integerrimus* Hook & Arn.** *C. andersonii* Parry	**deerbrush ceanothus,** sweet-birch, blue bush, deer brush	N California, Oregon, Washington to S California, Arizona, & New Mexico (300–2,100 m, in ponderosa pine to western hemlock, white fir forests; chaparral in SW)
***C. leucodermis* Greene**	**chaparral whitethorn**	S California to N Baja California (to 1,800 m in chaparral, dry slopes)
***C. megacarpus* Nutt.**	**bigpod ceanothus**	California
***C. oliganthus* Nutt.** *C. hirsutus* Nutt. *C. divaricatus* Nutt.	**hairy ceanothus,** jimbrush	Coast Ranges, San Luis Obispo & Santa Barbara Cos. & San Gabriel Mtns to Humboldt Co., California (to 1,300 m in chaparral)
***C. prostratus* Benth.**	**prostrate ceanothus,** squaw-carpet, mahala mat, squaw mat	Sierra Nevada & N Coast Range S to Calaveras Co., California; higher mtns of Oregon & Washington, W Nevada (900–2,200 m, common in ponderosa & Jeffrey pine forests)
***C. sanguineus* Pursh** *C. oreganus* Nutt.	**redstem ceanothus,** Oregon-tea tree	N California, Oregon, Idaho, Washington, & W Montana to S British Columbia (around 1,200 m in ponderosa pine Douglas-fir/mixed conifer, western hemlock zones)
***C. sorediatus* Hook. & Arn.** *C. intricatus* Parry *C. oliganthus* var. *sorediatus* (Hook. & Arn.) Hoover	**jimbrush ceanothus,** jimbrush	Coast Range in Los Angeles & Riverside Cos., Parry to Humboldt Co., California (150–1,000 m, in chaparral)
***C. thyrsiflorus* Eschsch.** *C. thyriflorus* var. *repens* McMinn	**blueblossom,** wild lilac	Coastal mountains Santa Barbara Co., California, to Douglas Co., Oregon (from sea level to 600 m in coast redwood, mixed-evergreen, Douglas-fir forest, & chaparral
***C. velutinus* Dougl. ex Hook.**	**snowbrush ceanothus,** mountain balm, sticky-laurel, tobacco brush	Coast Ranges, British Columbia to Marin Co., California, Siskiyou Mtns, Sierra Nevada/Cascade axis E to SW Alberta, Montana, South Dakota, & Colorado (to 3,000 m, in many forest types, ponderosa pine to subalpine)
***C. velutinus* var. *hookeri* (M.C. Johnston)** *C. velutinus* var. *laevigatus* Torr. & Gray	**varnish-leaf ceanothus**, Hooker ceanothus, snowbrush	Same as above, but more common near coast

Sources: Franklin and others (1985), Hitchcock and others (1961), Lenz and Dourley (1981), McMinn (1964), Munz and Keck (1968), Reed (1974), Sampson and Jesperson (1963), Schmidt (1993).

Figure 1—*Ceanothus*, ceanothus: capsules of *C. americanus*, New-Jersey-tea (**top**) and *C. velutinus*, snowbrush (**bottom**).

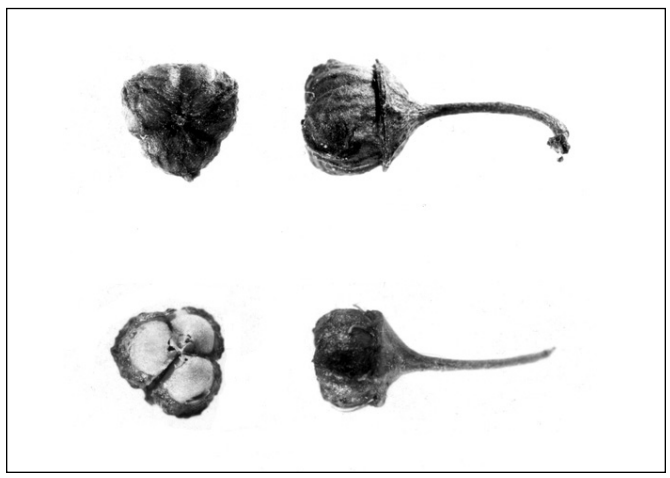
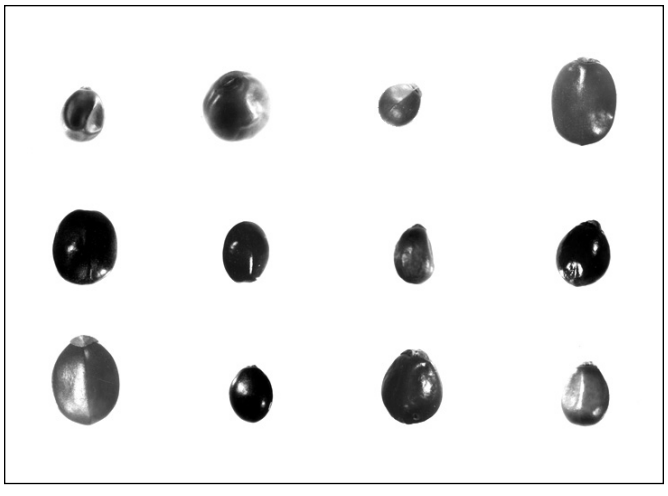
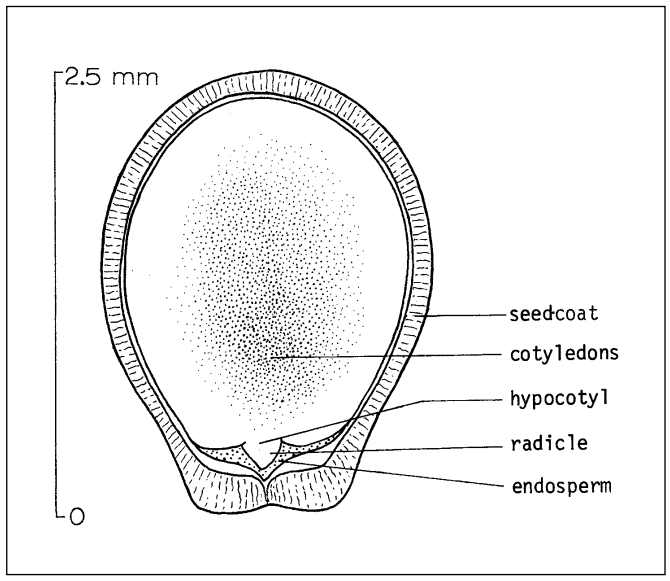


Figure 2—*Ceanothus*, ceanothus: seeds of *C. americanus*, New-Jersey-tea; *C. arboreus*, feltleaf ceanothus; *C. cordulatus*, mountain whitethorn; and *C. crassifolius* (**top, left to right**); *C. cuneatus*, buckbrush ceanothus; *C. impressus*, Santa Barbara ceanothus; *C. integerrimus*, deerbrush ceanthosus; and C. *oliganthus*, hairy ceanothus (**middle, left to right**); *C. prostratus*, prostrate ceanothus; *C. sorrediatus*, jimbrush ceanothus, *C. thyrsiflorus*, blueblossom; and *C. velutinus*, snowbrush ceanothus (**bottom, left to right**).



hoaryleaf ceanothus at 5 years (Everett 1957), desert ceanothus at 6 to 8 years (Zammit and Zedler 1992), and snowbrush ceanothus at 6 to 10 years (McDonald and others 1998). Thus it appears that most species can be expected to begin producing seeds by about 5 to 10 years of age. Fendler ceanothus has been reported to bear good seedcrops annually (Reed 1974). However, in hoaryleaf ceanothus, desert ceanothus, chaparral whitethorn, and other species,

Figure 3—*Ceanothus americanus*, New-Jersey-tea: longitudinal section through a seed.



both annual seed production and the amount of seeds stored in the soil may be quite variable (Conard and others 1985; Keeley 1977, 1987b; Zammit and Zedler 1988).

Collection, extraction, and storage. Several useful points on collecting ceanothus seeds have been described (Van Rensslaer and McMinn 1942; Emery 1988). Seeds should be collected only from vigorous plants, as weak, diseased plants do not produce sound seeds. To obtain plants similar to mature specimens, seeds should be collected in single-species stands in the wild or from isolated garden plants. Because many species hybridize freely, asexual propagation is the only certain way of maintaining species or varieties free from hybridization (Lenz and Dourley 1981). As the capsules split, ripe seeds are ejected with considerable force, such that about two-thirds of the seeds fall outside the shrub canopy, to distances up to 9 m (Evans and others 1987). Therefore, a common method of seed collection is to tie cloth bags—preferred to paper—securely over clusters of green seedpods. It is also possible to cut seedpod clusters before capsules have split, but the degree of maturity of the seeds is critical, as few prematurely collected seeds will germinate. Seeds that contain milky or gelatinous substances are not mature enough to harvest (Emery 1988). Green seeds should be air-dried at 29 to 38 °C.

If necessary, the seeds can be separated from capsule fragments by screening and blowing (Reed 1974), or seeds can be passed through a mill and floated (Plummer and others 1968). Average number of cleaned seeds per weight ranges from 90,000 to over 350,000/kg (41,000 to

Table 2—*Ceanothus, ceanothus:* phenology of flowering and fruiting, height, and year of first cultivation

Species	Flowering	Fruit-ripening	Height at maturity (m)	Year first cultivated
C. americanus	May–July	Aug–early Oct	0.5–1	1713
C. arboreus	Feb–Aug	May–early Oct	3–9	1911
C. cordulatus			0.6–2.5	—
California	May–June	July–Sept	—	—
Oregon	June–July	Aug–Sept	—	—
C. crassifolius	Jan–June	May–June	1.2–3	1927
C. cuneatus	Mar–June	Apr–July	1–4.5	1848
C. cuneatus var. *rigidus*	Dec–Apr	May–June	1–2.1	1847
C. diversifolius	Spring	June–July	0.3 or less	1941
C. fendleri (Arizona)	Apr–Oct	Aug–Dec	0.2–1	1893
C. greggii (Arizona*)	Mar–Apr	July	0.6–1.8	—
C. impressus	Feb–Apr	June	—	—
C. integerrimus	Apr–Aug	June–Aug	1–5.5	1850
C. leucodermis	—	July–Aug	—	
C. oliganthus	Feb–Apr	May–June	1.2–7.5	—
C. prostratus	Apr–June	July	.05–.15	—
C. sanguineus	Apr–June	June–July	1.5–3	1812
C. sorediatus	Mar–Apr	May–July	1–5.5	—
C. thyrsiflorus	Jan–June	Apr–July	1.2–8	1837
C. velutinus			0.6–2.4	1853
California	June–Aug	July–Aug	—	—
N Idaho†	May 20–July 25	July 15–Aug 1	—	—
W Montana‡	June 25–July 15	Aug 10–Sept 10	—	—
SW Oregon	May–July	July–Sept	—	—
Utah	—	Aug 1–Aug 30	—	—

Sources: Evans and others (1987), Furbush (1962), Hitchcock (1961), Hubbard (1958), Kearney (1951), McMinn (1964), Mirov and Kraebel (1939), Plummer and others (1968), Reed (1974), Rowntree (1948), Sampson and Jesperson (1963), Swingle (1939), Van Dersal (1938), Van Rensslaer (1942).
Elevations: * 900–1,500 m. † 700 m. ‡ 1,650 m.

178,000/lb), depending on the species (table 3). Adequate information on long-term storage is not available, but the seeds are apparently orthodox in storage behavior. Dry storage at around 4.5 °C should be satisfactory. Quick and Quick (1961) reported good germination in seeds of a dozen ceanothus species that had been stored for 9 to 24 years, with no apparent effect of seed age on viability. Seeds are apparently long-lived in litter; viable seeds of snowbrush ceanothus have been found in the surface soil of forest stands that were between 200 to 300 years old (Gratkowski 1962).

Germination. The long-term viability of seeds of ceanothus species apparently results from a strong seed coat dormancy, which in nature is typically broken by fire but may occasionally be broken by solar heating or mechanical scarification, such as from forest site preparation activities (Conard and others 1985). Germination of ceanothus seeds generally increases with increasing fire intensity (Conard and others 1985; Moreno and Oechel 1991), although at very high intensities, soil temperatures may be high enough to kill substantial numbers of seeds, resulting in decreased germination (Lanini and Radosevich 1986). In varnish-leaf ceanothus, Gratkowski (1962) observed that when seeds were exposed to drying conditions at normal air temperature, the hilum (the attachment scar on the seed, through which the radicle would normally emerge) functioned as a one-way hygroscopic valve that allowed moisture to pass out but prevented moisture uptake by the seeds. Heat caused a permanent, irreversible opening of the hilar fissure, which rendered the seed permeable to water. However, the seedcoat itself remained impermeable to moisture even after heating. This mechanism likely accounts for the abundant germination of ceanothus species that often occurs after fire on both chaparral and forest sites (Conard and others 1985).

In the laboratory, germination has been induced by soaking in hot water or heating in an oven, with or without a subsequent period of cold stratification (table 4). The typical pattern is that germination increases with the temperature of heat treatments up to a maximum, at which point seed mortality begins to occur. Seed germination and mortality are a function of both temperature and length of exposure, but for most species these optima are poorly defined. For hoaryleaf ceanothus, for example, maximum germination was obtained after heat treatments of 10 minutes to 1 hour at

Table 3—*Ceanothus*, ceanothus: thousands of cleaned seeds per weight

Species	Range /kg	Range /lb	Average /kg	Average /lb	Samples
C. americanus	212–291	96–132	247	112	5
C. arboreus	106–110	48–50	108	49	2
C. cordulatus	311–396	141–179	366	166	4
C. crassifolius	73–143	33–65	117	53	3
C. cuneatus	80–123	36–56	108	49	3
C. cuneatus var. *rigidus*	—	—	159	72	1
C. diversifolius	—	—	185	84	1
C. greggii	—	—	51	23	—
C. impressus	—	—	245	111	1
C. integerrimus	128–179	58–81	154	70	2
C. oliganthus	137–161	62–73	148	67	2
C. prostratus	82–98	37–45	90	41	3
C. sanguineus	282–291	128–132	287	130	2
C. sorediatus	267–269	121–122	—	—	2
C. thyrsiflorus	106–400	48–181	—	—	—
C. velutinus	135–335	61–152	207	94	5

Sources: Emery (1964), Hubbard (1958), Mirov and Kraebel (1939), Plummer and others (1968), Quick (1935), Quick and Quick (1961), Reed (1974), Swingle (1939).

70 to 80 °C. At higher temperatures, germination dropped off increasingly rapidly with duration of treatment, until at 100 °C there was a linear decrease in germination with times over 5 minutes (Poth and Barro 1986). In the wild, this range of time and temperature optima gives the advantage of allowing dormancy to be broken at a range of soil depths as a function of fire temperature and residence times. Quick and Quick (1961) reported that germination of mountain whitethorn and, to a lesser extent, deerbrush ceanothus began to drop off rapidly after a few seconds to several minutes in boiling water. Although "steeping" treatments at cooler temperatures (for example, 70 to 95 °C) were also found effective on several species (Quick 1935; Quick and Quick 1961), many investigators have continued to use treatments of boiling water (table 4). Dry heat treatments may be less damaging at higher temperatures than wet heat (table 4), although careful comparisons have not been made. In place of hot water treatments, seeds can also be immersed in sulfuric acid for 1 hour (Reed 1974).

Seeds of species found at high elevations also require cold stratification for good germination (Quick 1935; Van Rensslaer and McMinn 1942). Although some lower-elevation species from chaparral sites can germinate reasonably well without this cold treatment, their germination rates generally increase with stratification (table 4). Cold stratification is accomplished by storing seeds in a moist medium for periods of 30 to 90 days at temperatures of 1 to 5 °C. In general, longer periods of cold stratification are more effective than short ones. For example, Radwan and Crouch (1977) observed increasing germination of redstem ceanothus as cold stratification was increased from 1 to 3 or 4 months; no germination occurred without stratification. Similar patterns were observed by Quick and Quick (1961) for deerbrush ceanothus (increased germination up to 2 months of stratification) and Bullock (1982) for mountain whitethorn (increased germination up to 3 months). In lieu of cold stratification, a chemical treatment with gibberellin and thiourea was used to induce germination of buckbrush ceanothus (Adams and others 1961). Treatment with potassium salts of gibberellin also sucessfully replaced cold stratification in germination tests on redstem ceanothus seeds (Radwan and Crouch 1977). Following chemical treatments, seeds may then be germinated or dried again and stored (Adams and others 1961). Although emphasis has been on more natural methods of stimulating germination, seeds of snowbrush ceanothus and other species can be germinated quite successfully with acid scarification followed by a gibberellin treatment (Conard 1996).

Specific germination test conditions have not been well defined for most species of ceanothus. Sand or a mixture of sand and soil has been used as the moisture-supplying medium in most of the reported germination tests (Emery 1964; Quick 1935; Reed 1974), but filter paper has also been used successfully (Keeley 1987a). Diurnally alternating tempera-

Table 4—*Ceanothus*, ceanothus: pregermination treatments and germination test results

Species	Pregermination treatments: Hot water soak Temp (°C)	Pregermination treatments: Hot water soak Time* (min)	Pregermination treatments: Cold stratification (days)	Germination test days	Germination rate: Avg (%)	Germination rate: Samples
C. americanus	—	0	90	50	65	4
	77–100	ttc	60	30	32	1
C. arboreus	71–91	ttc	0	40–112	90	3+
C. cordulatus	90	ttc	94	35	74	4
	85	ttc	94	35	90	4
	80	ttc	94	35	74	4
C. crassifolius	71	ttc	90	21–90	76	1+
	71	ttc	0	90	48	1+
C. cuneatus	71	ttc	90	21–90	92	1+
	120†	5	30	21	28	3
	100	5	30	21	38	3
	70	60	30	21	3	3
	—	0	30	21	10	3
C. cuneatus var. *rigidus*	71	ttc	0	60–112	85	2+
C. diversifolius	77–100	ttc	60	60	61	1+
C. fendleri	—	0	0	—	16	—
C. greggii	100	1	30–60	17	51	—
C. impressus	77–100	ttc	60	30	73	1+
C. integerrimus	85	ttc	56	—	100	1
	71	ttc	90	20	85	1+
C. leucodermis	120†	5	30	21	68	3
	100	5	30	21	50	3
	70	60	30	21	47	3
	—	0	30	21	7	3
C. megacarpus	120†	5	30	21	88	3
	100	5	30	21	53	3
	70	60	30	21	54	3
	—	0	30	21	6	3
C. oliganthus	71	ttc	0	70	62	1+
C. prostratus	100	0.5	115	—	92	—
	77–100	ttc	90	30	71	1+
C. sanguineus	100	1	120	32	97	3
	100	5	120	32	92	3
	100	15	120	32	41	3
	100	1–5	0	32	0	3
C. sorediatus	100	5	90	30	100	1+
	100	5	0	30	38	1
C. thyrsiflorus	71	ttc	90	60	83	1+
	71	ttc	0	60	73	1
C. velutinus	90	ttc	63–84	—	82	1
	71	ttc	90	30	70	2+

Sources: Emery (1964), Keeley (1987a), Mirov and Kraebel (1939), Quick (1935), Quick and Quick (1961), Radwan and Crouch (1977), Reed (1974), Van Dersal (1938).

* ttc = "time to cool" (to room temperature) varied from several hours to overnight.

† Results reported here are for dry heat treatments, with germination in the dark; see Keeley (1987) for data on light germination.

tures of 30 °C in light and 20 °C in darkness have been effective, but constant temperatures of 10 °C (Reed 1974) and 24.5 °C (Emery 1988) also have been suitable for germination. A need for light has not been reported (Keeley 1991), and at least 1 species (deerbrush ceanothus) appears to germinate significantly better in the dark (Keeley 1987a). Germination rates resulting from selected pregermination treatments are listed in table 4 for 19 species.

The genus includes both species that sprout vegetatively following fire (sprouters) and species that are killed by fire and reproduce only from seeds (obligate seeders). Obligate seeders appear to have overall higher germination following heat treatment and to tolerate higher temperatures and longer periods at high temperature without damage to seed viability (Barro and Poth 1987). Germination test results suggest that eastern species may not be dependent on fire to

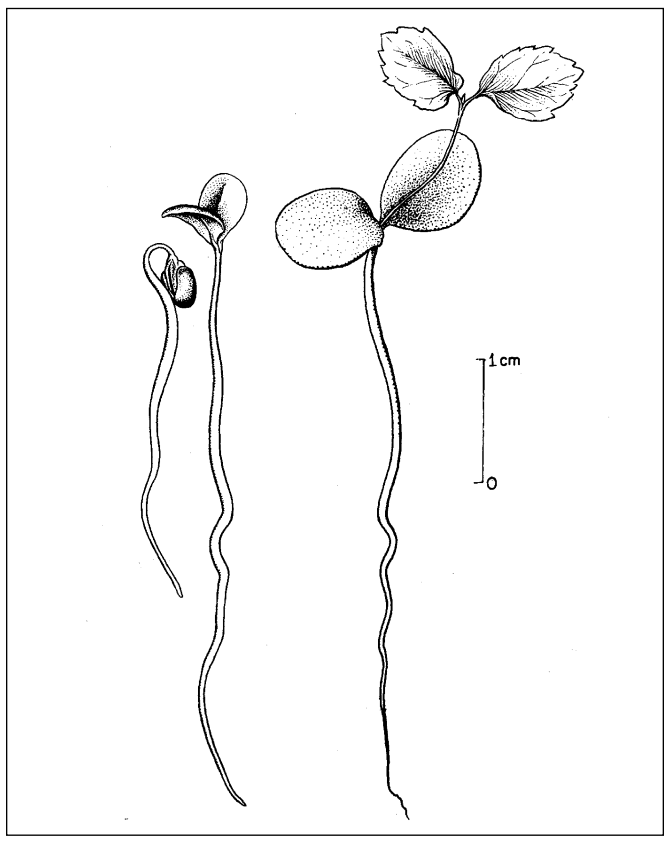
stimulate germination. For western species, however, some level of heat treatment, followed by stratification, will typically enhance germination. Although there has certainly been considerable variability in test results (table 4), a 5- to 10-minute dry heat treatment at 100 °C or a steeping treatment starting with 85 °C water, followed by several months of cold stratification, should effectively stimulate germination in most species.

Nursery practice. Seeding has been done in flats containing a medium of 5 parts loam, 4 parts peat, and 3 parts sand (Van Rensslaer and McMinn 1942). Leaf-mold may be substituted for the peat, but the peat is preferred because it is comparatively free of fungi. Sand is needed for drainage, a higher proportion being used in the seeding than in the potting medium. Seedlings are sensitive to sowing depth. In a trial by Adams (1962), deerbrush and buckbrush ceanothuses emerged best when sown at depths of 12 to 25 mm ($^1/_2$ to 1 in), and shading favored emergence of the first 2 species. However, some germination and emergence occurred at sowing depths ranging from 6 to 64 mm ($^1/_4$ to $2^1/_2$ in). Many species are sensitive to damping off, so for safety soil should be sterilized (Van Rensslaer and McMinn 1942). In California, seeding is usually done in November to January. Germination is epigeal (figure 4). Although all species of *Ceanothus* apparently fix nitrogen symbiotically, there has apparently been little or no research into the efficacy of or need for seed inoculation with *Frankia* to ensure nodulation of seedlings after outplanting. This is not likely to be a problem on soils where *Ceanothus* species are present, as nodulation appears to occur readily (Conard 1996) but may be of concern for horticultural uses of the genus.

Seedling care. When several sets of leaves have formed, the seedlings can be carefully planted into 2- or 3-inch (5- or 7.6-cm) pots. A good potting medium is 5 parts loam, 3 parts peat or leaf mold, and 1 part sand (Van Rensslaer and McMinn 1942). Care must be taken not to place the seedlings too deep in the soil, with root crowns should be just below the soil surface. Seedlings are susceptible to stem rot, and the loss will be greater if young plants are kept in moist soil that covers the root crown. The root development should be examined from time to time. When a loose root system has formed on the outside of the ball, the plant is ready for shifting to a larger pot or gallon can. It is best to discard potbound plants rather than to carry them along.

Planting stock of most common western ceanothus species is now available from commercial nurseries or botanic gardens, and numerous hybrids and cultivars have been developed for the nursery trade. Cultural notes on some of the commonly available species (table 1) and cultivars (Brickell and Zuk 1997) follow:

Figure 4—*Ceanothus americanus*, New-Jersey- tea: seedling development at 1, 5, and 15 days after germination.



- feltleaf ceanothus—*C. arboreus*—which can attain a height of 5 to 8 m and has pale blue flowers, grows best in coastal areas or with partial shade in areas with hot, dry summers.
- Fendler ceanothus—*C. fendleri*—up to 2 m tall with pale, bluish-white flowers, has been propagated from seeds sown in the spring and from cuttings in autumn. It grows best in light, well-drained soils and can tolerate cold.
- Carmel ceanothus—*C. griseus* var. *horizontalis* McMinn—a spreading, low-growing (to 1 m) variety, is used as ground cover and for slope stabilization. It performs best in mild coastal regions but will do well in partial shade in drier areas with adequate watering. Several named varieties are available.
- prostrate ceanothus—*C. prostratus*—a spreading, prostrate groundcover with small blue flower clusters, usually is propagated by layering. It is best if grown within its native range (for example, ponderosa pine zone of Sierra Nevada) and does not grow well at low elevations.

- Monterey ceanothus—*C. cuneatus* (Nutt.) Hoover var. *rigidus* cv. Snowball—a white-flowered cultivar, 1 to 1.5 m tall, recommended for coastal areas from southern California to the Pacific Northwest. Summer water should be restricted. It is a good bank and background plant.
- Sierra blue—*C. cyaneus* Eastw.—a medium to large shrub (to 6 m) with showy blue flowers, is a relatively fast grower that will tolerate hot, dry environments with some supplemental summer water.
- blueblossom—*C. thyrsiflorus*—a large shrub (2 to 7 m tall) with showy deep blue flowers, is a native of coastal forests. It grows well in its native range (Pacific coastal mountains) and needs shade from afternoon sun on dry inland sites, but requires little summer water once established.

There are many more ceanothus varieties that are excellent candidates for a range of domestic, commercial, or right-of-way landscaping situations. Although they are typically not widely available at retail nurseries, many native plant nurseries within the native range of ceanothus have wide selections. Additional information can be found in Kruckeberg (1982), Lenz and Dourley (1981), Perry (1992), Schmidt (1980), and the Sunset Western (1995) and National (1997) Garden Books, among others.

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Pinaceae—Pine family

Cedrus Trew

cedar

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Growth habit, occurrence, and use. The genus of true cedars—*Cedrus*—consists of 4 (or fewer) closely related species of tall, oleoresin-rich, monoecious, coniferous, evergreen trees, with geographically separated distributions (Arbez and others 1978; Bariteau and Ferrandes 1992; Farjon 1990; Hillier 1991; LHBH 1976; Maheshwari and Biswas 1970; Tewari 1994; Vidakovié 1991). The cedars are restricted to the montane or high montane zones of mountains situated roughly between 15°W and 80°E and 30 to 40°N (Farjon 1990). This discontinuous range is composed of 3 widely separated regions in North Africa and Asia (Farjon 1990): the Atlas Mountains of North Africa in northern Morocco and northern Algeria; Turkey, the mountains on Cyprus, and along the eastern border of the Mediterranean Sea in Syria and Lebanon; the Hindu Kush, Karakoram, and Indian Himalayas. The 4 species of cedars (table 1) are so closely related that habitual characteristics help differentiate the species (Farjon 1990). Isozyme analysis of cedar diploid tissue raises questions about the separation of Atlas cedar and cedar of Lebanon into 2 distinct species, because no distinguishing gene marker was detected (Panetsos and others 1992). There is disagreement as to the exact taxonomic status of the various cedars, with some authors suggesting that they be reduced to only 2 species: deodar cedar and cedar of Lebanon. In this writing, we will examine all 4 species.

The cedars are both valuable timber trees and quite striking specimen plants in the landscape. The wood of cedar of Lebanon is fragrant, durable, and decay resistant; and on a historical note, the ancient Egyptians employed cedar sawdust (cedar resin) in mummification (Chaney 1993; Demetci 1986; Maheshwari and Biswas 1970). Upon distillation of cedar wood, an aromatic oil is obtained that is used for a variety of purposes, from scenting soap to medicinal practices (Adams 1991; Chalchat and others 1994; Maheshwari and Biswas 1970; Tewari 1994).

Atlas cedar is a large tree that grows rapidly when young and is closely related to cedar of Lebanon. The Atlas cedar is distinguished by a taller crown, less densely arranged branchlets, bluish green leaves (needles) that vary from light green to silvery blue, smaller cones, and smaller

Table 1—*Cedrus,* cedar: nomenclature, occurrence, height at maturity, and date first cultivated

Scientific name	Common name	Occurrence	Height at maturity (m)	Year first cultivated
***C. atlantica* (Endl.) G. Manetti ex Carriere**	**Atlas cedar**	In Algeria on Mts. Babor & Tababort & in Hodna Mtns; in Morocco in Rif Mtns (at 1,370–2,200 m); planted in US	9–40	Before 1840
***C. breviifolia* (Hook. f.) A. Henry**	**Cyprian cedar**	Two separate locations on Mt Paphos in western Cyprus (at 900–1,525 m)	8–24	1879
***C. deodara* (Roxb. ex D. Don) G. Don F.**	**deodar cedar**	E Afghanistan (Hindu Kush), NW Pakistan (Karakoram), NW India (Kashmir & Gharwal Himalaya), rare in Nepal (1,700–3,000 m in western range & 1,300–3,300 m in eastern range); planted in US	15–50	1831
***C. libani* A. Rich.**	**cedar of Lebanon**	In S Turkey (Taurus Mtns), also Syria (Djebel el Ansiriya) & Lebanon (Djebel Loubnan); disjunct relict population in N Turkey near Black Sea (at 1,300–3,000 m); planted in US	15–40	Pre-1650

Sources: Dirr (1990), Farjon (1990), Hillier (1991).

seeds (table 2) (Dirr 1990; Farjon 1990; Hillier 1991; Loureiro 1990, 1994). Young trees appear stiff, with an erect leader and a pyramidal overall shape; with maturity this species assumes a flat-topped habit with horizontally spreading branches (Dirr 1990). Atlas cedar is hardy in USDA zones 6 to 9, with several beautiful cultivars that differ in color and characteristic habit (Dirr 1990; Hillier 1991; Vidakovié 1991). Of special note is '*Glauca*' (f. *glauca*), with very blue to silvery blue leaves, which is a spectacular specimen tree (Dirr 1990; Hillier 1991).

Cyprian cedar is a rare species that grows slowly but eventually develops into a medium-sized tree. This species is distinguished from cedar of Lebanon only by its habitual form and shorter leaves (table 2) and the broad and umbrella-shaped crown on older specimens (Farjon 1990; Hillier 1991; Vidakovié 1991).

Deodar cedar is an excellent specimen tree. The deodar cedar is broadly pyramidal when young, with gracefully pendulous branches (Dirr 1990; Tewari 1994). It is distinguished from the other species by its drooping leader and longer leaves (table 2) (Hillier 1991). Multi-stemmed crowns occasionally evolve from the higher branches turned erect, but the crown seldom becomes flat-topped, remaining conical or pyramidal (Farjon 1990). Deodar cedar is hardy in USDA zones 7 to 8, but young trees are prone to injury from frosts and cold wind (Dirr 1990). There are many cultivars of deodar cedar, but 2 worth mentioning are 'Kashmir' and 'Shalimar'. The former is winter-hardy—it tolerates cold winters to –30 °C—with silvery blue-green foliage (Dirr 1990; Vidakovié1991). The latter displays good blue-green leaf color and is the hardiest cultivar planted in the United States (Dirr 1990; Koller 1982).

Cedar of Lebanon is a majestic tree with innumerable historical and biblical references. It has a thick, massive trunk and wide-spreading branches; it is pyramidal when young but develops a flat-topped crown and horizontally tiered branches when mature (Chaney 1993; Dirr 1990; Farjon 1990; Hillier 1991). The dark green foliage, stiff habit, and rigidly upright cones (table 2) give this tree its splendor for landscape specimen planting. The morphological differences between cedar of Lebanon and Atlas cedar are small and not entirely constant (Farjon 1990; Maheshwari and Biswas 1970). Cedar of Lebanon is hardy in USDA Zones 5 to 7 (Dirr 1990; Dirr and others 1993). A geographical form—*C. libani* ssp. *stenocoma* (Schwarz) Davis—differs from the typical Lebanon cedar in having a broadly columnar habit and needle and cone characteristics that are intermediate between Atlas cedar and cedar of Lebanon; it is also more cold-hardy (Hillier 1991; Vidakovié 1991). There are also several dwarf cultivars of cedar of Lebanon that are of interest for use in the landscape (Hillier 1991; Vidakovié 1991).

Flowering and fruiting. The male flowers of cedar are erect catkins, up to 5 cm in length, whereas the female flowers are erect, cone-like inflorescences, 1 to 1.5 cm long, surrounded by needles at the base (Vidakovié 1991). Male and female strobili of the true cedars are borne (usually) on the same tree, but on separate branches (Farjon 1990; Maheshwari and Biswas 1970; Rudolf 1974). The male cones are solitary, grow more or less erect from the short shoots, and bear abundant yellow pollen (Farjon 1990; Maheshwari and Biswas 1970). Depending upon the altitude, locality, and weather, the pollen is shed late in the year (September through November), relating to the late development of the female strobilus (Farjon 1990; Maheshwari and Biswas 1970). The female cones are borne singly at the tips of the dwarf shoots, stand erect, and are less abundant than the male cones (Farjon 1990; Maheshwari and Biswas 1970). Although pollination takes place in the fall, the cones do not mature until the second year, requiring about 17 to 18 months for full development (Farjon 1990; Maheshwari and Biswas 1970; Rudolf 1974).

The mature, barrel-shaped cones (figure 1) are resinous and characterized by numerous closely appressed, very broad scales, each containing 2 seeds (table 2) (Rudolf 1974). The scales are attached to the persistent rachis with a narrowed, petiolate base and dismember from it by abscission at maturity, as in fir (*Abies*) (Farjon 1990; Rudolf 1974). The irregularly triangular mature seed is rather soft and oily, with resin vesicles present on each side of the seed,

Table 2—*Cedrus,* cedar: cone, seed, and leaf (needle) characteristics

	Cone characteristics			Seed size		Leaf characteristics	
Species	Ripe color	Length (cm)	Width (cm)	Length (mm)	Width (mm)	Length (cm)	No. in whorls
C. atlantica	Light brown	5–8	3–5	8–13	4–6	1–2.5	20–45
C. brevifolia	Light brown	5–10	3–6	8–14	5–6	0.5–1.6	15–20
C. deodara	Reddish brown	7–13	5–9	10–15	5–7	2–6.0	20–30
C. libani	Grayish brown	8–12	3–6	10–14	4–6	1–3.5	20–40

Sources: Farjon (1990), Rudolf (1974), Vidakovie (1991).

and it has a membranous, broad wing that is several times larger than the seed (figures 2 and 3) (Farjon 1990; Rudolf 1974). Seeding habits of the various species are given in table 3. Commercial seed bearing of deodar cedar begins from 30 to 45 years of age, and good seedcrops are borne every 3 years, with light crops in the intervening years (Doty 1982; Maheshwari and Biswas 1970; Rudolf 1974; Tewari 1994; Toth 1979).

Collection of fruits; extraction, cleaning, and storage of seeds. Cones should be collected directly from the trees, before the cones turn brown, or cone-bearing twigs may be cut from standing or felled trees just before ripening is complete (Dirr and Heuser 1987; Rudolf 1974; Singh and others 1992). One cubic meter (28.38 bu) of cones weighs from 12.2 to 15.9 kg (27 to 35 lb) and yields about 1.4 kg (3 lb) of cleaned seeds (Rudolf 1974). Cones should be allowed to dry until the scales loosen and the seeds can be removed (Dirr and Heuser 1987; Macdonald 1986; Toth 1980a). It is important to avoid any more drying than is absolutely necessary, because the seeds may be killed. Cones of cedar may be soaked in warm water for 48 hours to encourage them to disintegrate (Rudolf 1974; Macdonald 1986). Freezing moist cones (as a last resort) will also force the scales to open up (Macdonald 1986). After the cone scales are dry, they can be placed in a cone shaker to remove the seeds (Rudolf 1974), and seeds can be separated from the debris by fanning or sieving (Macdonald 1986). Seeds are de-winged by simply rubbing them in a dry cloth (Macdonald 1986), for resin from the resin pockets in the wings can make de-winging with bare hands difficult (Macdonald 1986). Purity of commercially cleaned seed has been 85 to 90% (table 4).

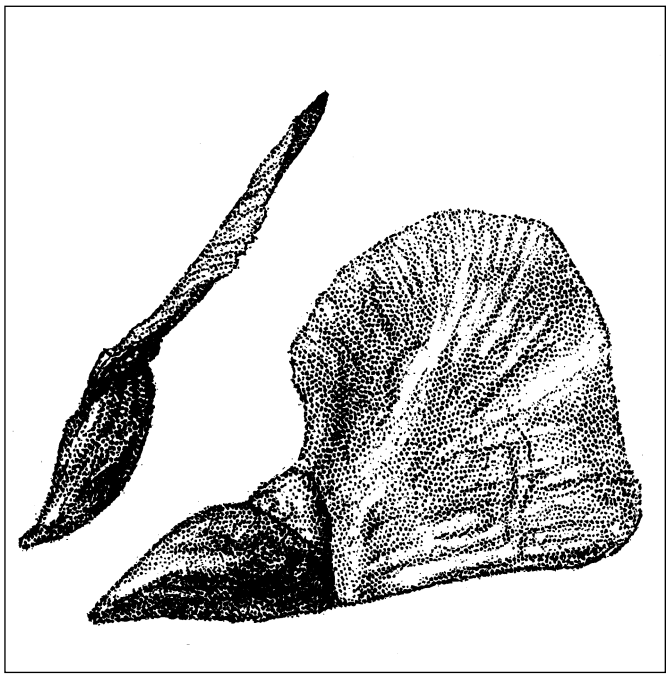
Even though cedar seeds are orthodox in storage behavior, they are very oily and do not keep well under many storage conditions (Allen 1995; Rudolf 1974). If cedar seeds are dried below a critical level, they will not imbibe water in a way that will allow the food reserves to be used by the embryo (Macdonald 1986). Cedar seeds have retained viability for 3 to 6 years when dried to a moisture content of less than 10%, placed in sealed containers, and held at temperatures of –1 to –5 °C (Erkuloglu 1995; Rudolf 1974).

Pregermination treatments. Cedar seeds exhibit little or no dormancy and will germinate without pretreatment. However, variable degrees of dormancy may be observed within a single lot of seeds (Dirr and Heuser 1987). Seeds should be stratified at 3 to 5 °C for 2 weeks (6.5 weeks for Cyprian cedar) to give more uniform germination (Allen 1995; Rudolf 1974). Thapliyal and Gupta (1980) found that 9 °C was a better temperature for stratification than 3 °C. Deodar cedar and cedar of Lebanon seeds are prone to damping-off disease and thus should be treated with an appropriate fungicide (Mittal 1983).

Germination tests. The AOSA (1993) prescribes germination tests of stratified seeds (14 days) on top of blotters for 3 weeks at 20 °C for all cedars (see also Toth 1980a). ISTA (1993) rules, however, specify diurnally alternating

Figure 1—*Cedrus libani*, cedar of Lebanon: mature cone.

Figure 2—*Cedrus libani*, cedar of Lebanon: seeds with membranous wing attached.



temperatures of 20 °C (night) and 30 °C (day) for a period of 4 weeks. Tests may also be made in sand flats (Rudolf 1974). Deodar cedar seeds stratified at 4 °C in moist sand for 30 days showed 45% germination versus 11% without stratification (Dirr and Heuser 1987). Thapliyal and Gupta (1980) also found that the percentage of germination without stratification to vary from 16 to 69%. Singh and others (1992) found that seeds from larger cones exhibited higher germination (66%) in Himalayan cedar. Singh and others (1997) also found that there were significant differences between tree-diameter classes in fresh and dry weight of seeds and also in germination in the laboratory and in the nursery. Germination of cedar seed is epigeal (figure 4).

Nursery practice and seedling care. Deodar cedar seeds should be sown in the fall (or in spring) at a rate of 200 to 250 seeds/m^2 (19 to 23/ft^2), in drills 10 to 15 cm (4 to 6 in) apart for lining-out stock and for root stocks (Macdonald 1986; Rudolf 1974). Chandra and Ram (1980) recommend sowing deodar seeds at a depth of 1 cm (0.4 in); further increase in depth results in decreased germination. Al-Ashoo and Al-Khaffaf (1997) reported that the best treatment for germination of cedar of Lebanon seeds was a 1.5-cm (0.6-in) sowing depth, with a covering medium of clay or alluvial soil. In northern areas, fall-sown beds should be mulched over winter, the mulch removed early in the spring, and the bed racks covered with burlap on critical spring nights to prevent freezing (Heit 1968). Cedar seeds can be sown in containers in the fall, transplanted into other containers during the winter, and kept in shaded beds in the summer to produce $^1/_2$- to 1 $^1/_2$-year-old planting stock (Rudolf 1974). The size of the propagation container, growth media, transplanting date, and handling of seedlings is important in container or field grown stock (Appleton and Whitcomb 1983; Burger and others 1992; Doty 1982; Guehl and others 1989; Puxeddu and Alias 1991; Toth 1980b).

Deodar cedar 'Shalimar' can be propagated by collecting cuttings in late fall to early winter; 67% of such cuttings given a quick dip in 5 g/liter (5,000 ppm) indole-3-butyric acid (IBA) solution and placed in a sand–perlite medium with bottom heat (Nicholson 1984) rooted. Shamet and Bhardwaj (1995) reported 69% rooting of deodar cedar cut-

Figure 3—*Cedrus brevifolia*, Cyprian cedar: longitudinal section through a seed (**top**) and exterior view of a de-winged seed (**bottom**).

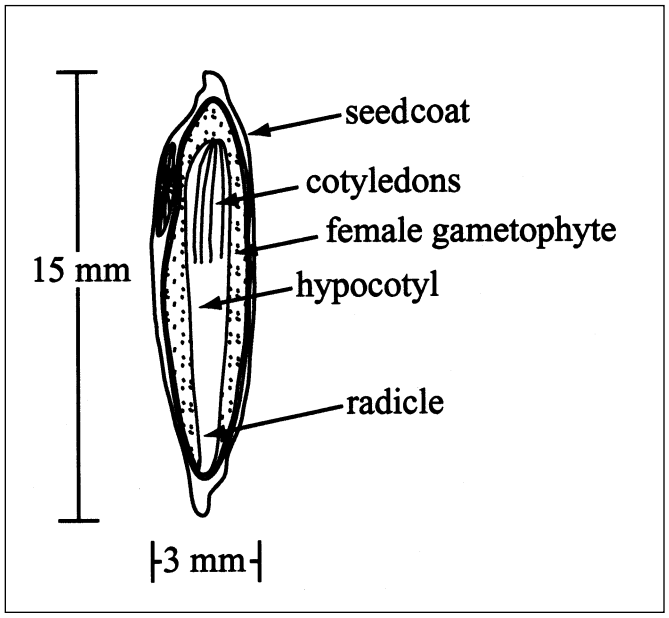


Table 3—*Cedrus*, cedar: phenology of flowering and fruiting

Species	Flowering	Cone ripening	Seed dispersal
C. atlantica	June–Sept	Sept–Oct	Fall–spring
C. deodara	Sept–Oct	Sept–Nov	Sept–Dec
C. libani	June–Sept	Aug–Oct	Fall–spring

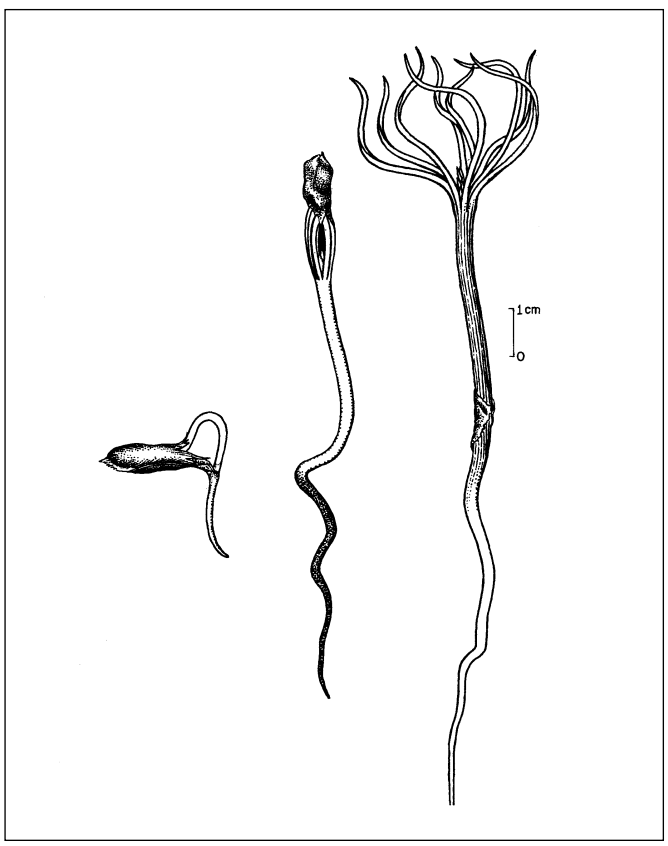
Sources: Rudolf (1974), Vidakovic (1991).

Table 4—*Cedrus*, cedar: seed data

Species	Avg no. cleaned seeds /kg	Avg no. cleaned seeds /lb	Commercial seed purity (%)
C. atlantica	13,900	6,300	89
C. brevifolia	13,000	5,890	—
C. deodara	8,150	3,700	85
C. libani	11,700	5,300	87
C. libani ssp. *stenocoma*	17,600	8,000	—

Sources: Allen (1995), Rudolf (1974).

Figure 4—*Cedrus libani*, cedar of Lebanon: seedling development at 1, 4, and 8 days after germination.



tings treated with 0.5% indole-3-acetic acid–talc or 1% naphthaleneacetic acid–activated charcoal, both supplemented with 10% captan and 10% sucrose. However, cuttings taken from Atlas cedar and cedar of Lebanon are difficult to root, although some rooting may occur on cuttings taken in late winter and treated with 8 g/liter (8,000 ppm) IBA–talc (Dirr and Heuser 1987). Cultivars of cedar species are more routinely propagated by grafting (Blomme and Vanwezer 1986; Dirr and Heuser 1987; Hartmann and others 1990; Lyon 1984; Macdonald 1986; Richards 1972). Two reports have been published on the *in vitro* culture of deodar cedar (Bhatnagar and others 1983; Liu 1990). A method for *in vitro* propagation of cedar of Lebanon through axillary bud production, a study of bed dormancy *in vitro*, and detection of genetic variation of *in vitro*–propagated clones has also been described (Piola and Rohr 1996; Piola and others 1998, 1999).

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Celastraceae—Bittersweet family

Celastrus scandens L.

American bittersweet

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Other common names. climbing bittersweet, shrubby bittersweet.

Growth habit, occurrence, and use. American bittersweet is a deciduous climbing or twining shrub of eastern North America (Brizicky 1964; Fernald 1950) that occurs in thickets, in stands of young trees, along fence rows, and along streams, usually in rich soil. It occurs naturally from southern Quebec; west to southern Manitoba; and south to Oklahoma and central Texas, Arkansas, Tennessee, northern Alabama, and western North Carolina (Brizicky 1964). Some authors (Fernald 1950; USDA FS 1948) reported it in Louisiana, New Mexico, Georgia, and Mississippi, but its occurrence has not been verified in Georgia, Louisiana, or Mississippi (Brizicky 1964).

The plant is valuable for ornamental purposes and game food and cover; the bark has been used for medicinal purposes (USDA FS 1948). Among the animals and birds feeding on American bittersweet are the bobwhite quail (*Colinus virginianus*), ruffed grouse (*Bonasa umbellus*), ringneck pheasant (*Phasianus colchicus*), eastern cottontail (*Silvilagus floridanus*), fox squirrel (*Sciurus niger*), and various songbirds (Van Dersal 1938). It was introduced into cultivation in 1736 (USDA FS 1948).

By 1970, oriental or Asiatic bittersweet—*C. orbiculatus* Thunb.—had become naturalized on at least 84 sites from Georgia to Maine and west to Iowa (McNab and Meeker 1987), occupying many of the same sites as American bittersweet. It is listed as an invasive plant by the United States Government (USDA NRCS 1999). In some locales, the species is found mainly along fence lines, resulting from the germination of seeds contained in the droppings from frugivorous birds (McNab and Meeker 1987). The stem, leaves, and berries of oriental bittersweet are reported to be toxic for human consumption (McNab and Meeker 1987).

Flowering and fruiting. The small greenish, polygamo-dioecious or dioecious flowers open from May to June and are borne in raceme-like clusters at the end of branches (Brizicky 1964; Fernald 1950). Hymenopterous insects, especially bees, seem to be the main pollinators, although wind may also be involved (Brizicky 1964). Seeds are about 6.3 mm long and are borne in bright orange to red, fleshy arils, 2 of which are usually found in each of the 2 to 4 cells composing the fruit, a dehiscent capsule (figure 1). The yellow to orange capsules ripen from late August to October. They split open soon thereafter, exposing the seeds covered with showy red arils (figures 2 and 3). Good seedcrops are borne annually and may persist on the bushes throughout much of the winter (USDA Forest Service 1948). In Pennsylvania, only 1 seedcrop failure was reported in a 14-year period (Musser 1970). Sunlight is reported necessary for abundant fruiting to occur (Musser 1970).

Collection of fruit. The ripe fruits should be collected as soon as the capsules separate and expose the arils, or from about mid-September as long as they hang on the vines (USDA FS 1948), but rarely later than December (Van Dersal 1938). In Pennsylvania, the fruits are collected from late October through November (Musser 1970).

Figure 1—*Celastrus scandens*, American bittersweet: fruiting branch.

Extraction and storage of seeds. Collected fruits should be spread out in shallow layers and allowed to dry for 2 or 3 weeks (USDA FS 1948). In Pennsylvania, the fruits are allowed to air-dry for 1 week in shallow trays (Musser 1979). The seeds are then removed from the capsules by flailing or running the fruits through a hammermill or macerator with water (Musser 1970; USDA FS 1948). Then the seeds are allowed to dry for another week and the chaff is separated by windmilling (Musser 1979). The dried arils are left on the seeds (USDA FS 1948) except when seeds are to be stored.

American bittersweet has 4 to 8 seeds/fruit. On the basis of 10 samples, the number of seeds per weight ranged from 26,000 to 88,000/kg (12,000 to 40,000/lb) with an average of 57,000/kg (26,000/lb). Average purity was 98% and average soundness 85% (USDA FS 1948).

In Pennsylvania, the seeds usually are sown in the fall soon after collection and extraction or stored in cloth bags until used (Musser 1970). For longer storage periods, viability has been retained for 4 to 8 years by cleaning the fleshy material from the seeds, air-drying the seeds at low humidity, and then storing them in sealed containers at a temperature between 1 and 3 °C (Heit 1967).

Pregermination treatments. Seeds of American bittersweet have a dormant embryo and thus require afterripening for germination. There is also some evidence that the seedcoat may have an inhibiting effect on germination (Hart 1928; USDA FS 1948). Good germination is obtained by fall-sowing or by stratification in moist sand or peat for 2 to 6 months at 5 °C (Heit 1968; Musser 1970; USDA FS 1948). Three months of cold stratification has resulted in good germination for American bittersweet (Dirr and Heuser 1987). It seems to make little difference whether cleaned seeds or dried fruits are sown; however, it appears that both cleaned seeds and fruits should be dried at room temperature for 2 to 3 weeks before they are sown (USDA FS 1948).

Figure 2—*Celastrus scandens*, American bittersweet: seeds with aril removed.

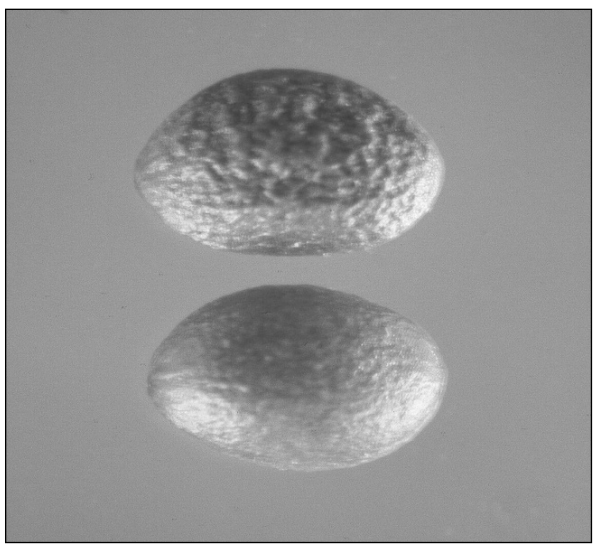
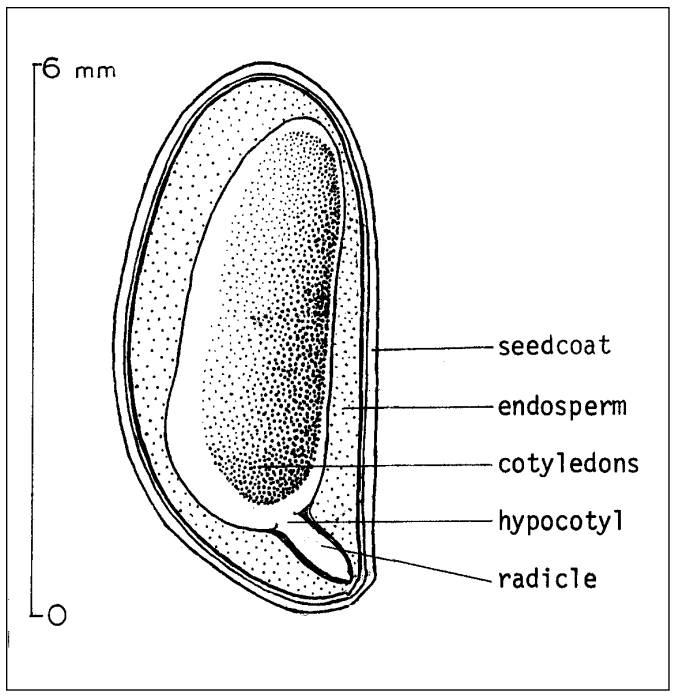


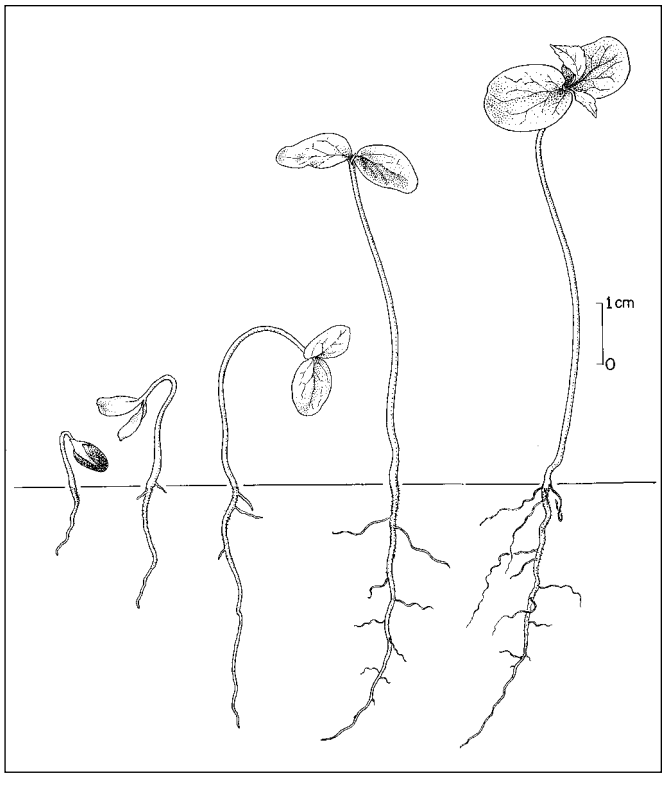
Figure 3—*Celastrus scandens*, American bittersweet: longitudinal section through a seed.



Germination tests. On the basis of 6 tests, using stratified seedlots in sand flats, at temperatures alternating from 10 to 25 °C, germinative capacity was found to range from a low of 9 to a high of 80% in 30 days, with an average of 47%. Potential germination varied from 9 to 93% (USDA FS 1948). Seedlots of oriental bittersweet showed 100% germination after 3 months of cold stratification (Dirr and Heuser 1987). Germination of American bittersweet is epigeal (figure 4).

A good estimate of germination can be obtained by the excised embryo method (Heit and Nelson 1941). The seeds are soaked until plump; seedcoats are removed and the embryos excised. The excised embryos are placed on moistened filter paper in covered petri dishes. A room temperature of 21 to 22 °C appears to be most satisfactory. Viable embryos will either show greening of the cotyledons, remain perfectly white in color but grow larger, or exhibit radicle elongation. Embryos exhibiting such characteristics can be counted as being from healthy seeds, capable of germinating

Figure 4—*Celastrus scandens,* American bittersweet: seedling development at 1, 2, 5, 10, and 30 days after germination.



with proper afterripening treatment. Five to 20 days are required to secure approximate germination by the excised embryo method.

Nursery practice. In Pennsylvania, good results have been obtained by sowing cleaned seeds in the first fall after collection and extraction. The seeds are broadcast on seedbeds and firmed in with a roller; then covered with a mixture of 1 part of sand to 2 parts of sawdust. The beds are covered with shade until germination occurs. Germination usually begins about 20 days after conditions become favorable (Musser 1970).

Another practice is to stratify cleaned or dried seeds in the pulp in January, and then sow them in the early spring. Young seedlings are somewhat susceptible to damping-off (USDA FS 1948). About 6,600 usable plants can be produced per kilogram of seeds (3,000/lb) (Van Dersal 1938). Propagation by root cuttings, layers, or stem cuttings is also sometimes practiced (Sheat 1948).

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C

Ulmaceae—Elm family

Celtis L.

hackberry

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Growth habit, occurrence, and use. The genus *Celtis*—hackberry—is a large, widespread genus that includes about 70 species of shrubs and trees in the Northern Hemisphere. The 3 species listed in table 1 are all medium to large deciduous trees.

Flowering and fruiting. The small, greenish flowers of all 3 species appear in the spring as the new leaves emerge (table 2). These species are polygamo-monoecious (Krajicek and Williams 1990; Kennedy 1990; Vines 1960). Hackberry fruits are spherical drupes 6 to 13 mm in diameter with a thin pulp enclosing a single bony nutlet (figures 1–3). Good seedcrops are borne practically every year, and the fruits persist on the branches into winter (Bonner 1974; Krajicek and Williams 1990; Kennedy 1990). Other fruit and seed data (Little 1950; Preston 1947; Rehder 1940; Swingle 1939) are presented in tables 2 and 3.

Collection of fruits. Mature fruits can be picked by hand from trees as late as midwinter. Collection is much easier after all leaves have fallen (Bonner 1974). Limbs of sugarberry can be flailed to knock the fruits onto sheets spread under the trees. Fruits collected early in the season should be spread to dry to avoid overheating and molding (Williams and Hanks 1976). Fruits collected later in the season, unless the collection is done in wet, rainy weather, usually do not require additional drying (Bonner 1974).

Extraction and storage. Twigs and trash can be removed by screening or fanning, and the fruits can be depulped by wet or dry maceration. If wet maceration is used, the seeds will have to be dried for storage. If they are to be planted immediately, drying is not necessary. The pulp on dried fruits can be crushed and the resulting debris removed by washing on a screen under water pressure (Williams and Hanks 1976).

Table 1—*Celtis*, hackberry: nomenclature and occurrence

Scientific name & synonym	Common name(s)	Occurrence
***C. laevigata* Willd.** *C. mississippiensis* Spach	**sugarberry,** sugar hackberry, hackberry, sugarberry, *palo blanco*	Maryland & Virginia to Florida & Texas; N to Kansas, Texas, Illinois, & Kentucky
***C. laevigata* var. reticulata (Torr.) L. Benson** *C. reticulata* Torr.	**netleaf hackberry,** hackberry, western hackberry, *palo*	Washington & Colorado S to W Texas, S California, & central Mexico
***C. occidentalis* L.** *C. crassifolia* Lam.	**common hackberry,** hackberry, sugarberry, northern hackberry	New England to North Dakota; S to NW Texas & N Georgia

Source: Little (1979).

Table 2—*Celtis*, hackberry: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
C. laevigata	Apr–May	Sept–Oct	Oct–Dec
C. laevigata var. *reticulata*	Mar–Apr	Late fall	Fall–winter
C. occidentalis	Apr–May	Sept–Oct	Oct–winter

Source: Bonner (1974).

Figure 1—*Celtis*, hackberry: fruits (**left**) and seeds (**right**) of *C. laevigat*a, sugarberry (**top**) and *C. laevigata* var. *reticulata,* netleaf hackberry (**bottom).**

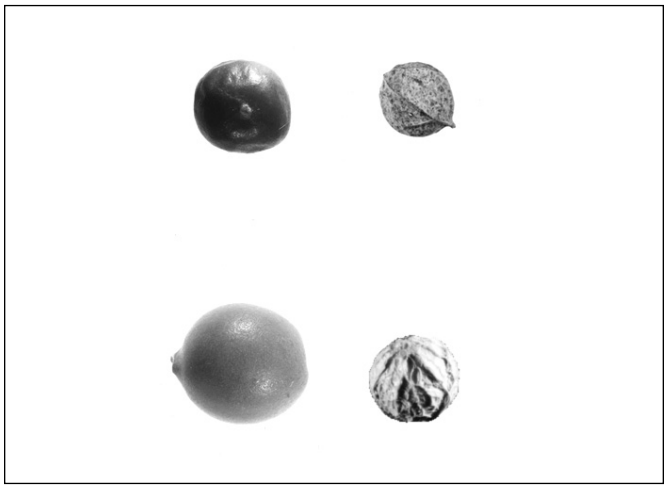
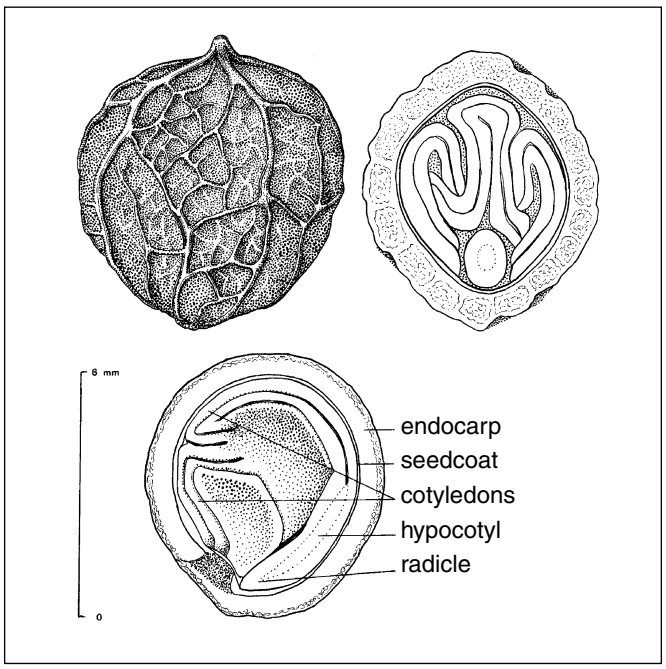
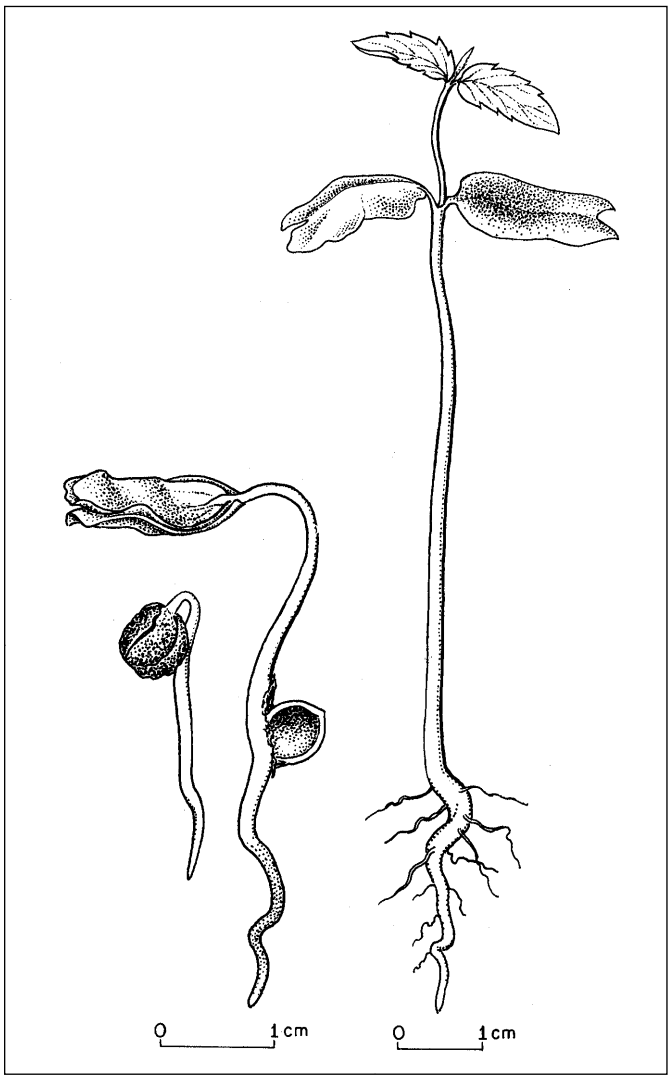


Figure 2—*Celtis occidentalis*, common hackberry: exterior view of seed (**top left**) and transverse section (**top right**) and cross section (**bottom**) of a seed.



Removal of the pulp may not be absolutely necessary, but it has been reported to aid germination of all 3 species (Bonner 1974; Vines 1960). Seed yield data are listed in table 4. Dry fruits or cleaned seeds store equally well in sealed containers at 5 °C. Dried fruits of hackberry were stored in this manner for 5 $^{1}/_{2}$ years without loss of viability (Bonner 1974), proving that they are orthodox in storage behavior.

Figure 3—*Celtis laevigata*, sugarberry: seedling development at 1, 2, and 5 days after germination.



Pregermination treatments. Hackberry seeds exhibit dormancy that can be overcome with stratification at 5 °C in moist media. Sugarberry, common hackberry, and netleaf hackberry all should be stratified for 90 to 120 days (Bonner 1974, 1984). In the southernmost part of sugarberry's range, no pretreatment was required for timely germination, but depulping prior to sowing was very beneficial (Vora 1989). Fermenting the fruits for 3 days at room temperature and then depulping before stratifying gave excellent results for common hackberry (Bonner 1974).

Germination tests. Germination test recommendations for treated seeds are the same for all 3 species (table 5). Untreated seeds should be tested for 90 days (Bonner 1974). Because of the long periods necessary for germination tests, rapid estimates of viability are very useful in this genus. Tetrazolium chloride staining works well with sugarberry. Incubation of clipped and imbibed seeds in a 1% solution for 24 hours at 26 °C has given good results (Bonner 1984).

Table 3—*Celtis,* hackberry: height, seed-bearing age, and fruit color

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yrs)	Fruit color	
				Preripe	Ripe
C. laevigata	18–24	1811	15	Green	Dark orange to red
C. laevigata var. *reticulata*	9–14	1890	—	—	Orange-red or yellow
C. occidentalis	9–40	1656	—	Orange-red	Dark reddish purple

Source: Bonner (1974).

Table 4—*Celtis,* hackberry: seed yield data

Species	Fruits/weight		Cleaned seeds/weight			
			Range		Average	
	/kg	/lb	/kg	/lb	/kg	/lb
C. laevigata	4,850	2,200	8,150–15,600	3,700–7,080	13,200	6,000
C. laevigata var. *reticulata*	—	—	5,150–14,500	2,340–6,600	10,500	4,870
C. occidentalis	4,520	2,050	7,700–11,900	3,500–5,400	9,500	4,300

Source: Bonner (1974).

Table 5—*Celtis,* hackberry: germination test conditions and results

Species	Germinative test conditions *			Germination rate		Germination %	
	Temp (°C)			Amount			
	Day	Night	Days	(%)	Days	Avg	Samples
C. laevigata	30	20	60	30–50	25–30	55	6+
C. laevigata var. *reticulata*	30	20	60	—	—	37	7
C. occidentalis	30	20	60	39	37	47	7

Source: Bonner (1974).

* Media used: sand, a sand–peat mixture, or a sandy loam soil.

Nursery practice. Both fall-sowing of untreated seeds and spring-sowing of stratified seeds are satisfactory. Seeds may be broadcast or drilled in rows 20 to 25 cm (8 to 10 in) apart and covered with 13 mm ($^1/_2$ in) of firmed soil. Beds should be mulched with straw or leaves held in place with bird screens until germination starts. Germination is epigeal (figure 4). These species can be propagated by cuttings (Bonner 1974), and grafting and budding success has been reported for common hackberry and sugarberry (Williams and Hanks 1976).

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Rubiaceae—Madder family

Cephalanthus occidentalis L.

buttonbush

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Other common names. common buttonbush, honeyballs, globe-flowers.

Growth habit, occurrence, and use. Buttonbush is a deciduous shrub or small tree that grows on wet sites from New Brunswick to Florida, west to southern Minnesota, Kansas, southern New Mexico, Arizona, and central California. It also occurs in Cuba, Mexico, and Central America (Little 1979). In the southern part of its range, buttonbush reaches heights of 4.5 to 6 m at maturity (Maisenhelder 1958), but it is shrubby in other areas. The seeds are eaten by many birds, and the tree has some value as a honey plant (Van Dersal 1938). Cultivation as early as 1735 has been reported (Vines 1960).

Flowering and fruiting. The perfect, creamy white flowers are borne in clusters of globular heads and open from June to September (Vines 1960). There is good evidence that buttonbush is largely self-incompatible (Imbert and Richards 1993). The fruiting heads (figure 1) become reddish brown as they ripen in September and October. Single fruits are 6 to 8 mm long (figure 2). Each fruit is composed of 2 or occasionally 3 or 4 single-seeded nutlets (figure 3) that separate eventually from the base (Bonner 1974b).

Collection and extraction. Collection can begin as soon as the fruiting heads turn reddish brown. Many heads disintegrate after they become ripe, but some persistent through the winter months. When the heads are dry, a light flailing will break them into separate fruits. Data from 4 samples of scattered origin showed 295,000 fruits/kg (134,000/lb), with a range of 260,000 to 353,000 (118,000 to 160,000). Purity in these seed lots was 96% (Bonner 1974b). The number of seeds per weight is about twice the number of fruits. Longevity of buttonbush seeds in storage is not known, but they appear to be orthodox in nature and thus easy to store. The principal storage food in the seeds is carbohydrate (Bonner 1974a).

Figure 1—*Cephalanthus occidentalis*, common buttonbush: fruiting heads.

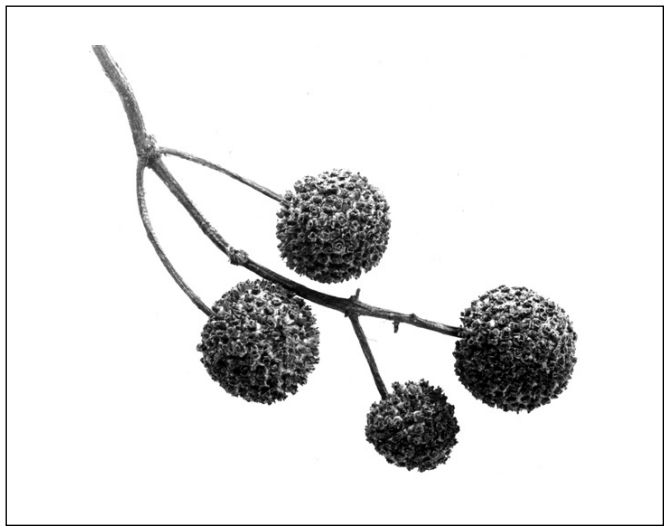
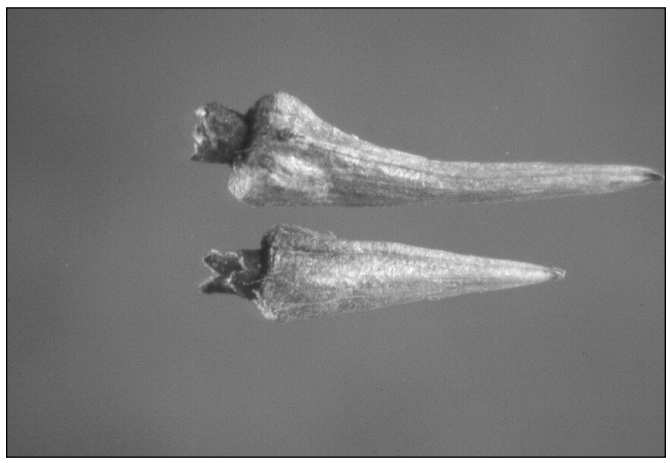


Figure 2—*Cephalanthus occidentalis*, common buttonbush: single fruits.



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Germination tests. Buttonbush seeds germinate promptly without pretreatment. Germination is epigeal (figure 4). Results with 2 test methods on seed from Louisiana (DuBarry 1963) and Mississippi (Bonner 1974b) were as follows:

	Louisiana	Mississippi
Medium	Water	Blotter paper
Temperature (°C)	24–34	30
Light	Yes	No
Test duration (days)	30	10
Germination (%)	86	78
No. of samples	4	4

Figure 3—*Cephalanthus occidentalis*, common buttonbush: longitudinal section through the 2 nutlets of a single fruit.

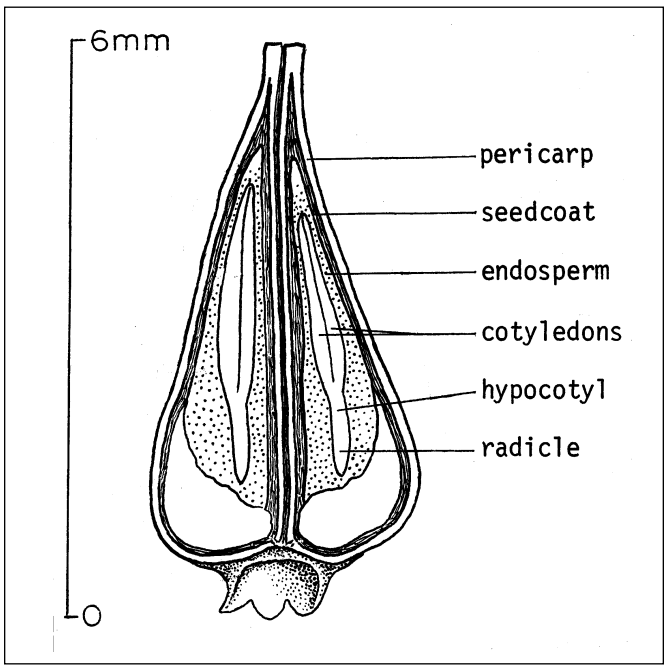
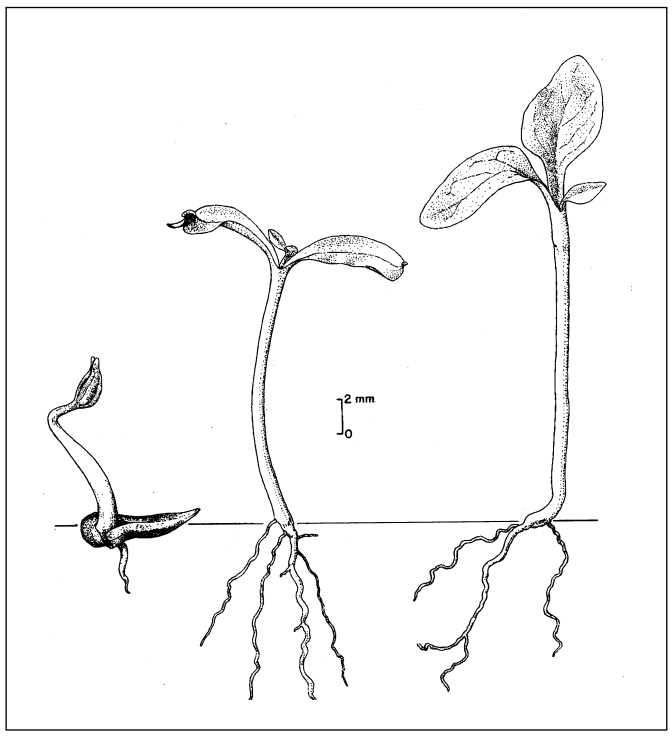


Figure 4—*Cephalanthus occidentalis,* common buttonbush: seedling development at 1, 23, and 40 days after germination.



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Fabaceae—Pea family

Ceratonia siliqua L.

carob

Wayne D. Shepperd

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Growth habit. *Ceratonia siliqua* L.—carob, St. John's bread, or locust—is a small to medium-sized broadleaf, evergreen tree that may grow to 20 m in height under ideal climatic conditions (Catarino 1993) but usually reaches heights of 8 to 15 m (Goor and Barney 1968). Carob is thought to be a tropical plant that has adapted well to Mediterranean climates by utilizing its deep rooting habit and xerophilous leaves to avoid water stress (Catarino 1993). The deep taproot's penetration into moist regions of the soil profile effectively lengthens the active growth period for carob leaves during the Mediterranean dry season (Rhizopoulou and Davies 1991).

Occurrence. Carob is native to the eastern Mediterranean from the southern coast of Asia Minor to Syria (Goor and Barney 1968; Griffiths 1952; Karschon 1960). It has been cultivated for thousands of years as a forage crop on a wide variety of soils in Asian, European, and North African countries along the coast of the Mediterranean Sea (Bailey 1947; Catarino 1993). Carob's sensitivity to low temperatures limits its area of distribution (Catarino 1993). Since its introduction to the United States in 1854, carob has done well only in the warm subtropical climates (southern Florida, the Gulf States, New Mexico, Arizona, and southern California) where annual rainfall is not below 30 to 35 cm (Bailey 1947; Coit 1951, 1962).

Use. Carob legumes (pods) are commonly used as animal feed or ground into flour and mixed with other cereals for human consumption. The legumes are rich in protein and sugar and are a highly nutritious livestock feed, comparable to barley and superior to oats (Bailey 1947; Coit 1962). However, the high sugar content (< 50%) is offset by a high tannin content (16 to 20%) that inhibits protein assimilation (Catarino 1993). Techniques are currently being developed to enzymatically separate and extract the phenolic tannin compounds to increase utilization (Catarino 1993). Legumes are also used in making health foods (as a chocolate "substitute"), carob syrup, and medicines such as laxatives and diuretics (Binder and others 1959; Coit 1951, 1962). In addition, they can be used as a cheap carbohydrate source for ethanol production, yielding 160 g of ethanol/kg of dry legumes (Roukas 1994). The annual production of carob legumes is 340,000 to 400,000 metric tons (374,800 to 441,000 tons), with Greece, Spain, Italy, and Portugal being primary producers (Roukas 1994; Catarino 1993).

Carob seeds are extremely hard, but the endosperm contains 30 to 40% by weight of galactomanane polysaccharides collectively known as carob-, or locust-bean gum (Catarino 1993). The compound is a valuable stabilizing and thickening additive used in the food processing, pharmaceutical, textile, paper, and petroleum industries.

The adaptability, ease of cultivation, and aesthetic appeal of carob also make it a desirable landscape plant (Catarino 1993). It is chiefly valuable in the United States as an ornamental evergreen but has been used to some extent in environmental plantings (Toth 1965).

Flowering and fruiting. The flowers, borne in small, lateral, red racemes, are polygamo-trioecious (Loock 1940). Nearly all cultivated species are dioecious, although flowers of both sexes may possess vestigial components of the other sex. Rarely, plants will possess both male and female flowers on the same stalk or completely hermaphroditic flowers (Catarino 1993). Flowers bloom from September to December in California, depending on the variety and the weather (Bailey 1947; Coit 1951).

The fruit is a coriaceous, indehiscent legume 10 to 30 cm long, 6 to 20 mm thick, filled with a sweet, pulpy substance bearing 5 to 15 obovate, transverse, brown, bony seeds about 6 mm wide (figures 1 and 2) (Bailey 1947; Coit 1951). Legumes ripen, turn dark brown, and begin to fall from September to November (California), depending on the variety and the weather (Bailey 1947; Coit 1951, 1962). Natural seedlings appear in Greece in November, even though temperatures do not favor shoot growth (Rhizopoulou and Davies 1991). Plants begin to bear fruit when 6 to 8 years old, and crops are abundant every second year (Bailey 1947). Average annual yield per tree at maturity

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Figure 1—*Ceratonia siliqua*, carob: seed.

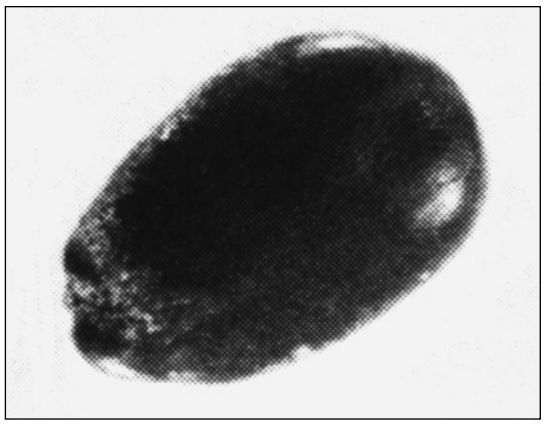
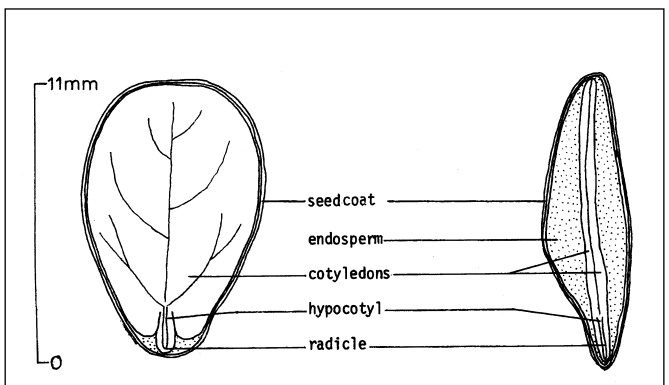


Figure 2—*Ceratonia siliqua*, carob: longitudinal sections through a seed.



is about 90 to 113 kg (200 to 250 lbs) of fruit (Coit 1951, 1962).

Collection of fruits. Fruits may be collected on the ground, or the ripe legumes may be shaken from the trees onto canvas sheets (Coit 1951). Legumes shaken from the tree should be allowed to remain on the ground for 2 to 3 days until completely dry (Coit 1962). Because of their high sugar content, legumes are likely to become moldy and quickly infested with a small scavenger worm—*Paramycelios transitella* Walker—if wet weather occurs during the harvesting season (Coit 1951, 1961, 1962). Because the worms infect the legumes while they are still attached to the tree, it is advisable to limit collections to dry years.

Extraction and storage of seed. Seeds are easily extracted after the legumes have been air-dried for a few days (Coit 1951; Goor and Barney 1968). If the legumes are to be stored for a time before extracting the seeds, they should be fumigated with an acceptable substitute for methyl bromide, which was recommended by Coit (1962) but is scheduled to be removed from use in the future. One kilogram (2.2 lb) of legumes yields about 50 to 140 g (1.8 to 4.9 oz) of cleaned seeds (Binder and others 1959). Cleaned seeds average 4,400 to 5,500 seeds/kg (2,000 to 2,500 seeds/lb) (Alexander and Shepperd 1974; Goor and Barney 1968). Soundness appears to be relatively high (<80% for 2 samples) (Alexander and Shepperd 1974). Seeds have remained viable for as long as 5 years when stored dry at low temperatures in sealed containers (Goor and Barney 1968).

Pregermination treatments. Seeds sown from recently ripened legumes germinate well without pretreatment (Rhizopoulou and Davies 1991), but if the seeds dry out they become very hard and do not readily imbibe water (Coit 1951). The best treatments to overcome seedcoat impermeability are soaking in concentrated sulfuric acid (H_2SO_4) for 1 hour and then in water for 24 hours, or alternatively, soaking for 24 hours in water that has first been brought to a boil and then allowed to cool (Goor and Barney 1968; Karschon 1960). Mechanical scarification is also effective in increasing the rate of water absorption with small lots of seeds (Coit 1951).

Germination tests. Germination tests have been run in moist vermiculite for 34 days at 21 °C. The germination rate was 66% for 16 days and the percentage germination was 80% (Alexander and Shepperd 1974).

Nursery practice. Seeds should be scarified by acid or hot water treatment and sown immediately afterwards in sterile soil or vermiculite under partial shade (Coit 1962; Karschon 1960). Seeds can be sown in either the spring or fall (Goor and Barney 1968). Seedlings have also been grown at 14 to 17 °C greenhouse temperatures with a 12-hour photoperiod of natural light supplemented with 250-W metal halide lamps (Rhizopoulou and Davies 1991). Seedlings develop a single deep taproot with a few small lateral roots less than 1.0 cm in length (Rhizopoulou and Davies 1991). Because the long taproot is easily injured, seeds should be sown in flats, pots, or containers so that seedlings can be outplanted with the original rooting medium intact (Coit 1951; Loock 1940). An alternate practice is to soak the legumes in water for 2 to 3 days and then plant without removing the seeds, but the germination rate is usually low (Coit 1951).

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C

Fabaceae—Pea family

Cercis L.

redbud

Valerie A. Banner and William I. Stein

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Growth habit, occurrence, and uses. The genus *Cercis L.*—redbud—includes 8 species of trees and shrubs; 2 are indigenous to North America, 5 to China, and 1 to an area from southern Europe eastward to Afghanistan (Little 1979; Robertson and Lee 1976). Eastern redbud is widely distributed from southernmost Canada to central Mexico, spans about 24 degrees of longitude and 23 degrees of latitude, and has at least 1 well-defined variety, Texas redbud (table 1). This species shows clinal variation and substantial differences in morphological, dormancy, and hardiness characteristics associated with climatic and geographic conditions (Donselman 1976; Donselman and Flint 1982; Raulston 1990). California redbud also has variable characteristics (Smith 1986) within its much more restricted range in the southwestern United States. About 15 cultivars of eastern redbud have been developed and cultivars of other redbuds also are propagated (Raulston 1990).

Redbuds are deciduous, small- to medium-sized trees or shrubs with unarmed slender branchlets that lack terminal buds. Eastern redbud typically is a straight-trunked tree up to 12 m tall (table 2); the tallest on record reaches 13.4 m (AFA 1996). Although they also reach tree size, California and Texas redbuds are more commonly described as multiple-stemmed shrubs. California redbud grows from 2 to 6 m tall; the tallest one on record is 8.8 m and the tallest Texas redbud is about the same (AFA 1996). Eastern redbud occurs on many soils in moist open woodlands, flood plains, river thickets, and borders of small streams, whereas the variety, Texas redbud, often inhabits drier locations, primarily paleozoic limestone formations such as xeric pastures, hills, outcrops, and bluffs (Hopkins 1942). California redbud is unevenly distributed at elevations of 70 to 1,524 m along foothill streams, flats, draws, low slopes and canyons and on dry gravelly and rocky soils (Chamlee 1983; Jepson 1936; Sudworth 1908).

Redbuds are valued particularly for their showy buds and flowers that appear before the leaves (Clark and Bachtell 1992; McMinn and Maino 1937). They exhibit cauliflory—flowering directly along older branches and trunks—which is rare among temperate species (Owens and Ewers 1991) and contributes greatly to flowering showiness. Flowers typically are a deep reddish purple (magenta) but vary among localities (Coe 1993; Smith 1986) and species (table 3). Some white ones occur naturally, and cultivars have been developed for particular flower and leaf colors (Raulston 1990). Ornamental uses are extensive within each species' indigenous range and several species have proven hardy more extensively (McMinn and Maino 1937;

Table 1—*Cercis*, redbud: nomenclature and occurrence

Scientific name & synonym	Common name(s)	Occurrence
***C. canadensis* L.**	**eastern redbud**, redbud, Judas-tree	Connecticut W to S Ontario, Michigan, Iowa, & E Nebraska; S to Texas & central Mexico; E to Florida
***C. canadensis* var. *texensis* (S. Wats.) M. Hopkins**	**Texas redbud**	S Oklahoma to SE New Mexico & Texas
***C. canadensis* var. *mexicana* (Rose) M. Hopkins**	**Mexican redbud**	E-central Mexico
***C. orbiculata* Greene** *C. occidentalis* Torr. ex Gray var. *orbiculata* (Greene) Tidestrom	**California redbud**, Arizona redbud, western redbud	Utah, Nevada, California, & Arizona

Sources: Clark and Bachtell (1992), Hopkins (1942), Hosie (1969), Little (1979), Robertson and Lee (1976), Sargent (1933).

Table 2—*Cercis,* redbud: growth habit, height, legume color, and size

Species	Growth habit	Height at maturity (m)	Legume color	Legume size		Seed diameter (mm)
				Length (cm)	Width (mm)	
C. canadensis	Tree or shrub	7–12	Reddish brown	5–10	8–18	4–5
C. canadensis var. *texensis*	Shrub or tree	4–10	Reddish brown	6–10	8–25	4–5
C. orbiculata	Shrub or tree	2–6	Reddish purple, dull red, to reddish brown	4–9	13–25	3–4

Sources: Fernald (1950), Hopkins (1942), Hosie (1969), Jepson (1936), McMinn (1939), Munz and Keck (1959), Sargent (1933).

Table 3—*Cercis,* redbud: phenology of flowering and fruiting

Species	Flowering	Flower color	Fruit ripening
C. canadensis	Mar–May	Magenta–purplish pink	July–early autumn
C. canadensis var. *texensis*	Mar–Apr	Magenta pink	Aug–Sept
C. orbiculata	Feb–May	Magenta pink–reddish purple	July–Sept

Sources: Abrahms (1944), Clark and Bachtell (1992), Fernald (1950), Hopkins (1942), Jepson (1936), Mirov and Kraebel (1939), Van Dersal (1938).

Robertson 1976). Where redbuds are numerous, they provide valued bee pasture in early spring (Magers 1970). The buds, flowers, and legumes (pods) of redbuds are edible and have been used in salads or batter (Coe 1993). Native Californians used the roots and bark of California redbud in basketry (Coe 1993; Jepson 1936); remedies for diarrhea and dysentery were also made from the astringent bark (Balls 1962).

Redbuds also are used for borders, erosion control, windbreaks, and wildlife plantings. Eastern redbud is browsed by white-tail deer (*Odocoileus virginiana*) and the seeds are eaten by birds, including bobwhite (*Colinus virginianus*) (Van Dersal 1938). California redbud is moderately important as fall and spring browse for deer but has been rated only fair to poor for goats and poor or useless for other livestock (Sampson and Jespersen 1963).

Two fungal diseases affect the flowering and attractiveness of eastern redbud—verticillium wilt (*Verticillium* sp.) and botryosphaeria canker (*Botryosphaeria dothidea* (Moug.:Fr.) Ces. & De Not.)—by causing die-back of branches. The canker has become more common and destructive in the eastern United States, appearing to attack trees that are under stress (Geneve 1991a; Raulston 1990; Vining 1986).

Flowering and fruiting. Flowering occurs from February to May, varying somewhat by species and location (table 3). The bisexual redbud flowers are brilliant pink to reddish purple and develop on older wood from dormant axillary buds laid down 1 to several years earlier (Owens and Ewers 1991). The flowers are borne sessile or on short, thin pedicels in umbel-like clusters densely covering the branches and trunk. Flowers of California redbud are somewhat larger than those of eastern redbud (Hopkins 1942; Robertson 1976). Eastern redbud begins flowering in 3 to 4 years from seed when trees are 1.5 to 2 m tall, and trees in open or semi-open locations flower most abundantly (Clark and Bachtell 1992; Raulston 1990). Pollination is usually done by long- and short-tongued bees (Robertson 1976). Crops of legumes are produced abundantly by both eastern and California redbud but seed set is more variable (Hopkins 1942; Jepson 1936).

Redbud fruits are pendulous, flattened legumes (figure 1) 4 to 10 cm long (table 2). The generic name *Cercis* (Greek *kerkis*, weaver's shuttle) apparently alludes to the shape of the legume (Robertson and Lee 1976). The legumes of California redbud are somewhat wider and shorter than those of eastern redbud. Legumes of eastern redbud contain 4 to 10 seeds each; those of California redbud only a few (Hopkins 1942; Robertson 1976). Legume color varies from lustrous reddish brown to dull red and turns tan or brown as the fruits mature and dry in July or later. Some legumes open and release their seeds in autumn, but many remain closed for most of the winter. Seeds are released from legumes on the tree or on the ground when the legume

Figure 1—*Cercis canadensis*, eastern redbud: 4 to 10 seeds (**left**) are in each legume (**right**).

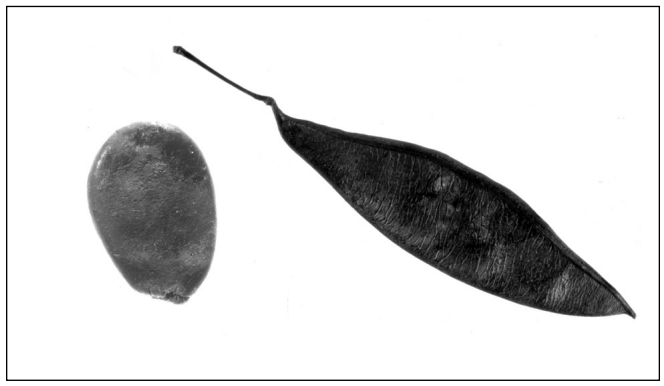
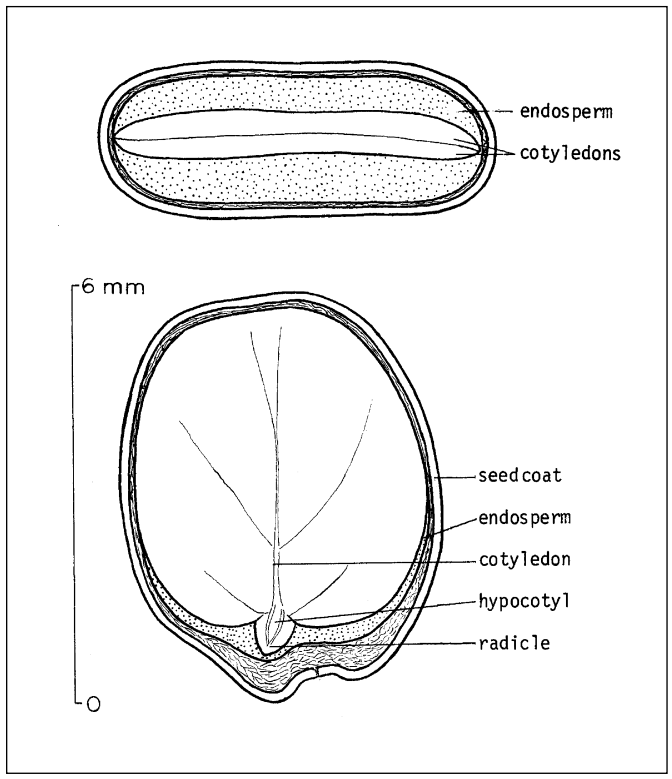


Figure 2—*Cercis canadensis*, eastern redbud: the flattened seed in transverse section (**above**) and longitudinal section (**below**).



sutures open or the walls decay (Robertson 1976). The seeds are dispersed by wind, birds, and animals, with the proportions carried by each varying by location.

Redbud seeds are somewhat flattened, oval to rounded, and hard (figures 1 and 2). Those of eastern redbud are 4 to 5 mm in diameter; those of California redbud are slightly smaller (table 2). The light tan to dark brown seedcoats are thin but made up of thick-walled cells impermeable to water (Afanasiev 1944). At maturity the embryo is straight, well-developed, and surrounded by endosperm (figure 2).

Collection, extraction, and storage. Legumes can be collected any time after they turn tan or brown. Although legumes remain closed on trees for lengthy periods, prompt collection is prudent to minimize the substantial seed losses that might occur from insects or other factors (Afanasiev 1944). Legumes can be picked by hand or loosened by flailing or shaking the branches and caught on ground cloths. Collected legumes should be temporarily stored and transported in loosely woven sacks.

If legumes are not fully dry when collected, they should be spread thinly and dried until brittle in the sun, under shelter, or in a kiln at 38 to 41 °C. The legumes can be threshed manually or in a variable speed, modified seed separator, hammermill, or grinder. Seeds are separated from the chaff by screening and fanning. Nearly 100% purity is readily obtainable in cleaning the smooth redbud seeds (Lippitt 1996).

After thorough air-drying, seeds can be stored in cloth bags or in closed glass, metal, or fiberboard containers. Because of their impermeable seedcoats, redbud seeds should store dry reasonably well at room temperature or in cool or cold storage, but little storage experience has been reported. Zins (1978) obtained substantial germination from an eastern redbud seedlot stored for 13 years in a glass jar at –25 °C. Seeds of California redbud have been stored satisfactorily for 12 years or more under the same conditions as many conifers at a moisture content of 5 to 9% and temperature of –18 °C (Lippitt 1996).

Seeds of California redbud average about half again as heavy as those of eastern redbud but seed weight varies widely among lots for both species (table 4).

Pregermination treatments and germination tests. Redbud seeds generally require pregermination treatment to overcome dormancy attributable both to a hard, impermeable seedcoat and to some demonstrated, but not fully identified, embryo dormancy (Afanasiev 1944; Geneve 1991b; Hamilton and Carpenter 1975; Heit 1967a7b; Jones and Geneve 1995; Profumo and others 1979; Rascio and others 1998; Riggio-Bevilacqua and others 1985; Tipton 1992; Zins 1978). Test results indicate that the level of dormancy varies by species, seed source, seedlot, age of seeds, and perhaps other factors. Given such variable dormancy, pretreatment might involve using the one demonstrated to be most broadly applicable, or determining sufficiently the nature of dormancy in local lots and applying a customized pretreatment.

Three pretreatments have proven satisfactory for overcoming redbud's seedcoat impermeability—mechanical scarification, immersion in sulfuric acid, or in hot water (table 5). In comparison tests, the acid treatment has generally produced more consistent or slightly better results (Afanasiev 1944; Liu and others 1981), but good imbibition of water has resulted after all 3 treatments. Acid treatment involves immersing redbud seeds in concentrated sulfuric acid for 15 to 90 minutes at room temperature followed by thorough washing in water (Afanasiev 1944; Frett and Dirr 1979; Liu and others 1981). Length of treatment required can be determined on a small sample; if immersion is too short, seedcoats remain impermeable, if too long, the seeds are damaged. Well-rinsed, acid-scarified seeds can be placed immediately in stratification or surface-dried and stored several months until sown by hand or seeder (Heit 1967a).

Abrading, clipping, or piercing the seedcoat to expose the endosperm and allow ready entry of water (Hamilton and Carpenter 1975; Riggio-Bevilacqua and others 1985; Zins 1978) can be done easily for small test lots but not as readily in quantity. Immersing small or large quantities of seeds in hot or boiling water can be done easily, but results have been more variable than for acid treatment—sometimes reasonably good (Fordham 1967; Mirov and Kraebel 1939), other times poor to mediocre (Afanasiev 1944; Liu and others 1981). Hot water treatment clearly makes redbud seedcoats permeable but may cause internal damage. Better calibration of time–temperature effects appears needed—

Table 4—*Cercis,* redbud: seed yield data

Species	Seeds/100 wt of legumes	Seed wt/ legume vol		Cleaned seeds/wt				Samples
				Average		Range		
		kg/hl	lb/bu	/kg	/lb	/kg	/lb	
C. canadensis	20–35	—	—	39,570	17,950	30,870–55,100	14,000–25,000	18
C. orbiculata	44	2.10	1.64	27,460	12,455	20,950–40,100	9,500–18,169	24

Sources: Lippitt (1996), Roy (1974), USDA FS (1948, 1996).

Table 5—*Cercis,* redbud: scarification, stratification, germination test conditions, and test results*

Species	Scarification		Stratification		Germination test conditions			Germination (%)	Samples
	Treatment	Time (min)	Days	Temp (°C)	Medium	Temp (°C)	Days		
C. canadensis	H_2SO_4	45	Var.	5	Peat	—	48	77	2
	H_2SO_4	45	Var.	5	Peat	—	107	78	2
	H_2SO_4	30	42	5	Cotton	21	8	97	2
	H_2SO_4	25–30	35–91	3–7	Cotton	—	—	88–100	7†
	H_2SO_4	30	60	5	Sand	20–30	30	80	2
	Mech.	—	60	5	Peat–perlite	25	24	90	5
	H_2SO_4	30	60	5	Peat–perlite	25	24	88	5
	Mech	—	—	—	Peat–perlite	25	24	82	5
	H_2SO_4	30	—	—	Peat–perlite	25	24	91	5
	H_2SO_4	15–60	60	5	Vermiculite	18–21	42	87	3
	H_2SO_4	30–90	60	5	Soil	20–27	14	67–72	12
	—	—	0	1	Paper	20–30	28	43	1
	—	—	28	1	Paper	20–30	28	83	1
C. canadensis	H_2SO_4	62	35	5	Paper	21	14	95	25‡
var. *texensis*	H_2SO_4	62	35	5	Paper	28	14	100	81‡
C. orbiculata	Heat§	Overnight	—	—	Vermiculite	—	118	38	1
	Heat	9	—	—	Vermiculite	—	118	52	1
	H_2SO_4	60	90	2–4	Cotton	—	10	84	1

Sources: Afanasiev (1944), Flemion (1941), Frett and Dirr (1979), Hamilton and Carpenter (1975), Heit (1967a), Liu and others (1981), Roy (1974), Tipton (1992), USDA FS (1948, 1996), Williams (1949).

* Only the better results for each test series are listed. In several studies, only full seeds were tested.

† Best results from a set of tests on each of 7 seedlots.

‡ Test combinations used to develop a response surface.

§ Moist heat applied by immersing seeds in 82 °C water that cooled gradually.

// Dry heat applied in oven at 121 °C.

whether to dip the seeds for 15 or more seconds in boiling water or immerse them overnight in 60 to 88 °C water that cools gradually. Application of dry heat also appears to have promise (Williams 1949).

After scarification, cold stratification is generally required to overcome some degree of internal dormancy and maximize seed germination. Germination differences between unstratified and cold-stratified seeds range from none (Hamilton and Carpenter 1975), to fractional differences in the response of excised embryos (Geneve 1991b), up to major differences for intact seeds (Afanasiev 1944; Fordham 1967; Frett and Dirr 1979; Geneve 1991b). Stratification of eastern redbud for 28 to 60 days at 1 to 7 °C has proven satisfactory (table 5) and 90 days for California redbud (Heit 1967a; Van Dersal 1938). Up to a point, seed response improves with longer stratification, and extended stratification generally does no harm. Seeds should be sown promptly after stratification; drying out for more than 6 days at room temperature reduced germination of eastern redbud seeds (Afanasiev 1944).

A pretreatment and germination test protocol has not yet been specified for redbud seeds due perhaps to extensive variability in seedlot characteristics, length of time required, and low demand for a standard test. Pretreated seeds of eastern redbud will germinate at temperatures of 1 to 38 °C; Afanasiev (1944) concluded 8 days at 21 °C was most satisfactory. Texas redbud seeds germinate at 24 to 31 °C and 28 °C was optimum (Tipton 1992). Germination test methods currently used for many species—14 to 28 days at alternating temperatures of 20 and 30 °C—seem to nicely bracket conditions that yielded high germination from pretreated redbud seeds (table 5).

Viability of redbud seeds is most easily and rapidly determined by a tetrazolium (TZ) test or a growth test of excised embryos. The TZ test is the only method prescribed by the International Seed Testing Association; preparation and evaluation procedures to use are listed in a published handbook (Moore 1985). In brief, the seeds are cut at the distal end of the cotyledons either dry or after overnight soaking in water at room temperature. Soaking in a 1% TZ solution follows for 6 to 24 hours at 35 °C. The embryos are then cut longitudinally, and the staining pattern of cotyledons, hypocotyl, and radicle evaluated. A growth test of excised embryos requires making the seedcoats permeable with acid, hot water, or mechanical scarification; soaking the seeds overnight, excising the embryos, and incubating them for 4 to 6 days on moist filter paper at 20 °C (Flemion 1941; Geneve 1991b). Viability determined by tetrazolium or excised embryo test reveals that the seeds' maximum potential and generally is higher than indicated by a germination test (Flemion 1941; Hamilton and Carpenter 1975; USDA FS 1996).

Nursery practice. Redbuds are propagated most readily from seeds sown either in the fall or spring. Fall-sown seeds may or may not be scarified, and stratification occurs naturally in the seedbeds (Lippitt 1996; Raulston 1990). In one reported instance, immature seeds of eastern redbud collected, extracted, and sown before the seedcoats hardened yielded 90% germination the following spring (Titus 1940). When seeds need to be scarified for either fall- or spring-sowing—acid treatment for 15 to 60 minutes, rinsing, and a 24-hour soak in water; a boiling water dip for 15 seconds or more followed by a 24-hour soak in cooler water; or immersion overnight in 88 °C hot water that gradually cools—can be generally used to overcome seedcoat dormancy (Frett and Dirr 1979; Heit 1967b; Lippitt 1996; Raulston 1990; Robertson 1976; Smith 1986). After scarified seeds have imbibed water, they may need to be sorted to separate those not swollen and still impermeable for further treatment. When necessary, seeds are stratified at 1 to 5 °C for 30 to 90 days. Stratification requirements are uncertain for 2 reasons: variability among seedlots and the unknown stratification effect produced by low temperature storage of the seeds.

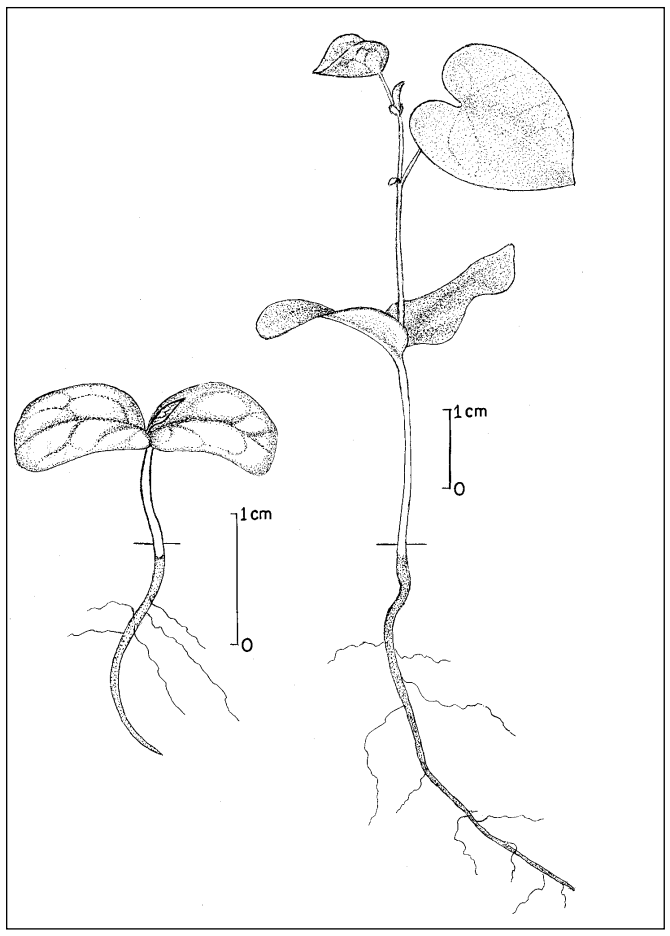
Surface-dried seeds are drill- or broadcast-sown and covered 0.6 to 2.5 cm (0.2 to 1 in) deep with soil, sand, sawdust, or bark. Some nurseries fumigate, then reinoculate before sowing seedbeds. Presence of an endomycorrhizal fungus is important; inoculation with *Glomus fasciculatum* (Thaxter) Gerdemann and Trappe has increased first-season growth of eastern redbud as much as 72% (Maronek and Hendrix 1978). Mulching of fall-sown beds can be beneficial but the mulch must be removed when germination starts. Germination is epigeal (figure 3).

Seedling return from nursery sowings is very variable. For eastern redbud, an average of 2,425 usable seedlings (range 617 to 7,055) were produced per kilogram of seeds (1,100 usable seedlings/lb, range 280 to 3,200/lb) (Roy 1974). Germination is fairly consistent year to year for California redbud, averaging 54 to 60% (Lippitt 1996). Under favorable conditions, seedling height growth of eastern redbud can be rapid: about 0.5 m (20 in) in reinoculated soil (Maronek and Hendrix 1978), 1 m (40 in) or more under an intensive nitrogen fertilizer schedule, and about 2 m (80 in) if started in January in a greenhouse under long-day conditions and transplanted outdoors after the danger from frost is over (Raulston 1990).

Redbud seedlings are also produced in pots and tube containers in both greenhouses and shadehouses where production practices and growth conditions can be closely controlled. To gain the benefits of natural stratification, containers may be sown in the fall and overwintered in shadehouses. Treatments to prevent botrytis are necessary soon after late February germination of California redbud (Lippitt 1996). Seedlings suitable for outplanting—15 to 30 cm (6 to 12 in)—can be produced readily in one season (Clark and Bachtell 1992; Lippitt 1996).

Redbuds are relatively difficult to propagate vegetatively, but that must be done to produce the desired cultivars. Redbud cultivars are generally budded or grafted. Field-grown stock is easier to bud then container-grown stock, and summer budding is much more successful then winter budding (Raulston 1990). Much effort and some progress has been reported on reproducing redbud from stem cuttings (Tipton 1990) and tissue cultures (Bennett 1987; Geneve 1991a; Mackay and others 1995).

Figure 3—*Cercis orbiulata*, California redbud: young seedlings grow rapidly: first leaf stage (**left**) and about 1 month old (**right**).



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Rosaceae—Rose family

Cercocarpus Kunth

mountain-mahogany

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Growth habit, occurrence, and use. The mountain-mahoganies—genus *Cercocarpus*—are 8 to 10 species of moderately to intricately branched shrubs or small trees that are endemic to dry coastal and interior mountains of the western United States and Mexico (Stutz 1990). Leaves are generally persistent and stems are unarmed. Two of the most widely distributed and utilized species are described here (table 1).

Curlleaf mountain-mahogany populations demonstrate considerable variability in height (Davis 1990; Stutz 1990). In some areas, the species occurs as a medium-statured shrub of 1 to 2 m. More commonly, it is a small tree of 4 to 10 m at maturity. Trunk diameter of mature trees measures 30 to 100 cm (Johnson 1970). Schultz and others (1990) estimated the mean age of trees in central and western Nevada stands to be 352 years. Mean plant age in Utah stands (85 years) is less than that in Nevada stands but greater than that in Oregon and Montana stands (Davis 1990).

True mountain-mahogany is a deciduous shrub of 1 to 5 m. Both species occur as components of mixed communities and as dominants in extensive stands and are important cover and browse species for wildlife, especially big game (Davis 1990). When burned, true mountain-mahogany resprouts from the crown, resulting in relatively rapid stand recovery following fire. Recovery of curlleaf mountain-mahogany stands following fire is from seed only and can be extremely slow. Because they are long-lived, produce an extensive root system, and survive well on dry steep slopes, mountain-mahogany plants play an important role in erosion control. Nitrogen fixation in root nodules has been described for both curlleaf (Lepper and Fleschner 1977) and true mountain-mahoganies (Hoeppel and Wollum 1971), suggesting a significant role by these species in improving fertility in otherwise infertile soils. The wood of curlleaf mountain-mahogany is extremely dense and heavy and has had limited use, primarily as fuel wood (Johnson 1970).

Geographic races and hybrids. Two distinct subspecies or varieties of curlleaf mountain-mahogany occur in the western United States (Stutz 1990). Although considerable overlap in distribution exists, *C. ledifolius* ssp. *ledifolius* (formerly ssp. *intercedens)* has a more northeastern distribution, whereas the distribution of ssp. *intermontanus* is centered to the west of its sister taxon. In northern Idaho, northern Wyoming, and southern Montana, ssp. *ledifolius* is the only mountain- mahogany taxon present (Stutz 1990). The leaves of ssp. *ledifolius* plants differ from those of ssp. *intermontanus* in being narrower, more strongly involute, and densely pubescent ventrally. The leaves of ssp. *intermontanus* are broadly elliptic and glabrous. Habit of ssp.

Table 1—*Cercocarpus*, mountain-mahogany: nomenclature and occurrence

Scientific name(s)	Common name(s)	Occurrence
***C. ledifolius* Nutt.**	**curlleaf mountain-mahogany**, curlleaf cercocarpus, curlleaf mahogany, desert mahogany	Washington & Oregon E to Montana & Wyoming, S to Arizona, California, & Mexico (Baja)
***C. montanus* Raf.** *C. betuloides* Nutt. *C. parvifolius* Nutt. *C. flabellifolius* Rydb.	**true mountain-mahogany,** mountain cercocarpus, birchleaf cercocarpus, birchleaf mountain-mahogany, alderleaf mountain-mahogany, blackbrush, deerbrush, tallowbrush	Oregon E to South Dakota S to Mexico, incl. parts of Wyoming, Colorado, Nebraska, Kansas, Texas, New Mexico, Arizona, Utah, & California

ledifolius is more shrubby (or less tree-like) than that of ssp. *intermontanus,* especially in its northern distribution. Although it is treated as a separate species, littleleaf mountain-mahogany—*C. intricatus* Wats.—is taxonomically and phenotypically close to curlleaf mountain-mahogany spp. ledifolius. It is distinguished by its smaller leaves and stature, fewer stamens, and shorter style on mature fruits (Stutz 1990). The evolutionary processes that produced littleleaf mountain-mahogany are still proceeding and intermediates between the 2 taxa are common.

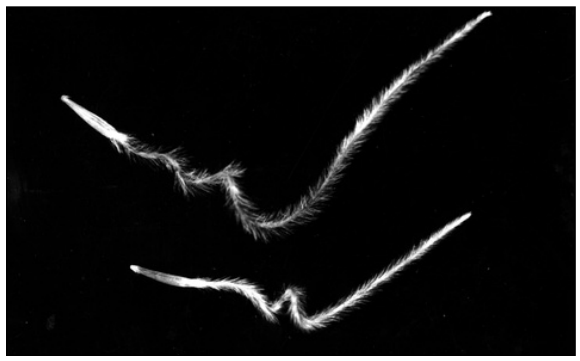
As reflected in its taxonomy, true mountain-mahogany is also quite variable across its range. *C. montanus* ssp. *montanus* has the most widespread distribution (Stutz 1990). Separate taxa have been described for parts of the Pacific Coast (ssp. *betuloide*s Nutt.) and in the Southwest (ssp. *paucidentatus* S. Wats and *argenteus* Rydb). *Cercocarpus mexicanus* Hendrickson, *C. rzedowski* Hendrickson, and *C. fothergilloides* Kunth. are closely related Mexican species.

Inter-specific hybrids are common between curlleaf and true mountain-mahoganies (Stutz 1990). Fertility in hybrids of true mountain-mahogany and curlleaf mountain-mahogany ssp. *ledifolius* is good in contrast to the low fertility encountered in hybrids of true mountain-mahogany × curlleaf mountain-mahogany spp. *intermontanus* (Stutz 1990). Hybrids between true and littleleaf mountain-mahoganies are rare.

Flowering and fruiting. Small perfect flowers bearing no petals are borne individually or in small clusters. Flowering for these wind-pollinated shrubs occurs some time between late March and early July depending on latitude, elevation, and aspect. Fruits are cylindrical achenes bearing a single seed and are distinguished by a 3- to 10-cm plumose style that facilitates wind dispersal (figure 1). Ripened fruits disperse from July through October. Abundant fruit production occurs at 1- to 10-year intervals (Plummer and others 1968); however, a high percentage of nonviable (empty) fruits is not uncommon. Plants may reach reproductive maturity in 10 to 15 years (Deitschman and others 1974).

Fruit collection. Fruit maturation within a stand is generally somewhat asynchronous. Because of this and because fruits will not dislodge before they are fully ripe, harvests are most productive when delayed until the fruits on a majority of plants ripen. Optimal timing for harvest varies between July and September. Delays may result in diminished or lost harvests due to wind dispersal. Fruits of several plants must be examined for fill and insect damage before starting collection. Ripe, dry mountain-mahogany fruits are easily shaken from branches onto tarps or hand-held hoppers using a beating stick. During harvest and handling, short hairs dislodge from the fruits. These hairs cause considerable discomfort to eyes and skin, thus the cowboy epithet of "hell feathers" (Plummer and others 1968). Fruits may collect in harvestable depths on the ground during years of superior production. However, collections from ground accumulations are often of poor quality due to the removal of viable seeds by rodents.

Figure 1—*Cercocarpus*, mountain-mahogany: achenes with feathery style; the size of the achene varies greatly within each species.

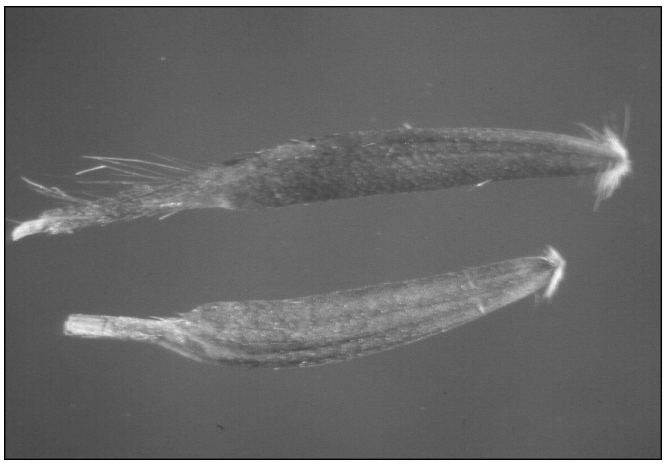


Cleaning and storage. Highest purity values are obtained by removing most broken branches from fruits during collection. For large collections, empty fruits, styles, and fine hairs are best removed using a variable-speed debearder and a 9.5-mm (#2) screen fanning mill (figure 2). Hammermilling causes excessive breakage and should not be used. Minimum standards accepted by the Utah Division of Wildlife Resources for both species are purity values of 95%, and viability values of 85% (Jorgensen 1995).

Cleaned-fruit sizes differ by species, ecotype, and year of collection. In one study, average number of fruits per weight for curlleaf (8 collections) and true mountain-mahoganies (10 collections) was 106,000 and 88,000/kg (48,000 and 40,000/lb), respectively (Kitchen and others 1989a&b). These fruit weights were either equivalent to or somewhat heavier than those previously reported (Deitschman 1974). Curlleaf and true mountain-mahogany fruits stored under warehouse conditions experienced no significant loss of viability during 15 and 7 years, respectively (Stevens and others 1981).

Germination. Reported germination responses to moist chilling for curlleaf mountain-mahogany range from no response after 12 weeks (Young and others 1978), to good germination with 4 weeks (Heit 1970). In most of these studies, interpretation of results is difficult because fruit fill percentage was not determined. Dealy (1975) reported 20% germination in response to 60 days of moist

Figure 2—*Cercocarpus montanus*, true mountain-mahogany: achenes with styles removed (cleaned seeds).



chilling (4 °C) followed by 30 days at 20 °C for a 2-year old Oregon source that had tested 78% viable. He also observed germination during extended chilling (75 to 270 days). Kitchen and Meyer (1990) found the length of wet chilling (1 to 2 °C) required to make 90% of viable seeds germinable at 15 °C ranged from 6 to 10 weeks for 6 fresh collections from Utah, Idaho, and Nevada. They observed that cold-temperature germination began at about 8 weeks. Chemical treatments that have provided limited success in breaking dormancy with curlleaf mountain-mahogany seeds include: gibberellins (GA_3), thiourea, hydrogen peroxide, and sulfuric acid (Dealy 1975; Stidham and others 1980; Young and others 1978).

Some collections of true mountain-mahogany seeds have tested largely nondormant (Deitschman and others 1974). More typically, 2 to 12 weeks of moist chilling are required to break dormancy (Kitchen and Meyer 1990). Kitchen and Meyer (1990) found that cold-temperature germination (1 to 2 °C) for 9 Colorado and Utah collections began after 7 to 10 weeks of moist chilling.

Consistent estimations of embryo viability using standard TZ (tetrazolium) staining procedures are difficult to obtain for both species (Kitchen and others 1989a, 1989b). This is because the embryo is held tightly in the cylindrical pericarp and is difficult to extract for staining and examination (figure 3). Technical experience with mountain-mahogany TZ evaluations appears to be a major factor in accuracy of test results.

Figure 3—*Cercocarpus ledifolius*, curlleaf mountain-mahogany: longitudinal section through an achene.

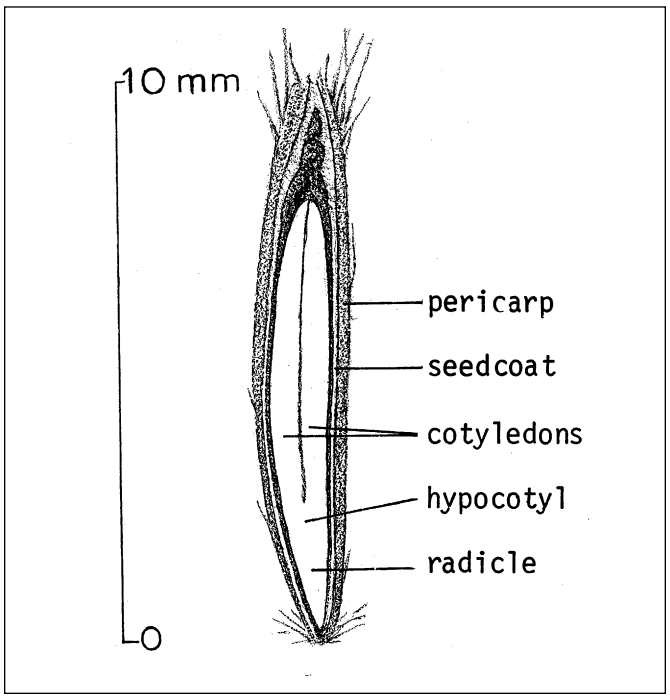
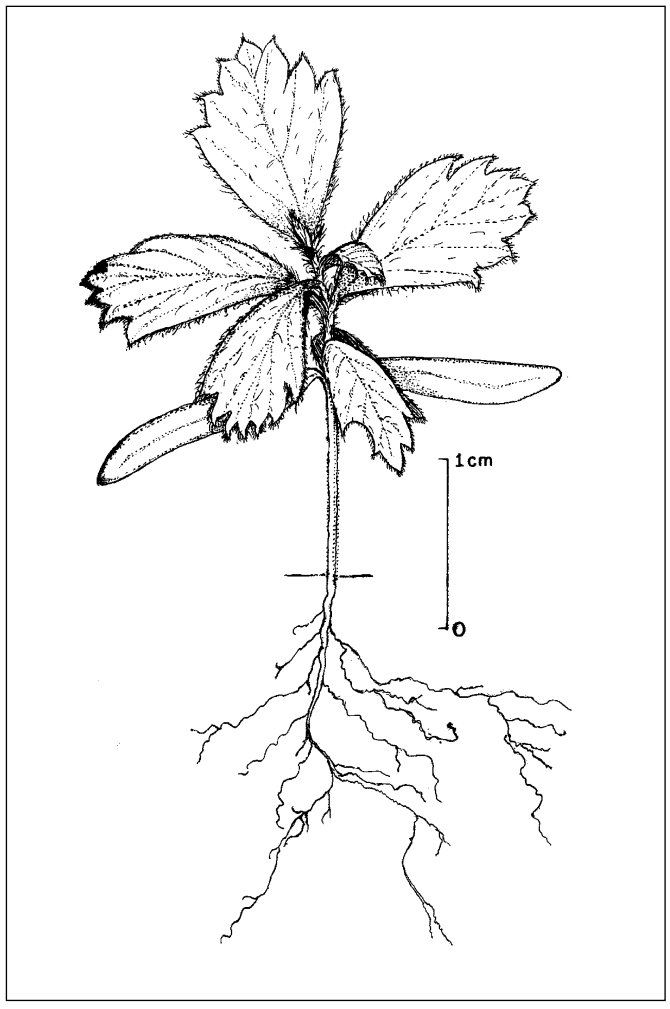


Figure 4— *Cercocarpus montanus*, true mountain-mahogany: seedling with primary leaves and well-developed secondary leaves.



C

Nursery and field practice. Curlleaf and true mountain-mahoganies were first cultivated in 1879 and 1872, respectively (Deitschman and others 1974). Bareroot and container nursery stock are commercially available for both species, generally as 1- or 2-year-old stock. Unless nondormant collections are used, cleaned fruits are either prechilled or fall-sown. Seedbeds should be kept moist until seeds have germinated (Deitschman and others 1974). Deep-rooting containers filled with a minimum of 0.2 liter (13 in^3) standard potting mix is recommended for container stock production (Landis and Simonich 1984). With optimum rearing conditions a minimum of 4 to 6 months is required to develop an adequate root system. Figure 4 illustrates a seedling with well-developed secondary leaves. Direct seeding of mountain-mahogany should be carried out in fall or early winter in conjunction with seedbed preparations that minimize competition to first-year seedlings (Plummer and others 1968).

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Rosaceae—Rose family

Chamaebatia foliolosa Benth.

bearmat

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Other common names. southern bearmat, mountain-misery, Sierra mountain-misery, San Diego mountain-misery, bearclover, tarweed, and running-oak.

Growth habit, occurrence, and use. Two varieties of this species—*Chamaebatia foliolosa* Benth.—are recognized. The typical variety, bearmat, is an evergreen shrub, 15 to 60 cm tall, that grows between 600 and 2,100 m elevation on the western slopes of the Sierra Nevada in California. It occurs in open ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and in California red fir *(Abies magnifica* A. Murr.) forests (Munz and Keck 1963). Southern bearmat—*C. foliolosa* var. *australis* Brandg.—grows to a height of nearly 2 m on dry slopes in the chaparral type from San Diego County to Baja California.

The typical variety is normally regarded as a pest because it inhibits the establishment and growth of trees (Adams 1969; Dayton 1931). From an aesthetic viewpoint, the plants can provide attractive ground cover, but their glutinous leaves are highly aromatic (Bailey 1928; McMinn 1959). It is useful for watershed stabilization and is a potential landscape plant (Magill 1974).

Flowering, seed production, and seed use. Bearmat produces perfect flowers throughout its range from May through July; southern bearmat flowers from November through May (McMinn 1959). The fruits are brown achenes about 5 mm in length (figures 1 and 2). Seeds require from 1 to 3 months of moist stratification at temperatures ranging from 1 to 5 °C before they will germinate (Emery 1964; Magill 1974). In the nursery, seeds should be sown in spring (Bailey 1928).

Figure 1—*Chamaebatia foliolosa*, bearmat: achene (**left**) and extracted seed (**right**).

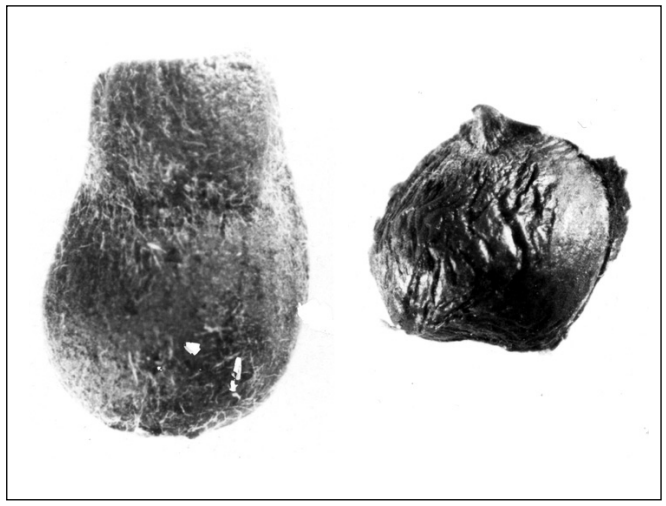
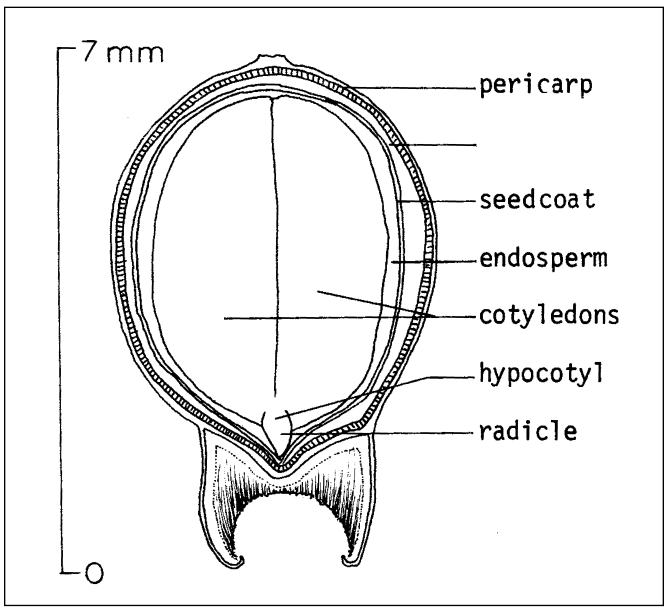


Figure 2—*Chamaebatia foliolosa*, bearmat: longitudinal section through an achene.



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Rosaceae—Rose family

Chamaebatiaria millefolium (Torr.) Maxim.

fernbush

Nancy L. Shaw and Emerenciana G. Hurd

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Other common names. desert sweet, fern-bush, desert-sweet.

Synonyms. *Spiraea millefolium* Torr., *Sorbaria millefolium* Focke, *Basilima millefolium* Greene, *Chamaebatiaria glutinosa* Rydb., and *Spiraea glutinosa* Fedde (Davis 1952; Hitchcock and others 1961; Peck 1961; Young and Young 1986).

Growth habit, occurence and use. Fernbush—*Chamaebatiaria millefolium* (Torr.) Maxim.—the only species in its genus, is endemic to the Great Basin, Colorado Plateau, and adjacent areas of the western United States. It is an upright, generally multistemmed, sweetly aromatic shrub 0.3 to 2 m tall. Bark of young branches is brown and becomes smooth and gray with age. Leaves are leathery, alternate, simple, bipinnatisect, stipulate, and more or less clustered near the ends of the branches. Foliage and young branches are viscid and pubescent, with simple and stellate hairs that are sharp-pointed or glandular-capitate. Southern populations are more or less evergreen (Phillips 1949), whereas northern populations are largely deciduous, retaining a few leaves near the branch tips through winter and initiating leaf development in early spring (Hitchcock and others 1961; Kirkwood 1930).

Fernbush is distributed east of the Cascade and Sierra Nevada Mountains from Deschutes Co., Oregon, to southern California and eastward across southern Oregon and Idaho, Nevada, Utah, northern Arizona, and New Mexico (Hitchcock and others 1961; Phillips 1949; Welsh and others 1987; Young and Young 1992). Fernbush is often present as an early successional species on cinder cones and basalt lava flows but is also found on soils derived from limestone and granite (Eggler 1941; Everett 1957; Merkle 1952). It occurs in cracks and fissures of rock outcrops and on well-drained soils of dry, rocky, gravelly canyons and mountain slopes at elevations ranging from 900 to 3,400 m (Albee and others 1988; Hickman 1993). Fernbush grows in isolated populations or as an associated species in sagebrush scrub (*Artemisia* spp.), sagebrush, northern juniper, mountain brush, aspen, limber pine, ponderosa pine, spruce–fir, and western bristlecone pine communities (Hickman 1993; Munz and Keck 1959; Welsh and others 1987).

Fernbush is occasionally browsed by mule deer (*Odocoileus hemionus*), sheep, and goats, but only rarely by cattle (Mozingo 1987; van Dersal 1938). Native Americans used a tea made from its leaves for treatment of stomach aches (Mozingo 1987).

Unlike its namesake genus—*Chamaebatia* Benth., bear-mat or mountain misery—fernbush is not nodulated by nitrogen-fixing actinomycetes (McArthur and Sanderson 1985). Plants are cyanogenic (Fikenscher and others 1981). The species is a very rare host of juniper mistletoe—*Phoradendron juniperinum* Engelm. (Hawksworth and Mathiasen 1978).

First cultivated in 1878 (Rehder 1940), fernbush has long been recognized as an attractive ornamental because of its profuse and conspicuous inflorescences of white- to cream-colored flowers, long flowering season, and aromatic, fernlike foliage (Bailey 1902; Hitchcock and others 1961; Phillips 1949; Young and Young 1986). It is used effectively in mass plantings, xeriscapes, screens, and hedges when planted in full sun. Specimen plants provide color and texture accents (Phillips 1949).

Genetic variation, hybridization, and origin. McArthur (1984) and McArthur and others (1983) described *Chamaebatiaria* and other monotypic western North American genera of the Rosaceae as showing little variation compared to larger genera such as *Rosa* (rose) or *Cercocarpus* (mountain-mahogany). Typical of shrubby western North American members of subfamily Spiraeoideae, fernbush has x = n = 9 chromosomes (McArthur and Sanderson 1985). Hybridization of fernbush with other species has not been reported.

Chamaebatiaria (subfamily Spiraeoideae) was named for its morphologic resemblance to *Chamaebatia* (subfamily

Rosoideae). McArthur and Sanderson (1985) suggest that shrubby Spiraeoideae and Rosoideae of western North America may be rather closely related based on similarities in morphologic and other characteristics of the 2 groups. Wolfe and Schorn (1989) and Wolfe and Wehr (1988) discuss evidence from Paleogene montane floras of the Rocky Mountains indicating the possible divergence of *Chamaebatiaria* and *Chamaebatia* from a common Eocene ancestor. They suggest both lines adapted to progressively drier post-Eocene conditions than the mesic coniferous forest environment inhabited by the ancestor.

Flowering and fruiting. The showy, white, insect-pollinated flowers develop in profuse, terminal, leafy-bracteate panicles up to 20 cm in length. Flowers are complete, regular, and about 0.8 to 1.5 cm in diameter. The calyx consists of 5 persistent green sepals. A glandular disk lining the hypanthium bears 5 petals and numerous stamens. Pistils are 5 (rarely 4), ovaries superior, and styles free. The ovaries are more or less connate below in flower, but separate in fruit. The pubescent, coriaceous, few-seeded follicles dehisce along the ventral suture and upper half of the dorsal suture (figure 1). Seeds are erect, yellowish to brownish, linear to narrowly fusiform, and somewhat flattened at each end (figure 2). The outer layer of the soft thin seedcoat is ridged, giving the body of the seed a 3-angled appearance; the inner layer is thin and translucent. A fleshy endosperm layer adheres to the seedcoat. The embryo is linear-oblong with 2 flat cotyledons and occupies the central portion of the seed (figure 3). Germination is epigeal (Hickman 1993; Hitchcock and others 1961; Hurd 1995; Kirkwood 1930; Welch and others 1987).

Figure 1—*Chamaebatiaria millefolium,* fernbush: follicle.

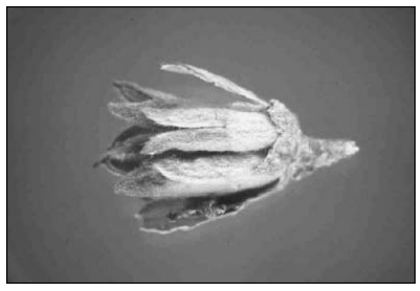


Figure 2—*Chamaebatiaria millefolium*, fernbush: seeds.

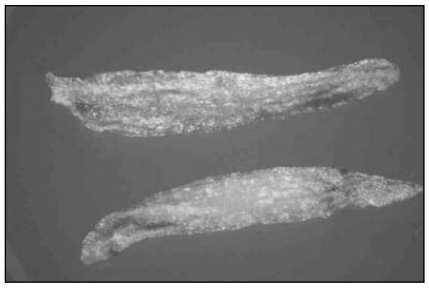
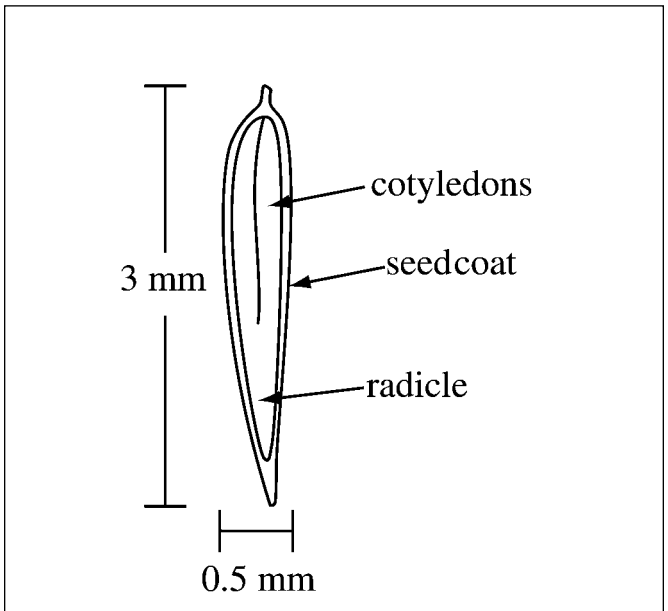


Figure 3—*Chamaebatiaria millefolium*, fernbush: longitudinal section through a seed.



Irrigated plants may begin flowering during the second growing season (Shaw 1995). Plants flower from June to September (Hitchcock and others 1961; Phillips 1949) with irrigation prolonging the flowering season (Shaw 1995). Fruits ripen from August to October.

Collection of fruits, seed extraction, cleaning, and storage. Fruits are harvested by clipping or stripping inflorescences when they are dry and brown, but before follicles open. Seeds can also be collected by briskly shaking or beating the inflorescences once the follicles begin dehiscing. Most follicles open during air-drying, releasing the seeds. Debris may then be removed with screens or a seed blower. Larger collections may be cleaned using air-screen machines. For 2 Idaho seedlots produced with irrigation, the number of seeds per seed weight averaged 3,700,000/kg (1,700,000/lb) (Hurd 1995). Storage requirements and seed longevity have not been determined, but the seeds are probably orthodox in storage behavior.

Pregermination treatments and germination and viability tests. Fresh seeds are nondormant, whereas stored seeds require 1 to 3 months of chilling to relieve dormancy (McDorman 1994; Phillips 1949; Young and Young 1986, 1992). The optimum temperature range for germination of southwestern populations is 18 to 26 °C (Phillips 1949).

Fernbush germination has received little study. Shaw (1995) examined the germination of 3 seed collections. Nampa, ID, and Sun Valley, ID, collections were harvested from irrigated plantings of seeds from a single unknown source. The third collection was from an irrigated Sante Fe, NM, planting of seeds from a western New Mexico source. All 3 collections were cleaned and held in dry storage for 4 to 5 months before testing. Total germination percentage of the Sante Fe, NM, and Sun Valley, ID, seed collections (but not the Nampa, ID, seed collection) was greater when untreated seeds were incubated at 20/10 °C (8 hours/16 hours) than at 15 °C for 28 days. A 28-day wet chilling at 3 to 5 °C (table 1) improved the total germination percentage of all seed collections when they were subsequently incubated at either 15 °C or 20/10 °C for 28 days.

Viability of fernbush seeds may be tested as follows: first, the seeds are soaked in water at room temperature for 1 hour, then the water is drained away. A horizontal slit should be made across the center of each seed without cutting it in half. Seeds are then submerged in a 1% solution of 2,3,5-triphenyl tetrazolium chloride for 6 hours at room temperature. Evaluate as described by Peters (2000) for Rosaceae III. The embryos may be read in place. The endosperm of viable seeds is living and will stain red (Hurd 1995).

Nursery practice. Nursery plantings should be made in late fall or early winter. As an alternative, artificially wet-chilled seeds may be planted in early spring. Fernbush seeds are small and must be sown on the soil surface or with a very light covering of sand or soil. Seedlings develop rapidly with irrigation and reach an adequate size for lifting after 1 growing season (Shaw 1995).

Seeds for production of container stock should be wet-chilled before planting. Survival of germinants moved from seeding flats to production containers is low (Everett 1957). Better establishment is obtained by sowing seeds directly into containers and thinning to 1 seedling per container. Developing seedlings are easily moved from small to larger containers (Phillips 1949). Seedlings should be grown in a well-drained medium.

Direct seeding. Seeds should be planted in fall or early winter. Seedlings emerge in spring from seeds naturally dispersed in late summer on rough or mulched soil surfaces (Mackie 1995; McDorman 1994; Shaw 1995). Naturally occurring seedlings generally establish where vegetative competition is limited (Shaw 1995).

Table 1—*Chamaebatiaria millefolium*, fernbush: germination test conditions and results

Source	Elevation (m)	Origin	Cold, wet chill (days)*	% Germination‡ 15 °C Incub†	% Germination‡ 20/10 °C Incub†	Seed fill (%)	Seed viability (%)
Nampa, ID	831	Unknown§	0	3	1	100	96
			28	72	65	100	96
Sun Valley, ID	1,773	Unknown§	0	12	20	100	86
			28	33	44	100	86
Santa Fe, NM	2,134	W New Mexico	0	9	22	100	85
			28	58	60	100	85

* Chilling temperature = 3 to 5 °C.

† Incub = incubation time = 28 days; seeds were exposed to 8 hours of light (PAR = 350 M m/sec) each day with temperatures of either constant 15 °C or 8 hours of 20 °C and 16 hours of 10 °C. In the alternating temperature regime, plants were exposed to light during the high-temperature period.

‡ Based on the percentage of viable seeds to germinate normally.

§ The Nampa and Sun Valley, ID, plants were grown from the same unknown seed source.

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Cupressaceae—Cypress family

Chamaecyparis Spach

white-cedar

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Growth habit, occurrence, and use. The genus *Chamaecyparis* occurs naturally on the Atlantic and Pacific Coasts of North America and in Japan and Taiwan. Three species are native to North America, 2 to Japan, and 1 to Taiwan (Sargent 1965). The North American species (table 1) are long-lived evergreens that attain large size. Port-Orford-cedar, the largest, has reached diameters of more than 1 m and heights of near 70 m in old-growth stands (Zobel 1990a). Branching is distinctive, with many-branched twigs and small paired scalelike leaves arranged in fernlike sprays. Another common name is "false cypress" (Little 1979); they are not true cedars (*Cedrus* spp.). Because of their somber beauty and variety of form, white-cedars are often used for ornamental plantings, hedges, and windbreaks (Rehder 1940). They produce valuable timber, the wood being sought for poles, posts, construction timbers, specialty items, and other uses where durability is desired. Atlantic white-cedar wood is especially popular for boats, outdoor furniture, posts, and utility poles (Kuser and Zimmerman 1995).

Geographic races and hybrids. Two geographic races of Atlantic white-cedar have been proposed: var. *henryae* (Li) Little in Georgia, Florida, Alabama, and Mississippi and var. *thyoides* in the area from South Carolina to Maine (Little 1966). Great variation exists within the genus, and numerous horticultural selections have been made of the 3 North America species as well as the Asian ones (Dirr and Heuser 1987; Harris 1990; Little and Garrett 1990; Zobel 1990a). Both interspecific and intergeneric crosses have been successful with certain of the cedars. Alaska-cedar and 2 of the Asian species have been crossed (Yamamoto 1981), and Alaska-cedar has also been crossed with several species of Cupressus (Harris 1990). The most well-known of these crosses is with Monterey cypress (*Cupressus macrocarpa* Hartw. ex Gord.) to produce the widely planted Leyland cypress (*Cupressocyparis* × *leylandii*).

Flowering and fruiting. White-cedars are monoecious. Their tiny inconspicuous yellow or reddish male pollen-bearing flowers and greenish female flowers are borne on the tips of branchlets (Harris 1974). Staminate flowers of Atlantic white-cedar, for example, are about 3 mm long, and the pistillate flowers are approximately 3 mm in diameter (Little and Garrett 1990). Pollination occurs generally from March to May, and cones ripen in September to October. Cones are slow to open fully, and seed dispersal occurs from fall into the following spring (table 2). Cones of Port-Orford-cedar and Atlantic white-

Table 1—*Chamaecyparis,* white-cedar: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***C. lawsoniana* (A. Murr.) Parl.** *Cupressus lawsoniana* A. Murr.	**Port-Orford-cedar,** false cypress, Lawson cypress, Oregon-cedar, Port-Orford white-cedar	SW Oregon (Coos Bay) S to NW California (Klamath River)
***C. nootkatensis* (D. Don.) Spach** *Cupressus nootkatensis* D. Don	**Alaska-cedar,** yellow-cedar, Alaska yellow-cedar, Nootka yellow-cypress, Sitka cypress, yellow cypress	Pacific Coast region from Prince William Sound, Alaska, SW to W British Columbia & W Washington, & S in Cascade Mtns to W & NW & SW British Columbia to California; local in NE Oregon
***C. thyoides* (L.) B.S.P.** *Cupressus thyoides* L	**Atlantic white-cedar,** white-cedar, swamp-cedar, southern white-cedar	Narrow coastal belt from S Maine to N Florida, W to S Mississippi

Source: Little (1979).

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Table 2—*Chamaecyparis*, white-cedar: phenology of flowering and fruiting

Species	Location	Flowering	Cone ripening	Seed dispersal
C. lawsoniana	Oregon	March	Sept–Oct	Sept–May
C. nootkatensis	Pacific Coast	Apr–May	Sept–Oct*	Oct–spring
C. thyoides	Atlantic Coast	Mar–Apr	Sept–Oct	Oct 15–Mar 1

Sources: Harris (1974), Little (1940).
* Cones require 2 years to reach maturity in the northern part of the range.

cedar mature the same year that they are pollinated, whereas cones of Alaska-cedar, in most of the species' range, take a second year to complete maturation (Harris 1974, 1990). In the extreme southern portion of the range of Alaska-cedar, cones may mature in only 1 year (Owens and Molder 1975). This condition even occurs on trees from more northern origins or from higher elevations when established in seed orchards in warm, southern, coastal sites (El-Kassaby and others 1991). The seeds from these 1-year cones are of size and germination quality equal to seeds from 2-year cones.

The white-cedars bear cones at an early age—5 to 20 years for Port-Orford-cedar (Zobel 1990a) and 3 to 5 years for Atlantic white-cedar (Little and Garrett 1990). Sprays of gibberellin (primarily GA_3) will induce flowering in even younger seedlings of Port-Orford-cedar and Alaska-cedar (Owens and Molder 1977; Pharis and Kuo 1977). The use of GA_3 and supplemental pollination on container-grown Port-Ordford-cedar trees 4 to 6 years from rooting or grafting has shown good potential to produce a large amount of seeds in a short period (Elliott and Sniezko 2000). Mature cones are 6 to 12 mm in diameter, spherical, and are borne erect on branchlets (figure 1). Cones have from 6 to 12 scales, each bearing from 1 to 5 seeds with thin marginal wings (figures 2 and 3) (Harris 1974). The average number of seeds per cone is 7 for Alaska-cedar (Harris 1990) and 8 for Atlantic white-cedar, but less than a third of these seeds may be filled. With controlled crosses in a seed orchard, Port-Orford-cedar averaged as high as 8.6 filled seeds per cone (Elliott and Sniezko 2000). Cone ripeness is normally determined by their exterior color (table 3).

Seedcrops of both western white-cedars can be damaged by larvae of the seedworm *Laspeyresia cupressana* (Kearfott) feeding on seeds in the cones. Larvae of the incense-cedar tip moth—*Argyresthia libocedrella* Busck—mine the cones and seeds of Port-Orford-cedar and can destroy practically the entire seedcrop (Hedlin and others 1980).

Collection of cones. Cones may be collected by hand or raked from the branchlets of standing or felled trees. As with many species, cone production is usually less in dense stands, although local conditions cause much variation (Zobel 1979), and open stands should be favored in collections from natural stands. In a North Carolina study,

Figure 1—*Chamaecyparis nootkatensis*, Alaska-cedar: mature cones.

Figure 2—*Chamaecyparis thyoides*, Atlantic white-cedar: seeds.

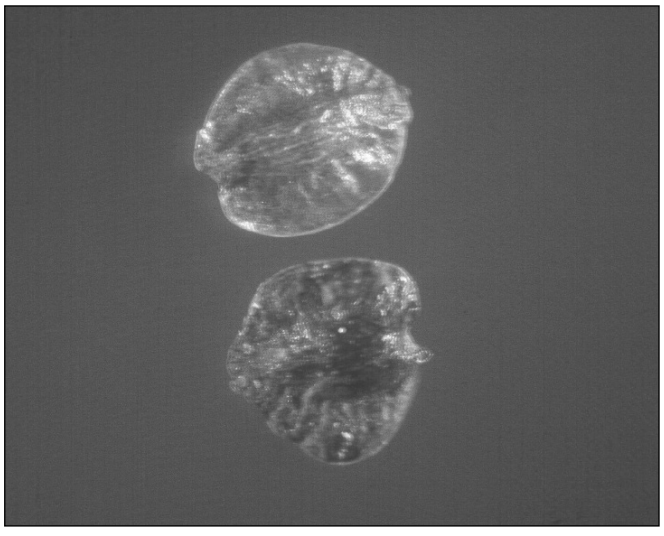
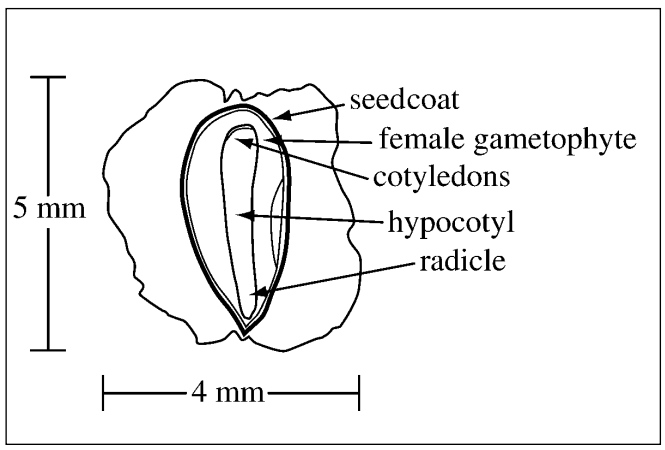


Table 3—*Chamaecyparis,* white-cedar: height, seed-bearing age, seed crop frequency, and color of ripe cones

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yrs)	Years between large seedcrops	Color of ripe cones
C. lawsoniana	to 73	1854	5–20	3–5	Greenish yellow to red brown
C. nootkatensis	to 53	1851	—	4 or more	Yellow brown to red brown
C. thyoides	12–27	1727	3–20	1 or more	Greenish with glaucous bloom to bluish-purple & glaucous, finally red brown

Sources: Little (1950), Korstian and Brush (1931), Ouden (1965), Rehder (1940), Sargent (1965).

Figure 3—*Chamaecyparis lawsoniana*, Port-Orford cedar: longitudinal section through a seed.



8- to 10-year-old plantations of Atlantic white-cedar produced good seedcrops that were easy to collect (Bonner and Summerville 1999). When collecting cones of Alaska-cedar in the northern part of the range, precautions are needed to limit the collection to mature, second-year cones. The smaller, greenish-blue, immature, first-year cones are often present on the same branches with the yellow-brown mature cones (Harris 1974).

Extraction, cleaning, and storage of seeds. Cones of white-cedars may be dried by spreading them in the sun or in a warm room, or they may be kiln-dried at temperatures below 43 °C (Harris 1974). Over 90% of the seeds can be recovered from cones of Atlantic white-cedar dried at 35 to 40 °C if 2 or 3 cycles of drying, interspersed with re-wetting of the cones, are used (Bonner and Summerville 1999). Each time the cones are redried, they open a little more. Mature cones of all white-cedars open when dried properly, and their seeds may be extracted by gentle shaking or tumbling. The thin-coated seeds of all species are easily injured and de-winging should not be attempted (Harris 1974).

Cleaning seeds of white-cedars to high purity values is difficult because the small, scalelike leaves are similar to the seeds in size and weight. For seedlots of Atlantic white-cedar, large trash can be removed with round-hole screens, and small trash can be blown off with any number of pneumatic cleaners or seed blowers. These same blowers can be used to upgrade Atlantic white-cedar seedlots by removing many of the empty seeds that occur naturally in this species. Separation is not absolute, of course, and many smaller filled seeds will be lost. With care, however, purities above 90% and filled seed percentages close to 90% can be obtained (Bonner and Summerville 1999). Similar data on the other 2 species are not available. Numbers of cleaned seeds per weight are listed in table 4.

Seeds of the white-cedars are orthodox in storage behavior. They should be stored at or below freezing at a seed moisture content of 10% or below (Allen 1957; Harris 1974). Seeds of Port-Orford-cedar from several origins stored at –15 °C lost no germination capacity over an 11-year period (Zobel 1990b). There are no comparable storage data for Alaska-cedar or Atlantic white-cedar, but the latter species is known to survive at least 2 years of similar storage without loss of viability (Bonner and Summerville 1999). Atlantic white-cedar seeds will also survive for at least 2 growing seasons in natural seedbeds (Little 1950).

Pregermination treatments and germination tests. Germination of white-cedar species is reported to be extremely variable and usually low, but this is due primarily to the naturally low percentages of filled seeds and the failure of seed managers to remove these empty seeds from the seedlots. Port-Orford-cedar germinates readily in the laboratory without pretreatment, and cold stratification does not appear to even improve germination rate (Zobel 1990b). Alaska-cedar exhibits a dormancy that can be somewhat overcome by warm incubation followed by cold stratification, but optimum schedules have not been determined (Harris 1990). In laboratory testing of germination, stratifi-

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Table 4—*Chamaecyparis*, white-cedar: seed yield data

Species	Seed wt/ cone wt	Cleaned seeds/weight			
		Range		Average	
		/kg	/lb	/kg	/lb
C. lawsoniana	20	176,400–1,323,000	80,000–600,000	463,000	210,000
C. nootkatensis	—	145,500–396,900	66,000–180,000	238,140	108,000
*C. thyoides**	20	926,100–1,102,500	420,000–500,000	1,014,300	460,000

Sources: Harris (1974), Korstian and Brush (1931), Swingle (1939).

* 1.64 kg (3.46 lb) of seeds were obtained from 1 bushel of cones (Van Dersal 1938).

cation of 21 days at 3 to 5 °C has been recommended (ISTA 1993). In nursery sowing, however, environmental conditions are seldom as favorable as those in the laboratory, so longer pretreatments are usually beneficial. One promising pretreatment schedule is moist stratification for 30 days at alternating temperatures of 20 and 30 °C, followed by 30 days at 5 °C (Harris 1974). The beneficial effect of warm incubation suggests that many of the seeds are not quite fully matured, and the incubation period enhances maturation in the same manner as warmer temperatures were shown to speed up cone ripening (Owens and Molder 1975).

Atlantic white-cedar has a variable dormancy also, although probably not as deep as that of Alaska-cedar. Some lots will germinate completely in the laboratory without any pretreatment (table 5). Recent tests with samples from North Carolina indicate that maximum germination in 28 days at good rates requires 4 weeks of moist stratification at 3 °C. Official test prescriptions (ISTA 1993) call for 90 days of stratification at 3 °C for germination within the same time period. Extremely slow germination has been reported in nursery beds in New Jersey (Little 1950), so some stratification would certainly be recommended. Germination is epigeal.

Nursery practice. For all 3 species of North American white-cedars, spring-sowing of stratified seeds is recommended. Port-Orford-cedar has the least dormancy and may only require 30 days of cold stratification. In England this species is normally not stratified at all (Aldous 1972). Alaska-cedar and Atlantic white-cedar have deeper levels of dormancy, and more extended pretreatments are necessary. Warm incubation at alternating temperatures, followed by cold stratification (as described in the previous section), has been recommended for both of these species (Dirr and Heuser 1987). Seeds from the more southern sources of Atlantic white-cedar seem to be not so dormant, and 30 to 60 days of cold stratification alone may be sufficient. Experience with Port-Orford-cedar in western nurseries suggests covering the sown seeds with 3 to 6 mm ($^1/_{10}$ to $^1/_4$ in) of soil and calculating sowing rates to produce 320 to 530 seedlings/m^2 (30 to 50/ft^2). One kilogram (2.2 lb) of Port-Orford-cedar seeds should produce about 284,000 plantable seedlings (Harris 1974). Shading the seedbeds until midseason of the first year may also be beneficial. For field planting, 2+0 stock is commonly used in the western United States, although 2+1 transplants are favored for Port-Orford-cedar in England (Harris 1974). For Atlantic white-cedar, 2+0 seedlings are used in New Jersey and 1+0 seedlings in North Carlina (Kuser and Zimmerman 1995).

All white-cedars can be propagated vegetatively and are commonly produced this way for the ornamental market. Port-Orford-cedar cuttings should be taken between September and April, treated with indole butyric acid (IBA) powder (3,000 to 8,000 ppm), and placed in peat or perlite with mist and bottom heat (Dirr and Heuser 1987). Zobel (1990a) suggests taking cuttings from tips of major branches from lower branches of young trees. Alaska-cedar cuttings need 8,000 or more ppm of IBA, and cuttings should be taken in late winter to early spring (Dirr and Heuser 1987). After 4 years, growth of outplanted rooted cuttings was equal to that of seedlings in British Columbia (Karlsson 1982). Atlantic white-cedar cuttings taken in mid-November and treated with auxins also root very well (Dirr and Heuser 1987). With auxins and bottom heat in mistbeds, 90% rooting can be expected. Early comparisons show that growth of seedlings and stecklings (rooted cuttings) to be about the same (Kuser and Zimmerman 1995).

Table 5—*Chamaecyparis*, white-cedar: stratification periods and germination test conditions and results

Species	Test conditions: Stratification (days) Warm*	Cold†	Temp (°C) Day	Night	Days	Test results: Germ energy (%)	Days	Germ capacity (%)	Soundness (%)	Samples
C. lawsoniana	0	0	30	20	28	44	14	48	48	9
	0	0	30	20	60	24	34	52	—	60
C. nootkatensis	58	30	30	20	22	10	11	12	51	1
	0	30–90	30	20	41	0	—	0	57	3
	0	0	30	20	28–55	0	—	0	54	8
C. thyoides	0	0	30	20	60	—	—	84	—	11
	0	90	30	20	28	—	—	—	—	—

Source: Harris (1974).

* At alternating temperatures of 30 and 20 °C.

† At 5 °C.

‡ Seeds were exposed to light during the warm period.

§ A constant temperature of 20 °C is also suitable (ISTA 1993).

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C

Bignoniaceae—Trumpet-creeper family

Chilopsis linearis (Cav.) Sweet

desert-willow

Arthur W. Magill, Carol Miller, and Jane E. Rodgers

Dr. Magill retired from USDA Forest Service's Pacific Southwest Forest and Range Experimental Station; Ms. Miller was a propagationist at the USDI National Park Service Joshua Tree National Park Center for Arid Lands Restoration and Native Plant Nursery, Twentynine Palms, California; Ms. Rodgers, is a restoration ecologist at the Point Reyes National Seashore Point Reyes Station, California

Synonyms. *C. saligna* D. Don, C. *linearis* var. *originaria* Fosberg, *C. linearis* var. *glutinosa* (Engelm.) Fosberg, C. *linearis* var. *arcuata* Fosberg.

Other common names. false-willow, *jano,* flowering-willow, desert catalpa, catalpa-willow.

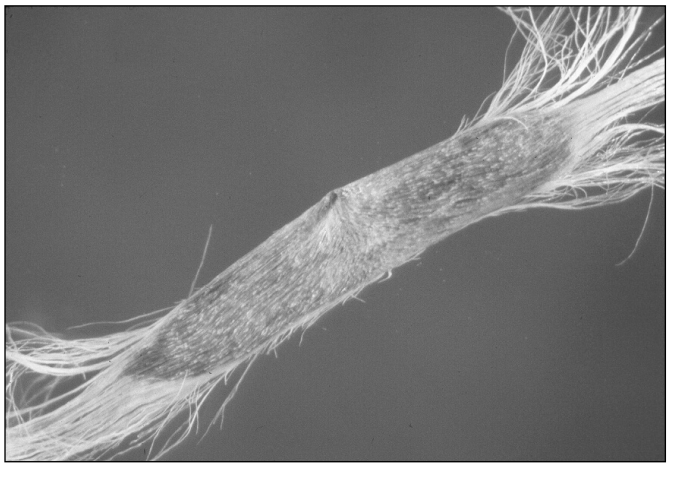
Growth habit, occurrence, and use. Desert-willow grows along dry washes and streams in the desert between 450 and 1,500 m of elevation from southern California through southern Utah to western Texas and southward into Mexico and Lower California. It is a deciduous shrub or small tree that attains heights of 3 to 7.5 m or occasionally more. Growth can be rapid, up to 1 m annually (Munz 1979). The plant is useful for wildlife cover, erosion control, restoration, stream stabilization, and ornamental plantings in arid regions (McMinn 1959; Bainbridge and Virginia 1989; Munz 1959). Seed pods and flowers are edible, but the major use for Native American people was the wood (for house frames, granaries, and bows) and the fibrous bark (for weaving nets, shirts, and breechclouts) (Bainbridge and Virginia 1989).

Flowering and fruiting. Desert-willow produces perfect flowers between April and August throughout its range (Magill 1974; McMinn 1959). The fruit is a 2-celled capsule about 6 mm in diameter and from 10 to 30 cm long. It ripens from late summer to late fall (Afanasiev 1942) and persists through winter (Little 1950). The numerous light-brown oval seeds are about 8 mm long and have a fringe of soft white hairs on each end (figures 1 and 2).

Collection, extraction, and storage. Seedpods can be hand-picked after late September and through the winter months. Care must be taken not to pick unripened fruits—the fruits on a tree may mature unevenly because of their long flowering period (Engstrom and Stoeckeler 1941). Seed extraction simply requires that the pods be spread out, dried, beaten lightly, and shaken, and then the seeds screened out. Each 45 kg (100 lb) of dried pods should produce 14 to 23 kg (30 to 50 lb) of clean seeds, which number from 88,200 to 282,240/kg (40,000 to 128,000/lb) and average 189,130/kg (86,000/lb) (Magill 1974). Commercial seedlots have averaged 92% in purity and 87% in soundness (Magill 1974). These seeds are orthodox in storage behavior, so cold, dry storage conditions are recommended for storage. Seeds have been successfully propagated after 4 years of refrigerated storage at 7 °C (CALR 1993).

Germination. Desert-willow seeds are not dormant, but storage for several days in wet sand or between wet blotter paper will speed germination. In germination tests 1,000 seeds were placed in a sand or water medium for 21 to 60 days with a night temperature of 20 °C and a day temperature of 30 °C (Engstrom and Stoeckeler 1941; Magill 1974). Germination averaged 14 to 60% in 9 to 30 days and germinative capacity ranged from 26 to 100% (Magill 1974). Average germination using blotter paper is 80% (CALR 1993).

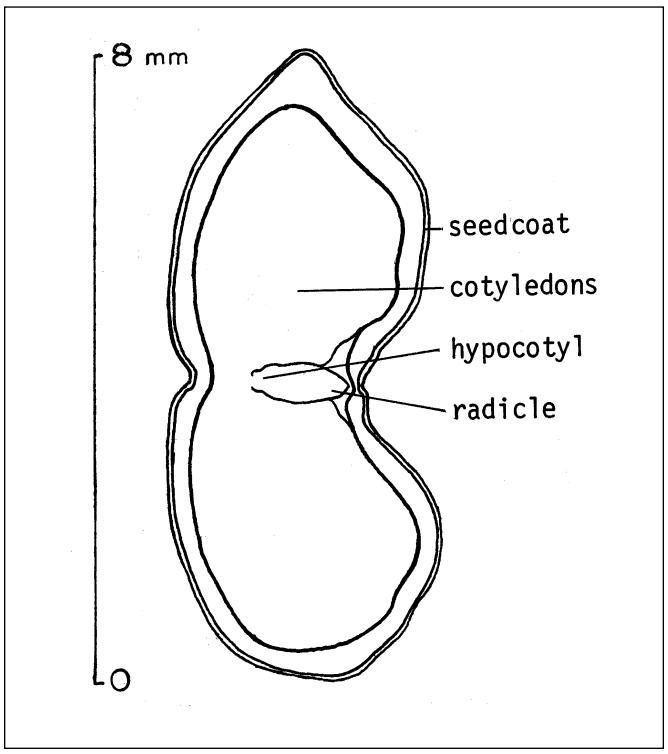
Figure 1—*Chilopsis linearis*, desert-willow: seed.



Nursery field practice and seedling care. Desert-willow seeds may decay unless sown in spring soon after the soil warms up. Sowing depth should be 6 mm ($^1/_4$ in). A ratio of seven times as many viable seeds as the desired number of usable seedlings is required to grow nursery stock (Magill 1974). Damping-off can be a problem.

Desert-willow may also be propagated from cuttings (Magill 1974); cuttings should be handled carefully and allowed to produce an extensive rootball before transplanting. Mature plants grown in ~57-liter (15-gal) pots and 0.8-m (30-in) tubes have been successfully outplanted as windbreaks and for desert restoration at Joshua Tree National Park (CALR 1993).

Figure 2—*Chilopsis linearis*, desert-willow: longitudinal section through a seed.



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C

Pyrolaceae—Shinleaf family

Chimaphila Pursh

chimaphila

Don Minore

Dr. Minore retired from the USDA Forest Service's Pacific Northwest Research Station

Growth habit, occurrence, and use. Taxonomists sometimes differ when classifying plants in the genus *Chimaphila* (Blake 1914; Camp 1939; Hitchcock and others 1959; Stapf 1930; Takahashi 1987; Traulau 1981; Wordsdell and Hill 1941), but there are at least 4 clearly defined species (table 1). All have a chromosome number (2n) of 28 (Haber and Cruise 1974), and all occur in the Northern Hemisphere (table 1). Pipsissewa, the most widespread species, has been divided into 5 geographically delimited subspecies: *C. umbellata* ssp. *occidentalis* (Rydb.) Hult. in western North America; ssp. *acuta* (Rydb.) Hult. in Arizona and New Mexico; ssp. *mexicana* (DC) Hult. in Mexico; ssp. *cisatlantica* (Blake) Hult. in eastern North America; and ssp. *umbellata* in Europe and Asia (Takahashi 1987).

The chimaphilas are low, usually creeping, evergreen subshrubs (Krüssmann 1984) with alternate leaves that are crowded near the summit of each year's annual growth, giving the appearance of being whorled on the short shoots ("pseudo-whorls"). Those shoots produce annual growth rings (Copeland 1947) and are connected by elongate rhizomes that are as much as 2.5 m long. The rhizomes are slender (not more than a few millimeters in diameter) and yellow or brown. They bear distant buds that are subtended by small scales and associated with single roots. The leaves may persist as long as 7 years in pipsissewa and 8 years in little pipsissewa (Copeland 1947).

Chimaphila leaves are purported to have antibacterial properties. They contain taraxerol, beta-sitosterol, ursolic acid, nonacosane, hentriacontane, isohomoarbutin, renifolin, arbutin, avicularin, hyperoside, several flavonoids, and a compound called chimaphilin (Lucia 1991; Sheth and others 1967; Trubachev and Batyuk 1968; Walewska 1971). Chimaphilin has a quinone structure similar to that of 1,4-naphthoquinone (DiModica and others 1953), and it may be responsible for the medicinal properties attributed to the chimaphilas. The boiled leaves are taken as a liver remedy (Altschul 1973). The plants also have been used as diuretics and to treat rheumatism and fever (Krüssmann 1984). Large quantities of pipsissewa are now being harvested for use as flavoring in a popular beverage.

Flowering and fruiting. Striped pipsissewa usually flowers in its third growing season, but flowering may be delayed in pipsissewa and little pipsissewa until 7 or 8 annual pseudo-whorls of leaves have been produced (Copeland 1947). Flowers are choripetalous, pentacyclic, pentamerous, actinomorphic, and protogynous (Holm 1927; Pyykko

Table 1—*Chimaphila*: nomenclature and occurrence

Scientific name	Common name(s)	Distribution
***C. japonica* Miq.**	**Japanese chimaphila**	Japan, Korea, China, & Taiwan
***C. maculata* (L.) Pursh**	**striped pipsissewa,** striped prince's-pine, spotted wintergreen	Maine & New Hampshire to Ontario, Michigan, & Illinois S to Georgia, Alabama, & Tennessee
***C. menziesii* (R. Br. ex D. Don) Spreng.**	**little pipsissewa,** little prince's-pine	British Columbia, Montana, & Washington S through Oregon & California to Mexico
***C. umbellata* (L.) W. Bart.**	**pipsissewa,** prince's-pine	North America from Alaska to Mexico & from Ontario & New Brunswick to Georgia; Europe (incl. Scandinavia), Eurasia, Japan, & West Indies

Sources: Barrett and Helenurm (1987), Blake (1914), Camp (1939), Fernald (1950), Hill (1962), Nordal and Wischmann (1989), Ohwi (1965), Prain (1960), Traulau (1981).

1968). They have 5-parted calyxes, 5 petals, 10 stamens, 5-chambered ovaries, and short thick styles with wide, 5-pointed stigmas (Krüssmann 1984). The ovary is superior, and there is a well-developed, collar-like disk at the base of the pistil that secretes nectar. Placentation is central-axile, with a massive, 2-lobed placenta intruding into each locule (Pyykko 1968). Those placentae are beset with numerous minute ovules (Copeland 1947). The 1 to 3 (little pipsissewa and Japanese chimaphila) or 2 to 6 (striped pipsissewa and pipsissewa) flowers are borne in pendulous, terminal inflorescences (Krüssmann 1984; Ohwi 1965). In pipsissewa those inflorescences are corymbs; in striped and little pipsissewas, they are cyme-like clusters (Copeland 1947). Flowers are pink or white and slightly fragrant.

Chimaphila pollen grains are packed into polyads composed of indefinite numbers of tetrads (Knudsen and Olesen 1993; Takahashi 1986). Pollination is by insects. In pipsissewa, bumble bees are the most important pollinators but the flowers also are visited by staphylinid beetles (Barrett and Helenurm 1987; Knudsen and Olesen 1993), and there is a small amount of self-pollination (Barrett and Helenurm 1987). Differences in the flower preferences of the bumble bee species involved may help to prevent interbreeding between pipsissewa and striped pipsissewa during a short overlap in flowering periods where these inter-fertile species grow together (Standley and others 1988).

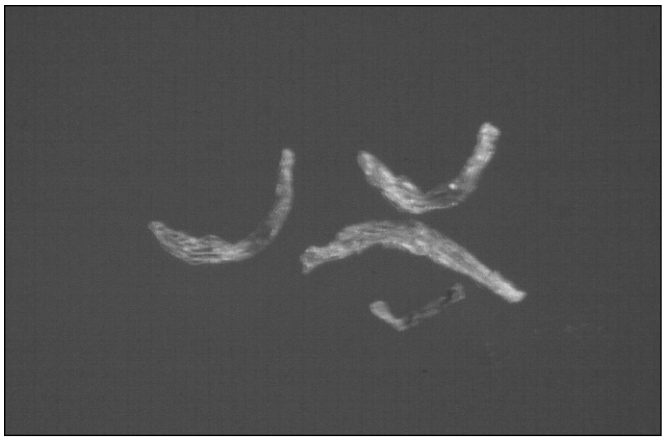
An average pipsissewa flower produces 308,800 pollen grains and 5,587 ovules—a pollen to ovule ratio of 58 (Barrett and Helenurm 1987). In central New Brunswick, Canada, anthesis occurs over a 30-day period in July (Helenurm and Barrett 1987). In the Pacific Northwest, pipsissewa flowers may be found from June until August (Hitchcock and others 1959). The fruits matured in about 70 days in New Brunswick, where an average fruit weighed 23 mg, and fruit set was 75% for both self-pollinated and cross-pollinated flowers (Barrett and Helenurm 1987).

The chimaphila fruit is a 5-celled, loculicidally dehiscent capsule that contains very large numbers of tiny seeds (Barrett and Helenurm 1987; Copeland 1947; Pyykko 1968) that sift out of the capsule openings to be borne away by the wind. The embryos of those seeds develop no distinct parts during seed development, but they eventually absorb all of the endosperm except a single layer of cells. The inner integumental cells die and remain in existence as more or less shriveled empty spaces at the ends of the seeds (Copeland 1947). The seedcoat consists only of the outer cell layer of the integument, which loses protoplasm and tannin to become transparent (Pyykko 1968). Although the inner periclinal walls of those transparent testa cells are smooth or slightly pitted in all species, intraspecific differences occur in pipsissewa (Takahashi 1993).

Chimaphila seeds are characterized by very small size, few cells, and little differentiation (figure 1). Each contains a central ellipsoidal mass consisting of an embryo covered by a single layer of endosperm cells, surrounded by a transparent seedcoat that is hollow and shriveled at each end. Ripe seeds are 0.6 to 0.9 mm long and 0.1 mm wide. There are about 1,500,000 seeds/g (42,524,250/oz) (Minore 1994).

Collection and storage of seeds. Seeds can be collected in the field by tapping recently dehisced capsules to dislodge the tiny seeds, which can then be captured in a jar or plastic bag as they drift downward. Recently dehisced capsules may be difficult to find, however, because mature capsules often are not open or have already lost their seeds. Mature closed capsules can be collected, dried, and macerated to recover the seeds. Unfortunately, this latter procedure creates debris that is difficult to separate from the seeds, and seed maturity is not assured. Optimal storage conditions and seed longevity are unknown.

Figure 1—*Chimaphila umbellata*, pipsissewa: seeds (0.1 mm wide and ~ 0.7 mm long, at center) with central embryo and elongate, transparent seedcoat.



Pregermination treatments; germination tests; and nursery practice. Chimaphila seeds have not been sown and germinated successfully. Forest soil that had been sifted to remove debris and rhizome material and then stored outdoors all winter produced pipsissewa seedlings in the spring, however, indicating that there are viable seeds in the soil seed bank and that extensive stratification may be necessary (Wilson 1994). No formal pregermination treatments or germination tests are known. Chimaphila seedlings are seldom found in nature (Holm 1927). Therefore, most natural regeneration may be accomplished by the spread of rhi-

zomes. Cultivation attempts often fail (Kruckeberg 1982), but division of the rhizome has been recommended as a suitable method of propagation (Bailey and Bailey 1976). The chimaphilas may be partial root parasites (Kruckeberg 1982). If they are, special practices that include an unknown host may be needed to achieve successful large-scale nursery production.

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Oleaceae—Olive family

Chionanthus virginicus L.

white fringetree

John D. Gill, Franz L. Pogge, and Franklin T. Bonner

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Other common names. old-man's-beard, flowering-ash, grandfather-graybeard.

Growth habit, occurrence, and uses. White fringetree—*Chionanthus virginicus* L.—occurs on rich, well-drained soils of streambanks, coves, and lower slopes but is most abundant in the understory of pine–hardwood forests, especially on moist, acid, sandy loam soils (Goodrum and Halls 1961). It develops best in semi-open situations but is moderately shade-tolerant, being found occasionally in dense understories. Though widely distributed, it usually is a minor part of the total vegetation. White fringetree is a relatively short-lived shrub or small tree and may attain 11 m in height (Rehder 1940). Its range is from southern Pennsylvania and Ohio south to central Florida and westward through the Gulf Coast region to the Brazos River in Texas and to northern Arkansas (Brown and Kirkman 1990).

Fringetrees are planted as ornamentals throughout the South and elsewhere beyond their natural range. The bark is used as a tonic, diuretic, and astringent; it is also used to reduce fever. In Appalachia, a liquid of boiled root bark is applied to skin irritations (Krochmal and others 1969). Twigs and foliage are preferred browse for deer (*Odocoileus* spp.) in the Gulf Coastal Plain but are less preferred in the Piedmont and mountains. Browsing is least in winter. The species is only moderately resistant to browsing, and plants may die when more than a third of the annual growth is removed. The date-like fruits are eaten by many animals, including deer, turkey (*Meleagris gallopovo*), and quail (*Callipepla* spp.). Cattle may eat the foliage (Goodrum and Halls 1961). The date of earliest known cultivation is 1736 (Rehder 1940).

Flowering and fruiting. White fringetree's flowering habit is polygamo-dioecious, although it is functionally dioecious (Brown and Kirkman 1990; Gleason 1963). The white, fragrant flowers are borne in pendant axillary panicles 10 to 25 cm long that appear from March to June, depending on latitude (Brown and Kirkman 1990; Gill and Pogge 1974). The fruit is a dark blue to purple ovoid drupe about 2 cm long (figure 1). It is usually single-seeded (figures 1 and 2); rarely 2- or 3-seeded. Fruits ripen and drop from the trees in July in eastern Texas and as late as October in the northern part of the range (Lay 1961; Van Dersal 1938). Seeds are dispersed beyond the immediate vicinity of the tree by birds and rodents. Plants first produce seeds at 5 to 8 years of age. In eastern Texas, they produced some fruit each year; no seedcrop failure occurred (Lay 1961).

Collection, extraction, and storage. The fruits should be collected from the branches after they have turned purple and before birds remove them, which should be August in the South and September and October in the North (Dirr and Heuser 1987). The pulpy pericarp should be removed by maceration with either mechanical macerators for large lots or kitchen blenders for small lots, or by rubbing the fruits over hardware cloth fine enough to retain the seeds. The pulp may then be washed away. The seeds contain about 40% moisture when they are shed and must be dried to at least 22% if they are to be stored at low temperatures (Carpenter and others 1992). There have been no long-term storage tests of white fringetree seeds reported,

Figure 1—*Chionanthus virginicus*, white fringetree: fruit (drupe, **left**) and seed (**right**).

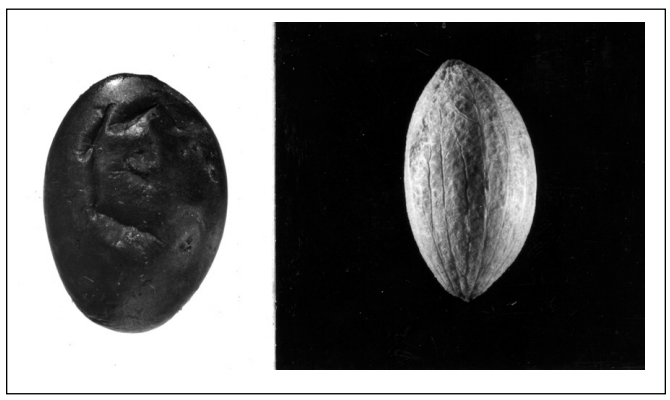
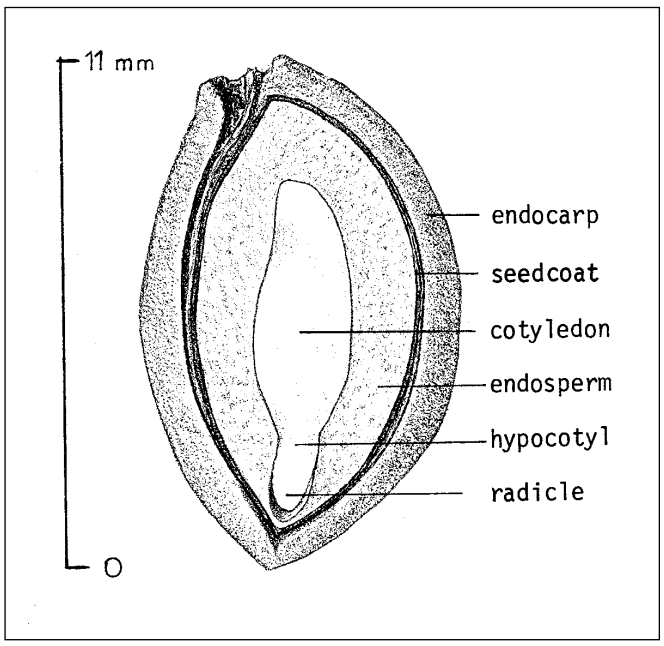


Figure 2—*Chionanthus virginicus*, white fringetree: longitudinal section through a seed.

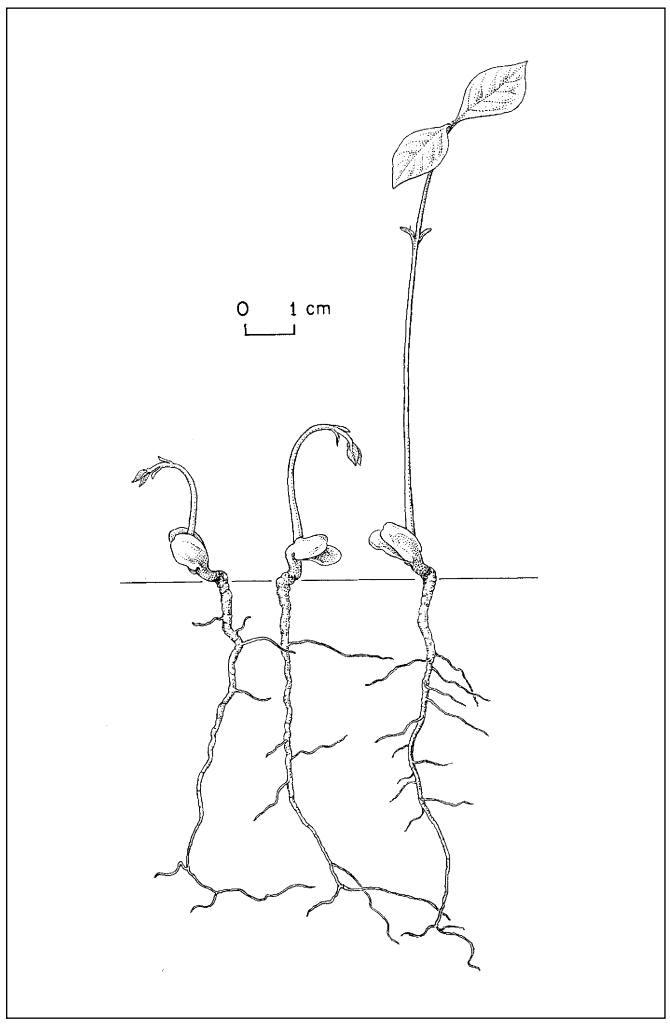


although seeds have remained viable in cold stratification for 1 to 2 years (Gill and Pogge 1974). It is not known if these seeds are orthodox or recalcitrant. There are about 1,400 fruits/kg (630/lb); 1 kg of fruits yielded 330 g of seeds and 1 lb yields 5 1/4 oz. The average number of seeds per weight is 4,000/kg (1,800/lb) with a range of 2,420/kg to 4,410 (1,100 to 2,000/lb) (Gill and Pogge 1974; Swingle 1939; VanDersal 1938).

Germination. Natural germination usually occurs in the second spring after seedfall, the results of an apparent double dormancy or combined dormancy in the seeds. Fringetree seeds first need a period of warm temperatures, commonly 3 to 5 months, during which the radicle develops while the shoot remains dormant. Subsequently, cold exposure during winter overcomes the shoot dormancy (Flemion 1941; Schumacher 1962). In the wild, these temperature exposures occur during the first summer and second winter after seedfall. In a test with 2 seedlots, seeds were held at 20 °C for 1 or more months; stratified at 5 °C for 1 month or more; then sown in flats and held at 20 to 30 °C for 1 year. Germination was about 40% (Gill and Pogge 1974). Good germination (80%) can also be obtained with removal of the hard endocarp; soaking in 1,000 ppm solution of gibberellin (GA_3) for 6 hours; then germinating at 25 °C (Carpenter and others 1992). No official test methods have been prescribed, and the embryo excision method has been recommended for quick viability estimates (Barton 1961; Flemion 1941; Heit 1955). Germination is hypogeal (figure 3).

Nursery practice. Seeds may be sown in either fall or spring. Seeds can be sown soon after they are cleaned, but no later than mid-October in the northern part of the range (Heit 1967). Drills should be set 20 to 30 cm (8 to 12 in) apart and the seeds covered with 6 to 12 mm ($^1/_4$ to $^1/_2$ in) of firmed soil. Beds should be covered with burlap or mulched with straw or leaf mulch until after the last frost the following spring. If spring-sowing is desired, then seeds should be given 3 months of warm storage, then 3 months of cold stratification (Dirr and Heuser 1987). As an alternative for the amateur gardener, seeds can be sown under glass, in boxes with standard compost, during February–March (Sheat 1948). Propagation by layering, grafting, or budding onto ash seedlings is sometimes practiced, but the species is almost impossible to root (Dirr and Heuser 1987).

Figure 3—*Chionanthus virginicus*, white fringetree: seedling development at 1, 4, and 7 days after germination.



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C

Fagaceae—Beech family

Chrysolepis Hjelmqvist

chinquapin

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Synonyms. The 2 species of *Chrysolepis* found in the United States are distinct from their Asian relatives in the genus *Castanopsis* and were placed by Hjelmqvist (1948) in their current genus. This genus was accepted in Hickman's extensive and long-researched flora of California (1993). These American species, which have a floral morphology that is intermediate between *Castanopsis* and *Lithocarpus*, represent the ancient condition of the family Fagaceae (McKee 1990). The common name also has changed throughout the years. Early workers called the species "chinquapin." Later, it became "chinkapin" but more recently it was changed back to "chinquapin" (Hickman 1993; Keeler-Wolf 1988).

Occurrence and growth habit. In North America, the genus *Chrysolepis* consists of 2 species and 1 variety (Hickman 1993), all located in the Pacific Coast region. Giant chinquapin—*Chrysolepis chrysophylla* var. *chrysophylla* (Dougl. ex. Hook) Hjelmqvist —is a tree that ranges from southwestern Washington southward to San Luis Obispo County in the Cascade, Klamath, and Coastal Mountains of California. A remnant stand also exists in El Dorado County in the north central Sierra Nevada. This species achieves its best form from Marin County, California, northward (Griffin and Critchfield 1972) to Lane County, Oregon. Giant chinquapin also has a shrub form—*C. chrysophylla* var. *minor* (Benth.) Munz, often called "golden chinquapin"—that is found throughout the range of its taller brethren.

The second species—*C. sempervirens* (Kellogg) Hjelmqvist—which is always a shrub, has the common name "bush chinquapin." This species is found from the Cascade Mountains of southern Oregon westward in the Siskiyou Mountains of northern California, and southward along the east-facing slopes of the north Coast Range and the west-facing slopes of the Sierra Nevada, San Jacinto, and San Bernardino Mountains (McMinn 1939). Throughout its range, the habitat is characterized as being of low quality with shallow, rocky, and often droughty soils. In western Siskiyou County, California, and in other places where the ranges of the 2 shrub forms overlap, hybridization probably occurs (Griffin and Critchfield 1972).

Giant chinquapin is often found as a single tree or in groves; it rarely occupies extensive areas. This shade-tolerant tree is rarely found in a dominant position; it is more often found in intermediate and codominant crown positions. Pure stands are uncommon and rarely exceed 10 ha (McKee 1990). In the Klamath Mountains of northern California, giant chinquapin shows a distinct preference for mesic conditions, with highest basal areas occurring on north-facing slopes or in mesic canyon bottoms (Keeler-Wolf 1988). In general, best growth is achieved in moist environments with deep and infertile soils (Zobel and others 1976). The shrub forms occupy a plethora of topographic/edaphic sites over an elevational range that varies from 300 to 3,000 m. The shrub forms can be quite extensive and achieve greatest coverage in the extreme environments of xeric sites at higher elevations. Here they dominate, with their area corresponding to the extent of past disturbance. The amount of time that they dominate also can be lengthy, given a lack of seed source for inherently taller competitors. Over a long time span, however, disturbance is necessary for the continued presence of chinquapin. Because of its wide ecological amplitude, chinquapin is part of many associations that include most of the forest-zone conifers and hardwoods on the Pacific Coast. A general pattern for all the species and varieties is that they are at their competitive best on infertile soils (McKee 1990).

Chinquapins are vigorous sprouters and most trees originate as root crown sprouts. The sprouts grow rapidly and outstrip natural conifer seedlings for several years. Mature trees tend to have straight boles and narrow crowns. The largest trees may reach over 33 m in height and 1 to 1.2 m in girth (Sudworth 1908). For shrubs, var. *minor* tends to be stiff and upright in exposed areas and semiprostrate in shaded environments. Bush chinquapin is stiff and upright in all environments.

Use. The light, fairly hard, and strong wood of chinquapin has been used for veneer, paneling, cabinets, furniture, turned products, pallets, and fuel (EDA 1968).

Flowering and fruiting. The flowers of giant chinquapin, which bloom from June through midwinter, and the flowers of the shrubs, which bloom throughout the summer, are unisexual, with staminate and pistillate flowers being borne on the same plant. The staminate flowers are borne in groups of 3 in the axils of bracts, forming densely flowered, erect cylindrical catkins 2.5 to 7.6 cm long; 1 to 3 pistillate flowers are borne in an involucre, usually at the base of the staminate catkins or borne in short separate catkins. At the time of peak blooming in June, each tree is covered with erect creamy white blossoms, which provide a pleasing contrast to the more somber foliage (Peattie 1953).

The fruit consists of 1 to 3 nuts (figures 1 and 2) enclosed in a spiny golden brown bur. The nuts mature in fall of the second year (Hickman 1993). The minimum seed-bearing age (from root crown sprouts) is 6 years (McKee 1990). Giant chinquapin trees have been reported as producing seeds at 40 to 50 years of age but probably do so before this age (McKee 1990). Controversy exists over seed productivity. Sudworth (1908) reported that the tree form is an abundant seeder, but Peattie (1953) noted that although flowering is abundant, fruiting is "strangely shy." Insects, squirrels, and birds often consume most of a given crop. Indeed, Powell (1994) observed tree squirrels (*Sciurus* spp.) cutting burs of large chinquapins during a bumper seed year. By late fall, the ground beneath the trees was covered with burs.

Collection, extraction, and storage. Because of heavy predation by many animals, collectors should hand-pick the burs in late summer or early fall, after they ripen but before they open (Hubbard 1974). The collected burs should be spread out to dry in the sun or in a warm room. After drying, the nuts can be separated from the burs mechanically. The following number of nuts per weight have been recorded (Hubbard 1974; McMinn 1939):

	Nuts/kg	Nuts/lb
giant chinquapin (*C. chrysophylla* var. *chrysophylla*)	1,826–2,420	830–1,100
golden chinquapin (*C. chrysophylla* var. *minor*)	1,540	700
bush chinquapin (*C. sempervirens*)	—	2,640 1,200

Figure 1—*Chrysolepsis chrysophila* var. *chrysophila*, giant chinquapin: nut.

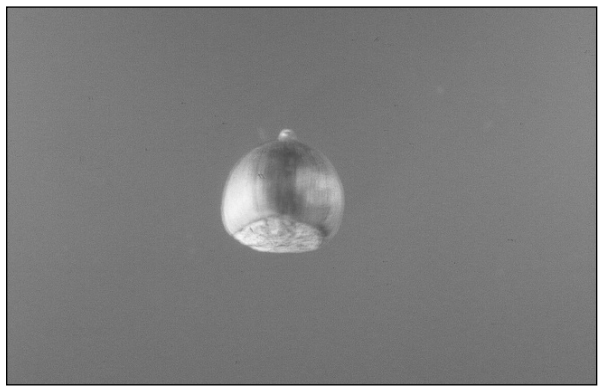
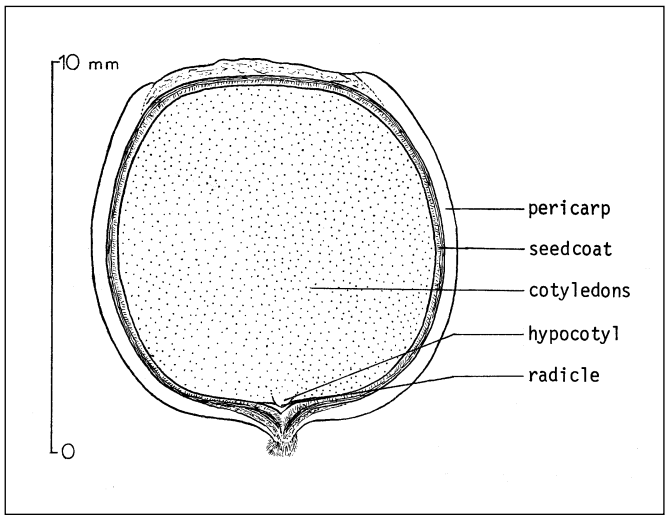


Figure 2—*Chrysolepsis*, chinquapin: longitudinal section through a seed.

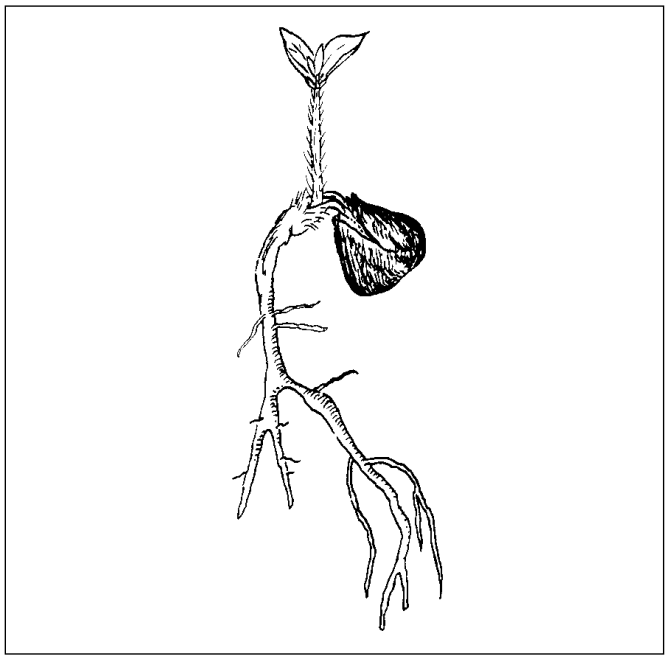


When stored in sealed containers at 6 °C, chinquapin seeds retain their viability well for at least 2 years and probably longer. Viability of 1 sample of giant chinquapin seeds stored in this manner dropped only from 50 to 44% in 5 years (Hubbard 1974).

Pregermination treatments. Mirov and Kraebel (1937) found that no stratification was needed.

Germination. Germination of untreated seeds of giant chinquapin in 3 tests ranged from 14 to 53% (Hubbard 1974)—the poorest of all hardwoods in the Klamath Mountains provenance of southwestern Oregon and northern California (McDonald and others 1983). Mirov and Kraebel (1937) found highest germination values for giant chinquapin to be 50% in 24 days and for bush chinquapin was 30% in 16 days. Germination is hypogeal (figure 3) and best in peat.

Figure 3—*Chrysolepsis,* chinquapin: seedling at 1 month after germination



Nursery practice. Little is known about raising chinquapins in nurseries. In a study at the Rancho Santa Ana Botanic Gardens in California, the 3 native species were raised in pots. Some survived through 1 or more potting stages, but none survived after outplantings (Hubbard 1974). Propagation by layering, grafting, or budding is feasible (Hubbard 1974).

Seedling care. Natural regeneration of giant chinquapin usually is sparse or totally lacking. Powell (1994) noted that not a single seedling was present on ground covered with burs beneath large seed trees. McKee (1990) also inferred that regeneration was lacking in environments of deep litter and dense understory vegetation. Sudworth (1908) noted that regeneration was best if seeds were covered, apparently by eroded soil. Keeler-Wolf (1988) found sexually reproduced seedlings and saplings to average about 19/ha (7/ac) in the Klamath Mountains but only in shaded mesic environments. In the Oregon Cascade Mountains, McKee (1990) noted that chinquapin reproduction occurred in light leaf mulch in partial shade, with plantlets that were 15 to 45 cm tall at ages 4 to 12. For bush chinquapin in the northern Sierra Nevada on 10 study areas over a 10-year period, not 1 seedling was found. Although tiny plants looked like seedlings, a gentle tug showed that they were connected to parent-plant root systems. The number of new sprouts averaged over 39,000/ha (16,000/ac) 6 years after site preparation by bulldozer bared the ground (McDonald and others 1994).

Altogether, this evidence suggests that for both natural and artificial regeneration, best seedling care will be achieved with covered seeds in partially shaded, moist conditions. Seedling growth in this environment, however, is unknown.

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Asteraceae–Aster family

Chrysothamnus Nutt.
rabbitbrush

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Growth habit, occurrence, and use. Members of the rabbitbrush genus—*Chrysothamnus* spp.—are among the best-known of western shrubs (Johnson 1987; McArthur and Welch 1986; McArthur and others 2004, 1979). The genus is endemic to western North America and is made up of 16 species (Anderson 1986; McArthur and Meyer 1987). It has recently been partially subsumed under the new genus *Ericameria*, formerly an infraspecific taxon within the related genus *Haplopappus* (Anderson 1995; USDA NRCS 2001). Because the durability of this nomenclatural change has yet to be demonstrated, the decision here is to follow the traditional nomenclature (table 1).

Rabbitbrush commonly occurs on sites of natural or human disturbances such as washes, drainage-ways, and quarries; they may also occur as subdominants in later seral vegetation. Their conspicuous golden flowers are a familiar sight in autumn along roadsides throughout the West. Three of the species—rubber rabbitbrush, Parry rabbitbrush, and green rabbitbrush—are widespread, polymorphic taxa made up of multiple subspecies, whereas the remainder are taxonomically simpler and more restricted in distribution. Rubber rabbitbrush is made up of 22 subspecies, many of which are ecologically distinctive. Its more ecologically specialized subspecies are restricted to dunes, rock outcrops, shale badlands, alkaline bottomlands, or montane riparian communities. Most of the widely distributed subspecies are also broad in their ecological requirements but tend to be commonest on disturbed ground. Common garden studies have shown that marked ecotypic differentiation occurs within subspecies for such traits as growth form, growth rate, cold and drought hardiness, competitive ability, flowering time, achene weight, and germination patterns (McArthur and others 1979; Meyer 1997; Meyer and others 1989). Such ecotypic variation is to be expected in other widely distributed species as well. It is therefore important to consider ecotype as well as species and subspecies when selecting seed sources for artificial seeding projects.

Species, subspecies, and populations of rabbitbrush also vary widely in their palatability to livestock and wildlife. Certain unpalatable taxa such as threadleaf rubber rabbitbrush tend to increase on abused rangeland, and considerable energy has been invested in control methods (Whisenant 1987). A tendency to resprout after herbicide spraying, chopping, or burning, combined with an ability to reestablish from seeds, can make rabbitbrush difficult to eradicate (Young and Evans 1974).

Basin and mountain whitestem rubber rabbitbrush races are highly palatable as winter forage for deer (*Odocoileus* spp.), sheep, and cattle, and have been included in seeding mixes for the rehabilitation of big game winter range for over 30 years (Monsen and Stevens 1987). Other species and subspecies also provide winter forage for wildlife and livestock (McArthur and others 2004). Rabbitbrushes are extensively used for mined-land rehabilitation in the West (Romo and Eddleman 1988). Thousands of pounds of wildland-collected seed are bought and sold annually (McArthur and others 2004; Monsen and others 2004, 1987). Rabbitbrushes may be seeded as pioneer species on harsh mine disturbances for erosion control and site amelioration and often invade such sites on their own (Monsen and Meyer 1990). They can act as nurse plants to facilitate establishment of later seral species, as they generally offer little competition to perennial grasses or later seral shrubs (Frischknecht 1963).

Rabbitbrushes have potential uses in landscape plantings, especially with the recent emphasis on xeriscaping. Rubber rabbitbrush has also been examined as a commercial source of natural rubber and other plant secondary metabolites such as resins (Weber and others 1987).

Flowering and fruiting. The perfect yellow disk flowers of rabbitbrushes usually occur in groups of 5 in narrowly cylindrical heads subtended by elongate, often keeled bracts. The heads are numerous and are clustered in often flat-topped terminal or lateral inflorescences that can be

Table 1—*Chrysothamnus*, rabbitbrush: ecology and distribution of some common species and subspecies

Taxon & species	Common name(s)	Geographic distribution	Habitat
SECTION CHRYSOTHAMNUS			
***C. linifolius* Greene** *Ericameria linifolia* (Greene) L.C. Anders.	**spearleaf rabbitbrush,** alkali rabbitbrush	Colorado Plateau N to Montana	Deep alkaline soils; low to mid-elevation
***C. viscidiflorus* (Hook.) Nutt.** *E. viscidiflora* (Hook.) L.C. Anders.	**green rabbitbrush**	Intermountain	Wide amplitude
***C. v.* ssp. *lanceolatus* (Nutt.) Hall & Clements** *E. viscidiflora* spp. *lanceolata* (Nutt.) L.C. Anders.	**Douglas rabbitbrush**	Intermountain	Montane
***C. v.* ssp. *viscidiflorus* (Hook.) Nutt.** *E. viscidiflora* (Hook.) L.C. Anders.	**low rabbitbrush**	Intermountain	Low to mid-elevation
SECTION NAUSEOSI*			
***C. nauseosus* (Pallas ex Pursh) Britt.** *E. nauseosa* (Pallas ex Pursh) Nesom & Baird	**rubber rabbitbrush**	W North America	Wide amplitude
***C. n.* ssp. *albicaulis* (Nutt.) Hall & Clements**	**mountain whitestem rubber rabbitbrush**	Mostly Intermountain Rocky Mtn	Mostly coarse soils; mid-elevation
***C. n.* ssp. *hololeucus* (Gray) Hall & Clements**	**basin whitestem rubber rabbitbrush**	Mostly Great Basin	Mostly coarse soils; low to mid-elevation
***C. n.* ssp. *consimilis* (Greene) Hall & Clements** *E. nauseosa* ssp. *consilimus* (Greene) Nesom & Baird	**threadleaf rubber rabbitbrush**	Mostly Great Basin	Mostly fine soils; low to mid-elevation
***C. n.* ssp. *graveolens* (Nutt.) Piper**	**green rubber rabbitbrush**	W Great Plains; Colorado Plateau	Wide amplitude; low to mid-elevation
***C. n.* ssp. *salicifolius* (Rydb.) Hall & Clements**	**willowleaf rubber rabbitbrush**	N Utah	Montane
***C. parryi* (Gray) Greene** *E. parryi* (Gray) Nesom & Baird	**Parry rabbitbrush**	Scattered; W US	Mostly montane
SECTION PUNCTATI*			
***C. teretifolius* (Dur. & Hilg.) Hall** *E. teretifolia* (Dur. & Hilg.)	**Mojave rabbitbrush,** Jepson green rabbitbrush	Mojave Desert	Rocky washes; hot desert

Sources: Anderson (1995), Deitschman and others (1974), USDA NRCS (2001).

quite showy. Flowering occurs from late July through October, with higher elevation populations flowering earlier. The fruits ripen in September in the mountains but may not be ripe until December in warm desert populations. There may be considerable variation in flowering and fruiting phenology within populations and even on individual plants (Meyer 1997). Each flower has the potential of producing a single narrowly cylindrical achene that is completely filled by the elongate embryo (figures 1 and 2). The achene is topped with a ring of pappus hairs that aid in dispersal by wind. The pappus may also be involved in orienting and anchoring the achene during seedling establishment (Stevens and others 1986). Fully ripened fruits are easily detached from the plant by wind under dry conditions. Abundant flowering occurs most years, but fill is variable. Sometimes there is considerable damage by noctuid moth larvae during seed development. The damaged fruits remain attached to the plant, creating the appearance of an abundant harvest after all the sound fruits have dispersed.

Seed collection, cleaning, and storage. Dry, calm conditions are best for the harvest of rabbitbrush seeds. Fully ripe fruits are fluffy and easily detachable, and they may be stripped or beaten into shoulder hoppers, bags, or boxes. Seed fill must average 30 to 50% in order to attain purities high enough for commercially profitable harvest. On favorable upland sites, harvestable crops occur in 4 of 5 years (Monsen and Stevens 1987). The purity of the bulk-harvested material is usually near 10%. Seeds are often moist at harvest and must be dried before cleaning.

Rabbitbrush seeds are difficult to clean. The elongate achenes are brittle and easily damaged in most mechanical cleaning equipment. Using flail-type cleaners such as barley debearders results in less damage than using hammermills. After initial cleaning, the material can be fanned and screened in a fanning mill to achieve the desired purity. Cleaning removes sticks and large debris, separates the achenes from the inflorescences, detaches the pappus from the achenes, and removes unfilled fruits and other fine debris.

Figure 1—*Chrysothamnus*, rabbitbrush: achenes with pappi intact of *C. viscidiflorus*, Douglas rabbitbrush (**left**) and *C. nauseosus*, rubber rabbitbrush (**right**).

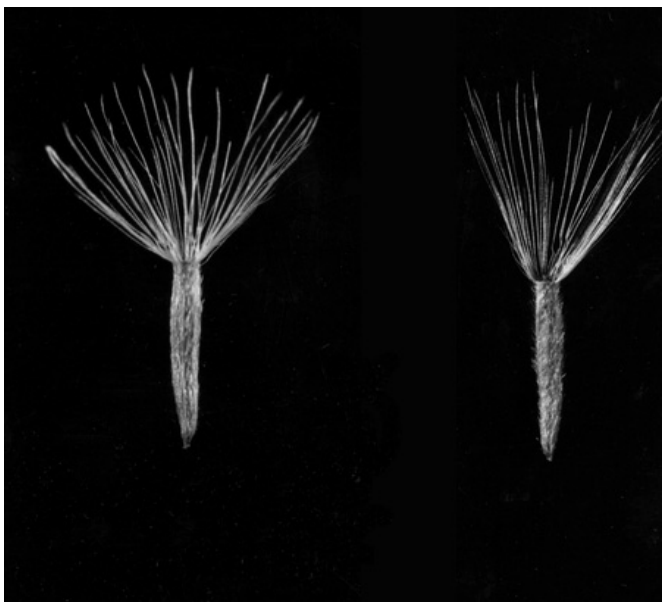
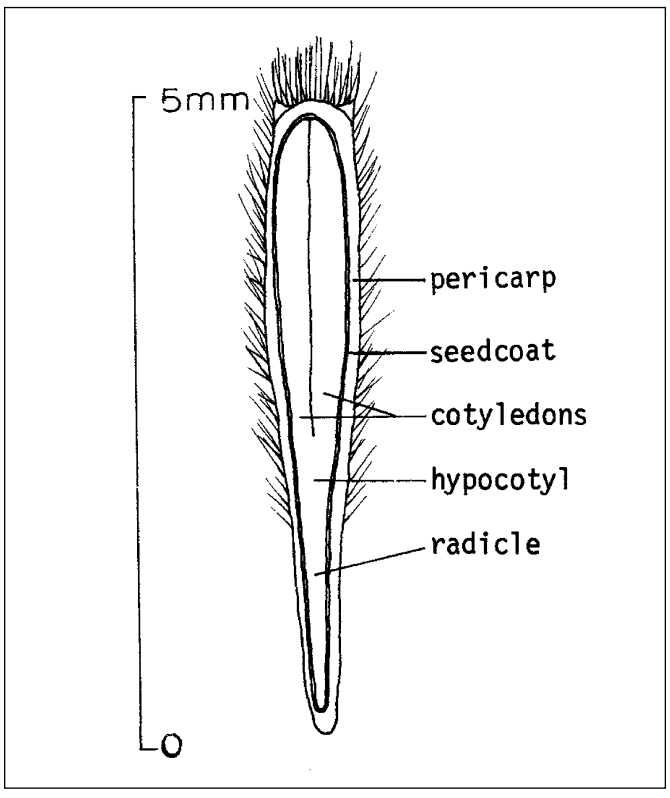


Figure 2—*Chrysothamnus viscidiflorus* spp. *lancedatus*, Douglas rabbitbrush: longitudinal section through an achene.



These steps are necessary to raise purities to 20% or higher and to make it possible to use conventional seeders (Monsen and Stevens 1987).

Achene weight varies substantially among species, subspecies, and populations of rabbitbrush (table 2). In rubber rabbitbrush, weight is correlated with habitat; the largest achenes come from plants that are specialized for growing on dune and badland habitats, and the smallest come from populations on temporarily open saline bottoms (Meyer 1997). There is a ninefold difference in achene weight among populations of rubber rabbitbrush, and other species also show achene weight variation (table 2). This makes it important to consider achene number per unit weight explicitly when calculating seeding rates.

Rabbitbrush seeds are not long-lived in warehouse storage. Substantial loss of viability may occur within 3 years, and storage beyond 3 years is not recommended (Monsen and Stevens 1987; Stevens and others 1981). Seeds should be retested immediately before planting so that seeding rates can be based on current values for pure live seed. Rabbitbrush seedlots with initially low vigor and viability values tend to lose their remaining viability more quickly in storage (Meyer and McArthur 1987). Because of late ripening dates, rabbitbrush seeds are usually held for a year (until the following autumn) before planting. Careful attention to moisture content (7 to 8% is probably near optimum) and storage at low temperature may prolong storage life, but data to substantiate this are lacking.

Germination. Germination requirements for rabbitbrush vary both among and within species. Rubber rabbitbrush germination is best understood (Khan and others 1987; McArthur and others 1987; Meyer and McArthur 1987; Meyer and Monsen 1990; Meyer and others 1989; Romo and Eddleman 1988). Seeds are usually nondormant at high incubation temperatures (30 °C) even when recently harvested, but display variable levels of dormancy at the intermediate temperatures characteristic of autumn seedbeds. Seeds of early-ripening high-elevation collections are most likely to be dormant or slow to germinate at autumn temperatures, whereas seeds of late-ripening warm-desert collections germinate completely and rapidly over a wide temperature range. The conditional dormancy of recently dispersed seeds is removed through moist chilling, so that all seeds are nondormant in the field by late winter. Germination rate at near-freezing temperature is even more closely tied to habitat. Collections from montane sites may

Table 2—*Chrysothamnus,* rabbitbrush: seed yield data

Species	Cleaned seeds* (x 1,000)/seed weight			
	Mean		Range	
	/kg	/lb	/kg	/lb
SECTION CHRYSOTHAMNUS				
C. linifolius	1.8	0.8	—	—
C. viscidiflorus	1.8	0.8	1.5–2.0	0.7–0.9
ssp. *lanceolatus*	1.8	0.8	1.1–2.2	0.5–1.0
	1.8	0.8	—	—
ssp. *viscidiflorus*	1.5	0.7	1.1–2.2	0.5–1.0
SECTION NAUSEOSI				
C. nauseosus	1.7	0.8	1.5–2.0	0.7–0.9
ssp. *albicaulis*	1.1	0.5	0.9–1.4	0.4–0.6
	1.5	0.7	—	—
ssp. *hololeucus*	1.3	0.6	1.1–1.5	0.5–0.7
	1.5	0.7	—	—
ssp. *consimilis*	1.5	0.7	0.9–2.4	0.4–1.1
	1.7	0.8	—	—
ssp. *graveolens*	1.3	0.6	0.9–1.1	0.4–0.5
ssp. *salicifolius*	0.9	0.4	0-9–1.1	0.4–0.5
C. parryi	0.9	0.4	—	—
SECTION PUNCTATI				
C. teretifolius	1.3	0.6	—	—

Sources: Belcher (1985), Deitschman and others (1974), Meyer (1995, 1997), McArthur and others (2004).

* 100% purity.

require more than 100 days to germinate to 50% at 3 °C, whereas warm desert collections may reach 50% germination in as few as 5 days. These germination features act in concert with seasonal patterns of temperature and precipitation in each habitat to ensure complete germination in mid to late winter. Germination is often completed just before the snow melts, with little or no carryover of seed between years. The ecotypic variation in germination phenology results in reduced emergence and survival when seed-source habitat is not matched to planting site habitat (Meyer 1990; Meyer and Monsen 1990).

Preliminary data for Intermountain and Mojave Desert populations of other species of rabbitbrush suggest that they share the same basic habitat-correlated germination patterns. Information on germination response to temperature for 6 collections of green rabbitbrush indicates that it differs from rubber rabbitbrush in having 25 °C rather than 30 °C as an optimum germination temperature and in showing some dormancy even at this optimal temperature (table 3) (Meyer 1997). Habitat-correlated germination responses at autumn and winter temperatures were similar for the 2 species and also for collections of Parry, spearleaf, and Mojave rabbitbrushes.

Evaluation of the seed quality for rabbitbrush is not without pitfalls. Reasonably repeatable purity values are obtained when only filled achenes are included as pure seed (Meyer and others 1989). Germination tests for rubber rabbitbrush should be carried out at alternating temperatures of 20 to 30 °C or a constant 25 °C for 28 days (Meyer and others 1989). This procedure is the only one listed in the official testing rules for this genus (AOSA 1993). Seedlots from low and middle elevations should complete germination within 14 days, whereas seedlots from high elevations may still show some dormancy even after 28 days, making post-test viability evaluation essential. Tests at 30 °C are not recommended, even though relative germination percentage (that is, percentage of viable seeds germinating) may be higher because there are indications that 30 °C is more stressful to marginally viable seeds.

Tetrazolium viability testing of rabbitbrush seeds is also somewhat problematical. The embryos must be removed from the achene prior to immersion in the stain because of poor penetration of the stain, even with piercing or cutting of the achene wall. The process of removal often damages the embryo, making the staining patterns hard to interpret. We frequently obtained higher viability estimates from germination tests than from tetrazolium evaluation for these species (Meyer 1997).

Nursery and field practice. Rabbitbrush species are easily propagated as container stock (Deitschman and others 1974). Seeds are sown directly into containers that provide depth for root development, sometimes after a short wet chill to ensure uniform emergence (Long 1986). The seedlings grow rapidly and are ready for outplanting in 3 to 4 months, after a hardening period. They may be outplanted in fall or spring, whenever moisture conditions are optimal. Bareroot propagation of rabbitbrush has also been successful. In spite of considerable among-lot and among-plant variation in seedling size, transplants survive quite well. Fall-seeding in nursery beds is recommended. Plants require less water than most other shrubs and should not be overwatered or fertilized excessively (Monsen 1966).

Rabbitbrushes are among the easiest shrubs to establish from direct seeding, and most plantings on wildland sites use this method. Minimal seedbed preparation is required. Surface planting onto a firm but roughened seedbed in late fall usually results in adequate stands. This planting may be accomplished through aerial seeding; hand-broadcasting; or seeding with a thimble seeder, seed dribbler, browse seeder, or a drill with the drop tubes pulled so that the seed is placed on the disturbed surface behind the disk furrow openers (McArthur and others 2004). Seeds should not be planted too deeply. One millimeter of soil coverage is sufficient. Seeding rates of about 20 to 30 live seeds/m^2 (2 to 3/ft^2) are usually adequate. This is equivalent to about 200 g/ha (ca 3 oz/ac) on a pure live seed basis for a seedlot that averages 1.5 million seeds/kg (680,400/lb). If the seedlot is cleaned to high purity, it may be necessary to dilute it with a carrier such as rice hulls in order to achieve uniform seeding rates. Seedlings emerge in early spring, and young plants grow rapidly, often producing seeds in their second growing season.

Table 3—*Chrysothamnus,* rabbitbrush: germination percentage (as percentage of total viable seeds) after 28 days at 15 °C or at 25 °C, and days to 50% of total germination during 20 weeks at 3 °C for some common species and subspecies

Species	Germination percentage at 15 °C			Germination percentage at 25 °C			Days to 50% germination at 3 °C		
	Mean	Range	No.	Mean	Range	No.	Mean	Range	No.
SECTION CHRYSOTHAMNUS									
C. linifolius	—	—	—	—	—	—	21	—	1
C. viscidiflorus									
ssp. *lanceolatus*	37	29–49	3	64	58–70	3	60	35–82	5
ssp. *viscidiflorus*	58	31–98	3	68	40–96	3	60	35–82	5
SECTION NAUSEOSI									
C. nauseosus									
ssp. *albicaulis*	37	29–45	2	85	78–92	2	41	9–88	2
ssp. *hololeucus*	75	17–97	8	91	74–96	8	21	7–70	12
ssp. *consimilis*	70	26–96	6	91	80–100	6	33	5–108	17
ssp. *graveolens*	76	28–100	7	91	58–100	7	33	10–105	17
ssp. *salicifolius*	25	9–55	6	65	44–92	6	89	60–100	6
C. parryi	—	—	—	—	—	—	34	12–54	4
SECTION PUNCTATI									
C. teretifolius	—	—	—	—	—	—	5	5	1

Sources: Meyer (1997), Meyer and McArthur (1987), Meyer and others (1989).

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Fabaceae—Pea family

Cladrastis kentukea (Dum.-Cours.) Rudd

yellowwood

David F. Olson, Jr., R. L. Barnes, and Jill R. Barbour

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Synonym. *Cladrastis lutea* (Michx. f.) K. Koch

Other common names. Kentucky yellowwood, virgilia, American yellowwood.

Growth habit, occurrence, and use. Yellowwood—*Cladrastis kentukea* (Dum.-Cours.) Rudd—is a small deciduous tree that attains a height of 12 to 18 m at maturity (Sargent 1965). The native range of yellowwood is restricted; it extends from western North Carolina into eastern and central Tennessee, northern Alabama, Kentucky, southern Illinois, and Indiana; it also occurs in the glades country of southwestern Missouri and in central and northern Arkansas. Locally, it grows on limestone cliffs in rich soils, and its greatest abundance is in Missouri and in the vicinity of Nashville, Tennessee. The wood is hard, close-grained, and bright yellow, turning to light brown on exposure to light; commercially, it is a substitute for walnut in gunstocks and a source of clear yellow dye. Yellowwood is hardy as far north as New England and is often planted for its ornamental value. It was introduced into cultivation in 1812 (Olson and Barnes 1974).

Flowering and fruiting. The fragrant, perfect, white, showy flowers bloom in June, usually in alternate years, and the fruit ripens in August or September of the same year (Bailey 1949; Radford and others 1964; Sargent 1965). The fruit is a legume (pod), 7.5 to 10 cm long (figure 1) (Fernald 1950), that falls and splits open soon after maturing. The seeds are dispersed by birds and rodents. Each legume contains 4 to 6 short, oblong, compressed seeds with thin, dark brown seedcoats and without endosperm (figure 2). Weights of seeds in legumes containing 2 to 4 seeds decreased from the base of the legume to the style (Harris 1917). Good seedcrops are produced generally in alternate years.

Collection of fruits. The legumes may be collected soon after maturity by handpicking them from trees or by shaking or whipping them onto outspread canvas or plastic sheets. Legumes turn brown and split open easily at maturity.

Extraction and storage of seeds. After the legumes are allowed to dry, they can be opened by beating them in sacks or running them through a macerator. The seeds may be separated from the legume remnants with screens or air separators.

Cleaned seeds average about 24,900 to 32,200/kg (11,300 to 14,600/lb). Average purity and soundness of seeds from commercial sources have been, respectively, 82 and 67% (Olson and Barnes 1974). Seeds of yellowwood are orthodox in storage behavior and may be stored dry in sealed containers at 5 °C (Olson and Barnes 1974). For overwinter storage, seeds may be stratified in sand or a mixture of sand and peat (Olson and Barnes 1974), or they may be dried and sown the following spring (Wyman 1953).

Pregermination treatments. Natural germination of yellowwood is epigeal (figure 3) and takes place in the spring following seedfall. Dormancy is chiefly caused by an impermeable seedcoat and to a lesser degree by conditions in the embryo (Burton 1947). Burton (1947) found that shaking yellowwood seeds for 20 minutes at 400 strokes per minute made 82% of the seed permeable to water. A successful dormancy-breaking treatment is sulfuric acid scarification for 30 to 60 minutes (Heit 1967). Dormancy may be overcome also by stratification in sand or sand and peat for 90 days at 5 °C or by scarification and storage for 30 days (Olson and Barnes 1974).

An early method of overcoming dormancy includes soaking the seeds in water that is nearly at the boiling point (Jenkins 1936). The water should be preheated to 71 to 100 °C at the time the seeds are immersed; the heating element is then removed and the seeds are allowed to soak and cool for 12 to 24 hours in water (Heit 1967).

Germination tests. There are no official test prescriptions for yellowwood. Germination has been tested on pretreated seeds in sand or sand and peat flats in 30 to 42 days at 20 to 30 °C (Olson and Barnes 1974) and on moist filter paper medium for 24 days at 0, 25, and 50 °C (Rivera and others 1937). Acid-treated seeds germinated from 51 to 67% in 11 days; final germination ranged from 56 to 67% (Olson and Barnes 1974). Acid treatment for 0, 30, 60, and 120 minutes produced 5, 41, 92, and 96% germination, respectively (Frett and Dirr 1979).

Figure 1—*Cladrastis kentukea*, yellowwood: legumes.

Figure 2—*Cladrastis kentukea*, yellowwood: longitudinal section (**left**) and exterior view of a seed (**right**).

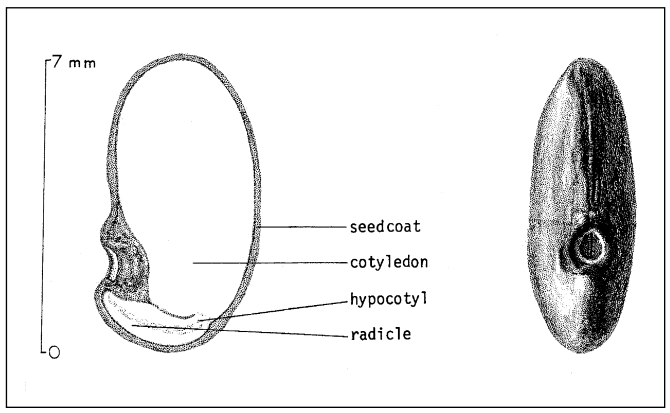
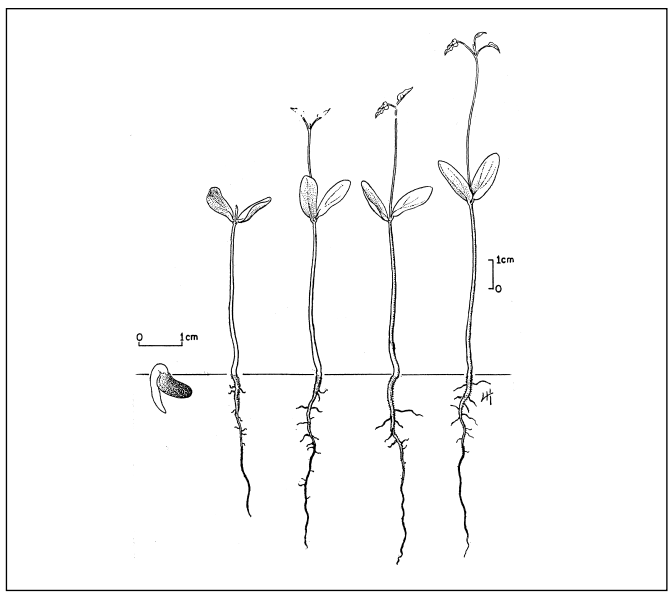


Figure 3—*Cladrastis kentukea*, yellowwood: seedling development at 1, 6, 10, 16, and 20 days after germination.



Applying hydrostatic pressure to yellowwood seeds increased their permeability in the region of the hilum and greatly increased the speed of germination (Rivera and others 1937). Pressures of 68,950 kN/m^2 (10,000 lb/in^2) applied for 10 minutes at 0 °C, 1 minute at 25 °C, and 1 minute at 50 °C resulted in 100% germination within 24 days (Rivera and others 1937). At 206,850 kN/m^2 (30,000 lb/in^2) of pressure for 1 minute or 5 minutes at 25 °C, 100% of the seeds germinated by the 12th day. However, a 20-minute exposure to a pressure of 68,950 kN/m^2 (10,000 lb/in^2) at 50 °C proved injurious to the seeds, with 15.5% of the seeds appearing soft and dead (Rivera and others 1937).

Nursery practice. Seeds may be sown in autumn or spring. Beds should be well prepared and drilled with rows 20 to 30 cm (8 to 12 in) apart, and the seeds covered with about 6 mm ($^1/_4$ in) of firmed soil. Untreated seeds may be sown in autumn and the seedbeds should be mulched and protected with bird or shade screens until after late frosts in spring. Side boards simplify mulching and screening. Stratified seeds or dry-stored seeds that have been treated to break dormancy are used for spring-sowing. If seeds were soaked in hot water at 49 °C for 24 to 36 hours until swollen and then surface-dried and planted in the nursery, they germinated readily in the spring (Dirr and Heuser 1987). Shading of seedlings is unnecessary.

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Ranunculaceae—Buttercup family

Clematis L.

clematis

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Dr. Rudolf (deceased) retired from the USDA Forest Service's North Central Forest Experiment Station

Growth habit, occurrence, and use. The genus *Clematis* includes more than 200 species of climbing vines, and erect or ascending perennial herbs (sometimes woody) widely that are distributed through the temperate regions, chiefly in the Northern Hemisphere (Rehder 1940). *Clematis* is subdivided into 3 sections—Flammula (western and eastern virgin's-bowers), Atragene (western blue clematis and *C. occidentalis* (C.L. Hitchc.) Pringle), and Viorna (traveler's-joy). The taxonomy and distribution of section Atragene are described by Pringle (1971). Many horticultural varieties are grown for ornamental purposes (Dirr 1990; Lloyd 1977; Markham 1935). The 8 species included here (table 1) are also useful for erosion control, ground cover, and wildlife food (Bailey 1939; Dirr 1990; Fernald 1950; Rehder 1940; Van Dersal 1938).

Species occupy different site types within their range. In Wisconsin, for example, eastern virgin's-bower was found in 13 community types but was most abundant in the wet alder thicket community. Rock clematis is present in 2 communities and most abundant in northern dry mesic forests (Curtis 1959). Western species seem to be more common on drier well-drained sites than species native east of the Mississippi (table 1).

Geographic races. Two varieties of western virgin's-bower—*C. ligusticifolia* var. *californica* Wats. and var. *brevifolia* Nutt.—are separated geographically within the species' range (Vines 1960). These and a variety of eastern virgin's-bower—*C. virginiana* var. *missouriensis* (Rydb.) Palmer & Steyrm.—may be geographic races. Wild plants intermediate between Drummond clematis and western virgin's-bower may be of hybrid origin (Vines 1960). Several hybrids of Italian clematis are known (Rehder 1940).

Flowering and fruiting. There are both monoecious and dioecious species. Eastern virgin's-bower and western virgin's-bower (section Flammula) are dioecious, but their female flowers have non-functional stamens. Species in the sections Atragene and Viorna are monoecious (Fernald 1950). Flower size differs significantly among species, for example, eastern virgin's-bower flowers occur in clusters (panicles) containing several flowers, and their sepals are about 0.5 cm in diameter, whereas rock clematis flowers are borne singly, and their sepals are about 4 cm. Fruits are borne in heads of 1-seeded achenes with persistent feathery styles. Achenes (figures 1 and 2) are produced annually (Rudolf 1974) and are dispersed by wind in late summer or fall. Some species have been shown to produce viable seeds the first year after sowing (neoteny) (Beskaravainya 1977).

Table 1—*Clematis*, clematis: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***C. columbiana* (Nutt.) Torr. & Gray** *C. verticillaris* var. *columbiana* (Nutt.) Gray	**rock clematis,** mountain clematis, purple clematis	Quebec to Manitoba, S to New England, West Virginia, Ohio, Wisconsin, &
***C. drummondii* Torr. & Gray**	**Drummond clematis,** Texas virgin's-bower, graybeard	NW Iowa Central & E Texas, Arizona & in Mexico on dry, well-drained soils
***C. flammula* L.** *C. pallasii* J. F. Gmel.	**plume clematis**	Mediterranean region to Iran
***C. ligusticifolia* Nutt.** *C. brevifolia* Howell	**western virgin's-bower,** western clematis, traveler's-joy	British Columbia & North Dakota S to New Mexico & California
***C. pauciflora* Nutt.**	**rope-vine**	California on dry, well-drained sites
***C. virginiana* L.** *C. catesbyana* Pursh	**eastern virgin's-bower,** Virginia virgin's-bower, eastern clematis	Maine to Georgia to Louisiana to Kansas in low woods & along streambanks
***C. vitalba* L.**	**traveler's-joy,** old-man's-beard	S Europe, N Africa, & the Caucasus Mtns.
***C. viticella* L.**	**Italian clematis,** vine-bower	S Europe & W Asia

C

Dates of flowering and fruiting are listed in table 2. Effects of day length and temperature on flowering and flowerbud development were reported by Goi and others (1975). Other characteristics of 8 common species are presented in table 3.

Collection of fruits and extraction and storage of seeds. Fruits are brown when ripe and may be gathered from the plants by hand, dried, and shaken to remove the seeds from the heads. Other characteristics of ripeness are when the styles have become feathery (figure 1) and the achene appears shrunken and separates easily from the head (Stribling 1986). Large quantities of fruits may be collected by means of a vacuum seed harvester, run dry through a hammermill to break up the heads, and fanned to remove debris (Plummer and others 1968).

Numbers of cleaned seeds per unit weight are listed for 7 species in table 4. Limited data for eastern virgin's-bower, traveler's-joy, and Italian clematis indicate that, in seeds not freed from the styles, purity runs from 90 to 95% and soundness about 85% (Rafn and Son 1928; Rudolf 1974). For hammermilled seeds of western virgin's-bower, a purity of 20% is acceptable in Utah (Plummer and others 1968) because separation of the broken styles from the seed is difficult and expensive. Viability of dry seeds of this species has been maintained for 2 years without refrigeration (Plummer and others 1968).

Germination. Clematis seeds have dormant or immature embryos (Dirr 1990; Dirr and Heuser 1987). Some species and hybrids may germinate over a period of from months to years (Lloyd 1977). Dirr (1990) and Dirr and Heuser (1987) also indicate that requirements for germination vary among the taxa.

Prechilling at 1 to 5 °C in moist sand, peat, or a mixture of the two for 60 to 180 days has been used to promote germination in some species (Dirr and Heuser 1987; Fordham 1960; Hartmann and others 1990; Heit 1968). Field-sowing responses of traveler's-joy and Italian clematis (Blair 1959) indicate that warm plus cold stratification may be needed. The presence of an immature embryo in Italian clematis suggests that the warm stratification allows the embryo to mature, which allows germination to occur (Clark and others 1989). Germination of seeds of *Clematis microphylla* F. Muell. ex Benth. was improved by removing the pericarp or by exposing them to a cycle of wetting and drying (Lush and others 1984). Germination of seeds of traveler's-joy collected and sown in November was lower and germination rate lower than that of seeds collected and sown in February (Czekalski 1987).

Germination tests can be run on pretreated seed in sand flats or germinators for 40 to 60 days at 20 °C (night) to 30 °C (day) (Rudolf 1974). Test results available for 4 species are shown in table 5.

Nursery practice. Only a few species are propagated from seeds because of unacceptable variation in form and flowering that detracts from their value as ornamentals (Evison 1977; Lloyd 1977). The most appropriate sowing schedule is based on species and winter conditions and will vary with geographic location. General recommendations

Figure 1—*Clematis virginiana*, eastern virgin's-bower: 1 achene with complete style (**upper left**) and 2 achenes with styles removed (**lower right**).

Figure 2—*Clematis virginiana*, eastern virgin's-bower: longitudinal section through an achene.

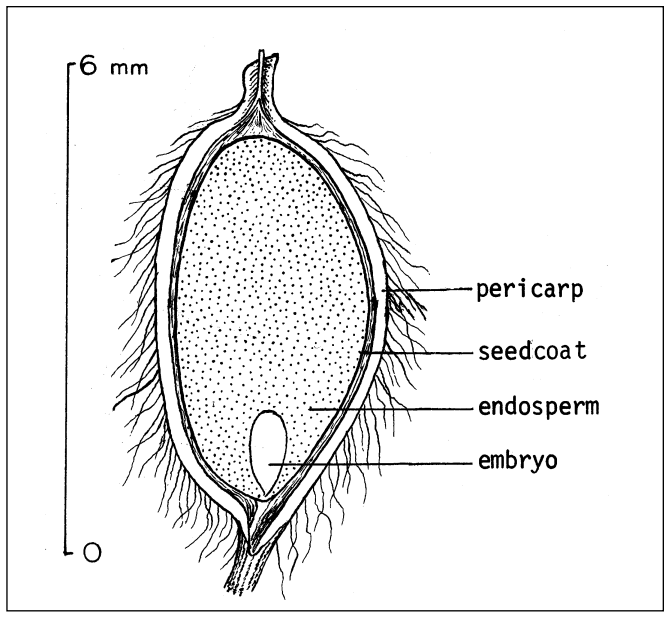

Table 2—*Clematis,* clematis: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
C. columbiana	—	May–June	July–Aug
C. drummondii	SW US	Mar–Sept	Aug–Oct
C. flammula	—	Aug–Oct	Aug–Oct
C. ligusticifolia	California	Mar–Apr	May–Aug
	Texas	Mar–Sept	Aug–Nov
	Colorado & Utah	May–Aug	Oct–Dec
C. pauciflora	California	Mar–Apr	May–July
C. virginiana	—	July–Sept	July–Sept
	Minnesota	June–July	Aug–Sept
C. vitalba	NE US	July–Sept	July–Sept
	France	June–July	Sept–Oct
C. viticella	NE US	June–Aug	June–Aug

Sources: Fernald (1950), Loiseau (1945), McMinn (1951), Mirov and Kraebel (1939), Radford and others (1964), Rehder (1940), Rosendahl (1955), Rydberg (1922), Van Dersal (1938), Vines (1960).

Table 3—*Clematis,* clematis: size, year first cultivated, and flower color

Species	Length at maturity (m)	Year first cultivated	Flower color
C. columbiana	2.8	1797	Purple
C. drummondii	—	—	White
C. flammula	3.1–4.6	1509	White
C. ligusticifolia	0.9–12.3	1880	White
C. pauciflora	—	Before 1935	White
C. virginiana	3.7–6.2	1726	Creamy white
C. vitalba	10.2	Long cultivated	White
C. viticella	4.6	1597	Purplish

Sources: Fernald (1950), McMinn (1951), Rehder (1940), Rosendahl (1955), Vines (1960).

Table 4–*Clematis,* clematis: seed yield data

		Cleaned seeds/weight			
		Range		Average	
Species	Place collected	/kg	/lb	/kg	/lb
C. columbiana	Minnesota	—	—	141,440	64,000
C. flammula	Europe	—	—	55,250	25,000
C. ligusticifolia	California	—	—	205,530	93,000
	Utah	663,000–724,880*	300,000–328,000*	696,150*	315,000*
C. pauciflora	California	—	—	187,850	85,000
C. virginiana	Baraga Co., Michigan	402,220–446,420	182,000–202,000	424,320	192,000
C. vitalba	Europe	—	—	707,200†	320,000
C. viticella	Europe	48,620-103-870	22,000-47,000	59,670	27,000

Sources: Mirov and Kraebel (1939), Rafn & Son (1928), Rudolf (1974).
* Styles removed.
† Styles presumably removed.

are to sow untreated seeds in the fall soon after collection or to sow in the spring using seeds stratified over winter (Bailey 1939). Untreated fall-sown seeds of traveler's-joy and Italian clematis have germinated the following fall (Blair 1959). Stribling (1986) recommends the following schedule for propagating Armand clematis—*C. armandii* Franch—in central California: store seeds collected in late May in a refrigerator until September; soak in cold water for

Table 5—*Clematis,* clematis: germination test results for stratified seeds

Species	Test duration (days)	Germination capacity (%)	# Tests
C. drummondii	40	76	1
C. ligusticifolia	200	11–84	8
C. pauciflora	—	36	1
C. virginiana	60	32	1

Sources: Mirov and Kraebel (1939), Plummer and others (1968), Rudolf (1974),

24 hours and treat with a fungicide; stratify for up to 180 days at 1 to 5 °C in sealed plastic trays; and sow in March or April.

Vegetative propagation is a common practice and used exclusively to propagate most of the popular species and varieties. Procedures for vegetative propagation from cuttings, grafting, and division are discussed by Dirr and Heuser (1987), Evison (1977), Lloyd (1977), and Markham (1935).

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Clethraceae—White alder family

Clethra L.

sweet pepperbush, summersweet

Jason J. Griffin and Frank A. Blazich

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Growth habit, occurrence, and uses. The genus *Clethra* L. comprises about 30 species native to eastern Asia, eastern North America, and Madeira (Huxley 1992; LHBH 1976). Of those, cinnamon-bark clethra and sweet pepperbush are native to eastern North America, occurring from southern Maine to Florida and west to Texas (LHBH 1976). Some taxonomists consider woolly summersweet to be a separate species in this same range, but others consider it to be a variety of sweet pepperbush (Huxley 1992; Kartesz 1994; Radford and others 1968). Japanese clethra, a native of Japan, is commonly cultivated in North America (Koller 1974). Specific geographic regions of occurrence differ among these species (table 1).

North American species of *Clethra* are deciduous shrubs or small trees with heights ranging from 3 to 10 m in their natural settings (Krüssmann 1984). Species generally grow as rounded, multi-stemmed plants that can be shaped easily into attractive small trees (Bir 1992b).

Valued for fragrant, late summer blooms and exfoliating, cinnamon-colored bark, cinnamon-bark clethra can be useful in the landscape as a specimen plant (Bir 1992b; Koller 1974) or as a hedge (Huxley 1992). Plants also fit nicely into shrub borders and are effective particularly along the edge of water (Dirr 1994). Adaptability to unfavorable environments make summersweets ideal selections for adverse planting sites. The species discussed herein perform well in both full sun and dense shade, while tolerating soil conditions ranging from drought-prone (once established) to saturated (Bir 1992b). Sweet pepperbush also has been cultivated successfully in coastal regions where it tolerates salt mist (but not salt spray), which frequently damages other plants (Bir 1993).

Geographic races and hybrids. Naturally occurring summersweets are quite variable. Although the exfoliating bark of cinnamon-bark clethra is typically cinnamon-red in color, variations of pink, chartreuse, gold, and mahogany

Table 1—*Clethra*, sweet pepperbush: nomenclature and occurrence of species cultivated in North America

Scientific name & synonym(s)	Common name (s)	Occurrence
***C. acuminata* Michx.**	**cinnamon-bark clethra,** mountain sweetpepperbush	Cliffs & mountain woods of SE Appalachian Plateau & inner Piedmont
***C. alnifolia* L.** *C. alnifolia* var. *paniculata* (Ait.) Rehd. *C. paniculata* Ait. *C. tomentosa* Lam. *C. alnifolia* var. *pubescens* Ait. *C. alnifolia* var. *tomentosa* (Lam.) Michx.	**sweet pepperbush,** summersweet, coastal sweetpepperbush	North American coastal plain, Maine to Texas, with extensions into the Carolina Piedmont; acid swamps & low moist woods
***C. barbinervis* Sieb. & Zucc.** *C. canescens* Forbes & Hemsl. *C. kawadana* Yanagita *C. barbinervis* var. *kawadana* (Yanagita) Hara *C. repens* Nakai	**Japanese clethra,** Asiatic sweet pepperbush	Hills & mountains of Japan & Korea
***C. tomentosa* Lam.** *C. alnifolia* var. *pubescens* Ait. *C. alnifolia* var. *tomentosa* (Lam.) Michx.	**woolly summersweet**	Swamps & coastal plain of North Carolina to N Florida & Alabama

Sources: Huxley (1992), Ohwi (1984), Sleumer (1967), Small (1933).

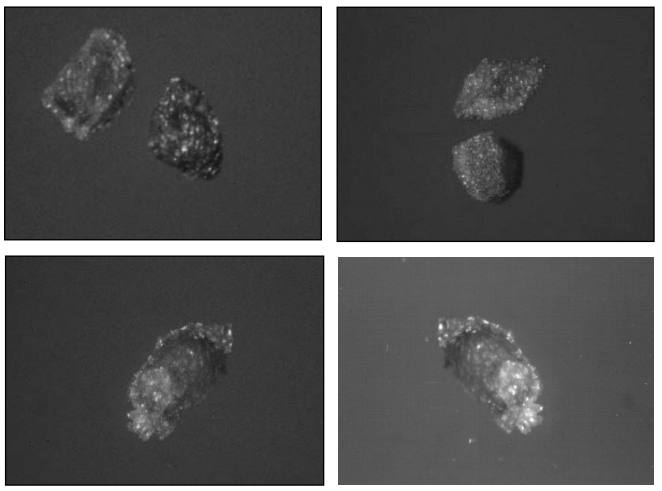
have been observed (Bir 1992b). The majority of named selections have originated from sweet pepperbush. Inflorescences of this species normally form erect racemes (LHBH 1976). However, inflorescences occur occasionally as branched panicles (Everett 1981), in which case the plants are often classified as C. *alnifolia* var. *paniculata* (Ait.) Rehd. or *C. paniculata* Ait. (Everett 1981; Huxley 1992; LHBH 1976). Dirr (1994) cited many cultivars in detail. Some of the more outstanding selections include *C. alnifolia* 'Compacta', a compact, 1.0- to 1.2-m-tall selection with lustrous, dark green foliage; 'Creel's Calico', the only variegated selection; 'Fern Valley Late Sweet', a late-flowering, almost columnar selection; and 'Hummingbird', unquestionably the most popular selection, which grows to a height of 0.8 to 1.0 m, with lustrous, dark green foliage that is covered by fragrant white flowers in mid to late summer. Of the pink-flowering forms, 'Pink Spires' and 'Rosea' are most common (Dirr 1994). These cultivars frequently are indistinguishable and may in fact be the same clone. 'Ruby Spice' occurred as a bud sport on 'Rosea' and is distinguished by deeper pink flowers that do not fade in late season. Another pink selection, 'Fern Valley Pink', produces inflorescences that can reach lengths of 20 to 25 cm for a spectacular floral display.

Flowering and fruiting. Fragrant white flowers, about 1 cm in diameter, are borne on upright or horizontally held terminal racemes or panicles, to 15 cm long (Huxley 1992), arising from the axils of leaves (Everett 1981). Flowering begins in July (with the exception of woolly summersweet, which flowers in August) and lasts to September (Krüssmann 1984), making summersweets excellent selections for late summer color. Pollination of perfect flowers most likely occurs by bees, which can be a nuisance if plants are located near walks or sitting areas (Bir 1992b; Dirr 1994; Koller 1974). Fruits are subglobose, 3-valved capsules, ranging from 2.5 to 5.0 mm in length with a persisting style and calyx (figure 1) (Huxley 1992). Upon maturation, capsules split to release many seeds. Seeds are quite small and irregularly angled, and dispersal is presumably by wind (figures 2 and 3) (Sleumer 1967). Sweet pepperbush in New Jersey averaged 6 to 17 seeds per capsule from 3 collection sites, with total seed production per plant ranging from 1,348 to 7,920 (Jordan and Hartman 1995).

Collection of fruits, seed extraction, cleaning, and storage. It appears that seeds do not mature until long after leaf abscission, November in North Carolina (Bir 1992a). Thus, collecting and sowing seeds before maturation may result in poor or no germination. Once seeds have matured, capsules can be collected before they open and

Figure 1—*Clethra*, sweet pepperbush: fruits (capsules) of *C. acuminata*, cinnamon-bark clethra (**top**); *C. alnifolia*, sweet pepperbush (**bottom**).

Figure 2—*Clethra*, sweet pepperbush: seeds of *C. acuminata*, cinnamon-bark clethra (**top left**); *C. alnifolia*, sweet pepperbush (**top right**); *C. barbinervis*, Japanese clethra (**bottom left**); and *C. tomentosa*, woolly summersweet (**bottom right**).



allowed to dry until they split. Seeds can then be shaken from the capsules and cleaned (Dirr 1994; Dirr and Heuser 1987). There are no reports of long-term storage, but seeds can be stored successfully for short periods at low temperatures (5 °C) and moisture contents (Bir 1992a; Dirr and Heuser 1987). The seeds are therefore apparently orthodox in storage behavior.

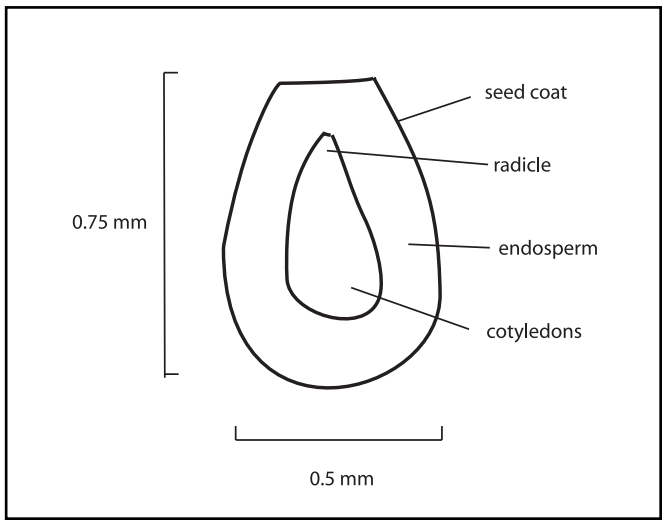
Pregermination treatments and germination testing. Jordan and Hartman (1995) reported up to 58% germination with New Jersey sources of sweet pepperbush after 5 months of stratification at 0 to 2 °C in the dark. Their germination regime was 16 hours of light at 30 °C and 8 hours in the dark at 15 °C. Other reports, however, suggest that no pretreatments are required and that germination occurs readily if seeds are sown immediately following collection (Bir 1992a; Dirr and Heuser 1987).

For successful germination seeds should be treated similar to those of azalea (*Rhododendron* L.) (Bir 1992a&b; Dirr and Heuser 1987). In general, when mature seeds are sown on the surface of a germinating medium and placed under mist at 24 °C, germination occurs within 2 weeks and is complete within 1 month (Bir 1992b).

Nursery practice. When seedlings are grown in a typical azalea growing medium of 3 parts pine bark to 1 part peat (vol/vol)—amended with 4.2 kg/m^3 (7.0 lb/yd^3) dolomitic limestone and fertilized following recommendations for azaleas—seedlings grow well, filling a 3.8-liter (1-gal) pot by the end of a growing season (Bir 1992b). Although naturally occurring as an understory species, seedlings of cinnamon-bark clethra show no symptoms of stress when grown in full sun and are visually no different than seedlings maintained under 50% shade (Bir 1992b). The species is well adapted to dry soils once established. However, if seedlings are exposed to drought conditions before a sufficient root system has developed, high mortality can be expected (Bir 1992b).

Asexual propagation of species of summer-sweet is very easy and is widely used for propagation of particular cultivars. Species listed in table 1 are propagated readily by stem cuttings taken during the summer, as well as by root cuttings taken during December and January (Dirr and Heuser 1987).

Figure 3—*Clethra alnifolia*, sweet pepperbush: longitudinal section of a seed.



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C

Rosaceae—Rose family

Coleogyne ramosissima Torr.

blackbrush

Burton K. Pendleton

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Growth habit, occurrence, and use. Blackbrush—*Coleogyne ramosissima* Torr.—grows in the transition zone between warm and cold deserts of southern California, southern Nevada, southern Utah, northern Arizona, and southwestern Colorado. It is found at elevations of 760 to 1,980 m. Ranging from 0.3 to 1.2 m in height, blackbrush forms almost monotypic stands in the lower Mojave–Great Basin ecotone, bounded by creosote bush (*Larrea tridentata* (Sesse & Moc.) ex DC. Coville.) communities at low elevations and by juniper–big sagebrush (*Artemesia tridentata* Nutt.) communities at higher elevations. In the eastern part of its range, blackbrush is bordered by Sonoran communities on the south and by big sagebrush, juniper, and mixed shrub communities of the Colorado Plateau in the north. Distribution of blackbrush is limited by soil depth, temperature extremes, and moisture availability.

Blackbrush occurs as a landscape dominant over much of its range and forms a major vegetational component of national and state parks in Utah, Nevada, and California. Blackbrush provides significant year-round forage for desert bighorn sheep (*Ovis canadensis*) and is eaten by mule deer (*Odocoileus hemionus*) in winter. Foliage may be grazed by domestic goats and sheep in spring, but receives minimal use by cattle. Blackbrush provides habitat to many small mammals, and its seeds are eaten by both rodents and birds.

Blackbrush, although a monotypic genus, occurs over a wide geographic and elevational range. Differences in plant size and germination characteristics suggest ecotypic variability. Use of locally adapted seed collection sites should improve chances for successful propagation and establishment.

Flowering and fruiting. Flowers are perfect, apetalous, with yellow sepals 4.5 to 6.5 mm in length; however, rare individuals with 1 to 4 yellow petals can be found in most populations (Welsh and others 1987). Flowering occurs from late March through early May, each population flowering for 2 to 3 weeks (Bowns and West 1976), with individual plants lasting some 7 to 10 days. Flowering is induced by fall and winter rains, and the timing and degree of flowering varies significantly from year to year (Beatley 1974). Ripe achenes are reddish brown in color (figure 1). The fruit is an ovate glabrous achene, somewhat curved in shape, and 4 to 8 mm long (figure 2). Blackbrush is wind-pollinated (Pendleton and Pendleton 1998).

Blackbrush is mast-fruiting: the size of the seedcrop is related to plant resource reserves. The mast crop comprises almost all of the seed production at low-elevation sites, whereas some seeds are produced in the more mesic higher-elevation sites in all but the driest intermast years. Periods between mast seedcrops often exceed 5 years. Late frosts can reduce or eliminate flowering and fruit production.

Seed collection, cleaning, and storage. The ripe seeds readily separate from the floral cup. Natural seed-fall is correlated with rain showers, which dislodge the achenes from the floral cup. The fruit ripens between late May and the third week of July, depending upon elevation and year-to-year variation. Harvesting is accomplished by beating the branches with a stick or board. Fruits can be collected onto a tarp spread under the shrub or into a basket or hopper (Nord

Figure 1—*Coleogyne ramosissima*, blackbrush: fruits with and without pubescence.

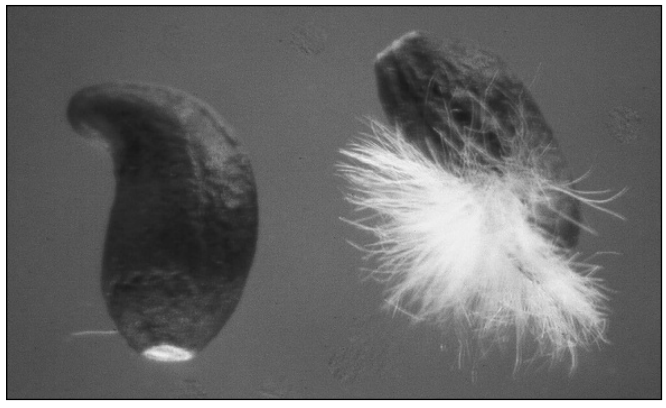
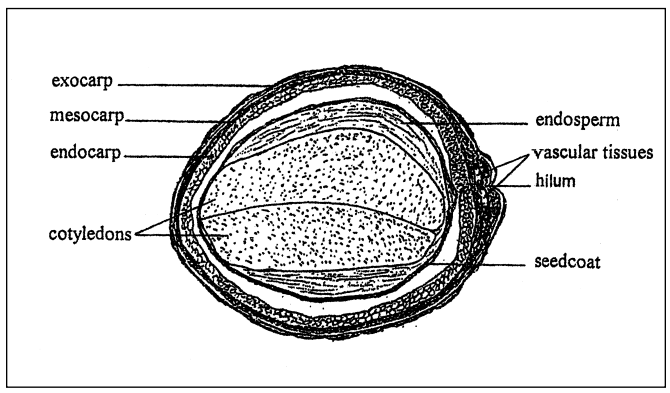


Figure 2—*Coleogyne ramosissima*, blackbrush: longitudinal section of achene with seed (drawing courtesy of Dr. Emerencia Hurd, retired, USDA Forest Service, Boise, ID).



1962). Seed collections contain a significant amount of debris and cleaning is required. Seeds can be cleaned in a fanning mill or with a gravity separator (Monsen 2004). A portion of the achenes are retained within the floral cup. These can be removed with a barley de-bearder or through use of a rubbing board.

Viability of cleaned seeds is generally high, and the incidence of insect damage is extremely low. Twenty-four collections from Utah and Nevada populations ranged in viability from 74 to 98%. Nineteen collections had viability percentages greater than 85%. The number of cleaned seeds per weight averages 60,000/kg (27,000/lb), with a range of 47,500 to 68,000/kg (21,500 to 31,000/lb).

Seeds of blackbrush are long-lived and orthodox in storage behavior; they can be stored in a cool dry location for long periods without loss of viability (table 1). Germination tests on seeds collected in Washington County, Utah, showed no loss in viability after 10 and 15 years. Plants were produced from this seedlot 12 years after collection. However, the vigor of older seeds (10+ years) in field plantings has not been determined.

Germination. Fresh blackbrush seedlots are 68 to 95% dormant and remain dormant in laboratory storage for the first year after collection (table 1). Seed dormancy increases with increasing elevation of the seed source. Five-year-old seeds are essentially nondormant and will readily germinate at cool temperatures (–15 °C) (Pendleton and others 1995). Stratification of fresh seeds for 4 to 6 weeks at 1 °C will produce rapid maximum germination of all collections when seeds are removed from chill and placed at temperatures between 5 and 25 °C. Under field conditions, seeds are nondormant by October, and germination can occur at this time given proper moisture conditions and cool soil temperatures. Field germination typically occurs during the winter and early spring (figure 3) (Meyer and Pendleton 2002).

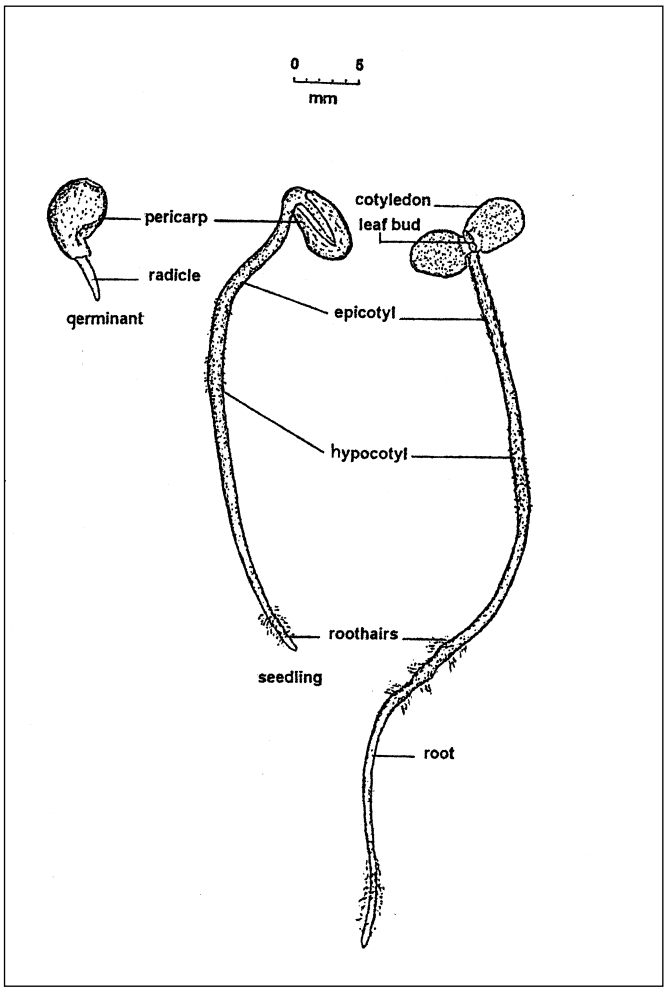
Nursery and field practice. Container stock can readily be produced from seeds. However, both stratified and unstratified seeds will germinate and emerge over a long period of time (up to 1 year). The most efficient method to synchronize germination and produce uniform-aged plants is to plant germinated seeds. Fresh seeds should be stratified between moist blotter paper for 6 weeks at 1 °C. When seedlots are removed from 1 °C and kept at room temperature, more than 75% will germinate in 24 to 48 hours. Seed collections 3 years old or older, stratified for 3 to 4 weeks, produce similar results. Germinated seeds, with radicals 2 to 10 mm (0.1 to 0.4 in) long, should be planted about 2 cm (0.8 in) deep in a well-draining soil mix. However, using a soil medium that retains moisture often leads to problems with damping-off diseases. Under experimental greenhouse conditions, blackbrush responds positively to inoculation with arbuscular mycorrhizal fungi (Pendleton and Warren

Table 1—*Coleogyne*, blackbrush: germination of nonstratified and stratified* seeds

Seed age	Percent germination†		Collections
	Range	Mean	
Fresh			
Stratified	5–32	17.6	10
Nonstratified	84–98	91.8	10
1 year			
Stratified	0–13	6.5	10
Nonstratified	85–95	92.0	10
5 years			
Nonstratified	82–96	90	6

Source: Pendleton and Meyer (2002).
* Stratification was a moist chilling for 4 weeks at 1 °C.
† Germination tests done on wet blotter paper with a 12-hour alternating temperature regime of 5 and 15 °C; mean percent viability of these collections > 90%.

Figure 3—*Coleogyne ramosissima*, blackbrush: germination and seedling development (courtesy of Dr. Emerencia Hurd, retired, USDA Forest Service, Boise, ID).



1996). Addition of mycorrhizal inoculum to the planting medium should be considered. Optimal growing temperature for seedling growth is about 20 °C (Wallace and others 1970; Wallace and Romney 1972). Warmer conditions result in slow growth and plants that enter dormancy. Greenhouse-grown plants are susceptible to aphid infestation, but blackbrush is tolerant of standard control methods.

When seeds are not available, plants can be produced from stem cuttings. About half of the cuttings taken from current-year growth (June or September) and treated with 0.8% indole butyric acid (IBA) or commercial rooting hormone produced roots (Hughes and Weglinski 1991).

Outplanted container stock, whether produced from seeds or cuttings, should be protected from herbivory by tree tubes or diamond netting. Container stock has successfully been outplanted at Joshua Tree National Monument in California (Holden 1994) and on a natural-gas pipeline right-of-way in Arches National Park in Utah.

A limited number of attempts to establish blackbrush through seeding have been reported. In general, these attempts have had poor success (Monsen 2004). Factors that may have been responsible include low moisture levels during the germination season, lack of sufficient seeds, seeding at a less than optimal time, weed competition, herbivory, and seed theft by rodents. Seed availability is a major limiting factor in blackbrush reestablishment. Mast crops of seeds occur infrequently (5- to 10-year periods) and should be collected and stored for future use. Blackbrush seeds maintain good viability when stored for these time periods.

Insufficient work has been done to firmly determine the seeding rates and seedbed conditions necessary to establish blackbrush stands from seeds, but experimental work and reported successful seedings do offer some guidelines. Rodent-cached seeds are found at depths of 1 to 3 cm (0.4 to 1.2 in), suggesting that conventional seeders should be set to this planting depth. Because blackbrush does exhibit ecotypic variation, locally collected seeds should be used. Seeding should be done in the late summer or fall. Germination and emergence occurs as early as November (Graham 1991) and, more typically, January to March (Bowns and West 1976; Meyer and Pendleton 2002).

Spring seedings have also been attempted. Blackbrush was included in seed mixes used in experimental restoration plantings at the Nevada Test Site in southern Nevada. The seedings were conducted during March 1993. Although no blackbrush seedlings emerged that spring, some seedlings were observed during subsequent springs (USDoE 1994). An experimental spring-seeding conducted in southeastern Utah in March 1992 included stratified and unstratified seeds from 4 populations. Of the stratified seedlots, 12.5% emerged during spring 1992; of the unstratified seedlots, <1%. During spring 1993, an additional 16% of the stratified and 62% of the unstratified seedlots emerged. Lots of stratified seeds produced half as many seedlings as unstratified seeds from March 1992 through May 1993 (Pendleton and Meyer 2002). Blackbrush will form a short-term seedbank during drought conditions, but most, if not all, seeds will germinate when moisture is adequate for winter germination.

As with all dryland and desert species, successful establishment from seeds depends on the availability of moisture during the germination and establishment periods. Spring and early summer precipitation is not the norm for Mojave and Sonoran blackbrush communities, a fact that makes blackbrush seeding establishment in these areas difficult, especially in lower-elevation sites.

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Fabaceae—Pea family

Colutea L.

bladder-senna

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Growth habit, occurrence, and use. The genus *Colutea*—the bladder-sennas—includes about 26 species of deciduous shrubs or small trees, with a distribution ranging from the Mediterranean region and southeastern Europe to northwest Africa and the western Himalayas (Browicz 1963, 1967; Hillier 1991; Krüssmann 1984; LHBH 1976). The 3 taxa of interest in the United States are common bladder-senna (*C. arborescens* L.), *C. orientalis* Mill., and *C.* × *media* Willd. (table 1). Bladder-senna species are cultivated in temperate climates primarily for ornamental purposes but may also be used for erosion control (Krüssmann 1984). In Spain, the potential use of common bladder-senna as a forage crop has been investigated because of its ligneous nature and summer utility (Allue Andrade 1983a). Antifungal compounds have been isolated from root bark of common bladder-senna (Grosvenor and Gray 1998). The bladder-sennas are very distinct shrubs, and the common name is derived from their large, inflated legumes (pods).

Common bladder-senna is a vigorous shrub of bushy habit, with medium to fast growth. It prefers a sunny location (Dirr 1990) but is easily grown in almost any soil type (except waterlogged). The cultivar 'Bullata' is a dwarf form with dense habit (about $^1/_3$ to $^1/_2$ the size of the species at maturity) whose 5 to 7 leaflets are small, rounded, and somewhat bullate (Dirr 1990; Krüssmann 1984). The cultivar 'Crisp' is a low-growing form with leaflets that are sinuate (Dirr 1990; Krüssmann 1984). *Colutea orientalis* is a rounded shrub with attractive glaucous leaflets (Hillier 1991; Krüssmann 1984). *Colutea* × *media* is a recognized as a hybrid (*C. arborescens* × *C. orientalis*), with bluish green foliage, that originated before 1790 (Dirr 1990; Krüssmann 1984).

Flowering and fruiting. The papillionaceous flowers are about 2 cm in length, bloom from May to July (with scattered blossoms into September), and occur in axillary, long-stalked racemes (Dirr 1990; Krüssmann 1984; LHBH 1976). The pea-shaped flowers of common bladder-senna are yellow, the standard petal having red markings; the flowers of *C. orientalis* are a reddish brown or copper color; and those of *C. media* range in color from the typical yellow to those which blend through markings or tints of copper, pink, or reddish brown (Krüssmann 1984; LHBH 1976). The fruit is a inflated, bladder-like legume, 6 to 7.6 cm long and 2.5 to 3.8 cm wide, that varies in color from lime green to tints of pink or bronze and is very ornamental (Dirr 1990; Krüssmann 1984). Fruits mature from July to September (Dirr 1990) and each legume contains several small seeds (figure 1) (Rudolf 1974). The legumes of *C. orientalis* dehisce at the tip.

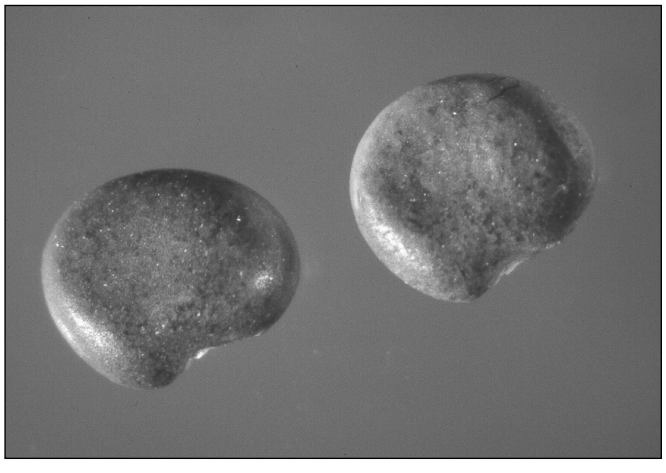
Collection of fruits; extraction, cleaning, and storage of seeds. Ripe legumes can be harvested from the shrubs in late summer or fall and then spread in a shed (with good air circulation) to dry (Rudolf 1974). The legumes are threshed to remove the seeds and the debris is fanned out (Rudolf 1974). Bladder-sennas average 74,956 seeds/kg (34,000/lb) (Allen 1995). Dry seeds stored at 5 °C in glass

Table 1—*Colutea*, bladder-senna: morphological characteristics, height at maturity, and date first cultivated

Scientific name	Leaflets	Flowers/ raceme	Height at maturity (m)	Year first cultivated
C. arborescens	9–13	6–8	1.8–4.5	1570
C. orientalis	7–11	2–5	2	1710
C. x media	11–13	Varies	1.8–3.0	1809

Sources: Dirr (1990), Hiller (1991), Krüssmann (1984), LHBH (1976).

Figure 1—*Colutea* arborescens, common bladder-senna: seeds.



containers will be viable for 1 to 3 years, depending upon the species. Like most genera in Fabaceae, this genus is orthodox in storage behavior. Seeds can be stored in liquid nitrogen without a significant loss in germination percentage (Gonzalez-Benito and others 1994; Iriondo and others 1992).

Pregermination treatments. Bladder-senna seeds do not germinate readily unless the impermeable seedcoat is ruptured by mechanical or chemical scarification. Soaking the seeds in concentrated sulfuric acid for 30 to 60 minutes, before sowing in nursery beds, results in good germination (Dirr 1990; Dirr and Heuser 1987). Steeping seeds in water that was initially brought to 88 °C and then allowed to cool 24 hours also results in good seed germination (Allue Andrade 1983b; Dirr 1990; Dirr and Heuser 1987).

Germination tests. Pretreated bladder-senna seeds can be tested in germinators at 20 °C night and 30 °C day for 30 days (Rudolf 1974).

Nursery practice and seedling care. Untreated seeds may be sown in the fall, but scarified seeds are required for spring-sowing (Allen 1995; Dirr and Heuser 1987). Seedlings germinate within 1 to 2 weeks and grow rapidly. Bladder-senna species may also be propagated by cuttings. In England, 29% of half-ripened cuttings taken in early November rooted without treatment; the cuttings failed to respond to naphthaleneacetic acid (NAA); and 73% rooted after treatment with 0.1 g/liter (100 ppm) indole-3-butyric acid (IBA) solution for 18 hours (Dirr 1990; Dirr and Hesuer 1987). Summer softwood cuttings should be treated with about 1 to 3 g/liter IBA solution (1,000 to 3,000 ppm) or talc formulation (Dirr and Heuser 1987). Bladder-senna plants develop a thin, rangy root system that makes transplanting difficult. Growing plants in containers is the preferred production method.

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C

Cornaceae—Dogwood family

Cornus L.

dogwood

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Growth habit, occurrence, and use. About 40 species of dogwood—*Cornus* L.—are native to the temperate regions of the Northern Hemisphere, and 1 is found in Peru. Most species are deciduous trees or shrubs (2 are herbs) useful chiefly for their ornamental qualities—flowers, fruit, foliage, or color of twigs. Many varieties have been developed for a number of the species for their landscape or horticultural value. The wood of flowering dogwood, the most commercially important species in the United States, is hard and heavy and was used extensively by the textile industry earlier in the 20th century for shuttle blocks. Today the species is widely known due to its popular use as an ornamental landscape tree. Some species produce edible fruits (Edminster 1950; Edminster and May 1951), and the bark of others contains a substitute for quinine. Roots and bark of several species have long been known to have medicinal properties that can be used to fight fevers. Distribution data and chief uses of 17 species of present or potential importance in the United States are listed in table 1.

Flowering and fruiting. The small, perfect flowers—white, greenish white, or yellow in color—are borne in terminal clusters in the spring. In flowering and Pacific dogwoods, the clusters are surrounded by a conspicuous enlarged involucre of 4 to 6 white or pinkish petal-like, enlarged bracts. Fruits are globular or ovoid drupes 3 to 6 mm in diameter, with a thin succulent or mealy flesh containing a single 2-celled and a 2-seeded bony stone (figures 1 and 2). However, in many stones, only 1 seed is fully developed, but larger stones generally have 2 developed seeds. The fruits ripen in the late summer or fall (table 2). Data on minimum seed-bearing age and fruiting frequency are limited (table 3). Stones are dispersed largely by birds and animals.

Collection of fruits. Dogwood fruits should be collected when the fruit can be squeezed and the stone will pop out. To reduce losses to birds, fruits should be collected as soon as they are ripe by stripping or shaking them from the branches. Short ladders may be useful for collecting fruits from the taller species, but ordinarily this can be done from the ground. Fruits of flowering dogwood should not be collected from isolated trees because these seem to be self-ster-

Figure 1—*Cornus*, dogwood: cleaned seeds of *C. alternifolia,* alternate-leaf dogwood (**top left**); *C. amomum*, silky dogwood (**top center**); *C. sericea* ssp. *orientalis*, California dogwood (**top right**); *C. drummondii*, roughleaf dogwood (**middle left**); *C. florida*, flowering dogwood (**middle center**); *C. nuttallii*, Pacific dogwood (**middle right**); and *C. racemosa*, gray dogwood **(bottom**).

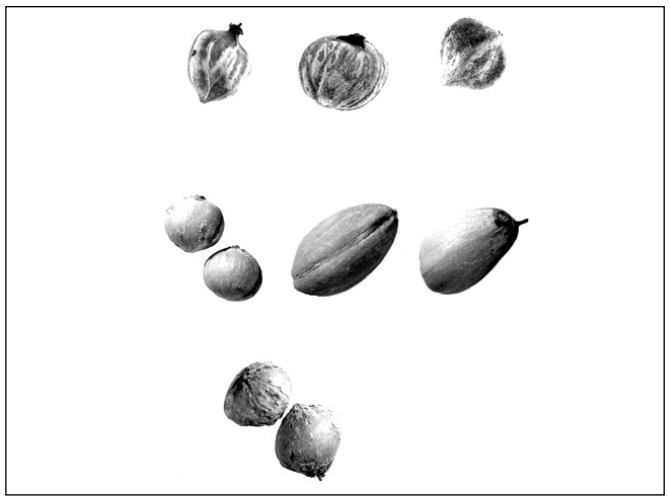


Figure 2—*Cornus sericea*, red-osier dogwood: longitudinal section through an embryo of a stone **(left)**; transverse section of a stone containing 2 embryos (**right top**) and transverse section of a stone containing 1 embryo (**right bottom**).

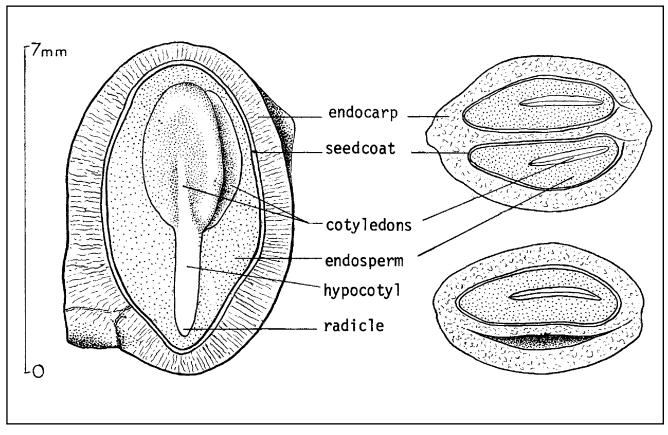


Table 1—*Cornus*, dogwood: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***C. alba* L.** *C. tatarica Mill.*	**Tatarian dogwood**	Siberia to Manchuria & North Korea
***C. alternifolia* L. f.** *Swida alternifolia* (L.f.) Small	**alternate-leaf dogwood,** blue dogwood, pagoda dogwood	Newfoundland to SE Manitoba, S to Missouri & E Arkansas, E to Georgia
C. amomum P. Mill.	**silky dogwood,** kinnikinnik, red-willow	Maine to Indiana, S to Georgia & Florida
***C. canadensis* L.** *Chamaepericlymenum canadense*(L.) Aschers & Graebn. *Cornella canadensis* (L.) Rydb.	**bunchberry,** bunchberry dogwood, dwarf cornel	S Greenland to Alaska, S to Maryland, W to South Dakota, New Mexico, & California
***C. controversa* Hems.**	**giant dogwood**	Japan, China, & Nepal
***C. drummondii* C. A. Mey.** *C. priceae Small*	**roughleaf dogwood**	S Ontario, Ohio, & Kentucky, W to Nebraska, S to Texas & Mississippi
***C. florida* L.** *Cynoxylon floridum* (L) Raf. ex. B.D. Jackson	**flowering dogwood,** dogwood	E United States
***C. kousa* Hance**	**Japanese dogwood,** kousa dogwood	Japan & Korea
***C. macrophylla* Wall.**	**bigleaf dogwood**	Japan, China, & Nepal
***C. mas* L.**	**cornelian-cherry,** cornelian-cherry dogwood	Central & S Europe & W Asia
***C. nuttallii* Audubon ex Torr. & Gray**	**Pacific dogwood,** western flowering dogwood, mountain dogwood	SW British Columbia, W Washington & Oregon, S in mtns to S California; also in central W Idaho
***C. officinalis* Siebold & Zucc.**	**Japanese cornelian-cherry,** Japanese cornel dogwood	Japan, Korea, & China
***C. racemosa* Lam.** *C. foemina* ssp. *racemosa* (Lam.) *C. circinata* L'Herit. J.S. Wilson *C. paniculata* L'Herit.	**gray dogwood,** western dogwood	Maine to Manitoba, S to Florida, W to Missouri & Oklahoma
***C. rugosa* Lam.** *C. circinata* L'Herit.	**roundleaf dogwood,** roundleaved dogwood, roundleaf cornel	Quebec to Manitoba, S to Virginia, W to NE Iowa
***C. sanguinea* L.** *C. sanguinea* var. *viridissima* Dieck *Swida sanguinea* (L.) Opiz	**bloodtwig dogwood,** common dogwood, dogberry, pegwood	Europe
***C. sericea* L.** *C. stolonifera* Michx. *C. baileyi* Coult. & Evans *Suida stolonifera* (Michx.) Rydb.	**red-osier dogwood,** American dogwood, kinnikinnik, squawbush	Newfoundland to Alaska, S to California, New Mexico, & Nebraska, in NE US from Wisconsin to New York
***C. sericea* ssp. *occidentalis* (Torr.& Gray) Fosberg**	**western dogwood,** California dogwood, creek dogwood	S British Columbia to N Idaho, S to S California

Source: Brinkman (1974).

ile, and a high percentage of the stones will be empty (Mugford 1969).

Extraction and storage of seeds. The stones can be readily extracted by macerating the fruits in water and allowing the pulp and empty stones to float away (see chapter 3 on seed processing) (Brinkman 1974; Mugford 1969). Stone yields and weights are summarized in table 4. If the fruits cannot be extracted immediately after fruits are collected, they should be spread out in shallow layers to prevent excessive heating; however, slight fermentation facilitates removal of the fruit pulp (Brinkman 1974; NBV 1946). Clean air-dried stones may be stored in sealed containers at 3 to 5 °C (Heit 1967; Mugford 1969; Sus 1925; Swingle 1939). Stones of flowering dogwood have been successfully stored at 4% moisture content at –7 °C for 7 years by the Georgia Forestry Commission with only a 1% decrease in viability (Brock 1997), thus demonstrating the orthodox nature of seeds of this genus. Brinkman (1974) wrote that dogwood stones could be sown without extracting them from the fruit and that stones were cleaned when storage was required and that commercial seedlots may or may not have the dried fruit attached. Presently, however, all commercial lots of dogwood seeds now are cleaned (table 4) and some nursery managers report that if the stones are not cleaned, the fruits may inhibit germination (Brock 1997). After the fruits are collected and cleaned, the stones may be sown immediately or stratified for spring-planting.

Pregermination treatments. Natural germination of most species occurs in the spring following seedfall, but some seeds do not germinate until the second spring. Germination is epigeal (figure 3). Seeds of all species show delayed germination due to dormant embryos; in most species, hard pericarps also are present. Where both types of dormancy exist warm stratification for at least 60 days in a

Table 2—*Cornus,* dogwood: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
C. alba	May–June	Aug–Sept	—
C. alternifolia	May–July	July–Sept	July–Sept
C. amomum	May–July	Aug–Sept	Sept
C. canadensis	May–July	Aug	Aug–Oct
C. controversa	May–June	Aug–Sept	Oct
C. drummondii	May–June	Aug–Oct	Aug–winter
C. florida	Mar & Apr (S US)–May (N US)	Sept (N US)–Oct (S US)	Sept–Nov
C. kousa	May–June	Aug–Oct	—
C. macrophylla	July–Aug	—	—
C. mas	Feb–March	Aug–Sept	—
C. nuttallii	April–May	Sept–Oct	Sept–Oct
C. officinalis	Feb–Mar	Sept	—
C. racemosa	late May–July	July–Oct	Sept–Oct
C. rugosa	May–July	Aug–Sept	—
C. sanguinea	May–June	Aug–Sept	—
C. sericea	May–July, June–Aug (N US)	July–Oct	Oct–winter
C. sericea ssp. *occidentalis*	Apr–Aug	July–Nov	—

Sources: Asakawa, (1969), Billington (1943), Brinkman (1974), Dirr (1990), Fernald (1950), Forbes (1956), Holweg (1964), Gordon and Rowe (1982), Lakela (1965), McMinn (1951), Ohwi (1965), Rehder (1940), Rosendahl (195), Rydberg (1932), Steyermark (1963), Van Dersal (1938), Vimmerstedt (1965), Weaver (1976), Wyman (1947).

Table 3—*Cornus,* dogwood: height, seed-bearing age, seedcrop frequency, and fruit ripeness criteria

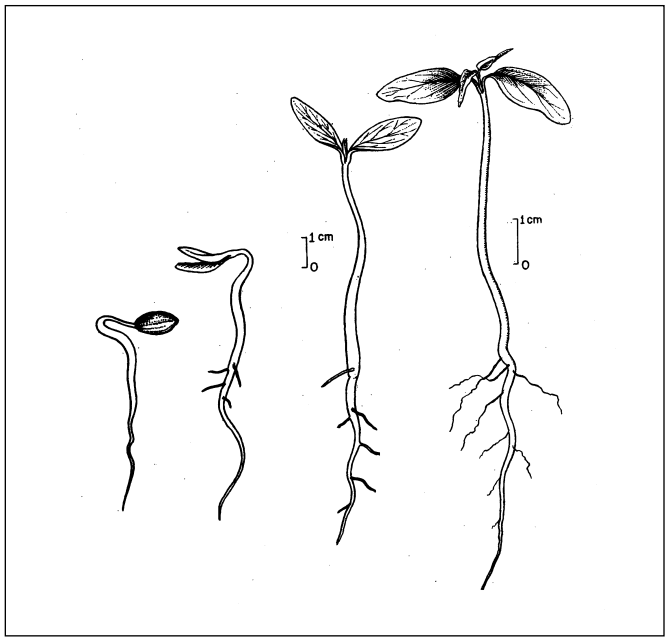
Species	Height at maturity (m)	Year first cultivated	Min seed-bearing age (yrs)	Years between large seedcrops	Ripe fruit color
C. alba	3	1741	—	—	Bluish white
C. alternifolia	5–8	1760	—	—	Dark blue
C. amomum	3	1658	4–5	1	Pale blue or bluish white
C. canadensis	0.3	—	—	—	Bright red or scarlet
C. controversa	9–18	1880	—	—	Red or purple to blue-black
C. drummondii	8–14	1836			White
C. florida	6–12	1731	6	1–2	Dark red
C. kousa	8	1875	—	2	Rose red pinkish
C. macrophylla	8–11	1827	—	—	Reddish purple to purple black
C. mas	8	Ancient	—	—	Scarlet
C. nuttallii	6–24	1835	10	2	Bright red to orange
C. officinalis	6–9	1877	—	—	Red
C. racemosa	4	1758	—	—	White
C. rugosa	3	1784	—	—	Light blue to white
C. sanguinea	2–5	—	—	—	Black
C. sericea	3–6	1656	—	—	White or lead colored
C. sericea ssp. *occidentalis*	5	—	—	—	White

Sources: Dirr (1990), Fernald (1950), Gordon and Rowe (1982), McMinn (1951), Rehder (1940), Weaver (1976).

moist environment followed by a longer period at a much lower temperature is required (table 5). A more complicated procedure has been recommended for cornelian-cherry by Tylkowski (1992). The warm phase of treatment is at alternating temperatures (15/25 °C) on 24-hour cycles for 18 weeks, then a cold phase at 3 °C for 15 to 18 weeks or until the first germination is observed. Immersion in concentrated sulfuric acid for 1 to 4 hours or mechanical scarification can be used in place of warm stratification for most species. Soaking stones in gibberellic acid for 24 hours also has been successful for roughleaf (Furuta 1960) and flowering dogwoods (Litvinenko 1959). In species having only embryo dormancy, this can be broken by low-temperature stratification.

Germination tests. Official testing rules for dogwoods call for germination tests for some species, but rapid tests, such as tetrazolium (TZ) staining or excised embryos, are also recommended (AOSA 1993; ISTA 1993). Flowering and western dogwoods can be tested on the top of moist blotters or creped paper for 28 days at alternating temperatures of 30 °C (day) and 20 °C (night). Excised embryo testing is an alternate method for flowering dogwood, and TZ is an alternate method for western dogwood (AOSA 1993). TZ

Figure 3—*Cornus florida*, flowering dogwood: seedling development at 2, 4, 8, and 31 days after germination.



staining is recommended for the European species Cornelian-cherry and bloodtwig dogwood (ISTA 1993). The seeds must be soaked in water for 48 hours, then cut transversely on the ends and soaked for another 6 hours. The TZ incubation should be for 48 hours in a 1% solution; presence of any unstained tissues is cause to consider the seeds non-viable (ISTA 1993).

Germination tests using 400 properly pretreated seeds per test can be performed using sand, soil, paper, or blotters, but long stratification periods of 3 to 5 months are usually required. The same diurnally alternated temperatures of 30/20 °C appear to be satisfactory for all species (table 6), although Heit (1968a) recommended 30 and 10 °C for silky dogwood. Estimating the viability of dogwood seed lots by TZ staining is the common practice at the USDA Forest Service's National Seed Laboratory and at other seed testing facilities. In many cases, this is the preferred testing method of seed collectors and dealers, nursery managers, and seed testing laboratories. TZ tests performed by trained personnel will provide accurate, reliable data that are comparable to field germination. A TZ test only takes a few days to conduct as compared to a germination test, which requires several months of stratification before the germination period. The quicker TZ test will provide nursery managers with more time to secure different seedlot for either fall-sowing or stratification if the first seedlot is substandard or dead. Excised embryos also have been used (Flemion 1948; Heit 1955).

Nursery practices. Best results for most species are obtained when freshly collected stones are sown in the fall as soon after cleaning as possible (Heit 1968a; Stevenson 1969). Seeds of most species will germinate the following spring. Seeds of species that require a warm-cold pretreatment (table 6) can be planted in the summer but should be left in the ground until the second spring because many will not germinate the spring following planting (Murphy 1997). Dry-stored stones probably should be soaked in water and sown before October (Heit 1968a). Fruits collected too late for fall-sowing should be cleaned, stored over winter and spring, stratified in summer and sown in the fall (NBV 1946; Shumilina 1949). An alternate procedure is to stratify the seeds at about 4 °C for 3 to 4 months during the winter

Table 4—*Cornus*, dogwood: seed yield data

Species	Stones/fruit wt		Cleaned stones/weight				Samples
			Range		Average		
	kg/100 kg	lbs/100 lb	/kg	/lb	/kg	/lb	
C. alba	—	—	27,900–40,900	12,700–18,600	33,000	15,000	33
C. alternifolia	—	—	13,000–20,500	5,900–9,300	17,600	8,000	6
C. amomum	15–18	17–20	22,400–30,800	10,200–14,000	26,800	12,200	6
C. canadensis	—	—	129,800–169,400	59,000–77,000	147,400	67,000	2
C. drummondii	16–24	18–27	18,900–46,200	8,600–21,000	34,500	15,700	5
C. florida	17–41	19–46	7,300–13,600	3,300–6,200	9,900	4,500	11
C. kousa	—	—	14,300–18,300	6,500–8,300	21,300	9,700	3
C. mas	13	15	3,500–7,500	1,600–3,400	5,000	2,300	22
*C. nuttallii**	11	12	8,800–13,400	4,000–6,100	10,300	4,700	4
C. racemosa	16–22	18–25	22,400–33,700	10,200–15,300	28,600	13,000	11
C. rugosa	—	—	—	—	41,800	19,000	1
C. sanguinea	—	—	16,100–26,000	7,300–11,800	20,200	9,200	70
C. sericea	13–18	15–20	30,400–58,700	13,800–26,700	40,700	18,500	9
C. sericea ssp. *occidentalis*	—	—	—	—	73,500	33,400	1

Sources: Asakawa (1969), Brinkman (1974), Edminster (1947), Forbes (1956), Gordon and Rowe (1982), Gorshenin (1941), Heit (1969), Mirov and Kraebel (1939), Mugford (1969), NBV (1946), Stevenson (1969), Swingle (1930).

* 0.036 cubic meters (1 bu) of fruit clusters weighed 15 kg (33 lb) and yielded 2 kg (4 lb) of stones (Brinkman 1974).

and sow them in the spring (Goodwin 1948; Shumilina 1949; Sus 1925). Seeds in nurserybeds should be covered with 6 to 13 mm ($^1/_4$ to $^1/_2$ in) of soil (Brinkman 1974; Heit 1968b; Mugford 1969; NBV 1946; Stevenson 1969). Seeds sown in the fall should be mulched during the winter with 13 to 25 mm ($^1/_2$ to 1 inch) of sawdust (Heit 1968a; Mugford 1969; Stevenson 1969).

Table 5—*Cornus,* dogwood: stratification treatments

Species	Warm period		Cold period		Duration (days)
	Medium	Temp (C°)	Days	Temp (C°)	
C. alba	—	—	—	5	90–120
C. alternifolia	Sand, peat, or mix	30–20	60	5	60
*C. amomum**	"Moist"	—	—	3–5	21–28
	Sand, peat, or moss	—	—	5	90–120
C. canadensis†	—	—	—	—	60–90
	Sand, peat, or mix	25	30–60	1	120–150
C. controversa	—	—	60–90	—	60–90
C. drummondii‡	Sand	21–27	1	5	30
		—	30–60	—	30–60
C. florida	Sand	—	—	5	120
C. kousa	Sand, peat, or vermiculite	—	—	1–5	40–120
C. macrophylla	—	—	90–150	—	90
C. mas	Soil or vermiculite	20–30	120	1–13	30–120
C. nuttallii§	Peat	—	—	3	90
C. officinalis	—	15–22	120–150	—	90
C. racemosa	Sand	20–30	60	5	60, 120
C. rugosa	Soil	—	—	Outdoors	Overwinter
C. sanguinea	—	—	60	—	60–90
C. sericea //	Sand	—	—	2–5	60–90
	Sand	—	—	5	60-90

Sources: Billington (1943), Brinkman (1974), Dirr and Heuser (1987), Emery (1988), Guan and others (1989), Goodwin (1948), Gordon and Rowe (1982), Heit (1967, 1968b), Jack (1969), Nichols (1934), Ohwi (1965), Pammel and King (1921), Peterson (1953), Soljanik (1961), Swingle (1939),

* Seeds were soaked for 3 hours in water at room temperature before stratification (Heit 1968b).

† Seeds were soaked for 1 hour in sulfuric acid before stratification (Dirr and Heuser 1987).

‡ Seeds were mechanically scarified before stratification (Brinkman 1974).

§ Seeds were soaked for 4 hours in sulfuric acid before stratification (Emery 1988).

// Seeds were soaked for 1 hour in sulfuric acid before stratification (Brinkman 1974).

Table 6—*Cornus,* dogwood: germination test conditions and results

Species	Germination test conditions*		Germination rate		Germination %		
	Daily light (hrs)	Days	Amt (%)	Days	Average (%)	Samples	Purity (%)
C. alba	—	—	—	—	—	—	—
C. alternifolia	8	60	8	50	10	2	63
C. amomum	8–24	14–28	86†	11	70	6	91
C. canadensis	—	60–90	6	26	16	5	90
C. drummondii	8	50	14	34	25	3	89
C. florida	8	60	14–45	15–20	35	7	97
C. kousa	—	30	—	—	85	2	—
C. macrophylla	—	—	—	—	—	—	—
C. mas	—	—	—	—	57	6	95
C. nuttallii	8–24	47	57	16	81	2	100
C. racemosa	8	60	22–30	14	20	8	83
C. rugosa	8	60+	8	15	46	4	95
C. sericea	—	60–90	35	13–18	57	18	99

Sources: Adams (1927), Asakawa (1969), Brinkman (1974), Heit (1968a&b, 1969), McKeever (1938), Nichols (1934), Peterson (1953), Soljanik (1961), Swingle (1939), Titus (1940).

*Temperatures were 30 °C for 8 hours and 20 °C for 16 hours each day. Sand was the medium used on all listed species. Additional tests were made on wet paper in germinators with seeds of *C. amomum, C. kousa,* and *C. nuttallii* (Brinkman 1974; Heit 1969).

†One test.

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Betulaceae—Birch family

Corylus L.

hazel

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Other common names. Filbert, hazelnut.

Growth habit, occurrence, and use. The hazels—*Corylus* L.—include about 15 species of large, deciduous shrubs (rarely small trees) that occur in the temperate parts of North America, Europe, and Asia. Some species are grown for their nuts or for ornament, and most species provide food for wildlife. In this country, 4 species have present or potential value for wildlife, shelterbelt, or environmental plantings (table 1). For many years, European hazel has been cultivated for the commercial production of its edible nutmeats, known as hazelnuts or filberts, mostly in Europe but to some extent in the United States, especially in the Willamette Valley of Oregon. Years of first cultivation for other species are as follows: American hazel (1798), beaked hazel (1745), and California hazel (1910).

Flowering and fruiting. Male and female flowers are borne separately on 1-year-old lateral twigs of the same plant. They are formed late in the summer and open the following spring before the leaves appear (table 2). The male flowers are borne in clusters of 2 to 5 pendulous catkins, consisting only of stamens. The female flower is budlike, each flower has a single ovary with 2 styles that are strikingly red at pollination (Hora 1981). By late summer or early fall, the fertilized female flowers develop into fruits. These are round or egg-shaped, brown or dark-tan, hard-shelled "nuts", each containing one embryo that is enclosed in a pericarp, or shell. These nuts are enclosed in an involucre (or husk) which consists of 2 more-or-less united hairy bracts (figures 1 and 2). The seeds are naturally dispersed by animals or birds. Large seedcrops are produced at irregular intervals, usually every 2 or 3 years (NBV 1946; Vines 1960).

Collection of fruits. Hazelnuts may be eaten by rodents, larger animals, or some birds even before they are fully mature. To reduce such losses, fruits should be picked as soon as the edges of the husks begin to turn brown, which may be as early as mid-August.

Extraction and storage of seeds. The fruits should be spread out in thin layers on wire-mesh screens to dry in a room with high humidity for about 1 month. A macerator can be used to separate the nut from the husk. The machine is operated without water, and the nuts and husks pour out of the spout (Horvath 1999). An aspirator or screen cleaning machine is then needed to separate the husk debris from the nut. Alternatively, a brush machine can be used to dehisce the nut in a square-wire cylinder and a vacuum to suck out the dust, with the seeds flowing out the opening in the door (Maloney 1999). Yields and number of seeds per weight vary even within the species (table 3).

Table 1—*Corylus*, hazel: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
C. americana Walt.	**American hazel,** American filbert	Maine to Saskatchewan, S to Georgia; W to Missouri & Oklahoma
C. avellana L.	**European hazel,** European filbert, common filbert	Europe, to 1,824 m in central Alps
***C. cornuta* Marsh.** *C. rostrata* Ait.	**beaked hazel,** beaked filbert	Newfoundland to British Columbia, S to Georgia, Missouri, & E Colorado
***C. cornuta* var. *california* Marsh. (A.DC.) Sharp**	**California hazel,** California filbert	Coast ranges from Santa Cruz N to British Columbia

Source: Brinkman (1974).

Table 2—*Corylus*, hazel: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
C. americana	—	Mar–May	July–Sept
C. avellana	Europe	Feb–Apr	Sept–Oct
C. cornuta	Tennessee	Jan–Feb	Aug–Sept
var. *california*	California	Jan–Feb	Sept–Oct

Sources: Fernald (1950), Loiseau (1945), Munz and Keck (1959), NBV (1946), Rosendahl (1955), Sus (1925), Van Dersal (1938), Vines (1960), Wappes (1932), Zarger

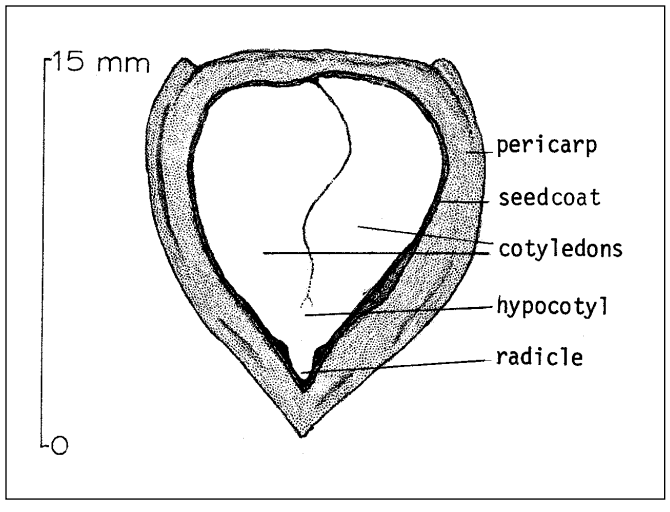
Table 3—*Corylus*, hazel: seed yield data

Species	Place of collection	Seed wt/fruit wt		Cleaned seeds/weight				Samples
				Range		Average		
		kg/45 kg	lb/100 lb	/kg	/lb	/kg	/lb	
C. americana	—	11–14	25–30	434–1,623	197–736	1,083	491	11
C. avellana	Europe	27	60	353–1,180	160–535	803	364	244
C. cornuta	—	—	—	937–1,490	425–676	549	249	3
var. *californica*	California	—	—	882–922	400–418	410	186	—

Sources: Brinkman (1974), Gorshenin (1941), NBV (1946), Rafn (1928), Swingle (1939), Vines (1960), Zarger (1968).

Figure 1—*Corylus cornuta* var. *californica*, California hazel: mature fruit including husk.

Figure 2—*Corylus cornuta* var. *californica*, California hazel: longitudinal section through a fruit.

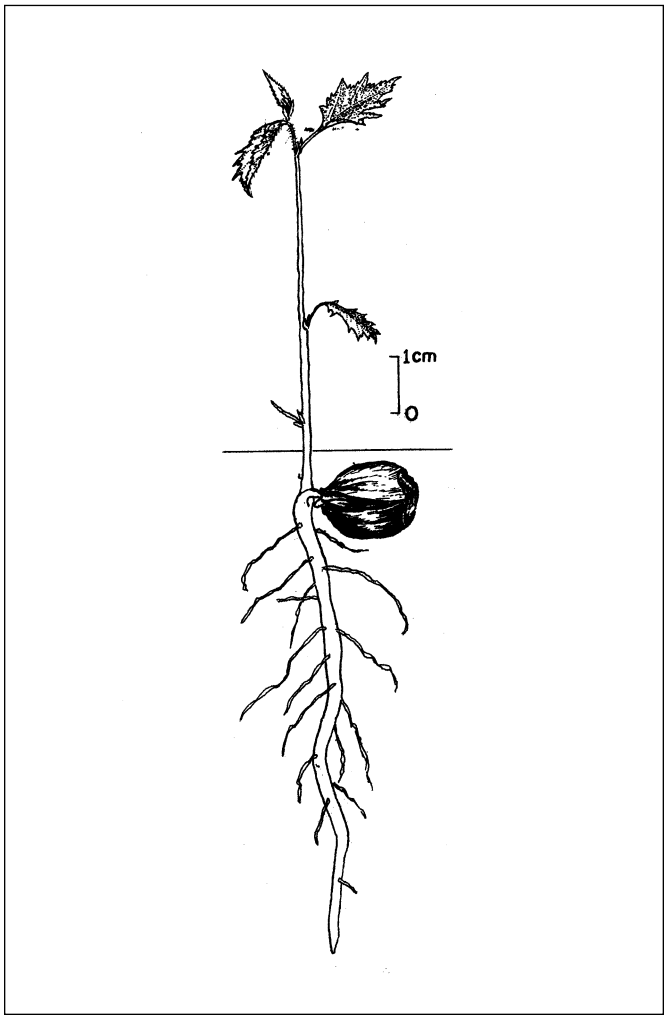


Because some dormancy is apparently induced by drying the nuts, seeds of hazel species were once thought to be recalcitrant and intolerant of any drying (Hong and Ellis 1996). Recommendations usually were to keep the hazelnuts moist after collection and store them moist over winter (stratification) before planting in the spring (Heit 1967; NBV 1946). Seeds of hazel species are now considered as orthodox in storage behavior, even though moist storage will prevent deep embryo dormancy for at least several months. Seeds of this genus will also remain viable for a year in unsealed containers at room temperature. Most of the viability of American hazelnut and some of beaked hazelnuts (Brinkman 1974) will be retained if seeds are stored in sealed containers at 5 °C. There are no long-term storage data for hazelnuts.

Pregermination treatments. Newly harvested hazelnuts are not dormant, but inhibitors present in the testa and pericarp are carried to the cotyledons and subsequently through the cotyledonary petioles into the embryonic axis (Bradbeer 1978; Jarvis 1975). Numerous studies have been

carried out on the nature of dormancy in European hazel, with most of them concerning the balance of gibberellins and inhibitors and starch synthesis (Arias and others 1976; Bradbeer and Pinnfield 1966; Jarvis 1975; Jarvis and Wilson 1978; Jeavons and Jarvis 1984; Li and Ross 1990). Stratification remains the method used to overcome dormancy, however. Hazel seeds require 2 to 6 months of prechilling before germination will occur (Heit 1968a&b). Three months of cold stratification has proven effective (Dirr and Heuser 1987). Stratification removes the block to gibberellin biosynthesis which begins when the seed is transferred to higher temperatures (Bradbeer and others 1978). In nurseries this can be accomplished by fall-sowing or by stratifying outdoors over winter before planting. Seeds may benefit from alternations of warm and cold stratification. Freshly harvested seeds of European hazel that were warm stratified for 3 weeks followed by 3 weeks at 4 °C germinated best (Dirr and Heuser 1987).

Figure 3—*Corylus cornuta* var. *californica*, California hazel: seedling development 30 days after germination.



Germination tests. Germination is hypogeal (figure 3). The seeds have a dormant embryo and germinate slowly without pretreatment. In one experiment, unstratified seeds of American hazel germinated throughout a year (Brinkman 1974). Giberillic acid (10^{-4} M) applied to European hazel seeds increased the germination from 64% for the control to 86% at 20 °C (Arias and others 1976). Seedlots of this species soaked in ethanol and then 0.1% (w/v) mercuric chloride, when put in a lighted chamber germinated 70% compared to seedlots germinated in total darkness, which germinated at only 9% (Jeavons and Jarvis 1996). Results of limited tests are listed in table 4.

Viability testing by staining the seeds with tetrazolium chloride (TZ) is the preferred method of ascertaining the seed's quality (ISTA 1993). Seeds should be cracked and soaked in water for 18 hours. After 1 to 2 mm of the cotyledons is cut off at the distal ends and the seeds are split longitudinally, the embryos should be incubated for 12 to 15 hours in 1% TZ, or 18 to 24 hours in a 0.5% solution. Some unstained tissue is allowed in viable seeds, but interpretation is difficult. Standard germination tests can also be performed once the pericarp is removed and the seeds are prechilled for 2 months at 3 to 5 °C (ISTA 1993).

Nursery practice. Although spring-sowing of stratified seeds is feasible, most nurseries plant hazel seeds in the fall (Sus 1925). In Holland, seeds of European hazel are mixed with moist sand for several months before sowing in the fall (NBV 1946). In Tennessee, good results with this species were obtained by storing fresh seed dry at 3 °C until planting in October; average tree percent was 98 based on 80% viability (Zarger 1968). Two seedlots of American hazel planted in November and December gave tree percents of 63 and 48, based on 70 and 60% viability. Seeds of both species were sown 2.5 cm (1 in) deep in drills and covered with 2.5 to 3.75 cm (1 to 1.5 in) of sawdust. In this report, the seedbeds had been fumigated with methyl bromide; other fumigants are now recommended. If seedling densities are kept low, from 43 to 65/m^2 (4 to 6/ft^2), hazel can be outplanted when 1 year old. European hazel and horticultural varieties are frequently propagated by cuttings, grafting, and tissue culture (Dirr and Heuser 1987).

Hazels are attacked by several fungi. The powdery mildew of hardwoods—*Phyllactinia guttata* (Wallr.:Fr.) Lév. (synonym *Phyllactinia corylea* (Pers.) P. Karst.)—will defoliate the plant. More serious attacks by the fungal parasite *Nematospora coryli* Peglion cause malformation of the nuts (Hora 1981). Hazelnuts are also attacked by the brown rot of pome and stone fruits—*Monilinia fructigena* Honey in Whetzel (synonym *Sclerotinia fructigena* Aderhold. ex Sacc.)—which enters through punctures caused by *Balaninus nuceum*, the nut weevil (Hora 1981).

Table 4—*Corylus,* hazel: germination test conditions and results

Species	Germination test conditions: Medium	Temp (°): Day	Temp (°): Night	Days	Germinative energy: Amt (%)	Germinative energy: Days	Germinative capacity: Average (%)	Germinative capacity: Purity: Samples	Germinative capacity: Purity (%)
C. americana	Sand	30	20	60	10	30	13	2	96
C. avellana	Sand or germinator	30	20	60	—	—	69	13	95
C. cornuta	Sand	30	20	60	1	26	1	1	99
var. *californica*	Sand	30	20	90	—	—	20	1	62

Sources: Brinkman (1974), NBV (1946), Rafn (1928), Shumilina (1949).

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C

Anacardiaceae—Sumac family

Cotinus P. Mill.

smoketree or smokebush

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Growth habit, occurrence, and use. The genus *Cotinus* P. Mill—smoketree— includes 3 or 4 species of deciduous, polygamous or dioecious, small trees or shrubs, widely distributed through central and southern Europe to the Himalayas, southwest China, and the southeastern United States (Hillier 1991; Krüssmann 1984). The smoketrees are cultivated primarily for ornamental purposes. The durable wood of American smoketree has been used for fence posts (Koller and Shadow 1991; LHBH 1976) and it also yields a yellow dye that was widely used during the Civil War (Vines 1960). Common smoketree is used in Bulgarian medicine for its anti-inflammatory, antibacterial, and wound-healing properties (Tsankova and others 1993). The 2 species of interest are described in table 1.

Common smoketree is an upright, spreading, multistemmed shrub that is grown because of its many ornamental landscape qualities and its adaptability to widely divergent soils and pH ranges (Dirr 1990). Several cultivars produce a long period of midsummer floral and fruit ornamentation, showy plumose inflorescences, and vivid autumn foliage color (Dirr 1990; Hillier 1991; Koller and Shadow 1991; Krüssmann 1984). Of special note are 'Nordine Red', the hardiest of the purple-leaf smokebushes, and 'Royal Purple', a cultivar with rich maroon-red foliage and purplish red inflorescences (Dirr 1990). The foliage of this last cultivar accumulates anthocyanin pigments in response to ultraviolet light of wavelengths between 300 and 400 nm and low temperatures (Oren-Shamir and Levi-Nissim 1997).

American smoketree is a large, upright shrub or small, round-headed tree with bluish to dark green leaves that turn a brilliant yellow, orange, red, and reddish purple color in the fall (Dirr 1990). The bark of the American smoketree is a beautiful gray to gray-brown, and scaly mature trunks (that is, with a fishlike scale effect), providing pattern and detail in the winter landscape (Dirr 1990; Koller and Shadow 1991). For a review of *Cotinus* and discussion of selected cultivars, see Tripp (1994).

Flowering and fruiting. The small, usually infertile, yellowish flowers, which bloom in June to July (April to May for American smoketree), are borne in large, terminal panicles (Krüssmann 1984). The pedicels and peduncles lengthen after flowering and are clad with fine hairs, creating the smokelike effect that gives the plant its common name (LHBH 1976). The plumelike inflorescences often persist through September (Dirr 1990). The fruit (figures 1 and 2) is a dry, reticulate drupe about 3 to 6 mm in length, light red-brown in color (ripening to near black), containing a thick, bony stone (Rudolf 1974). Seedcrops are produced annually but are often poor. The kidney-shaped drupe ripens in the fall, which is usually August to October for common

Table 1—*Cotinus*, smoketree: nomenclature, occurrence, growth habit, height at maturity, and date first cultivated

Scientific name(s)	Common name(s)	Occurrence	Growth habit	Height (m)	Year first cultivated
***C. coggygria* Scop.** *C. americanus* Nutt. *C. cotinoides* (Nutt. ex Chapm.) Britt.	**common smoketree**, smokebush, European smoketree, Venetian sumac	Central & S Europe, Himalayas & to SW China	Shrub	2.5–4.6	1656
***C. obovatus* Raf.**	**American smoketree**, yellowwood	Tennessee, S to Alabama & Missouri, W to Texas	Tree	6.1–9.1	1882

Sources: Dirr (1990), LHBH (1976).

Figure 1—*Cotinus obovatus*, American smoketree: seeds.

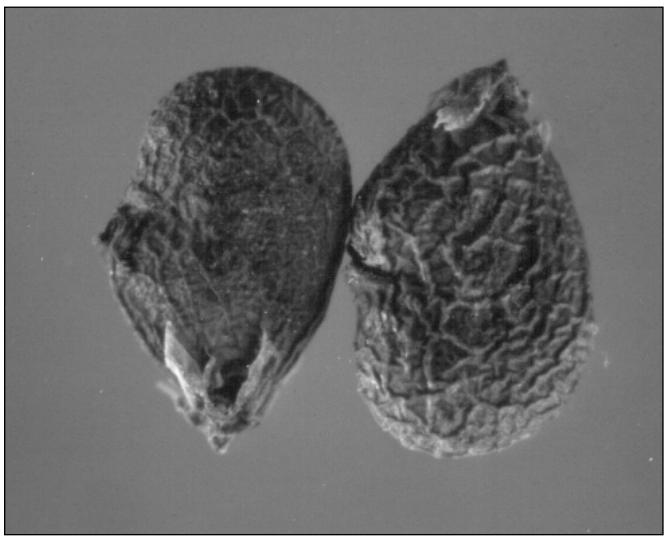
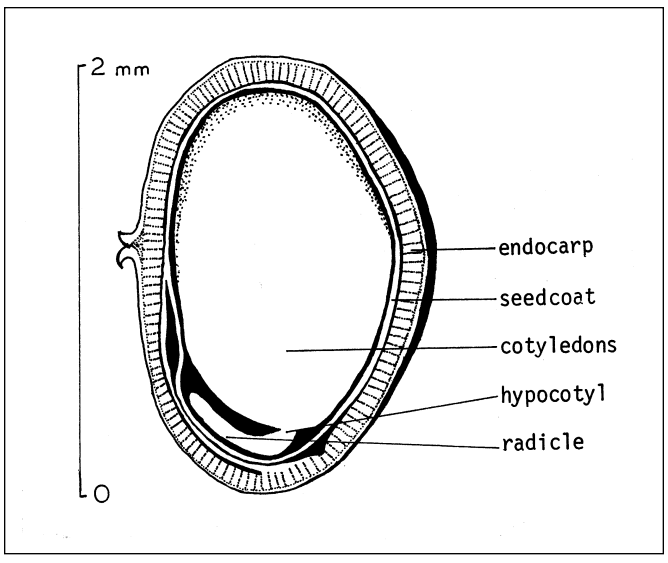


Figure 2—*Cotinus obovatus*, American smoketree: longitudinal section through a seed.



smoketree and June to September for American smoketree (Rudolf 1974).

Collection of fruits; extraction, cleaning, and storage of seeds. The fruits should be harvested by hand as soon as they are ripe (Rudolf 1974). Seeds of common smoketree that are collected green during late August–September and sown immediately can produce high germination percentages the following spring (Dirr and Heuser 1987). Seeds collected from purple-leaf forms produce a mixture of green-leaf and purple-leaf seedlings (Dirr and Heuser 1987). Dry fruits should be run through a hammermill and the debris fanned out (Rudolf 1974). The number of cleaned seeds per seed weight for common smoketree ranges between 99,978 to 118,999/kg (45,350 to 53,978/lb) with 75% germination and 97% purity, depending upon cleaning techniques (Allen 1994). The average number of cleaned seeds per weight for American smoketree is 111,111/kg (50,400/lb) (Rudolf 1974).

Information on smoketree seed storage is limited, but the indications are strong that these seeds are orthodox in storage behavior. One report states that seeds of common smoketree can be stored dry for several years in open or sealed containers at room temperature (Heit 1967, cited by Rudolf 1974). However, the best practice is to store dry seeds in a metal or rigid plastic container that is then sealed and stored in a refrigerator at 0 to 5 °C (Macdonald 1986). Seeds stored in this manner will be viable for a number of years.

Pregermination treatments. Smoketree seeds have both a hard seedcoat and an internal dormancy, thus causing slow and irregular germination. Seeds can be stimulated to germinate more uniformly by sulfuric acid scarification followed by cold stratification (table 2). Seeds from a recent introduction (Dummer hybrids) that were acid-scarified for 3 hours (no cold stratification given) and then planted germinated in 12 days (Dirr 1990).

Germination tests. Pretreated smoketree seeds may be tested for 30 days in sphagnum flats or in seed germinators (Rudolf 1974). Average test results for 2 species are shown in table 3. Tetrazolium staining can be used for rapid estimates. Seeds should be soaked in water for 24 hours before breaking open the seed coat and staining 24 hour at 30 °C in a 1% solution (Enescv 1991).

Nursery practice and seedling care. Smoketree seeds are fall-sown without pretreatment if the fruits are slightly green (Dirr 1990; Macdonald 1986; Rudolf 1974) or with pretreatment in the spring at a rate of 430/m^2 (40/ft^2) (Rudolf 1974). The seed should be covered with 6 to 9 mm ($^1/_4$ to $^3/_8$ in) of soil, and fall-sown beds should be mulched with sawdust (Rudolf 1974). Seedlings may be planted as 1+0 stock (Rudolf 1974).

Several references noted that common smoketree should be propagated by vegetative methods, because many seedlings are male plants lacking the showy flowering panicles (Dirr 1990; Dirr and Heuser 1987; Hartmann and others 1990; Macdonald 1986). In general, softwood cuttings taken in early June to July, treated with 1 to 3 g/liter (1,000 to 3,000 ppm) indole-3-butyric acid solution, and placed in a well-drained medium under mist will root in about 4 to 8 weeks (Blakesley and others 1991, 1992; Dirr 1990; Dirr and Heuser 1987; Hartmann and others 1990; Kelley and

Table 2—*Cotinus*, smoketree: seed pregermination treatments

Species	Scarification in H_2SO_4 (min)	Stratification treatments		
		Moist medium	Temp (°C)	Days
C. coggygria	30	Sand	3	45–60
	30/60	Sphagnum moss	5	90
	20/80	Peat	3	60–80
C. obovatus	20/40	Plastic bag	3	60

Sources: Dirr and Heuser (1987), Gonderman and O'Rourke (1961), Heit (1968) cited by Rudolf (1974), Stilinovic and Grbic (1988).

Table 3—*Cotinus*, smoketree: germination test conditions and results with pretreated seed

Species	Germination test conditions				Germination rate		Germination		Soundness (%)
	Medium	Temp (°C) Day	Temp (°C) Night	Days	%	Days	%	Samples	
C. coggygria	Germinator	20	20	30	—	—	80	2	70
	Sphagnum	21	21	21	—	—	93	2	—
C. obovatus	Kimpak in germinator	30*	20	46	37	11	39	3	60†

Source: Rudolf (1974).
* With light for 8 hours.
† Purity was 96%.

Foret 1977; Macdonald 1986; Siftar 1981). Rooted cuttings must be overwintered without disturbance and transplanted in the spring. Spellerberg (1985, 1986) reported improved shoot growth and higher rooting percentages of common smoke tree cv. 'Royal Purple' cuttings when they were taken in April from mother plants forced under glass than cuttings taken in June from outdoor-grown plants. After rooting, shoot growth was promoted by longer photoperiods, higher carbon dioxide levels, and gibberellic acid treatments. Howard (1996) reported that rooting of 'Royal Purple" cuttings was confined to the period of active shoot growth (late May to early August), and a small benefit was noted with severe stock plant pruning. Common smoketree can also be successfully propagated by French or continuous layering (Macdonald 1986).

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C

Rosaceae—Rose family

Cotoneaster Medik.

cotoneaster

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Growth habit, occurrence, and use. The genus *Cotoneaster* includes about 50 species of shrubs and small trees native to the temperate regions of Europe, northern Africa, and Asia (excepting Japan) (Cumming 1960). Growth habits range from nearly prostrate to upright. Cold-hardy types are more or less deciduous, whereas those native to warmer regions are evergreen (Heriteau 1990). Cotoneasters are valued as ornamentals for their glossy green foliage, attractive fruits, and interesting growth habits. Fall foliage color is often a showy blend of orange and red. Cotoneasters are adapted to sunny locations with moderately deep and moderately well-drained silty to sandy soils. Several hardy species are commonly used in mass plantings, hedges, shelterbelts, wildlife plantings, windbreaks, recreational areas, and along transportation corridors on the northern Great Plains, the southern portions of adjoining Canadian provinces, and occasionally in the Intermountain region and other areas (Plummer and others 1968; Shaw and others 2004; Slabaugh 1974). They require little maintenance and provide ground cover, soil stabilization, snow entrapment, and aesthetic values. Peking cotoneaster provides food and cover for wildlife (Johnson and Anderson 1980; Kufeld and others 1973; Leach 1956; Miller and others 1948). Six species used in conservation plantings are described in table 1 (Hoag 1965; Nonnecke 1954; Plummer and others 1977; Rheder 1940; USDA SCS 1988; Zucker 1966). Use of cotoneasters in some areas may be limited due to their susceptibility to fire blight (infection with the bacterium *Erwinia amylovora*), borers (*Chrysobothris femorata* (*Olivier*)), lace bugs (*Corythucha cydonia* (Fitch)), and red spiders (*Oligonychus platani* (McGregor)(Griffiths 1994; Krüssmann 1986; Wyman 1986).

Cotoneasters are apomictic and will, therefore, propagate true from seed (Wyman 1986). However, because of the apomictic habit, many variants occur within each species (Everett 1982). This variability has been exploited in cultivar

Table 1—*Cotoneaster,* cotoneaster: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***C. acutifolius* Turcz.** *C. acutifolia* Turcz. *C. pekinensis* Zab.	**Peking cotoneaster**	North China; introduced from North Dakota to Nebraska & upper mid-West, S Canadian prairie provinces
***C. apiculatus* Rehd. & Wilson** *C. apiculata* Rehd. & Wilson	**cranberry cotoneaster**	W China; introduced from North Dakota to Nebraska & upper mid-West
***C. horizontalis* Dcne.** *C. davidiana* Hort.	**rock cotoneaster,** rockspray cotoneaster, quinceberry	W China; introduced from North Dakota to Nebraska & upper mid-West, S central Washington
***C. integerrimus* Medic.** *C. vulgaris* Lindl.	**European cotoneaster**	Europe, W Asia, Siberia
***C. lucidus* Schltdl.** *C. acutifolia* Lindl., not Turcz. *C. sinensis* Hort.	**hedge cotoneaster**	Altai Mtns & Lake Baikal region of Asia
***C. niger* (Thunb.) Fries** *C. melanocarpus* Lodd.	**black cotoneaster,** darkseed cotoneaster	Europe to NE & central Asia, introduced from North Dakota to Nebraska

Source: Krüssmann (1986), LHBH (1976), Slabaugh (1974).

development (Krüssmann 1986; LHBH 1976). A number of hybrids have also been developed as ornamentals.

Flowering and fruiting. Cotoneaster flowers are perfect, regular, and white to pink. They develop singly or several to many together in corymbs produced at the ends of leafy lateral branchlets. Flowers are small, but in some species attractive due to their abundance. Fruits are black or red berrylike pomes that ripen in late summer or early fall and often persist into winter (Wyman 1949) (figure 1). The fruits contain 1 to 5 seeds (Rehder 1940) (figures 2 and 3), averaging 3 for Peking, hedge, and black cotoneasters; 2 for cranberry and rock cotoneasters; and 2 or 3 for European cotoneasters (Uhlinger 1968, 1970). Phenological data are provided in table 2.

Collection of fruits. Ripe fruits are collected by hand stripping or flailing in early autumn, preferably after leaf fall. Fruit firmness and color (table 3) are good criteria of ripeness. Leslie (1954) recommends that fruits of Peking, hedge, and black cotoneasters be collected slightly green. The minimum fruit-bearing age of hedge cotoneaster is 3 years. Fruit crops are produced annually.

Extraction, cleaning, and storage of seeds. Seeds may be extracted by macerating fresh fruits and skimming off or screening out the pulp. Seeds are best cleaned while fresh, because it is difficult to remove dry fleshy material by maceration. Most empty seeds can be eliminated by floating the seedlot twice in water (Uhlinger 1968, 1970). Seeds may be removed from dried fruits by abrasion (Slabaugh 1974) and the debris separated using a 2-screen fanning machine. Number of seeds per weight for 3 species are provided in table 4. About 0.5 kg (1 lb) of cleaned seeds of European cotoneaster are obtained from 2.7 kg (6 lb) of fruits (USDA SCS 1988). Seeds of the cotoneasters are orthodox in storage behavior. Leslie (1954) and USDA SCS (1988) recommend that seeds of cotoneasters be stored dry in sealed containers in a cool place. Seeds of European cotoneaster, however, can be stored in an unheated warehouse for at least 16 years without loss of viability (Jorgensen 1996; Plummer 1968).

Pregermination treatments. Seeds of many cotoneasters exhibit double dormancy due to their hard, impermeable seedcoats and the physiological condition of their embryos. First-year germination is enhanced by acid scarification followed by warm incubation and wet prechilling (USDA SCS 1988) (table 5). Addition of a commercial compost activator to the wet prechilling medium reportedly improved emergence of spreading cotoneaster—*C. divaricatus* Rehd. & Wilson (Cullum and Gordon 1994).

Figure 1—*Cotoneaster*, cotoneaster: fruits.

Figure 2—*Cotoneaster*, cotoneaster: seeds (**from top to bottom)** of *C. apiculanyus,* cranberry cotoneaster; *C. horizontalis,* rock cotoneaster; *C. lucidus,* hedge cotoneaster; *C. niger,* blackcotoneaster.

Figure 3—*Cotoneaster horizontalis*, rock cotoneaster: longitudinal section through a seed.

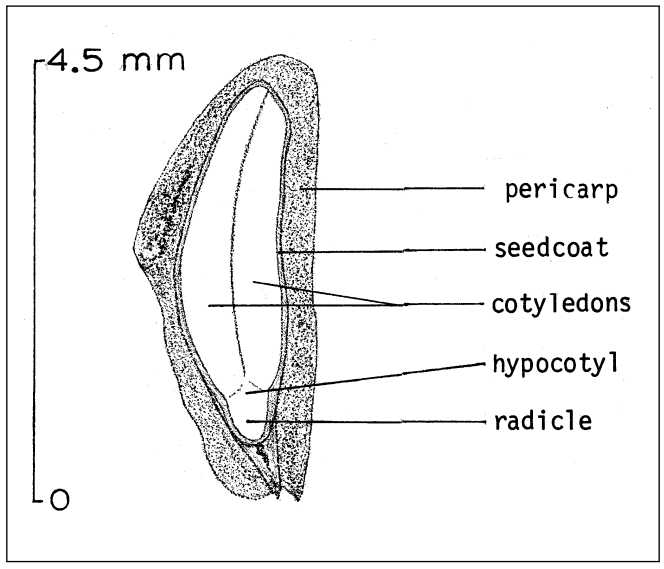

Table 2—*Cotoneaster,* cotoneaster: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
C. acutifolius	N Great Plains	May–June	Sept–Oct	Sept–winter
C. apiculatus	S Michigan	May–June	Aug–Sept	Fall–winter
C. horizontalis	—	June	Sept–Nov	Sept–winter
C. integerrimus	Great Plains	May–June	Aug–Sept	—
C. lucidus	North Dakota	May–June	Sept	—
C. niger	—	May–June	—	—

Sources: Krüssmann (1986), Macdonald (1986), Slabaugh (1974), USDA SCS(1988), Zucker (1966).

Table 3—*Cotoneaster,* cotoneaster: height, year first cultivated, and color of flowers and ripe fruit

Species	Height at maturity (m)	Year first cultivated	Flower color	Color of ripe fruit
C. acutifolius	1.8–3.9	1883	Pink	Black
C. apiculatus	0.3–1.5	1910	Pink	Scarlet
C. horizontalis	0.9–1.2	1880	White-pink	Light to dark red
C. integerrimus	1.2–3.6	—	Pinkish	Red
C. lucidus	1.8–2.7	1840	White, tinged w/pink	Black
C. niger	1.5–2.4	1829	Pinkish-white	Blackish red

Sources: Griffiths (1994), Hoag (1958, 1965), LHBH (1976), Leslie (1954), Krüssmann (1986), Rehder (1940), Rosendahl (1955), USDA SCS (1988).

Table 4—*Cotoneaster,* cotoneaster: seed yield data

	Cleaned seeds/weight			
	Range		Average	
Species	/kg	/lb	/kg	/lb
C. acutifolus	48,466–58,212	21,984–26,405	59,300	26,900
C. horizontalis	—	—	141,094	64,000
C. integerrimus	—	—	35,274	16,000
C. lucidus	—	—	51,560	23,390

Sources: Cumming (1960), McDermand (1969), Plummer and others (1968), Slabaugh (1974), Uhlinger (1968, 1970), USDA SCS (1988).

Table 5—*Cotoneaster,* cotoneaster: pregermination treatments

Species	Immersion time in conc H_2SO_4 (min)	Wet prechill at 4 °C	
		Medium	Period (days)
C. acutifolius	10–90	Peat	30–90
C. apiculatus	60–120	Sand & peat	60–90
C. horizontalis	90–180	Peat	90–120
C. integerrimus	120	—	120*
C. lucidus	5–20	Sand & perlite	30–90
C. niger	10–90	Peat	30–90

Sources: Dirr and Heuser (1987), Fordham (1962), Leslie (1954), McDermand (1969), Slabaugh (1974), Smith (1951), Uhlinger (1968, 1970), USDA SCS (1988).
*Wet prechilling was preceded by 90 days of warm incubation at 21 °C.

Duration of effective pretreatments varies with species, seedlot, and year due to differences in seedcoat thickness and degree of embryo dormancy. Meyer (1988), for example, found that seeds of cranberry and spreading cotoneasters scarified for 1.5 hours in concentrated sulfuric acid germinated over an increasing range of incubation temperatures as the duration of wet prechilling at 2 °C increased from 0 to 4 months. After 4 months of prechilling, germination of both species occurred at constant incubation temperatures from 4.5 to 26.5 °C. This variability in response adds to the difficulty of securing prompt, consistent germination (Uhlinger 1968, 1970).

Germination tests. Table 6 lists germination test conditions and results for 4 cotoneaster species (see table 5 for pretreatments). The effect of light on germination of seeds of Peking, hedge, and black cotoneasters varies among seedlots, but germination of black cotoneaster was generally improved by exposure to cool-white fluorescent light (Uhlinger 1968, 1970). Pretreatment with gibberellic acid partially replaced the effect of light (Uhlinger 1968, 1970).

Because of the dormancy in these seeds, the International Seed Testing Association recommends use of tetrazolium staining rather than germination tests for evaluation of seed quality (ISTA 1993). Seeds are stained by first soaking them in water for 18 hours, then removing the distal third of the seeds with a transverse cut; and finally placing the seeds in a 1.0% solution of tetrazolium chloride for 20 to 24 hours. Viable seeds usually stain completely, but seeds are considered viable if only the radicle tip and the distal third of the cotyledons are unstained (ISTA 1993).

The excised embryo method may also be used to test seed germinability of spreading cotoneaster (Smith 1951). Seeds are first scarified in sulfuric acid for 3 hours, then soaked in 27 °C tapwater for 2 days before the embryos are excised and incubated under conditions favorable for germination.

Nursery practice. Seeds of cotoneaster species may be given appropriate scarification pretreatments and seeded in midsummer to provide the warm incubation and overwinter wet-prechilling required to relieve dormancy and permit germination in the spring. Scarified seeds provided with warm incubation pretreatment in the laboratory may be fall-planted; however, scarification, warm incubation, and wet prechilling in the laboratory are required for spring-planting. A seeding rate of 250 seeds/m^2 (23/ft^2) is recommended for producing lining-out stock of rock cotoneaster (Macdonald 1993); 100 to 130 seeds/m^2 (10 to 12/ft^2) are recommended for European cotoneaster var. 'Centennial' (USDA SCS 1988). Seeds of this variety are planted 0.3 cm (0.1 in) deep and covered with 1.5 to 2 cm (3/5 to 4/5 in) of soil (USDA SCS 1988). European and hedge cotoneaster seedbeds may be mulched with hay or other suitable material (Hinds 1969; USDA SCS 1988). Filtered shade until August is recommended for seedlings of Peking, hedge, and black cotoneasters (Leslie 1954). For hedge cotoneaster, an average seedling yield of 30% was obtained in a North Dakota nursery (Hinds 1969). Seedlings of this species are usually ready for outplanting after 2 growing seasons.

Cotoneasters are propagated vegetatively from softwood and occasionally from hardwood cuttings (Dirr and Heuser 1987; Wyman 1986). Cuttings are taken from June to August (Dirr and Heuser 1987) and treated with 1,000 to 3,000 ppm IBA. Macdonald (1993) recommended that heel cuttings be used when evergreen species are rooted in cold frames. Cuttings, particularly those of evergreen species, root readily and are easily transplanted and overwintered. Layering and grafting are also used to obtain small numbers of plants.

Field planting. Nursery stock is generally used to establish conservation plantings. Wildland seedings of Peking cotoneaster have been only marginally successful

Table 6—*Cotoneaster,* cotoneaster: germination test conditions and results

	Germination test conditions				Percentage germination		
			Temp (°C)				
Species	Daily light (hrs)	Medium	Day	Night	Days	Avg (%)	Samples #
C. acutifolius	9	Wet paper	25	10	—	70–80	—
C. horizontalis	24	Wet paper	27	—	—	100	—
	24	Sand	30	20	100	30	5+
C. lucidus	9	Wet paper	25	10	—	70	—
C. niger	9	Wet paper	25	10	—	80	—

Sources: Smith (1951), Slabaugh (1954), Uhlinger (1968 & 1970).

(Shaw and others 2004). Germination is erratic and seedlings grow slowly, particularly if the site is not kept weed-free.

Bareroot plantings of European cotoneaster Centennial may be established using 1+0 or 2+0 bareroot seedlings with stem diameters of 0.5 to 1.3 cm ($^1/_5$ to $^1/_3$ in) just above the root collar (USDA SCS 1988). Seedlings should be planted in fallowed ground at 1.2- to 1.5-m (4- to 5-ft) spacings immediately after the soil thaws in spring. At least 5 years of weed control are often required. Average survival ranges from 70 to 95% (USDA SCS 1988). Fruit-producing stands are obtained in 3 to 4 years.

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Rosaceae—Rose family

Crataegus L.

hawthorn, haw, thorn, thorn-apple

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Growth habit, occurrence, and uses. The genus *Crataegus* L. is a complex group of trees and shrubs native to northern temperate zones (Mabberley 1997), mostly between latitudes 30° and 50°N (Phipps 1983). Although most species can attain tree-sized proportions, hawthorns in general do not form large trees or exist as canopy dominants in forests (Little 1980a&b). Some species are decidedly shrubby, whereas others can grow to heights of 12 m (table 1). There are about 250 currently recognized species, with most native to the New World (about 200 species), and the remainder (about 50 species) native to the Old World (Christensen 1992; Phipps and others 1990). Species native to the United States, as well as those that have been introduced and naturalized and some of those grown horticulturally, are included herein (table 1).

Historically, the taxonomy of the hawthorn genus has been rife with disagreement and confusion. The circumscriptions of species have varied widely, and authors of various floristic treatments have misidentified species that occur in regions treated in their works (Phipps 1998c). The genus has vexed so many authors that early experts on the group termed the situation "the Crataegus problem" (Eggleston 1910; Palmer 1932). Nearly 1,500 "species" were described in North America alone, mostly by W. W. Ashe, C. D. Beadle, and C. S. Sargent, from the 1890s through the 1910s (Christensen 1992; Phipps 1988; Phipps and others 1990; Robertson 1974). Palmer later reduced the number of species of hawthorns, such that only 20 to 100 were recognized, a range followed by subsequent authors (Phipps 1988). Recently, taxonomists have taken a middle approach, recognizing 100 to 200 species in North America (Kartesz 1994a&b; Phipps and others 1990), a larger number than that accepted in treatments of 20 to 30 years ago. Two primary references—Kartesz (1994a) and Phipps and others (1990)—offer the most complete survey of North American hawthorns (excluding Mexico).

Crataegus belongs to the subfamily Maloideae in the Rosaceae, a natural group of complex genera with the ability to interbreed freely (or hybridize), as they all possess the basal chromosome number of 17 (Phipps and others 1991; Robertson 1974; Robertson and others 1991). Authors have long regarded hybridization and apomixis as potential explanatory factors for the speciation phenomenon existing in hawthorns (Phipps 1988; Radford and others 1968; Vines 1960). Robertson (1974) related empirically derived data that implicated apomixis and hybridization as causes of the variation found within the genus. Specifically, he cited (1) widespread occurrence of pollen sterility; (2) cytological proof of triploidy or polyploidy in > 75% of plants observed; (3) similarity between offspring produced from triploid or pollen-sterile plants and parental plants; and (4) the ability of flowers that have stigmas removed at anthesis to set fruit.

Many authors allude to the existence of putative hybrids in New World hawthorns (Elias 1987; Harlow and others 1996; Jacobson 1996; Kartesz 1994a&b; Knees and Warwick 1995; LHBH 1976; Little 1980a&b; Phipps 1984; Vines 1960). However, despite widespread documentation of hybrid species complexes existing in Eurasia (Christensen 1992), few scientifically verified examples of hybrid species in North American hawthorns are known (Phipps 1998a). Several recent studies now demonstrate unequivocal proof that both apomixis and polyploidy are implicated in the complex variation seen in this genus in North America (Dickinson 1985; Muniyamma and Phipps 1979a&b, 1984, 1985; Phipps 1984). Apomixis and hybridization are also known in other Rosaceous genera, including *Alchemilla* L. (lady's-mantle), *Cotoneaster* Medik. (cotoneaster), *Potentilla* L. (cinquefoil), and *Rubus* L. (blackberries and raspberries) (Mabberley 1997).

Around the world, hawthorns are used for a wide range of purposes. Many hawthorn species are grown for their

Table 1—*Crataegus,* hawthorn: nomenclature, occurrence, and heights at maturity

Scientific name & synonym(s)	Common name(s)	Occurrence	Height at maturity (m)
***C. aestivalis* (Walt.) Torr. & Gray** *C. cerasoides* Sarg. *C. luculenta* Sarg.; *C. maloides* Sarg.	**eastern mayhaw**, shining, may, or apple hawthorn	N Florida & SE Alabama, N to E North Carolina	3–12
***C. x anomala* Sarg. (pro sp.)** *C. arnoldiana Sarg.*	**Arnold hawthorn**, anomalous hawthorn	Quebec & New England, S to New York	5–10
***C. berberifolia* Torr. & Gray**	**barberry hawthorn,** bigtree hawthorn	Virginia to Kansas, S to Georgia & Texas	5–11
***C. brachyacantha* Sarg. & Engelm.**	**blueberry hawthorn**, blue haw, pomette bleu	Arkansas to Oklahoma, S to Mississippi & Texas; Georgia also	6–15
***C. brainerdii* Sarg.**	**Brainerd hawthorn**	Quebec to Michigan, S to New England, North Carolina & Ohio	2–7
***C. calpodendron* (Ehrh.) Medik.** *C. calpodendron* var. hispidula (Sarg.) Palmer *C. fontanesiana* (Spach) Steud. *C. hispidula* Sarg.; *C. tomentosa* L.	**pear hawthorn,** sugar or black hawthorn	Ontario to Minnesota & Kansas, S to Georgia & Texas	4–6
C. chrysocarpa* Ashe var. *chrysocarpa *C. brunetiana* Sarg. *C. doddsii* Ramalay; *C. faxonii* Sarg. *C. praecoqua* Sarg.; *C. praecox* Sarg. *C. rotundifolia* Moench; *C. sheridana* A. Nelson	**fireberry hawthorn,** roundleaf or golden-fruit hawthorn	Newfoundland to British Columbia, S to North Carolina & New Mexico	5–10
***C. coccinoides* Ashe**	**Kansas hawthorn,** Eggert thorn	Indiana to Kansas, S to Arkansas & Oklahoma	4–7
***C. crus-galli* L.** *C. acutifolia* Sarg.; *C. bushii* Sarg. *C. canbyi* Sarg.; *C. cherokeensis* Sarg. *C. mohrii* Beadle; *C.operata* Ashe; *C.palmeri* Sarg. *C. regalis* Beadle; *C. sabineana* Ashe *C. salicifolia Medik*. *C. signata* Beadle *C. subpilosa* Sarg.; *C. vallicola* Sarg. *C. warneri* Sarg.	**cockspur hawthorn,** Newcastle thorn, hog-apple	Quebec to Michigan & Kansas, S to Florida & Texas	5–10
***C. dilatata* Sarg.** *C. conspecta* Sarg. *C. loculples* Sarg.	**broadleaf hawthorn,** apple-leaf hawthorn	Quebec to Michigan, S to New York, Kentucky, & Missouri	4–8
***C. douglasii* Lindl.** *C. columbiana* Howell	**black hawthorn,** Douglas or western black hawthorn, black thornberry	Alaska to S California, Ontario to Dakotas, S to Michigan & Nevada	7–12
***C. erythropoda* Ashe** *C. cerronis* A. Nelson	**cerro,** chocolate hawthorn	Wyoming to Washington, S to New Mexico & Arizona	2–6
***C. flabellata* (Spach) Kirchn.** *C. densiflora* Sarg.; *C. grayana* Egglest.	**fanleaf hawthorn**	Maine to Quebec to Michigan, S to Florida & Louisiana	4–6
***C. flava* Ait.** *C. cullasagensis* Ashe	**yellow hawthorn** summer haw	Maryland & West Virginia, S to Florida & Mississippi	5–8
***C. greggiana* Egglest**.	**Gregg hawthorn**	Texas & NE Mexico	3–6
***C. harbisonii* Beadle**	**Harbison hawthorn**	Tennessee, S to Georgia & Alabama	3–8
***C. intricata* Lange**	**thicket hawthorn,** entangled or Allegheny hawthorn	New England to Michigan to Missouri, S to Florida & Alabama	1–7
***C. lacrimata* Small**	**Pensacola hawthorn,** weeping or sandhill hawthorn	Florida	3–6
***C. laevigata* (Poir.) DC.** *C. oxyacantha* L., in part *C. oxycanthoides* Thuill.	**English hawthorn,** English midland or English woodland hawthorn	Central & W Europe	2–4
***C. marshallii* Egglest**. *C. apiifolia* (Marshs.) Michaux	**parsley hawthorn,** parsley haw	Virginia to Illinois, S to Florida & Texas	2–8
***C. mollis* (Torr. & Gray) Scheele** *C. albicans* Ashe *C. arkansana* Sarg. *C. brachyphylla* Beadle *C. cibaria* Beadle *C. coccinea* var. *mollis* Torr. & Gray *C. invisa* Sarg.; *C. lacera* Sarg.; *C. limaria* Sarg.	**downy hawthorn,** summer hawthorn red haw, turkey-apple	Ontario to the Dakotas, S to Alabama & Texas	6–12
***C. monogyna* Jac.** *C. oxyacantha* L. ssp. *monogyna* (Jacq.) Rouy & Camus	**oneseed hawthorn,** single-seed or common hawthorn, may, quickthorn	Europe, N Africa, & W Asia	5–12

Table 1—*Crataegus,* hawthorn: nomenclature, occurrence, and heights at maturity (continued)

Scientific name & synonym(s)	Common name(s)	Occurrence	Height at maturity (m)
***C. nitida* (Engelm.) Sarg.** *C. viridis* var. *nitida* Engelm.	**shining hawthorn,** glossy hawthorn, & shining thorn	Ohio to Illinois, S to Arkansas	7–12
***C. opaca* Hook. & Arn.** *C. nudiflora* Nutt. ex Torr. & Gray	**western mayhaw**, apple haw, may, or riverflat hawthorn	W Florida to Texas, N to Arkansas	6–10
C. pedicellata* Sarg. var. *pedicellata *C. aulica* Sarg.; *C. caesa* Ashe *C. coccinea* L. in part	**scarlet hawthorn,** Ontario hawthorn	Maine to Michigan, S to Virginia & Illinois; South Carolina & Florida also	4–8
***C. persimilis* Sarg.** *C. laetifica* Sarg.; *C. prunifolia* Pers.	**plumleaf hawthorn**	New York to Ontario, S to Pennsylvania & Ohio	7–10
***C. phaenopyrum* (L. f.) Medik.** *C. cordata* (Mill.) Ait. *C. populifolia* Walt. *C. youngii* Sarg.	**Washington hawthorn**, Virginia hawthorn, Washington thorn, hedge thorn, red haw	New Jersey to Missouri, S to Florida, Mississippi & Louisiana	4–10
***C. piperi* Britt.** *C. chrysocarpa* Ashe var. *piperi* (Britt.) Krushke *C. columbiana* auct. *C. columbiana* var. *columbiana* T.J. Howell *C. columbiana* Howell var. *piperi* (Britt.) Egglest.	**Columbia hawthorn,** Piper hawthorn	British Columbia, S to Idaho & Oregon	4–6
***C. pruinosa* (Wendl. f.) K. Koch** *C. formosa* Sarg. *C. georgiana* Sarg. *C. lecta* Sarg.; *C. mackenzii* Sarg. *C. leiophylla* Sarg.; *C. porteri* Britt. *C. rugosa* (Ashe) Kruschke; *C. virella* Ashe	**frosted hawthorn,** waxy-fruited hawthorn	Newfoundland to Wisconsin, S to West Virginia & Oklahoma	2–8
***C. pulcherrima* Ashe** *C. flava* Ait., not auctt. *C. opima* Beadle; *C. robur* Beadle	**beautiful hawthorn**	Florida to Mississippi	4–8
***C. punctata* Jacq.** *C. fastosa* Sarg. *C. punctata* var. *aurea* Ait. *C. verruculosa* Sarg.	**dotted hawthorn,** flat-topped, thicket, or large-fruited hawthorn	Quebec to Minnesota & Iowa, S to Georgia & Arkansas	5–10
***C. reverchonii* Sarg.**	**Reverchon hawthorn**	Missouri to Kansas, S to Arkansas & Texas	1–8
***C. rufula* Sarg.**	**rufous mayhaw**	N Florida, SW Georgia, & SE Alabama	3–9
***C. saligna* Greene**	**willow hawthorn**	Colorado	4–6
***C. sanguinea* Pall.**	**Siberian hawthorn**	E Russia & Siberia, S to Mongolia & China	5–8
***C. spathulata* Michx.** *C. microcarpa* Lindl.	**littlehip hawthorn,** small-fruited or pasture hawthorn	Virginia to Missouri, S to Florida to Texas	5–8
***C. succulenta* Schrad. ex Link** *C. florifera* Sarg.; *C. laxiflora* Sarg.	**fleshy hawthorn,** longspine or succulent hawthorn	Nova Scotia to Montana, S to North Carolina & Utah	5–8
***C. tracyi* Ashe ex Egglest.** *C. montivaga* Sarg.	**Tracy hawthorn,** mountain hawthorn	Texas & NE Mexico	3–5
***C. triflora* Chapman**	**three-flower hawthorn**	Tennessee, S to Georgia & Louisiana	4–6
***C. uniflora* Münchh.** *C. bisculcata* Ashe; *C. choriophylla* Sarg. *C. dawsoniana* Sarg.; *C. gregalis* Beadle	**dwarf haw,** one-flowered hawthorn, & dwarf thorn	New York to Missouri, S to Florida & NE Mexico	$^1/_2$–4
***C. viridis* L.** *C. amicalis* Sarg. *C. ingens* Beadle	**green hawthorn**, southern or tall hawthorn, green haw, green or southern thorn	Pennsylvania to Kansas, S to Florida & Texas	5–12

Sources: Beadle (1913), Brinkman (1974), Dirr (1998), Flint (1997), Foote and Jones (1989), Griffiths (1994), Jacobson (1996), Little (1980a&b), Palmer (1950, 1952), Phipps (1988, 1995, 1998a&b), Phipps and O'Kennon (1998), Phipps and others (1990), Sargent (1933), Strausbaugh and Core (1978), Tidestrom (1933), Vines (1960), Wasson (2001), Weakley (2002).

edible fruits in Asia, Central America, and various Mediterranean countries (Everett 1981; Guo and Jiao 1995; Mabberley 1997; Usher 1974). The fruits of some species contain higher concentrations of vitamin C than do oranges (*Citrus* L. spp.) (Morton 1981).

In recent years, cultivation of mayhaws native to the southeastern United States—including eastern, western, and rufous mayhaws—has increased (Bush and others 1991; Payne and Krewer 1990; Payne and others 1990). Mayhaws are atypical among the hawthorns in their early flowering period (from late February through mid-March) and their early fruit ripening dates (May) (table 2) (Payne and Krewer 1990). At least 12 cultivars have been selected for improved fruit size, yield, and ease of harvest, and these are grown for production of jellies, juices, preserves, and wine. Vitamin contents are comparable to those found in manzanilla (*Crataegus mexicana* Moc. & Sesse ex DC.) (Payne and others 1990), a species used for medicinal purposes in Central America (Morton 1981). However, until propagation, production, and harvest techniques are improved, limited supplies of fruits derived from orchard-grown plants will necessitate further collection of fruit from native stands (Bush and others 1991). Other North American *Crataegus* species cultivated for fruit production are black, yellow, and downy hawthorns (Mabberley 1997; Usher 1974).

Many hawthorn taxa are grown in North America and Europe solely as ornamental plants because of their small stature, brilliant flowers in spring, and brightly colored fruits in fall (Bean 1970; Christensen 1992; Dirr 1998; Everett 1981; Flint 1997; Griffiths 1994; Jacobson 1996; Knees and Warwick 1995; Krüssmann 1984; Mabberley 1997). In the United States, the most commonly encountered hawthorn taxa in cultivation include Washington,'Winter King', cockspur, plumleaf, and Lavalle hawthorns (*C.* × *lavallei* Henriq. ex Lav.) (Bir 1992; Dirr 1998; Everett 1981; Flint 1997). One caution, however, is necessary with regard to cultivated hawthorns. Because only a partial understanding of the taxonomy of native populations of hawthorns now exists, especially in North America, it is likely that identities of many cultivated hawthorns may be either incorrect or imprecisely defined.

Hawthorns are important for wildlife. They offer good nesting sites for birds because of their dense branching and their thorns, which deter predators (Martin and others 1961). Fruits of many species are consumed by songbirds, game birds, small mammals, and ungulates (Shrauder 1977). Hawthorns are recommended commonly by professionals as landscaping and shelterbelt plants that can attract wildlife (Bir 1992; Elias 1987; Foote and Jones 1989; Morgenson 1999; Petrides 1988).

Flowering and fruiting. Flowers always appear after leaf emergence and are borne either in flat-topped inflorescences termed corymbs or in globular inflorescences termed umbels (Phipps 1988). Flower color is usually white, but rarely, pink-flowered variants are found in horticultural selections. From 1 to 25 flowers can be produced per inflorescence (Christensen 1992; Phipps 1988). Flowers usually contain 5 petals and 5 to 20 stamens and have a fetid odor in many species.

Hawthorn fruits are known as pomes, although the seeds and their bony endocarps are termed pyrenes, or nutlets (figures 1 and 2). Between 1 and 5 pyrenes are produced in each pome. Although most species produce flowers in spring and fruits in fall, mayhaws are notable for their early flowering and fruit ripening period. Some species drop fruits in autumn, and others have fruits that persist through winter. Timing of these events is important to horticulturists and wildlife and game managers (table 2).

Collection of fruits, seed extraction, cleaning, and storage. Mature fruits of most hawthorn species are collected readily from the ground in autumn, whereas fruits of species that tend to hold their fruits through the winter must be hand-picked from the trees (Brinkman 1974). Harvested fruits can be macerated to separate the seeds from the fleshy pericarp (Munson 1986). The macerated pericarp material can be removed by water flotation, and the seeds should then be air-dried. Seed yield data are available for only a few species, and there is considerable variability among them (table 3).

As an alternative to macerating the fruits and subsequently storing the seeds, fermenting freshly collected, undried fruits of western mayhaw for 4 or 8 days yielded 93% germination. However, fermentation periods > 8 days adversely affected seed germination (Baker 1991). Most other reports stated that acid scarification and/or cold stratification are obligatory to enhance seed germination. Fermentation treatments may prove extremely beneficial in reducing the time required to produce seedlings of hawthorns. However, further research on a wide range of hawthorns is needed before making general conclusions about the usefulness of such treatments.

After extracting, cleaning, and drying, the seeds should be stored under refrigerated conditions (Dirr and Heuser 1987; Hartmann and others 2002). All indications are that hawthorn seeds are orthodox in storage behavior, but reports on long-term seed viability during storage do not all agree.

Table 2—*Crataegus,* hawthorn: phenology of flowering and fruiting, and color of ripe fruit

Species	Flowering	Fruit ripening	Color of ripe fruit*
C. aestivalis	Mar	May–June	Lustrous, scarlet
C. x anomala	May	Sept–Oct	Bright crimson
C. berberifolia	Mar–Apr	Oct	Orange with red face
C. brachyacantha	Apr–May	Aug	Bright blue with white wax
C. brainerdii	May–June	Sept–Oct	Red
C. calpodendron	May–June	Sept–Oct	Orange-red to red
C. chrysocarpa	May–June	Aug–Sept	Yellow to orange to crimson
C. coccinoides	May	Oct	Glossy, dark crimson
C. crus-galli	June	Oct	Dull red
C. dilatata	May	Sept	Scarlet with dark spots
C. douglasii	May	Aug–Sept	Lustrous, black to chestnut-brown
C. erythropoda	Apr–May	Oct	Red to wine purple, brown, or black
C. flabellata	May	Sept	Crimson
C. flava	Apr	Oct	Dark orange-brown or yellow
C. greggiana	Apr	Oct–Nov	Bright red
C. harbisonii	May	Oct	Bright red or orange-red
C. intricata	May–June	Oct	Greenish or reddish brown
C. lacrimata	Apr	Aug	Dull yellow or orange or red
C. laevigata	Apr–May	Sept–Oct	Deep red
C. marshallii	Apr–May	Oct	Bright scarlet
C. mollis	May	Aug–Sept	Scarlet with large dark dots
C. monogyna	May	Sept–Oct	Bright red
C. nitida	May	Oct	Dull red covered with white wax
C. opaca	Feb–Mar	May	Lustrous scarlet with pale dots
C. pedicellata	May	Sept	Glossy, scarlet
C. persimilis	May–June	Oct	Bright red
C. phaenopyrum	May	Sept–Oct	Lustrous scarlet
C. piperi	May–June	Aug–Sept	Salmon-orange to scarlet
C. pruinosa	May–June	Oct–Nov	Dark purple-red
C. pulcherrima	Apr–May	Sept–Oct	Red
C. punctata	May–June	Sept–Oct	Dull red or bright yellow
C. reverchonii	May	Oct	Shiny or dull red
C. rufula	Mar–Apr	June–July	Red
C. saligna	May	Oct	Red to blue-black
C. sanguinea†	May	Aug–Sept	Bright red
C. spathulata	Apr–May	Sept–Oct	Red
C. succulenta	May–June	Sept–Oct	Bright red
C. tracyi	Apr–May	Sept–Oct	Orange-red
C. triflora	May	Oct	Red, hairy
C. uniflora	Apr–May	Sept–Oct	Yellow to dull red to brown
C. viridis	Apr–May	Sept–Oct	Bright red, orange-red, yellow

Sources: Beadle (1913), Brinkman (1974), Dirr (1998), Everett (1981), Flint (1997), Foote and Jones (1989), Jacobson (1996), Little (1980a&b), Palmer (1950, 1952), Phipps (1988, 1998a), Phipps and O'Kennon (1998), Sargent (1933), Vines (1960).

* Color of ripe fruit is highly arbitrary and varies in interpretation amoung authors due to lack of standardization. Accurate determinations of fruit color cannot be ascertained from herbarium specimens.

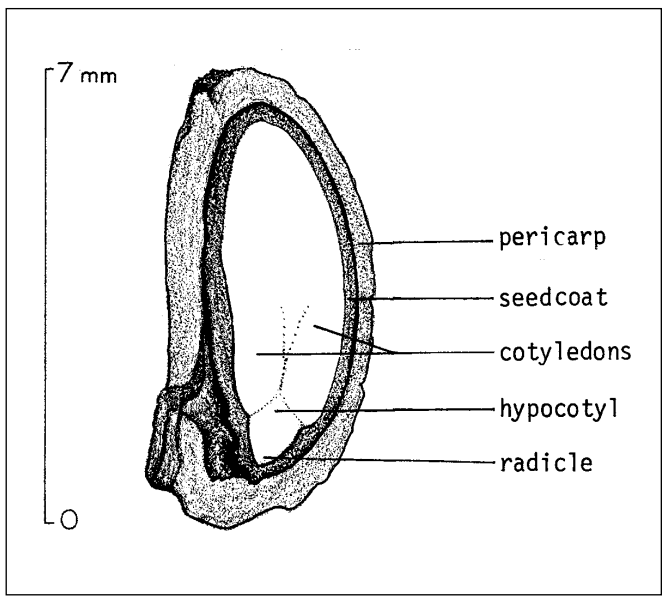
† Plants growing in Boston, Massachusetts, not in native habitat.

Dirr and Heuser (1987) stated that seeds of hawthorns, in general, can remain viable for 2 to 3 years in cold storage. St. John (1982), however, noted decreased seed viability in oneseed, cockspur, plumleaf, and scarlet hawthorns after storage for 2 years and recommended that seeds be stored for no more than 1 year. Bir (1992) found decreases in seed viability of Washington hawthorn after cold storage for 1 year. However, Christensen (1992) observed that under natural conditions, seeds of Eurasian species may require from 2 to 6 years to germinate.

Pregermination treatments and germination tests. Seeds of many hawthorns exhibit double dormancy (Hartmann and others 2002). Therefore, pregermination treatments usually consist of acid scarification followed by a period of cold stratification (Brinkman 1974; Hartmann and others 2002). Many authors also recommend periods of warm stratification for selected species (Brinkman 1974; Dirr and Heuser 1987; Morgenson 1999; St. John 1982; Young and Young 1992). Brinkman (1974) stated that "all" seeds of hawthorns exhibit embryo dormancy, therefore

Figure 1—*Crataegus*, hawthorn: cleaned pyrenes (nutlets) of *C. crus-galli*, cockspur hawthorn (**top**), *C. douglasii*, black hawthorn (**second**), *C. mollis*, downy hawthorn (**third**), *C. phaenopyrum*, Washington hawthorn (**fourth**), *C. punctata*, dotted hawthorn (**fifth**), *C. succulenta*, fleshy hawthorn (**bottom**).

Figure 2—*Crataegus*, hawthorn: longitudinal section of a pyrene (nutlet).



requiring cold stratification. This is reflected in the general recommendation by Hartmann and others (2002) that, following acid scarification, seeds should be stratified for 5 months at 4 °C. However, Kosykh (1972) reported that acid scarification and cold stratification for 6 months did not enhance germination of several species of hawthorns occurring in the Russian Crimea. In *C. mexicana*, cold stratification failed to enhance germination in seeds that were pretreated with 1 or 3 minutes of hot-water soaking at 80 °C (Felipe Isaac and others 1989). The fermentation work by Baker (1991) with western mayhaw also demonstrated high germination percentages without pretreating the seeds via acid scarification or cold stratification. Phipps (1998c) commented that hawthorns native to warm temperate climates possessed only endocarp dormancy, whereas those species native to regions with colder climates displayed embryo dormancy in addition to endocarp dormancy. In a large and geographically widely distributed group such as hawthorn, these different observations are not surprising.

Differences in endocarp thickness have been noted by several authors. Endocarp thickness in oneseed hawthorn varies not only among individual trees, but also over years (St. John 1982). Some species (for example, Washington hawthorn) lack thickened endocarps and can germinate without acid scarification (Bir 1992; Brinkman 1974; Dirr and Heuser 1987; Hartmann and others 2002). In contrast, other hawthorns exhibit highly thickened endocarps (up to 0.5 cm) and require up to 7 to 8 hours of acid scarification (Dirr and Heuser 1987) before other germination pretreatments can be imposed. Table 4 summarizes pregermination treatments that have been tested on various species of *Crataegus*.

Tipton and Pedroza (1986) studied germination requirements of Tracy hawthorn and failed to achieve germination > 54% in seeds pretreated with acid scarification for up to 4.5 hours, in combination with other pretreatments (table 4). They speculated that a combination of longer durations of acid scarification (for example, > 4.5 hours), lower germination chamber temperatures (for example, < 16 °C), shorter durations of warm stratification (for example, 0 to 60 days), and longer durations of cold stratification (for example, 100 to 322 days) might improve germination in this species. The low germination percentages observed may have been due to embryo decay caused by excessively long periods of warm stratification or high temperatures in the germination chamber, in combination with incomplete modification of the endocarp due to an inadequate duration of acid scarification. Interestingly, some seeds germinated during cold stratification before being placed into the germination chambers.

Morgenson (1999) noted differential responses of 3 hawthorns to acid scarification, as well as warm and cold stratification pretreatments. Specifically, he found that

Table 3—*Crataegus,* hawthorn: seed yield data

Species	Provenance	Seed wt/fruit wt		Average cleaned seeds/wt		Samples
		kg/kg	lb/100 lb	/kg	/lb	
C. chrysocarpa	South Dakota	—	—	21,500	10,750	1
C. douglasii	Washington, Idaho, Oregon	0.15	15.2	45,200	22,600	6
C. phaenopyrum	—	—	—	59,600	29,800	1
C. punctata	Minnesota	0.11	11.3	9,400	4,700	2
C. sanguinea	Russia	0.15	15.0	—	—	—
C. succulenta	—	—	—	41,200	20,600	1

Source: Brinkman (1974).

although 2 hours of acid scarification did not enhance seed germination of Arnold and downy hawthorns, some beneficial effects on seed germination in fireberry hawthorn were noted, especially in combination with warm and cold stratification pretreatments. Germination of both Arnold and downy hawthorn seeds was optimized under a 60-day warm and 120-day (or more) cold stratification regime, with 37 and 51% germination occurring, respectively. For fireberry hawthorns, 90 to 120 days of warm stratification, followed by 120 to 180 days of cold stratification resulted in 18 to 27% germination. In all 3 species tested, extreme radicle elongation was observed in some treatments, for example, in all 120-day cold stratification combination treatments for fireberry hawthorns, and in some 60 and 120-day cold stratification combination treatments for Arnold and downy hawthorns.

In *C. azarolus* L., cold stratification treatments reduced abscisic acid (ABA) content in seeds, especially during the first 20 days, but only yielded 24% germination (Qrunfleh 1991). Work in England with oneseed, cockspur, plumleaf, and scarlet hawthorns resulted in as much as 80% germination (see table 4 for pregermination treatments) (St. John 1982). Using alternating 3-month periods of warm stratification at 21°C and cold stratification at 4 °C, seeds of oneseed hawthorn exhibited 31% germination after a warm-cold cycle and 55% after a cold-warm-cold-warm-cold cycle (Deno 1993). Utilizing these alternating cold-warm regimes with Washington hawthorn, 50% germination was attained with a warm-cold scheme, and 51% germination occurred with cold stratification only (Deno 1993). This latter result for Washington hawthorn agreed with data reported by Brinkman (1974). Studying seeds of downy hawthorn sown into old-field vegetation patches, Burton and Bazzaz (1991) noted a negative correlation between germination percentage and the quantity of plant litter on the soil surface. This suggested that seed germination in downy hawthorn may be inhibited by the presence of organic acids or allelochemicals released by decaying organic matter.

Official seed testing prescriptions are in place for only 2 species. AOSA (1993) recommends 2 hours of soaking in concentrated sulfuric acid, followed by 90 days of incubation at room temperature and then 120 days of moist-prechilling for downy hawthorn. Germination should then be tested on moist blotters or creped paper at 20/30 °C for 14 days. For oneseed hawthorn, ISTA (1993) prescribes 90 days of incubation at 25 °C, followed by 9 months of moist-prechilling at 3 to 5 °C. Germination is to be tested in sand at 20/30 °C for 28 days. Both organizations also allow tetrazolium staining to determine viability as an alternative to actual tests. For all hawthorn species, ISTA (1996) recommends cutting transversely one-third from the distal end of the seeds, then incubating for 20 to 24 hours in a 1% solution at 30 °C. The embryos must be excised for evaluation. Maximum unstained tissue is one-third the distal end and the radicle tip. Some germination test results are summarized in table 5.

Because hawthorns produce apomictic seeds, reports have appeared on clonal production of plants by seed propagation (Hartmann and others 2002). In western mayhaw, this phenomenon occurs widely because of the production of nucellar embryos and may be exploitable for production of superior clones (Payne and Krewer 1990; Payne and others 1990). Further study of apomixis in *Crataegus* is needed.

Nursery practice. Hawthorns are produced in nurseries utilizing both sexual and asexual propagation techniques. In horticulture, sexual propagation of hawthorns (via seeds) is important for production of large numbers of rootstocks, to which superior, clonal scions (often cultivars) are budded (Bush and others 1991; Dirr and Heuser 1987). In particular, this is necessary for rapid build-up of clonal orchards of desirable species of hawthorns (such as those with potential pomological interest), for which there are limited scion material and little knowledge of vegetative propagation by stem cuttings. Western mayhaw is a good example of such a species (Bush and others 1991). Brinkman (1974)

recommended that if controlled seed pretreatment regimes (such as stored refrigerated conditions) are not used by nurseries, seeds should be sown in early fall (versus spring) to satisfy any potential requirements for cold stratification. This may be an adequate generalization for many hawthorns, although it is important to note the aforementioned exceptions for those species (for example, those from warm temperate climates) that will germinate either in shorter time periods without the cumbersome waiting periods involved in cold stratification or through innovative seed pretreatment techniques such as fermentation.

Research on vegetative propagation of hawthorns by stem cuttings is limited. Dirr and Heuser (1987) reported previous efforts as being "rarely successful," whereas Dirr

Table 4—*Crataegus,* hawthorn: pregermination treatments

Species	Scarification* (hrs)	Stratification treatments: Warm period Temp (°C)	Warm period Days	Cold period Temp (°C)	Cold period Days
C. anomala	4.5	—	—	2–9	180
	0	21–27	30–90	2–9	90–180
C. crus-galli	2–3	21–25	21	Low†	21–135
	0	21	120	7	135
C. douglasii	0.5–3	—	—	5	84–112
C. mollis	2	25	90	5	120
	0	30	21	10	180
C. monogyna	—	25	90	3–5	270
	0.5–2	20	14–28	2–4	70–84
C. pedicellata	2	20	28	2–4	84
C. persimilis	4	20	14–28	2–4	70–84
C. phaenopyrum	0	—	—	5–10	135
C. punctata	0	21	120	5	135
C. sanguinea	2	21–25	21	5	21
	0	20–25	30	4–7	—
C. succulenta	0.5	—	—	4	110–140
C. tracyi	0, 0.5, 2.5, 4.5	21–27	0, 20, 60, 120	4	0, 20, 100

Sources: Brinkman (1974), Felipe Isaac and others (1989), Qrunfleh (1991), St John (1982), Tipton and Pedroza (1986), Young and Young (1992).
* Immersion time in sulfuric acid (H_2SO_4).
† Outdoor winter temperatures.

Table 5—*Crataegus,* hawthorn: germination test conditions and results

Species	Germination test conditions*: Medium	Temp (°C): Day	Temp (°C): Night	Days	Germination: Avg (%)	Germination: Samples
C. anomala	Soil	8	2	180	35	1
C. crus-galli	Soil	21	21	21	73	1
C. douglasii	Peat or sand	21	21	35–45	30†	6
C. mollis	Soil	21	21	—	42–50	3
C. phaenopyrum	Soil	21	21	—	71	2
	Peat	5	5	135	92	1
C. punctata	Peat	21	21	21	60	1
C. sanguinea	Peat	21	21	21	73	1
	Peat	4	7	30	50	2
C. succulenta	Soil	—	—	—	35–40	2
C. tracyi ‡	Germination blotters	16	16	28	0	2

Sources: Brinkman (1974), Tipton and Pedroza (1986).
* Light provided ≥ 8 hours per day. For each species, seeds were pretreated as shown in table 4.
† Sound seed was approximately 45% of total seeds sown.
‡ 16/8 hour light/dark cycle used.

(1998) and Hartmann and others (2002) make no mention of stem cutting propagation. However, 35% rooting was achieved utilizing softwood stem cuttings of 2 cultivars of western mayhaw—'Super Spur' and 'T.O. Super Berry'—treated with 8,000 ppm of the potassium (K) salt of indolebutyric acid (IBA) in combination with 2,000 ppm of the K salt of naphthaleneacetic acid (NAA) (Payne and Krewer 1990). Hardwood stem cuttings of this species (no clone specified) exhibited poor rooting, with callus visible 12 weeks after sticking cuttings, and ultimately only 10% rooting occurring (Bush and others 1991). However, softwood stem cuttings taken from new growth in mid-spring (in Calhoun, Louisiana) rooted in percentages > 80% in 8 weeks under intermittent mist. No differences in rooting occurred for cuttings treated with talc formulations of 0, 3,000, or 8,000 ppm IBA (Bush and others 1991). Clearly, these latter results suggest potential for developing readily producible clonal hawthorns by stem cuttings. If so, this could reduce the importance of seed-propagated hawthorns.

Vegetative propagation of hawthorns by grafting and budding is used widely in the horticulture industry. T-budding is one of the most viable vegetative propagation procedures employed for a wide range of cultivars of hawthorns (Dirr and Heuser 1987; Hartmann and others 2002). Root-grafting is also mentioned (Hartmann and others 2002) but rarely practiced. In the United States, Washington hawthorn is the "universal" rootstock, due to the fact that (a) seedlings are commonly available (because seeds of this hawthorn species germinate more easily than those of other species) and (b) bark-slippage occurs over a long season (late summer to early fall) (Dirr and Heuser 1987). Cultivars budded onto Washington hawthorn can be expected to grow 0.9 to 1.2 m in the growing season following budding (Dirr and Heuser 1987). Cultivars of European species (for example, English and oneseed hawthorns) should be budded onto rootstocks of European species, whereas hawthorns native to North America should be budded onto rootstocks of North American species (Dirr and Heuser 1987; Hartmann and others 2002). Aside from these constraints, T-budded hawthorns appear to be highly compatible across many species.

Several grafting procedures are employed (rather than budding procedures) in production of plants of mayhaw. Cleft grafts for larger rootstocks or whip-and-tongue grafts for small diameter rootstocks are used widely in late winter (Payne and Krewer 1990). In Louisiana, cleft grafting is the most popular grafting method used for western mayhaw (Bush and others 1991). Other species, such as parsley, cockspur, Washington, and yellow hawthorns, also can be used as rootstocks for mayhaws (in particular, western mayhaw) due to graft compatibility (Payne and Krewer 1990).

Brinkman (1974) called for additional trials on hawthorns to acquire more knowledge on seed biology. However, little comprehensive research has been conducted in the intervening 30 years on this subject. Much work remains to be done before a comprehensive understanding of propagation of hawthorns will be possible.

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Taxodiaceae—Redwood family

Cryptomeria japonica (L. f.) D. Don

sugi or cryptomeria

Gerald A. Walters and John K. Francis

Dr. Walters retired from the USDA Forest Service; Dr. Francis retired from the USDA Forest Service's International Institute of Tropical Forestry

Synonyms. *C. fortunei* Hooibrenk, *C. mairei* (Leveille) Nakai, *C. kawaii* Hayata, *Cupressus japonica* L. f., *Cupressus mairei* Leveille.

Other common names. Japanese cryptomeria, Japanese-cedar, goddess-of-mercy-fir, peacock-pine.

Growth habit, occurrence, and use. *Cryptomeria* is a monotypic genus native of Japan and China (Streets 1956). *Sugi—Cryptomeria japonica* [L. f.] D. Don—has been cultivated there since about 1300 A.D. for timber, shelterbelts, and environmental forestry. It was introduced to Hawaii for the same purposes about 1870 by Japanese immigrants (Carlson and Bryan 1959). An evergreen tree, it reaches heights of 36 to 46 m (Carlson and Bryan 1959; Dallimore and Jackson 1967; Troup 1921). Its wood is soft and fragrant; the red heartwood is strong and durable (Dallimore and Jackson 1967). It is used for boxes, poles, and general construction (Tsutsumi and others 1982). This species is also used for Christmas trees (Carlson and Bryan 1959; Dallimore and Jackson 1967).

Flowering and fruiting. Sugi is a monoecious species, with the male and female strobili located on different parts of the same branch. The female strobili are formed in fall and are fertilized when pollen is shed the following spring (Dallimore and Jackson 1967). Seed weight and percentage filled seeds are higher and seedling growth rate is greater when flowers are wind-pollinated (outcrossed) rather than selfed (Tabachi and Furukoshi 1983). In the native range in Japan, female cones begin to open between late January and mid-February and flower for 54 to 57 days. The male strobili begin to open about 25 days after the female strobili (Hashizume 1973). The solitary cones are globular and measure 13 to 19 mm in diameter. In Hawaii, cones ripen from July to September.

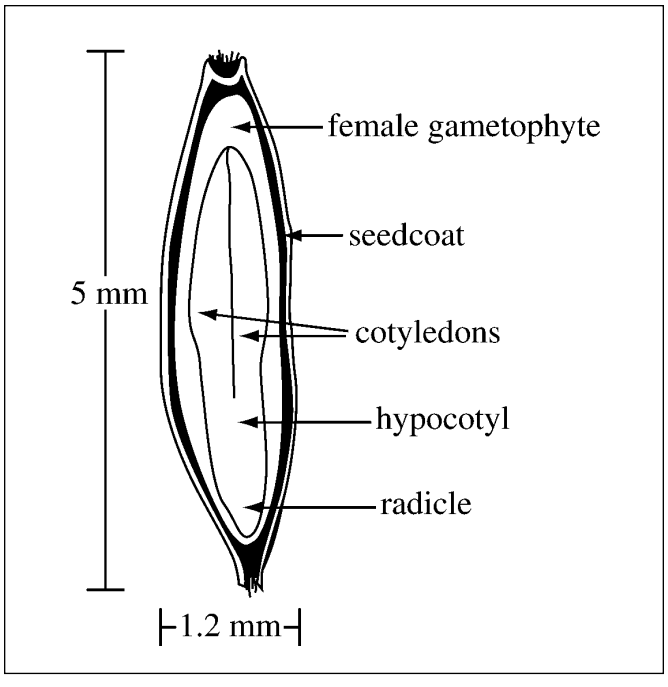
Seeds are shed during the same periods (Walters 1974). The seeds are dark brown and triangular, measuring 4 to 6 mm long and about 3 mm wide (Dallimore and Jackson 1967) (figures 1 and 2). Trees generally begin to produce seeds when 15 to 20 years old (Carlson and Bryan 1959). A 3-year-old orchard of rooted cuttings in Japan that was sprayed with gibberellic acid produced 1,082 kg/ha of seeds (967 lb/ac) 11 months later; 46% of the seeds were sound and 45% germinated (Itoo and Katsuta 1986).

Collection, cleaning, and storage. When the cones turn from grayish brown to reddish brown, they are ripe and should be picked. Cones should be immediately spread out to finish ripening. As the cones dry, seeds fall into trays; agitation aids in seed extraction. Seeds can be separated from chaff by winnowing. The number of seeds per weight ranges from 700,000 to 1,200,000/kg (320,000 to 550,000/lb) (Walters 1974; Ohmasa 1956). The optimal moisture content for storage is 10% (Shi 1985). After drying, the seeds should be stored in sealed polyethylene bags at 2 to 5 °C (Walters 1974). A drying agent placed in the bag aids storage (Ohmasa 1956).

Germination. Sugi seed germination is considered poor to very poor (Parry 1956). In Japan, the standard of sowing—30 g/m² (0.1 oz/ft²)—is based on 30% germination (Ohmasa 1956). Sugi seeds should be soaked in cold water (0 °C) for about half a day, then put moist into plastic bags, and stored at 1 °C for 60 to 90 days before sowing (Walters 1974). Bags should be left open for adequate aeration. A mild fungicide can be added (Ohmasa 1956). Constant day/night temperature, whether high or low, adversely affects germination (RFC 1973). Germination is better in

Figure 1—*Cryptomeria japonica*, sugi: seed.

Figure 2—*Cryptomeria japonica*, sugi: longitudinal section through a seed.



seeds kept in the light than seeds kept in the dark (Chettri and others 1987). Official test prescriptions for sugi call for germination on top of moist blotters at alternating temperatures of 20 and 30 °C for 28 days; no pretreatment is necessary (ISTA 1993).

Nursery and field practice. Sugi seeds are sown in Hawaii from November to March. Sowing is by the broadcast method or by using a planter that has been adjusted to the proper seed size. The planter places seeds in rows about 15 to 20 cm (6 to 7 in) apart. Seeds are covered with 3 to 6 mm (1 to $2^1/_2$ in) of soil (Ohmasa 1956; Walters 1974). No mulch is used in Hawaii (Walters 1974), but a single layer of straw is used in Japan (Ohmasa 1956). The seedbeds are given about 75% shade for about 2 months (Walters 1974). Seedling density in the beds is about 220 to 330 seedlings/m^2 (20 to 30/ft^2). Frost damage to seedlings in early winter can be avoided by shading or shortening the daily period of exposure to solar radiation (Horiuchi and Sakai 1978). Seedlings are outplanted as 1+0 stock in Hawaii (Walters 1974). Sugi can be started from cuttings (Carlson 1959). In an experiment in which the trees were measured after more than 26 years, there was no significant difference in any measure of growth between trees started from seeds and those started from cuttings (Yang and Wang 1984).

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Cupressaceae—Cypress family

Cupressus L.

cypress

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Growth habit, occurrence, and use. The true cypresses—genus *Cupressus* L.—are evergreen trees or shrubs native to the warm temperate areas of the Northern Hemisphere. The genus comprises about 15 species distributed throughout the western United States, Mexico, northern Central America, the Mediterranean region, northern Africa, and from southern Asia to Japan (Bailey 1923; Dallimore and Jackson 1967; Little 1966, 1979; Raizada and Sahni 1960; Wolf and Wagener 1948). The species native to North America are referred to as New World cypresses and those native to Europe, Africa, and Asia, as Old World cypresses (Gauseen 1968; Wolf and Wagener 1948).

Most New World cypresses are restricted in their occurrence (table 1). McNab and Sargent cypresses are often associated with serpentine soils (Griffin and Stone 1967; Hardham 1962). Arizona cypress and its subspecies are found in large stands confined mainly to north slopes, coves, benches, and canyon bottoms (Sudworth 1915). All reach their maximum sizes in moist, sheltered canyon bottoms. Of the 10 species, subspecies, and varieties native to California, none grow in large pure stands.

In the United States, cypresses are commercially propagated mainly for landscaping, Christmas trees, erosion control, windbreaks, and to a minor extent for lumber, fenceposts, fuelwood, and railroad ties. A factor limiting the widespread planting of cypresses in some parts of the United States is the cypress canker—*Seiridium cardinale* (W. Wegener) Sutton & I. Gibson—which attacks most species of cypress (Wolf and Wagener 1948). In California, this disease has eliminated some plantations of Monterey cypress. Only resistant species or strains of cypress should be planted where the cypress canker disease exists. In the South, Arizona cypress was at one time seriously considered for Christmas tree production (Goggans and Posey 1968; Grigsby 1969; Linnartz 1964; Posey and Goggans 1967), but its susceptibility to a foliage blight caused by *Cercospora sequoiae* Ellis & Everh. (Hepting 1971) has eroded this interest.

In Africa and New Zealand, Mexican and Monterey cypresses are planted for lumber and pulp production (Bannister 1962; Bannister and Orman 1960; Paterson 1963). Mexican cypress has become commercially important in Ethiopia, Kenya, and Tanzania (Bergsten and Sundberg 1990). Himalayan cypress is planted for timber, fuelwood, windbreaks, and animal fodder in Asia (Von Carlowitz 1986).

Italian cypress is the most widely planted of all the cypresses. It has been cultivated since ancient times (Bailey 1923; Bolotin 1964a); its columnar form and dark green foliage make it a popular tree for planting in formal gardens, along roads, and in cemeteries. This variety is propagated by seeds or cuttings. Seeds collected from pure stands or isolated columnar form varieties will breed true (Bolotin 1964b). The unusually narrow crown results from the ascending branches, which almost parallel the main trunk (table 2).

Monterey cypress is also extensively used in landscaping in spite of its high susceptibility to cypress canker disease. The rapid growth, lush green foliage, and dense crown make it ideally suited for planting around buildings, in windbreaks, and along roadsides.

Flowering and fruiting. Cypresses are monoecious. Staminate and ovulate strobili are produced on the ends of short twigs or branchlets. The staminate strobili are 3 to 7 mm long, cylindrical or oblong, and light green or rarely red. They become yellow as pollen-shedding time nears. Ovulate strobili at time of pollination are less than 6 mm long, subglobose to cylindrical, erect, greenish, and have 6 to 12 (rarely 14) distichously arranged scales. At maturity they may be 15 to 25 mm long.

Pollen is shed in late fall, winter, and spring. Planted trees of Arizona and Guadeloupe cypresses growing in the Eddy Arboretum, Placerville, California, shed their pollen in

Table 1—*Cupressus,* cypress: nomenclature and occurrence

Scientific name & synonym(s)	Common names	Occurrence
***C. abramsiana* C.B. Wolf** *C. goveniana* var. *abramsiana* (C.B. Wolf) Little	**Santa Cruz cypress**	California: Santa Cruz & San Mateo Co.
***C. arizonica* Greene**	**Arizona cypress**	Small, scattered areas in mtns of Arizona, New Mexico, S Texas, & N Mexico at 915–2,450 m
***C. arizonica* ssp. *arizonica* Greene** *C. arizonica* var. *glabra* (Sudsworth) Little *C. glabra* Sudsworth	**Arizona smooth cypress**	Mtn areas of central Arizona
***C. arizonica* ssp. *nevadensis* (Abrams) E. Murray** *C. arizonica* var. *nevadensis* (Abrams) Little *C. macnabiana* var. *nevadensis* (Abrams) Abrams *C. nevadendsis* Abrams	**Piute cypress**	California: Kern Co., Piute Mtns
***C. arizonica* ssp. *stephensonii* (C.B. Wolf) Beauchamp** *C. arizonica* var. *stephensonii* (C.B. Wolf) Little *C. stephensonii* C. B. Wolf	**Cuyamaca cypress**	California: San Diego Co., Cuyamaca Mtns
***C. bakeri* Jepson** *C. bakeri* ssp. *matthewsii* C.B. Wolf	**Modoc cypress,** Baker cypress, Siskiyou cypress	California & Oregon in Siskiyou Mtns & NE California
***C. forbesii* Jepson** *C. guadalupensis* var. *forbesii* (Jepson) Little *C. quadalupensis* ssp. *forbesii* (Jepson) Beauchamp	**tecate cypress**	San Diego Co., California, & Baja California, Mexico
***C. goveniana* Gord.**	**Gowen cypress**	California coast from Mendocino Co. to San Diego Co.
***C. goveniana* ssp. *pygmaea* (Lemmon) Bartel** *C. goveniana* var. *pygmaea* Lemmon *C. pygmaea* (Lemmon) Sarg.	**Mendocino cypress,** pygmy cypress	California coast in Mendocino Co.
***C. guadalupensis* S. Wats.**	**Guadalupe cypress**	Mexico, Guadalupe Island
***C. lusitanica* Mill.**	**Mexican cypress,** cedar-of-Gog, Portuguese-cedar	Central Mexico, S to Guatemala & Costa Rica
***C. macnabiana* A. Murr.**	**MacNab cypress**	N California: Sierra Nevada foothills & interior coastal range from Siskiyou to Napa Co.
***C. macrocarpa* Hartw. ex Gord.**	**Monterey cypress**	Central California coast in Monterey Co. between Monterey & Carmel Bays; scattered on inland ridges
***C. sargentii* Jepson** stands	**Sargent cypress**	California, in the coastal range in scattered from Mendocino Co. S to Santa Barbara Co.
***C. sempervirens* L.** *C. sempervirens* var. *stricta* Aiton	**Italian cypress,** Mediterranean cypress	Mediterranean area
***C. sempervirens* var. *horizontalis* (Mill.) Gord.**	**spreading Italian cypress**	Mediterranean area
***Cupressus torulosa* D.Don** *C. torulosa* var. *corneyana* Carr.	**Himalayan cypress,** *surai*	Temperate China to tropical India & Queensland, Australia

Sources: Johnson (1974), Sargent (1965), Sudworth (1967).

October and November (Johnson 1974). Native trees of Sargent cypress at Bonnie Doon, California, pollinate in December, and Monterey cypress at Point Cypress, California, pollinate in March (Johnson 1974).

The ovulate cones and their seeds ripen the second year, some 15 to 18 months after pollination. Mature cones (figure 1) are up to 30 mm in diameter, woody or leathery, and the peltate scales usually have a central mucro. Each cone produces 12 to 150 seeds (table 3).

Precocious cone production characterizes this genus. Male cones have developed on 1- and 2-year-old seedlings of Gowen and Mendocino cypresses, respectively (McMillan 1952). Female cone production often begins on trees younger than 10 years (Magini and Tulstrup 1955; McMillan 1952), but collectable quantities are usually not produced at such an early age. Treatment of seedlings of some species with various gibberellins can stimulate precocious flowering to a great degree. Mendocino, Mexican, and

Table 2—*Cupressus*, cypress: growth habit, height, cone and seed ripeness criteria

Species	Growth habit	Height at maturity (m)	Year first cultivated	Color ripeness criteria: Cones	Color ripeness criteria: Seed
C. arizonica	Straight central leader	15–21	1882	Dull gray to brown, sometimes purple	Medium to dark brown or deep purplish brown
ssp. *arizonica*	Straight trunk with or without turned up side branches	8–15	ca. 1909	Glaucous bloom over rich dark brown	Medium tan to brown or red brown
ssp. *nevadensi*	Erect tree with pyramidal crown	6–15	1930	Glaucous or silver gray	Rich light tan
ssp. *stephensonii*	Erect tree with straight central leader	9–15	1900	Dull gray or brown	Very dark brown
C. bakeri	Single stem, narrow crown	9–15	1917	Grayish to dull brown	Light tan
C. forbesii	Erect, irregularly branched tree	4.5–9	1927	Dull brown or gray	Rich dark brown
C. goveniana	Shrublike to small tree with single stem	6–18	1846	Brown to gray brown	Dull dark brown to nearly black
ssp. *pygmaea*	Shrublike to medium-sized tree	9–46	—	Weathered gray	Jet black to brownish
C. guadalupensis	Broad crown, trunk forking	12–20	ca. 1879	—	Dark brown & glaucous
C. lusitanica	Erect straight trunk with drooping branches	30	ca. 1670	Dull brown	Rich light tan
C. macnabiana	Brown crown lacking main trunk	6–12	1854	Brownish gray	Medium brown to glaucous brown
C. macrocarpa	Single trunk; symmetrical in sheltered areas	8–27	1838	Brown	Dark brown
C. sargentii	Single stem, slender or bushy tree	9–23	1908	Dull brown or gray often glaucous	Dark brown
C. sempervirens	Columnar with branches parallel to main trunk	46	B.C.	Shiny brown or grayish	—
var. *horizontalis*	Single stem with spreading crown	46	B.C.	Shiny brown or grayish	—

Sources: Dallimore and Jackson (1967), Raizada and Sahni (1960), Sargent (1965), Sudworth (1915), Wolf and Wagener (1948).

Arizona cypresses produced staminate strobili on seedlings 7 to 9 months old after foliar applications of gibberellin (GA_3), whereas the latter 2 species produced ovulate strobili at ages less than 24 months (Pharis and Morf 1967). Most native and planted cypresses produce an abundance of female cones. Guadelupe cypress rarely produces female cones under cultivation (Wolf and Wagener 1948), but the close relative, tecate cypress from Baja California, does (Johnson 1974). Occasional trees appear sterile, but this phenomenon is usually correlated with extremely heavy male cone production (Johnson 1974). Most cypresses have serotinous cones. Arizona and Italian cypresses open and shed their seeds when the cones ripen (Wolf and Wagener 1948). Cones on some trees within a stand will open and shed their seeds in July (Posey and Goggans 1967).

There is little information on the cone and seed insects that damage seed production in cypress. Larvae of the cypress bark moth—*Laspeyresia cupressana* Kearfott—are known to feed on maturing seeds of Gowen and Monterey cypresses and have earned the common name of "seedworm." Similar damage has been recorded on Monterey cypress from larvae of the moth *Henricus macrocarpan*a Walsingham (Hedlin and others 1980). Over a dozen microorganisms have been identified in association with cypress seeds (Mittal and others 1990), but their effects on seed production, if any, are not known.

Cypress seeds vary widely in shape and size (figures 2 and 3). Length with wings attached ranges from 2 to 8 mm; width dimensions are slightly less. Seeds are flattened or lense shaped, and the wings are tegumentary extensions of the seedcoat. Seed length within a cone of Sargent cypress ranged from 2 to 5 mm (Johnson 1974). X-ray examination of bulk collections of several species showed that the smallest seeds were hollow (Johnson 1974). This phenomenon is most likely caused by lack of pollination or abortion after pollination (Johnson 1974).

Seed color is an important criterion for determining ripeness and an aid in differentiating species (table 2). Some species and geographic sources within a species can be distinguished by seed color. Seeds of Mendocino cypress from the central coast of Mendocino Co., California, have shiny jet-black seedcoats; seeds of the Anchor Bay strain from southern Mendocino Co. have brownish black seedcoats. Seeds of Guadalupe and tecate cypresses have the same

Table 3—*Cupressus*, cypress: seed yield data

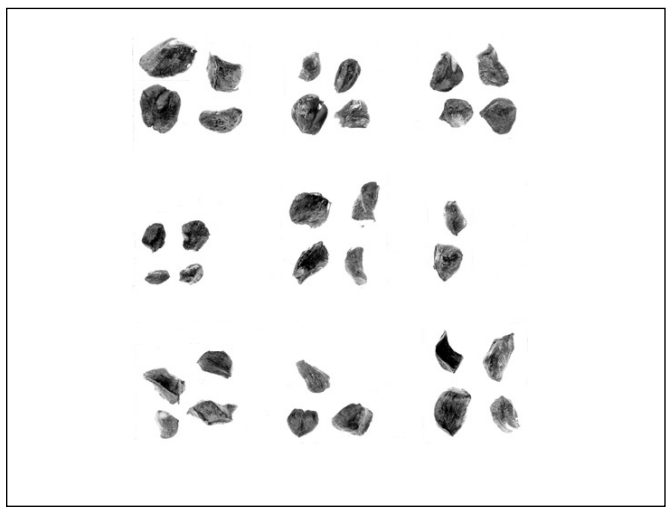
Species	Seeds (x1,000)/weight* Range /kg	Range /lb	Average /kg	Average /lb	Samples	Scales/cone	Seeds/cone
C. arizonica	387.6–103.2	176.2–46.9	182.6	83.0	77+	6–8	90–120
ssp. *arizonica*	210.3–65.1	95.6–29.6	121	55.0	22+	5–10	90–100
ssp. *nevadensis*	201.1–86.7	91.4–39.4	126.5	57.5	11+	6–8	93
ssp. *stephensonii*	123.2–95.0	56.0–43.2	109.1	49.6	2	6–8	100–125
C. bakeri	387.2–316.8	176.0–144.0	359.9	163.6	4	6–8	50-85
C. forbesii	112.6–84.5	51.2–38.4	98.6	44.8	2	6–10	—
C. goveniana	313.3–253.4	142.4–115.2	283.4	128.8	2	3–5	90–110
ssp. *pygmaea*	246.4-232.3	112.0–105.6	239.4	108.8	2	8–10	130
C. guadalupensis	—	—	55.0	25.0	1	8-10	>100
C. lusitanica	—	—	261.8	119.0	1	6-10	75
C. macrocarpa	356.4–100.1	162.0–45.5	167.4	76.1	20	8–12	140
C. macnabiana	200.6–147.8	91.2–67.2	174.2	79.2	2	6–8	75–105
C. sargentii	147.8–98.6	67.2–44.8	123.2	56.0	2	6–10	100
C. sempervirens	149.6–118.8	68.0–54.0	137.9	62.7	9	8–14	64–280
C. torulosa	238-200	108–91	219	99	—	—	—

Sources: Goggans and Posey (1968), Rafn (1915), Raizada and Sahni (1960), Toumey and Stevens (1928), Von Carlowitz (1986), Wolf and Wagener (1948).

* Figures are for samples that have foreign matter (twigs, leaves, cone scales, etc.) removed but no attempt was made to separate sound from hollow and other nonviable seeds.

Figure 1—*Cupressus goveniana*, Gowen cypress: cones.

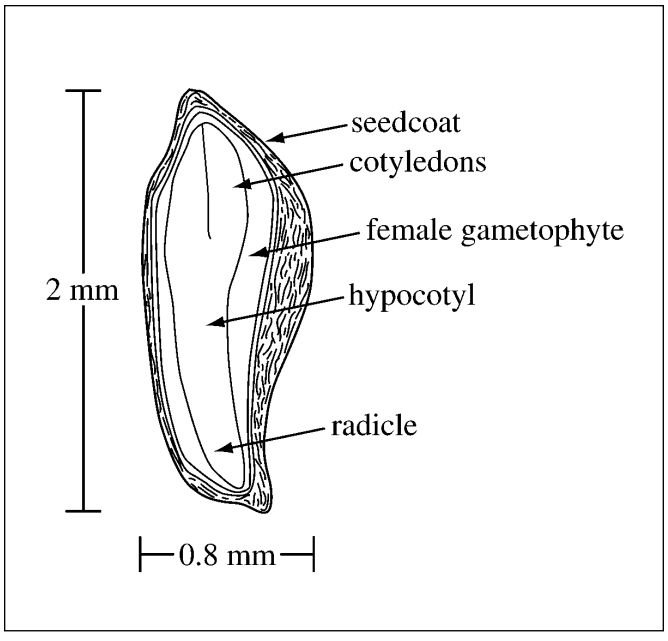
Figure 2—*Cupressus*, cypress: seeds of *C. arizonica*, Arizona cypress (**upper left**); *C. bakeri*; Modoc cypress (**upper center**); *C. goveniana*, Gowen cypress (**upper right**); *C. goveniana* ssp. *pygmaea*; Mendocino cypress (**middle left**); *C. forbesii*, tecate cypress (**middle center**); *C. lusitanica*, Mexican cypress (**middle right**); *C. macnabiana*, MacNab cypress (**bottom left**); *C. macrocarpa*, Monterey cypress (**bottom center**); and *C. sargentii*, Sargent cypress (**bottom right**).



color, but seeds of Guadalupe cypress have a glaucous bloom and those of tecate cypress are shiny (Wolf and Wagener 1948).

Collection of cones. Mature cones are normally collected by hand from standing trees, usually by cutting clusters of cones with hand clippers. To ensure that the seeds are mature, only seeds from cones that matured the previous season or seeds with thoroughly darkened coats from the current season should be collected (Wolf and Wagner 1948). Goggans and others (1974) confirmed this rule in collections of Arizona cypress made in Alabama plantations. Cones that had turned gray in Alabama were over 5 years old and yielded seeds of quality not much better than immature cones. It is advisable, therefore, to collect only cones 4 years old and younger. Insect-damaged cones should not be collected because they do not readily open, and many of the seeds have been destroyed by the insects (Wolf and Wagener 1948). The time of year for collecting cones for most species is not critical if older cones are collected. Seeds of Italian cypress and some Arizona cypress sspp. are

Figure 3—*Cupressus arizonica*, Arizona cypress: longitudinal section through a seed.



shed when the cones are mature, so they must be collected as soon as they ripen. Cone and seed color aid in determining when the seeds are ripe (table 2).

Extraction and storage of seed. Cypress cones must be dried for the seeds to be released. Cones dried at room temperature 22 °C require 1 to 2 months for the scales to separate and the seeds to fall out (Posey and Goggans 1967). The process of cone opening can be speeded up by boiling the cones for 30 to 60 seconds or cutting each cone in half. Either method hastens the process of cone opening by several weeks. Clusters of cones should be cut apart so the scales can freely separate.

Sun-drying is another good method, provided the weather is hot and dry. Ripe cones of Gowen and Monterey cypresses collected in July were stored in a refrigerator at 1 °C for 2 days, then placed in trays. The cones opened and shed their seeds within 2 weeks when sun-dried in day temperatures of 32 to 35 °C with relative humidity ranging from 20 to 39% (Johnson 1974). Case-hardening is a potential hazard when sun-drying. This problem is minimized or eliminated by storing the cones for several days in a refrigerator, which will act as a desiccator.

Seeds fall out readily from completely mature cones with little or no tumbling. Insect-attacked and immature cones keep their seeds tightly attached to the cone scales, but such seeds usually have low viability and are best discarded with the cones. De-winging is not necessary, as the seeds have minute or no wings.

The percentage of filled seeds varies widely among species and among individuals within a species (table 4). Values for Arizona cypress ranged from 10 to 29% filled seeds, whereas those for the subspecies Arizona smooth cypress ranged from 1 to 49% filled seeds (Goggans and Posey 1968). Major improvements in seed quality can result from careful cleaning that minimizes loss of good seeds. This may be done with either a well-controlled air separation or a specific gravity table. Bergsten and Sundberg (1990) reported an upgrading of a Mexican cypress seedlot from 20 to 60% filled seeds with incubate-dry-separate (IDS) techniques (see chapter 3).

Cypress seeds are orthodox in storage behavior and maintain viability very well at low temperatures and moisture contents. There are no long-term storage test data available, but seeds of 7 species of cypress retained good viability during 10 to 20 years storage at temperatures of 1 to 5 °C (Johnson 1974; Schubert 1954; Toumey and Stevens 1928).

Pregermination treatments. Seeds of most cypress species exhibit some dormancy, and treatments are required for prompt germination. Ceccherini and others (1998) reported that, for 14 species of cypress, 30 days of stratification at 20 °C stimulated seed germination of all except Guadalupe cypress, and that the greatest benefit was shown by Monterey and Arizona smooth cypresses. At the USDA Forest Service's Institute of Forest Genetics at Placerville, California, seeds were stratified for 30 days at 1 °C (Johnson 1974). Stratification for 60 to 90 days has been recommended for Monterey cypress (Von Carlowitz 1986). Goggans and others (1974) also found 30 days of prechilling effective in breaking dormancy of Arizona cypress. The stratification was supplemented slightly by first soaking the seeds in a 0.1% citric acid solution. When time was short, a 72-hour water soak gave some benefit over just a 24-hour water soak. Seeds are often heavily contaminated with mold and bacteria, but control of the mold is feasible with fungicides during stratification and germination. Local extension experts should be consulted for current treatment recommendations. Treated medium and seeds can then be stored in plastic bags, jars, or petri dishes for the duration of the stratification period. Seeds stratified in a petri dish can be germinated in the same dish.

Germination. Germination should be tested with seeds placed on the top of moist blotters. ISTA (1993) recommends alternating temperatures of 30 °C (day) for 8 hours and 20 °C (night) for 16 hours for Arizona and Monterey cypresses, and a constant 20 °C for Italian cypress. Test periods of 28 days are prescribed for Arizona and Italian cypresses and 35 days for Monterey cypress.

Table 4—*Cupressus*, cypress: germination test results on stratified seeds

Species	Days	Germination Average (%)	Germination Samples	Soundness Average (%)	Soundness Samples
C. arizonica	20	26	9	30	4
ssp. *nevadensis*	6	6	1	38	1
C. bakeri	30	12	2	36	2
C. forbesii	30	12	2	54	1
C. goveniana	30	22	2	93	2
ssp. *pygmaea*	30	31	2	—	—
C. macnabiana	30	1	1	5	1
	—	—	15	2	—
C. macrocarpa	30	24	4	82	4
	30	14	37	—	—
C. sargentii	30	13	2	41	2
C. sempervirens	—	—	—	27	9

Source: Johnson (1974).

* Soundness was determined by x-radiography examination before stratification (Johnson 1974).

Because of variable dormancy, AOSA (1998) also recommends paired tests for Arizona cypress, using unstratified and stratified (21 days) samples for each lot. Official test prescriptions have not been developed for the other cypress species, but similar conditions should be sufficient. For unstratified Himalayan cypress seeds (Rao 1988), the use of the alternating germination temperatures of 21 °C daytime and 9 °C night time gave 60% germination compared to 33% germination at constant 25 °C. Although light appears to be important, prechilling and alternating temperatures are the more significant promoters of germination. Light did not appear necessary for seeds of Arizona cypress (Goggans 1974). The seeds can be watered throughout the test with a mild solution of fungicide (the same formulation used above) with no phytotoxicity. Germination test results (table 4) have been low primarily because of the low percentages of sound seed that are common among seed lots of cypress. Good estimates of germination can be made with x-ray analysis of fresh seeds of Italian, Mexican, and Arizona cypresses (Bergsten and Sundberg 1990; Chavagnat and Bastien 1991).

Nursery practice. Fall-sowing of cypress seeds has been recommended (Johnson 1974; Wolf and Wagener 1948), but spring-sowing of stratified seeds is preferred. Germination of cypress is epigeal. Seeds should be sprinkled on the nurserybed and covered with a 4 to 5 mm (0.15 to 0.20 in) layer of soil and a light mulch. A density of 320 to 640/m^2 (30 to 60/ft^2) is recommended. Zeide (1977) was successful in direct seeding Italian cypress in Israel—annual precipitation, 447 mm (18 in)—in plots that were "mulched" with light colored stones of 2 to 5 cm ($^3/_4$ to 2 in) diameters. The seedlings grew out from under the stones.

Newly germinated cypress seedlings are particularly susceptible to damping-off fungus. When possible, nursery soil should be fumigated. As an added precaution, a fungicide should be used immediately after sowing and until the seedling stems become woody, which takes about 1 month's time. Cypresses can be outplanted as 1- or 2-year-old seedlings. A well-defined taproot and numerous lateral roots are formed in the first year. One-year-old seedlings of most species have only juvenile foliage.

Some species can be propagated vegetatively. Monterey cypress cuttings treated with indole-butyric acid (IBA) root well, whereas Italian cypress cuttings root well without treatment (Dirr and Heuser 1987).

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C

Fabaceae—Pea family

Cytisus scoparius (L.) Link

Scotch broom

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Growth habit, occurrence, and uses. The genus *Cytisus* comprises about 80 species native to Eurasia and North Africa. Many are cultivated as ornamentals, and several of these have become more or less naturalized in the United States, especially in California (Munz and Keck 1959). Scotch broom—*C. scoparius* (L.) Link—was planted extensively for erosion control during the first half of the century (Gill and Pogge 1974) but is now considered a serious invasive weed throughout the range of its introduction in North America, Australia, and New Zealand (Bossard 1991). It has become the dominant species on several hundred thousand hectares of coastal and cis-montane vegetation, from Santa Barbara, California, north to British Columbia. It is a drought-deciduous shrub with angled, photosynthetic stems that is able to root-sprout following fire (Bossard and Rejmanek 1994; Gonzales-Andres and Ortiz 1997). It is largely useless as a browse-plant because of its toxic foliage, a feature that may permit it to increase at the expense of more palatable species (Bossard and Rejmanek 1994; Gill and Pogge 1974). It increases in response to disturbance of native vegetation and is also a serious weed problem in pine plantations in California and New Zealand.

However, because of its beauty and exceptional summer drought-hardiness, Scotch broom is considered valuable as an ornamental shrub for low-maintenance landscapes. The species is very showy in flower and its evergreen stems add interest to winter landscapes. There are over 60 named varieties (Wyman 1986).

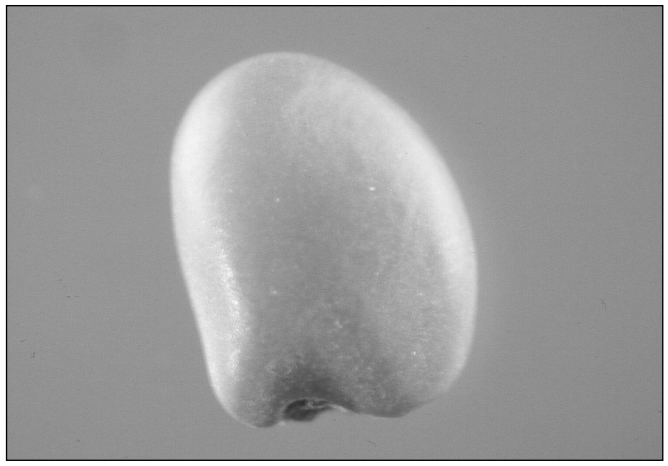
Flowering and fruiting. The perfect flowers are of typical pea-family form and appear on the plants in great profusion in May and June. Each flower must be "tripped" by an appropriate pollinator for fertilization to take place, so the mutualistic relationship with honey bees (*Apis mellifer*a L.) and native bumble bees is essentially obligatory (Parker 1997). Other native North American insects seem to ignore its fragrant blossoms, preferring to work the flowers of indigenous species. The result is that seed production may be severely pollinator-limited (Parker 1997). In spite of this, the plants may produce a prodigious number of seeds; the estimated mean annual production per plant was about 10,000 seeds in 2 California populations (Bossard and Rejmanek 1994). Host-specific pre-dispersal seed predators from Europe (a seed weevil and a bruchid beetle) have been introduced for biocontrol of Scotch broom in the Northwest, but so far these introductions have been largely ineffective, possibly because of asynchrony in the phenology of host and seed predator (Bravo 1980).

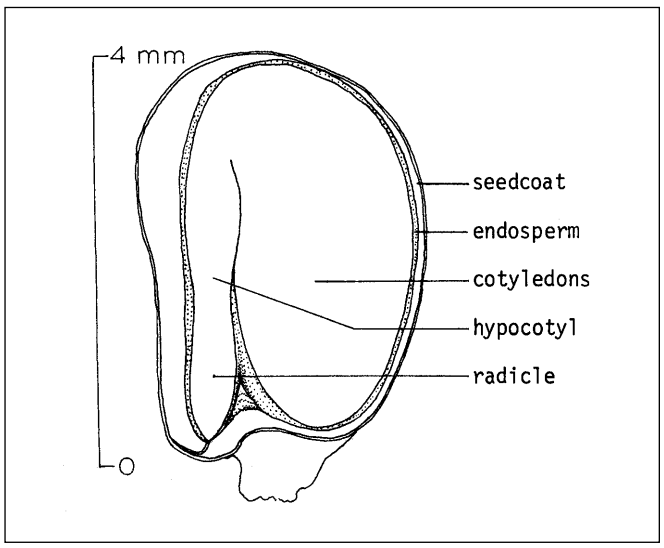
Plants reach reproductive maturity at about 4 years of age (Gill and Pogge 1974). The 5- or 6-seeded legumes (pods) ripen in August, and seeds are dispersed in September. The legumes open abruptly with a springing motion, vaulting the seeds some distance from the plant (Bossard 1991; Bossard and Rejmanek 1994). The seeds possess a strophiole or elaiosome at the hilar end (figure 1) and are secondarily dispersed by ants (Bossard 1991; Weiss 1909). At 2 California study sites, seeds were taken by mice and by ground-feeding birds, but these organisms were strictly seed predators and did not function as dispersers (Bossard 1991).

Seeds of Scotch broom have the capacity to form a persistent seed bank. Bossard (1993) found in seed retrieval experiments that 65% germinated the first year after dispersal, 20% germinated the second year, and 10% germinated the third year. About 5% of the seed population carried over for more than 3 years.

Seed collection, cleaning, and storage. After the fruits ripen but before they disperse, the legumes may be hand-stripped or picked up from beneath plants. They should be spread to dry, threshed, and screened to separate the seeds (Gill and Pogge 1974). Reported seed weights have averaged 125 seeds/g (57,500/lb) in 9 samples, and viability averaged 80% in 5 samples (Gill and Pogge 1974).

Figure 1—*Cytisus scoparius*, Scotch broom: longitudinal section through a seed (**bottom**) and exterior view (**top**).





No long-term storage data are available, but the seeds are orthodox and remain viable for many years in storage.

Germination and seed testing. Scotch broom seeds have water-impermeable (hard) seedcoats and require pretreatment in order to germinate. Once the seedcoats have been made permeable, the seeds germinate well over a wide range of temperatures and do not require any further pretreatment (Bossard 1993). Mechanical and acid scarification have been used to remove hard-seededness in this species, and the official seed-testing rules call for cutting or nicking the seedcoat at the cotyledon end, then soaking in water for 3 hours (ISTA 1993). Tests should be carried out on the tops of moist paper blotters for 28 days at 20/30 °C. More recently, the effect of heat on hard-seededness in Scotch broom has received attention. Tarrega and others (1992) report that dry-heating the seeds was as effective as mechanical scarification in terms of final percentage. Optimum time of heating varied with temperature from 1 minute at 130 °C to 15 minutes at 70 °C. Abdullah and others (1989) reported that repeated brief (3-second) immersion in boiling water resulted in complete elimination of hard-seededness, but low germination percentages indicated that some damage was occurring. They found that alternating the boiling water treatments with freezing treatments (immersion in liquid nitrogen for 15 seconds) resulted in the highest germination percentages as well as in complete removal of hard-seededness. This result was confirmed by Bossard (1993), who found that vigor of seedlings from hot/cold–treated seeds was much higher than that of seedlings from seeds subjected to dry heat only.

Nursery practice. Scotch broom is normally propagated from cuttings for ornamental planting in order to preserve varietal characters (Wyman 1986). If seed propagation is desired, seeds should be pretreated to remove hard-seededness prior to planting (Gill and Pogge 1974). The roots are delicate, and plants are more easily produced in container culture than as bareroot stock (Wyman 1986).

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D

Fabaceae—Pea family

Delonix regia (Bojer ex Hook.) Raf.

flamboyan

J. A. Vozzo

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Other common names. royal poinciana, flametree.

Occurrence and growth habit. A popular ornamental throughout the tropics, flamboyan—*Delonix regia* (Bojer ex Hook.) Raf.—is a small to medium-sized tree, typically 7 to 16 m high and up to 60 cm in diameter (Little and Wadsworth 1964). The champion Puerto Rican flamboyan, however, is 32 m high and 105 cm in diameter (Francis 1994). It grows well in moist soil derived from limestone, where it is common and reproduces well, but it is also tolerant of well-drained and somewhat droughty conditions (Francis and Liogier 1991). The species is briefly deciduous. Flamboyan has prominent buttresses and a broad, flat crown when grown in full sun. Its shallow but spreading root system limits the sites where it may be planted. The tree is susceptible to termites, shoot borers, and heart rot (Webb and others 1984). Although the genus is reported to have 3 species, flamboyan is the most cosmopolitan. A native of Madagascar, it has been planted in nearly every country in frost-free areas and is perhaps the most important flowering ornamental tropical tree of the world (Meninger 1962).

Use. This is a beautiful tree in form, shade, and flower. The flowers are predominantly red, although yellow and orange forms are cultivated; they are relatively short-lived as cut flowers. Trees remain in flower for several weeks, however. They are often seen planted along roadsides as living fence posts or as shade trees on both sides of the road that arch over the entire road. The wood is yellow-brown, weak, brittle, and soft, with a specific gravity of about 0.3. Although the species is not a good timber source, the wood is widely used as firewood. The legume (pod) is edible (Little and Wadsworth 1964; Menninger 1962; Webb and others 1984).

Flowering and fruiting. Showy flowers follow a dry season when the tree is almost leafless. The 5-pointed calyx is hairy and borne on racemes 15 to 25 cm long. Flowers are commonly red but may be white, yellow, orange, or yellow and vary from 8 to 25 cm across. Although flowers form after the dry season and during the wet season, they persist during leaf emergence so that the crown appears feathery green while the colorful flowers are dominant. The hard legumes are 35 to 50 cm long, 6 cm wide, and 5 mm thick, and they hang tenuously on trees year-round. When mature, the legumes split into 2 parts lengthwise and are dark brown to black (Little and Wadsworth 1964); seeds (figures 1 and 2) are shed at that time. There are about 4,500 seeds/kg (2,040/lb) from Puerto Rican sources (Marrero 1949), whereas Colombian sources report only 2,000 to 3,000 seeds/kg (900 to 1,360/lb) (Navarette nd).

Collection, extraction, and storage. Pruning poles should be used to collect dark brown to black legumes. Legumes open naturally on trees after about 6 months. If unopened legumes are collected, they should be dried in the sun for 1 month; then the woody legumes should be forced open and the seeds removed. Seeds are relatively loosely attached in lateral grooves inside the legume. Dry seeds store very well in either open or closed containers and do not require refrigerated storage (Francis 1994). Seeds stored for 12 months at 26 °C germinated at 60% (Marrero 1949). Webb and others (1984) reported viability after 4 years storage but do not give germination rate or percentage germination.

Figure 1—*Delonix regia*, flamboyan: mature seed.

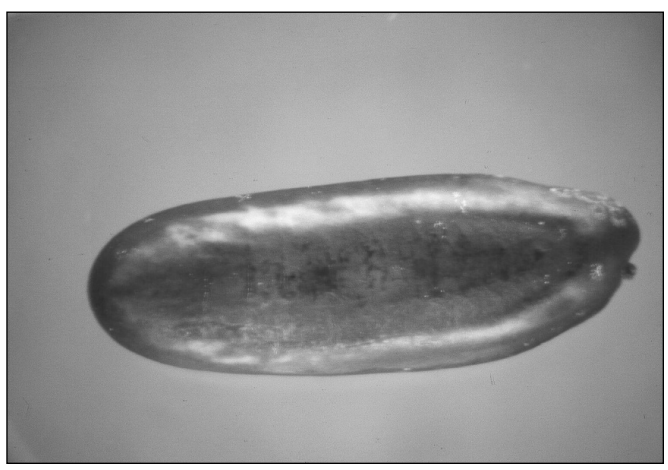
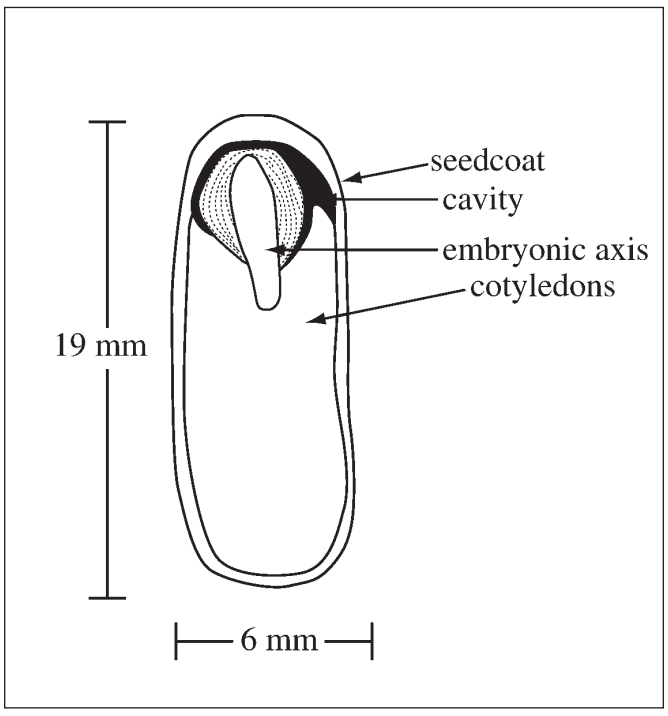


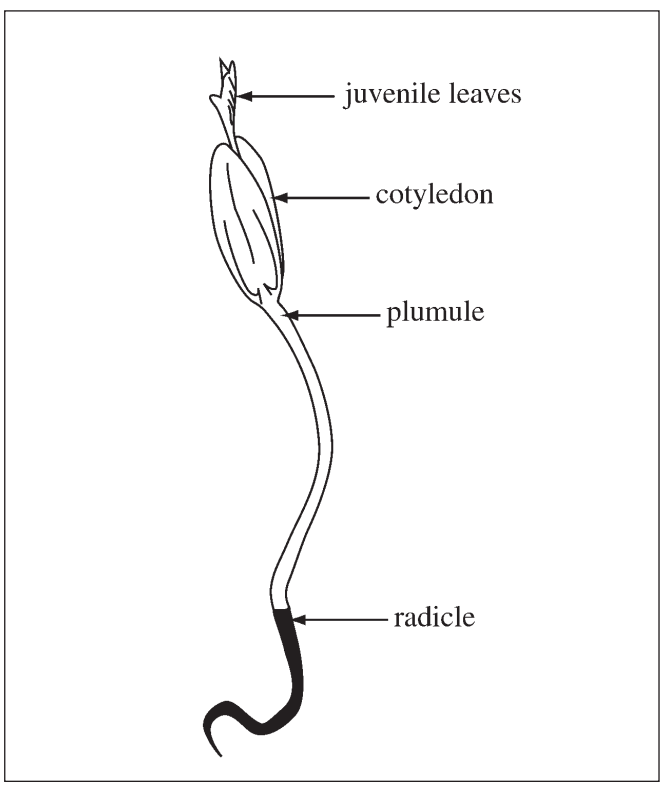
Figure 2—*Delonix regia*, flamboyan: longitudinal section through a seed.



Germination. Scarification—with either hot water, sulfuric acid, or abrasion—is required for germination. Millat-E-Mustafa (1989) recommends 90 °C water for 10 seconds followed by 24 hours of imbibition. A concentrated sulfuric acid soak for 0.5 to 5 hours improved germination for Duarte (1974), whereas a hot-wire scarification proved superior to other means described by Sandiford (1988). Seeds subjected to the various scarification treatments reported here had germination values superior to those of their respective controls. Within 8 days of fresh collections, expect 76% germination after 9 weeks.

Nursery practice. Seedlings (figure 3) are ready for outplanting after 3 to 4 months of growth in plastic nursery bags during the wet season. Saplings are also grown to 2 m, then "balled and burlaped" for large ornamental potted plants. Mature flowering and fruiting trees may be grown in 3 to 5 years in good sites (Francis 1994).

Figure 3—*Delonix regia*, flamboyan: seedling at 10 days after germination.



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D

Papaveraceae—Poppy family

Dendromecon Benth.

bushpoppy

W. Gary Johnson and Donald L. Neal

Mr. Johnson retired from the USDA Forest Service's National Seed Laboratory; Dr. Neal retired from the USDA Forest Service's Pacific Southwest Forest and Range Experiment Station

Growth habit, occurrence, and use. Bushpoppies (also known as treepoppies) are openly branched, evergreen shrubs from 0.6 to 2.5 m high, sometimes to 6 m. They have a woody base with gray or white shreddy-barked stems. The 2.5- to 10-cm-long leaves are mostly lanceolate, 3 to 8 times longer than wide (LHBH 1976). Environmental factors and shoot growth pattern affect leaf size (Bullock 1989). The 2 species considered here grow on dry chaparral slopes, ridges, and washes below 1,830 m. One species is found in California's Channel Islands and the other in the coastal range, from Sonoma County to the Sierra San Pedro Martir, Baja California, Mexico, and in the west foothills of the Sierra Nevada, from Shasta County to Tulare County (table 1). Bush-poppies rely on seed production to propagate. No lignotuber is formed on sprouts that appear after burning, so regrowth after fire is rare (Bullock 1989). The genus is useful for watershed protection (Sampson and Jespersen 1963) and for forage. Goats are especially fond of bushpoppies, and deer (*Odocoileus* spp.) and sheep eat the sprouts after fire.

Flowering and fruiting. Flowers are bisexual, yellow, showy, and solitary on stalks. At several locations, the shrubs first flowered in their second spring (Bullock 1989). Flowers appear in April through June and sometimes into August (Munz and Keck 1959). Bullock (1989) reports that the shrubs flower profusely from February through April in the Santa Monica Mountains. Several populations produce a few flowers throughout the year. Fruits are linear, grooved capsules measuring 5 to 10 cm long, with 2 valves that separate incompletely at maturity. Ripe fruits (those that explode when grasped) may be collected in May, June, and July (Neal 1974). Fruits are dehiscence, scattering the seeds (figure 1) up to several meters from the shrub, and ants disperse the seeds, some below and others above the ground. Concentrations of seeds can be found around the entrances of harvester ant—*Pogonomyrmex* and *Veromessor* spp.—nests (Bullock 1989).

Collection, cleaning, and storage. The black seeds are almost spherical, 2 to 4 mm in diameter, with a slightly

Figure 1—*Dendromecon harfordii*, island bushpoppy: seeds.

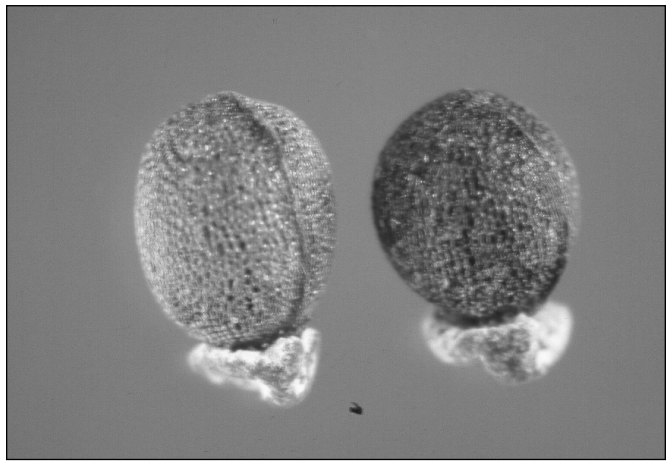


Table 1—*Dendromecon,* bush-poppy: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***D. harfordii* Kellogg** *Dendromecon rigida* ssp. *harfordii* (Kellogg) Raven *D. rigida* spp. *rhamnoides* (Greene) Thorne	**island bushpoppy,** Harford tree-poppy	Channel Islands, California
***D. rigida* Benth.**	**stiff bushpoppy**, tree-poppy	Central California to N Baja California

Source: Munz and Keck (1959).

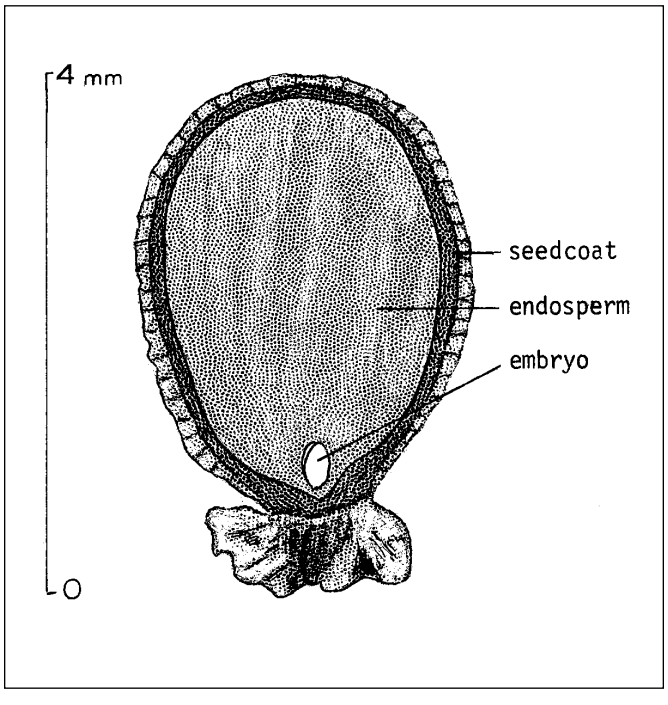
pitted, hard, brittle testa. The seeds are dispersed by ants; the prominent caruncle is removed and used by the ants for food. The endosperm is oily, and the minute embryo rudimentary (Berg 1966) (figure 2). The mean number of seeds per fruit ranged from 2.9 to 10.7 in 14 populations (Bullock 1989). In 2 samples of cleaned seeds, purity was 77% and soundness was 97%. There were 92,400 to 114,400 seeds/kg (42,000 to 52,000/lb) (Neal 1974). Four other samples had purities of 99.4 to 99.9%, with an average of 99.4%, and 100,300 to 106,300 seeds/kg, with an average of 103,200/kg (45,600 to 48,300/lb, average 46,900/lb) (Vivrette 1996). Bullock found that seed weights varied greatly among the 14 populations studied, ranging from 10.1 to 15.8 mg (Bullock 1989). Vivrette reported seed weights ranging from 9.38 to 9.90 mg, average 9.70 mg, on 4 samples (Vivrette 1996). Bullock's slightly heavier fresh seeds may have had attached caruncles or a higher moisture content than Vivrette's laboratory samples.

There are no reports of seed storage of these species, but they likely can be stored at low moisture contents and near-freezing temperatures.

Germination pretreatments. Bushpoppy seeds have been sown in a moist medium at temperatures alternating diurnally from 4.5 °C (night) to 21 °C (day). Germination started after 50 days at these temperatures and reached 21% at 102 days after sowing (Mirov and Krabel 1939; Neal 1974). Vivrette reported no germination in of 9 samples tested for 21 days at 15 °C. A few seeds germinated on blotters moistened with 400 ppm GA_3 (gibberellic acid). Total viable seeds as determined by staining in tetrazolium chloride ranged from 11 to 50%, average 27% (Vivrette 1996). Emery recommended fire treatment or 1 $^1/_2$ to 2 months of stratification and stated that 3 months of stratification with a diurnal fluctuation from 8 to 21 °C may improve germination (Emery 1988).

Nursery practice. Fire-treated bushpoppy seeds give the most reliable germination in nurseries (Emery 1988; Everett 1957). Seeds to be fire-treated should be sown in the fall in a slightly moist nurserybed. The seeds should be then covered with a layer of milled peat or sand 1 to 2 times as thick as the seeds' diameter and not watered. Then, a 10- to 15-cm (4- to 6-in) layer of dry pine needles or excelsior should be placed over the bed and burned. The seedbed should be watered after it has cooled. If wooden flats are being used, 2 layers of aluminum foil will protect the wood during the burning (Emery 1988).

Figure 2—*Dendromecon harfordii*, island bushpoppy: longitudinal section through a seed.



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D

Ebenaceae—Ebony family

Diospyros L.

persimmon

David F. Olson, Jr., R. L. Barnes, and W. Gary Johnson

Drs. Olson and Barnes retired from the USDA Forest Service's Southeastern Forest Experiment Station; Mr. Johnson retired from the USDA Forest Service's National Seed Laboratory

Growth habit, occurrence, and use. Nearly 200 species of persimmons—*Diospyros* L.—are widely distributed, mostly in tropical regions. Only 2 persimmons—common persimmon and Texas persimmon—are native to the 48 contiguous states. Two others are grown in mild regions: Japanese persimmon for fruit and date-plum for root stock (table 1). Other persimmons are native to the tropical regions of the United States—*Diospyros hillebrandii* (Seem.) Fosberg and *D. sandwicensis* (A. DC.) Fosberg in Hawaii (Little and Skolman 1989) and *D. revoluta* Poir. and *D. sintenisii* (Krug & Urban) Standl. in Puerto Rico (Little and others 1974).

Common persimmon is a small to medium-sized deciduous tree, normally attaining a height of 9 to 18 m at maturity (Sargent 1965). It occurs in open woods and as an invader of old fields from Connecticut west through southern Ohio to eastern Kansas, and south to Florida and Texas (Sargent 1965). Common persimmon develops best in the rich bottom lands along the Mississippi River and its tributaries and in coastal river valleys. In these optimum habitats, common persimmon trees often attain heights of 21 to 24 m and diameters of 51 to 61 cm (Morris 1965).

In past years, persimmon wood was used extensively for weaver's shuttles, golf club heads, and other products requiring hard, smooth-wearing wood (Olson and Barnes 1974). At present, such uses have diminished because of the use of laminates and other substitute materials.

The fruits are exceedingly astringent when green, but delicious when thoroughly ripe (Harlow and Harrar1958); they are eaten by humans, animals, and birds. The common persimmon is a valuable honey plant and has been cultivated for its handsome foliage and fruit since 1629. Several varieties have been developed for fruit production (Harlow and Harrar 1958).

Texas persimmon is a shrub or small tree of south Texas and northeast Mexico, usually 1.8 to 3 m tall but sometimes reaching 12 m, with 4-cm-long leaves (Everitt 1984; LHBH 1976). The fruits are important wildlife food, but the shrub is considered as undesirable in rangelands of the Southwest (Everitt 1984).

Japanese persimmon (*kaki*) and date-plum are small persimmons from Asia grown commercially in the milder regions of the United States. Japanese persimmon grows to 14 m, with 18-cm-long leaves and large delicious fruit; many varieties are listed. Date-plum grows to 14 m, with leaves 13 cm long; it is often used as a rootstock for Japanese persimmon (LHBH 1976).

Table 1—*Diospyros,* persimmon: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***D. kaki* L.f.** *D. chinensis* Blume	**Japanese persimmon,** *kaki,* keg fir, date-plum	NE Asia & Japan
***D. lotus* L.** *D. japonica* Siebold & Zucc.	**date-plum**	NE Asia & Japan
***D. texana* Scheele**	**Texas persimmon,** black persimmon	SE Texas to central & trans-Pecos Texas
***D. virginiana* L.** *D. mosieri* Small	**common persimmon,** eastern persimmon	S Connecticut to SE Nebraska, S to Gulf of Mexico

Sources: LHBH (1976), Sargent (1965).

Flowering and fruiting. Male and female flowers are borne on different plants, but a few plants have bisexual flowers. The female flowers are solitary, with 4 to many staminodes. The male flowers are in cymes or clusters with 4 to many stamens. The fruits are juicy, 1- to 10-seeded berries with enlarged, persistent calyxes at the base (LHBH 1976).

Common persimmon has small, dioecious, axillary flowers borne after the leaves from March to mid-June, depending on the latitude (Little and Delisle 1962; Morris 1965; Olson and Barnes 1974; Radford and others 1964). Flowers are most common in April and May and are pollinated by insects.

The fruits are green before ripening and may vary in color when ripe from green, yellow, orange, and yellowish brown to dark reddish purple and black (Olson and Barnes 1974; Sargent 1965) (figure 1). The fruit is a 2- to 5-cm plumlike berry, glaucous and with a conspicuous, persistent calyx, that contains 3 to 8 seeds (Olson and Barnes 1974; Sargent 1965). The fruits ripen from September to November; the flat, brown seeds, about 15 mm long, are dispersed from the time of ripening until late winter (Little and Delisle 1962; Olson and Barnes 1974; Morris 1965; Radford and others 1964) (figures 1 and 2). The seeds are disseminated by birds and animals that feed on the fruits, and to some extent, by overflow water in low bottom lands (Morris 1965).

Seed bearing may begin at age 10, but the optimum seed-bearing age is 25 to 50 years (Little and Delisle 1962; Morris 1965; Olson and Barnes 1974). Good seedcrops are borne about every 2 years, with light crops in intervening years (Olson and Barnes 1974).

Figure 1—*Diospyros virginiana*, common persimmon: mature fruit and a single seed.

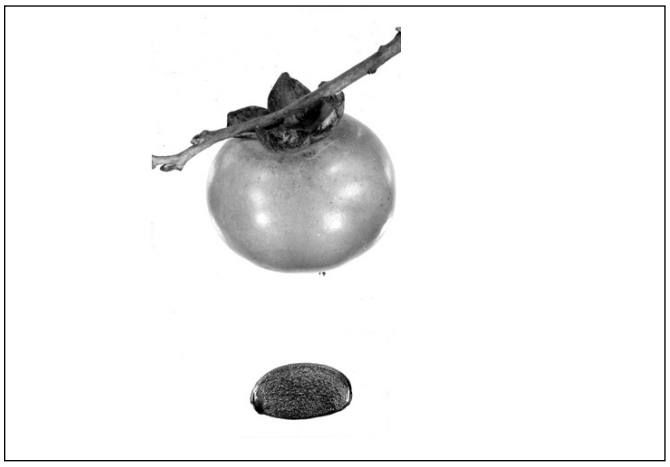
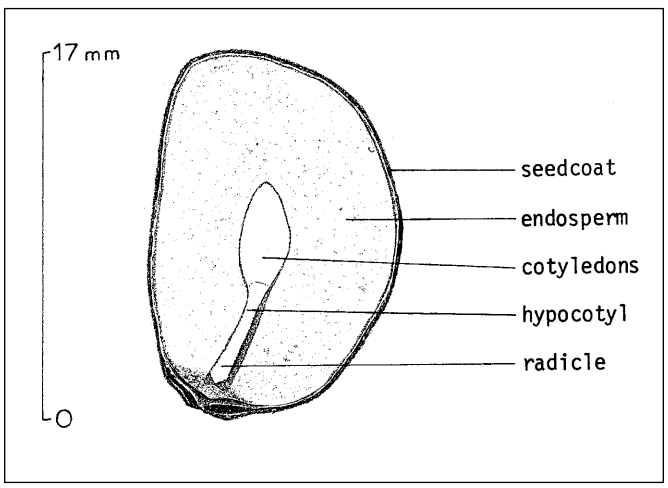


Figure 2—*Diospyros virginiana*, common persimmon: longitudinal section through a seed.



The small Texas persimmon flowers have 5 lobes. The black, globe-shaped fruits are 2.5 cm in diameter and have dark flesh (LHBH 1976). Animals and birds eat the fruits and disseminate the seeds (Everitt 1984).

Japanese persimmon flowers are yellowish white, about 2 cm long. Male flowers have 16 to 24 stamens and female flowers have 8 staminodes. The orange to reddish fruits are variable in shape, to 7.6 cm in diameter, with orange flesh (LHBH 1976).

Date-plum flowers are reddish to greenish, 7.5 mm long, with 4 lobes. Male flowers have 16 stamens. The small, yellow, globe-shaped fruits are 12.5 mm in diameter and turn blackish as they ripen (LHBH 1976).

Collection of fruits; extraction and storage of seeds. The fruits of common persimmon may be collected by picking them or shaking them from the trees as soon as they are ripe and soft in texture. They may also be picked from the ground after natural fall. If the fruits have started to dry, they should be softened by soaking in water (Myatt and others 1988). The seeds are easily removed by running the fruits with water through a macerator and allowing the pulp to float away or by rubbing and washing the pulp through 6.4-mm ($^1/_4$-in) mesh hardware cloth (Olson and Barnes 1974). For small quantities, ripe fruits can be placed in plastic bags and left until the pulp turns to juice, which can then be drained away before drying the seeds (Dirr and Heuser 1987).

After being cleaned, the seeds should be spread out to dry for a day or two. Spreading the seeds on screens to dry is common (Myatt and others 1988). Prolonged storage requires thorough drying. After the seeds are dried, they should be passed over a 9.9-mm (#25) screen on an air-

screen cleaner to remove trash and twigs. Use of a gravity table with high air may also be necessary (Myatt and others 1988). The seeds can then be safely stored in sealed dry containers at 5 °C (Engstrom and Stoeckler 1941).

One hundred kilograms (220 pounds) of fruit of the common persimmon will yield 10 to 30 kg (22 to 66 lbs) of cleaned seeds (Olson and Barnes 1974); the number of seeds per weight ranges from 1,460 to 3,880/kg (665 to 1,764/lb), with an average of 2,640 seeds/kg (1,200/lb) (table 2) (Aroeira 1962; Engstrom and Stoeckler 1941; Olson and Barnes 1974). Seedlots of 96% purity and 90% soundness have been obtained (Olson and Barnes 1974).

Japanese persimmon has about 3,400 seeds/kg (1,550/lb). Seeds stored at 0 °C at 45% moisture content retained the greatest viability after 18 months. Viability decreased rapidly as the seeds were dried, regardless of the speed of drying, with almost no germination at moisture contents below 10% (Kotobuki 1978). Date-plum has about 8,910 seeds/kg (4,040/lb).

Pregermination treatments. Natural germination of common persimmon usually occurs in April or May, but 2- to 3-year delays have been observed (Blomquist 1922; Olson and Barnes 1974). The main cause of the delay is the seed covering, which caps the radical, restricts the embryo, and causes a decrease in water absorption (Blomquist 1922). After removal of this cap, 100% germination was secured with mature seeds collected in the autumn (Blomquist 1922). Seed dormancy also can be broken by stratification in sand or peat for 60 to 90 days at 3 to 10 °C (Aroeira 1962; Crocker 1930; Olson and Barnes 1974; Thornhill 1968). Sulfuric acid scarification for 2 hours proved to be less effective in breaking dormancy than did stratification (Aroeira 1962).

Japanese persimmon does not have strong dormancy. Oh and others (1988) have shown that, although stratification was not essential, it improved germination. Rate of germination of date-plum seeds increased as the stratification length increased to 10 weeks (Oh and others 1988). No pretreatment is needed to germinate Texas persimmon seeds (Vora 1989).

Germination tests. Germination of stratified common persimmon seeds was tested in sand or peat flats at diurnally alternating temperatures of 20 to 30 °C. Germinative energies ranging from 54 to 94% were obtained in 20 to 34 days; and germinative capacities at 60 days varied from 62 to 100% (Olson and Barnes 1974). Payne achieved 90% uniform germination on common persimmon and date-plum by stratifying the seeds for 60 to 90 days in wet vermiculite after lightly dusting them with a fungicide. Scratching the seedcoat can shorten the stratification period (Payne 1996).

Fresh Japanese persimmon seeds taken from ripe fruits and sown immediately germinate best. Germination ranged from 20 to 77% in a study of 18 cultivars with fresh seeds sown immediately (Dirr and Heuser 1987). Date-plum seeds germinated best without light at alternating 18 to 30 °C with 10 weeks stratification at 5 °C. Germination of seeds stratified for 2 weeks was increased by treating them with 500 ppm gibberellin (GA_3) (Oh and others 1988). Fresh Texas persimmon seeds sown immediately after extraction germinated 33%. Germination was reduced with all other treatments (Dirr and Heuser 1987).

The tetrazolium chloride staining test is often used to estimate the viability of common persimmon and date-plum seeds due to the long stratification period needed to overcome dormancy. Clipping the radicle end of a seed with toenail clippers and soaking the seed for several days in water or 500 ppm GA_3 will soften it. Then it should be cut lengthwise to expose the embryo and storage tissue for staining.

Nursery practice. Common persimmon seeds may be fall-sown or stratified and sown in the spring. In Missouri, fall-sowing at a depth of 5 cm (2 in) is the normal practice, and seedbeds are mulched. Steavenson (Olson and Barnes 1974) reported a tree percent of 50%; an average tree percent of 25 to 33% is easily attainable. Seedlings of this

Table 2—*Diospyros*, persimmon: seed yield data

	Cleaned seeds/weight				
	Range		Average		
Species	/kg	/lb	/kg	/lb	Samples
D. kaki	3,015–3,790	1,370–1,720	1,550	3,400	2
D. lotus	—	—	8,910	4,040	1
*D. virginiana**	1,460–3,880	665–1,765	2,640	1,200	—

Source: Olson and Barnes (1974).

* Seed weight to fruit weight ratio (in kilograms/100 kg or pounds/100 lb) = 10 to 30.

species have a strong taproot (figure 3) and should be field-planted at the end of the first season. Root wrenching will cause the seedlings to form a compact, fibrous root system (Myatt and others 1988).

Figure 3—*Diospyros virginiana*, common persimmon: seedling development at 4, 6, and 8 days after germination.

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D

Thymelaeaceae—Mezereum family

Dirca palustris L.

eastern leatherwood

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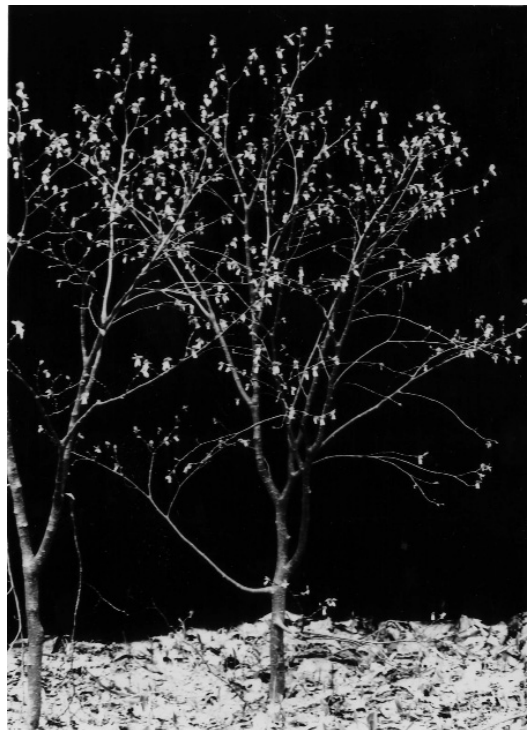
Growth habit, occurrence, and use. Eastern leatherwood—*Dirca palustris* L.—is also known as moosewood, rope-bark, and wicopy. Its natural distribution extends from New Brunswick to Ontario in the north and from northern Florida to Louisiana in the south (Fernald 1950). Within this range, the distribution is restricted to very specific site conditions. It is found almost exclusively in mesic, relatively rich hardwood forests or mixed conifer–hardwood forests (Alban and others 1991; Curtis 1959; Fernald 1950; Ferrari 1993; Jones 2000; Kotar and others 1988; Meeker and others 1993; Neveling 1962; Rooney 1996; Soper and Heimberger 1982; Voss 1985; Weir-Koetter 1996). In aspen ecosystems across the upper Great Lakes region, leatherwood is present in stands with a relatively high aspen site index and a significant northern hardwood component (Alban and others 1991). In Ontario, the northern limit of distribution is similar to that of beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.)(Soper and Heimberger 1982). The distribution of plants on a particular site can vary from apparently random to aggregated (Jones 2000). Forests in which leatherwood is common are characterized by a dense overstory that permits relatively little light to reach the forest floor during the growing season. It is often the only true understory shrub in these stands; the other woody understory species are tolerant to mid-tolerant trees—for example, sugar maple, ironwood (*Ostrya virginiana* (Mill.) K. Koch.), white ash (*Fraxinus americana* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and balsam fir (*Abies balsamea* (L.) Mill.)—having the capacity to grow into the overstory (Alban and others 1991; Buckley 1996; Ferrari 1993; Jones 2000).

Western leatherwood—*D. occidentalis* Gray—is very similar to eastern leatherwood (Neveling 1962). Its distribution is limited to the wooded hills of the San Francisco Bay region (Vogelman 1953). Flower descriptions and morphological comparisons of the 2 species are provided by Vogelman (1953). A related species in the Thymelaeaceae—*Daphne mezereum* L.—is an introduced species that has become established in some areas. The information presented here is for eastern leatherwood; some of it may also apply to western leatherwood.

In its natural habitat, eastern leatherwood reaches a height of 3 to 4 m and basal diameters of 5 to 10 cm. Crown width and depth of larger plants can be as much as 2 to 3 m; the largest crown volumes that we have measured are in the range of 15 to 25 m^3. Crown architecture can be fairly complex, with frequent branching and numerous apical growing points (figure 1). The largest individuals that we have observed are in old-growth northern hardwood forests where logging is prohibited and in older hardwood stands managed under a single-tree selection system. The maximum age attained by leatherwood is not known, but 30- to 50-year-old plants occur in older hardwood forests.

Figure 1—*Dirca palustris*, eastern leatherwood: mature forest-grown plant in full flower, with plant about 1.3 m tall.



Annual height growth varies considerably (Jones 2000). On mature plants, elongation of an individual apical meristem ranges from 1 to 25 cm, but cumulative annual growth over the many apical meristems comprising the crown may be 0.5 to 1 m or more. Complete removal or reduction of canopy cover to less than 50% seems to reduce the frequency of leatherwood, but more work is needed to understand effects of disturbance on the survival, growth, and reproduction of leatherwood. This reduction, however, may be more the result of physical damage during harvesting than to the change in the physical environment resulting from harvesting. In plants that have had branches completely or partially separated, callus growth covers the wound relatively quickly, giving wounded stems a distinct appearance. The flexible nature of the stem and branches is the result of a relatively low level of lignification in the wood (Neveling 1962). The specific gravity of the wood is 0.41, ranking it among the least dense woods of deciduous broadleafed species, comparable to poplar and basswood species (Alden 1995; Neveling 1962).

There is poor sprouting in leatherwood after the main stem is cut or broken. Layering of branches has been observed, but usually it does not occur, even on branches in good contact with an apparently suitable substrate layer. Seedling regeneration seems to be the most common way that the species is maintained in forests.

The only current documented use of eastern leatherwood is for landscaping. Even for this, it is not used to the extent possible, particularly in more northern areas (for example, in the northern Great Lakes region and northern New England), where the choice of plants is limited by climate. Although leatherwood provides a very early flowering, medium-sized shrub for these northern areas (Esson 1949), unfortunately its leaves are often infected by a rust and leaf miners in mid-summer, turning yellow prematurely and falling early. It can be planted and does best in moist, shaded areas. If the plant is naturally present in areas where development is planned, efforts should be made to protect it and provide conditions that favor growth, as older plants provide interesting form and structure to managed landscapes such as yards and gardens (del Tredici 1991; Dirr 1990). The plant appears to be browsed very little by deer (*Odocoileus* spp.), even in forests where other woody plants are repeatedly and severely browsed throughout the year (Weir-Koetter 1996). The lack of browsing could be due to the plants' diuretic qualities (Meeker and others 1993); the stem also contains large quantities of calcium oxalate crystals (Holm 1921). Ramsewak and others (1999) have described novel phenolic glycosides in leatherwood. The strong pliable bark (the source of the common name) was used by Ojibwa for making bowstrings, baskets, and fishing lines (Holm 1921; Meeker and others 1993; Weir-Koetter 1996). The wood is very easy to slice with a sharp knife.

Flowering and fruiting. Leatherwood is monoecious. The pale yellow, fragrant flowers are perfect and borne in clusters of 2 to 7 (figures 1 and 2) (Neveling 1962; Soper and Heimberger 1982; Vogelman 1953; Zasada and others 1996). The buds from which flowers develop are small and conical, with 4 distinct dark, silky scales that persist after flowering (figure 2). Clusters of 3 flowers are most common in northern Wisconsin–Michigan; clusters of 4 are somewhat less common, and clusters of 5 to 7 uncommon or rare. Mature plants commonly produce 300 to 1,500 flowers; the greatest number we observed on a plant was about 4,500 flowers (Zasada and others 1996). [Note: in the following discussion, we refer to unpublished data on fruits and seeds collected on or in the vicinity of the Ottawa National Forest in Michigan's Upper Peninsula and the Nicolet and Chequamegon National Forests in northern Wisconsin.]

Flowering occurs in April–May, 2 to 3 weeks before the overstory leafs out and generally before the spring ephemeral species flower. In 1994 and 1995 in northern Wisconsin-Michigan, fairly average years in terms of spring weather, pollination was mostly completed by May 11–15. In 1996, a relatively cold, wet spring, flowering began on May 14 on warm, south-facing aspects and several days later on north aspects. Flower buds opened as late as May 25 and some

Figure 2—*Dirca palustris*, eastern leatherwood: 3-flower cluster, subtending structures are silky bud scales.

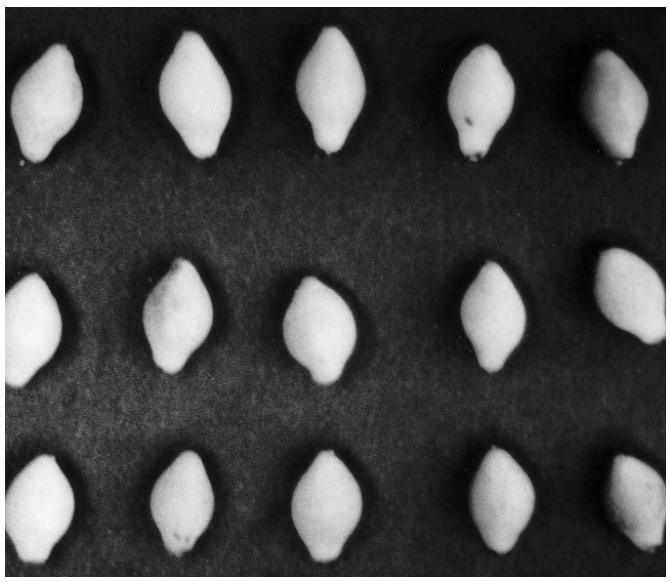
anthers still contained pollen in early June. Flower parts drop quickly if pollination/fertilization is not successful but remain attached to developing fruits for a longer period (figure 3). Fruits ripen in June and July, with one report of ripening as late as September–October (Vogelman 1953). About 1 month (mid-June) after the first flowers appear in northern Wisconsin–Michigan, 75% of seeds contained embryos that filled 80% or more of the seed; 5% of the seeds were less than 50% filled. When fully ripe, the endosperm is a minor component of the seed (figure 4) (Neveling 1962; Zasada and others 1996). The outermost fleshy portion of the fruit cannot be separated easily from the seed coat until mid-late June.

Immature fruits are green and change to a very light green; some fruits are almost white when they fall from the plant. There are some reports that fruits turn reddish when mature (McVaugh 1941; Meeker and others 1993; Neveling 1962). However, McVaugh (1941) summarized the literature and concluded that although the reddish fruit color can be observed in dried herbarium specimens, his own and other's observations led to the conclusion that mature fruits are light to yellowish green. We found no evidence in the 8 stands studied in Wisconsin and Michigan that fruits were reddish in color when mature. The fleshy outer fruit wall (figure 5) of naturally dispersed fruits turns black within about 24 hours in some fruits, but in others it remains light green for several days.

Each flower has the potential to produce 1 single-seeded fruit, and hence fruits can be in clusters of 3 to 7 if all flowers produce fruits. Fruits with 2 seeds were observed, but they were very rare. Clusters with 1 to 3 fruits were most common, as many flowers do not produce fruits. Clusters of more than 4 fruits are uncommon or rare. Number of flowers, fruit set, and number of fruits per cluster varies annually and among stands in the same year (table 1).

Figure 3—*Dirca palustris*, eastern leatherwood: fully developed but immature fruits. Flower parts are still attached to some fruits. Fruit length varies from 6.5 to 15 mm in the northern Wisconsin–Michigan area where fruits were collected.

Figure 4—*Dirca palustris*, eastern leatherwood: ripe fruits collected shortly after dispersal.



The fruit (figure 3) is a drupe and described as "bilaterally symmetrical, somewhat spindle-shaped....circular in cross-section at the widest point...and (having) a narrow, slightly elevated ridge...from the base of the style down the whole length of the fruit" (McVaugh 1941). Fruits are reported as 9 to 12 mm long for Ontario populations (Soper and Heimberger 1982), 12 to 15 mm long by 7 mm wide (Vogelman 1953) for Michigan and Indiana populations, and 12.5 to 15 mm long (McVaugh 1941) for New York populations. Average dimensions for fruits from 6 northern Wisconsin–Michigan populations were 8.5 to 9.5 mm long by 5.5 to 6.5 mm wide. Range in length was from 6.5 to 15.0 mm and width 4.5 to 7.5 mm for these latter populations (Zasada and others 1996). The fresh weight of individual fruits containing fully developed seeds varied from 0.08 to 0.23 g. Moisture content of whole fruits was 100 to 175% (dry weight basis) for dispersed fruits and those about to be dispersed.

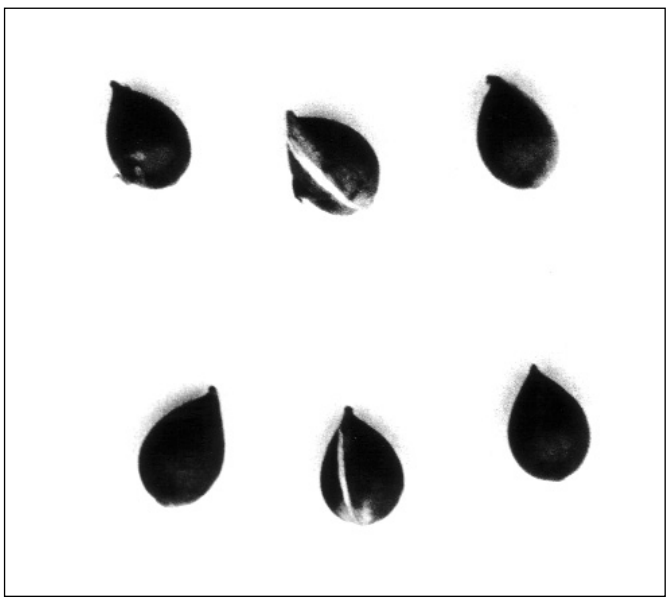
Individual seeds, with their fleshy coats removed (figure 4), were 5.5 to 8.5 mm long and 3.5 to 5.0 mm wide for northern Wisconsin–Michigan populations. Fresh seed weight varied from 0.04 to 0.08 g and percentage moisture content was 40 to 55% (dry weight basis; seeds dried to a constant weight at 65 °C) for seeds collected from the ground shortly after dispersal; individual seeds on plants

Table 1—*Dirca palustris*, eastern leatherwood: flowering and fruit production in 2 forest types in northern Wisconsin

Stand type*	No. 3-flower clusters/shrub† Mean	No. 3-flower clusters/shrub† Range	% cluster w/1–3 fruits	% of all clusters with fruits 1 fpc	% of all clusters with fruits 2 fpc	% of all clusters with fruits 3 fpc	Fruits/plant Mean	Fruits/plant Range
Hardwood forest								
1995	153	5–515	23	22	48	30	40	0–386
1995	198	21–695	—	—	—	—	194	13–840
1996	—	—	55	20	41	19	—	
Pine forest								
1995	59	0–255	2	0	77	23	3	0–45
1995	85	0–325	—	14	57	29	—	
1996	—	—	23	—	—	—	36	0–260

Note: fpc = fruits per cluster; these populations did not have 4-flower or 4-fruit clusters in the 2 years of observation.
* Based on 15 randomly selected shrubs in each stand.
† To obtain total number of flowers, multiply by 3.

Figure 5—*Dirca palustris*, eastern leatherwood: seeds with fleshy outer fruit wall removed. All seeds have a light-colored area along which the ovular trace is located; the 2 seeds in the center are positioned to show this area.



from which seeds were being dispersed but still firmly attached to the peduncle had moisture contents of 100 to 125% (Zasada and others 1996). Mature seeds are dark brown-black with a well-developed lighter longitudinal strip (figure 5). The strip is the point of attachment of the seed to the fruit wall in the area of the elevated ridge, which is a noticeable aspect of the shape of the fruit; the ovular trace is attached to the seed in this strip (figures 3 to 6) (McVaugh 1941; Neveling 1962).

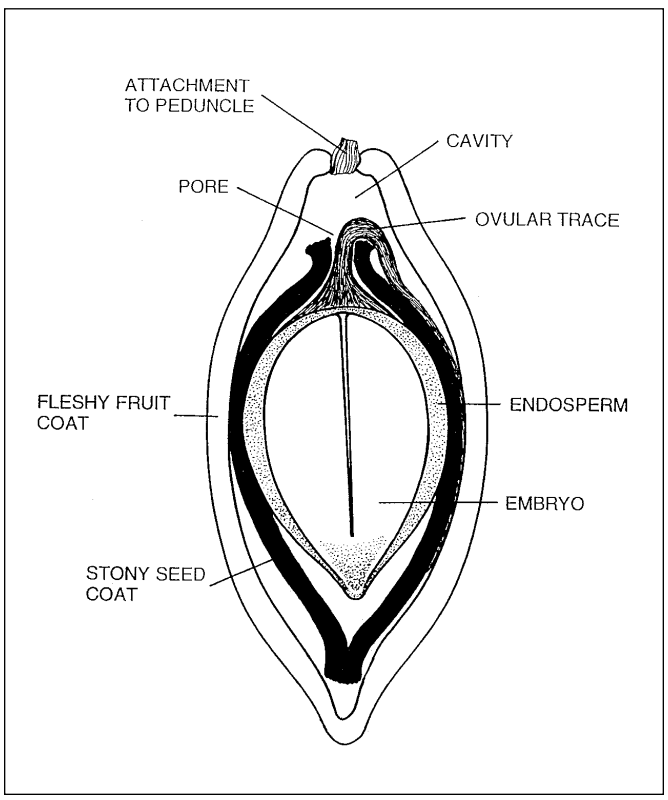
Embryo length varied from 4 to 6 mm and from 2 to 4 mm in width in the Wisconsin–Michigan populations. At maturity, the embryo fills 95% or more of the seed; a small cavity develops at both poles of the seed (figure 6). Multiple embryos, all poorly developed, occurred in less than 0.5% of the seeds (Zasada and others 1996).

The general anatomical features of a seed are illustrated in figure 6. The ovular trace and the pore through which it passes are an interesting feature of the seed (Neveling 1962). The pore appears filled with a fibrous material in seeds that have fallen from the plant. The black, stony seed-coat does not appear to completely seal the pore, even at maturity.

Collection of fruits; extraction and storage of seeds. Fruits ripen in June and July. McVaugh (1941) observed that dispersal for plants in New York was completed by the following dates during a 3-year period—June 20, July 1–3, and later than July 7. In northern Wisconsin–Michigan populations, fruits have been observed on plants as late as July 16, but as observed by McVaugh (1941), dispersal was completed by July 1 in some years. The seeds disappear fairly quickly once they are fully mature but are fairly obvious on the soil surface for several days after dispersal (Dirr and Heuser 1987; McVaugh 1941; Nevling 1962; Soper and Heimberger 1982). During windy periods, deposition rates were as high as 27 fruits/m^2/hr under 1 shrub. Timing of fruit abscission and fruit drop vary among plants in a stand, among branches within a plant and among fruits in a cluster (Zasada and others 1996). In an area where dispersal was followed on a daily basis, seeds from the entire population were dispersed over about a 2-week period; some plants shed all of their seeds in 2 to 3 days, whereas others dispersed seeds over a 6- to 8-day period.

Birds do not seem to be a critical factor in seed removal, but they do consume some seeds and may be more important than our observations suggest. They may remove entire fruits, but, in some cases, they remove only the seed, leaving the fleshy fruit coat attached to the plant. Although the level of fruit use by rodents after dispersal is not known, it seems that this might be an important way in which seeds are

Figure 6—*Dirca palustris*, eastern leatherwood: generalized longitudinal section of mature seed, based on Neveling (1962) and Buckley (1996).



removed from the seed pool. Remnants of the black, stony seedcoat are fairly common under plants about 1 month after dispersal.

If seeds are needed, we recommend keeping a close watch on shrubs with fruits and collecting the fruits soon as they are ripe. Once some fruits fall naturally, all fruits have fully developed seeds. Embryo development is easily checked by cutting seeds longitudinally; those that are fully developed will appear as in figure 6.

Fruits can be picked by hand from the plant. However, when fully ripened, they readily fall when the plant is shaken and could be collected from the ground. Because each fruit contains only 1 seed, the number of seedlings desired (plus additional seeds as insurance against poor germination) will determine the number of fruits required. Based on cutting tests, 90 to 100% of developed fruits contained seeds with apparently viable embryos.

The pulp can be removed by hand or mechanically. When the seeds are fully mature, a cavity, with the exception of the attachment between the ovular trace and fruit wall, develops between the fleshy fruit wall and the hard inner seed coat, making it fairly easy to hand-clean small quantities of seeds. The stony seedcoat is easily broken with the pressure of a fingernail and the seed can be squashed by squeezing between the thumb and forefinger with moderate pressure. Consequently, any type of mechanical cleaning must be done with care.

No information was found on the best ways to handle fruits or store seeds. Seeds remain viable in the forest floor from the time of dispersal until they germinate in the spring (del Tredici 1984), suggesting that storage for at least 8 to 10 months is possible. Seeds are exposed to a fairly wide range of temperature and moisture conditions between dispersal and germination.

Germination. Detailed information on the effects of environmental conditions on germination was not found. del Tredici (1984) used a number of standard methods to stimulate gemination, but untreated seeds planted in a nursery bed soon after they were collected were the only ones that produced seedlings (67% germination). Dirr and Heuser (1987) reported that both cleaned and uncleaned (fleshy fruit wall removed) seeds produced seedlings. In controlled environment studies, a seedlot was observed to produce germinants over at least a 3-year period (Zasada and others 1996).

Nursery. Based on the limited information available, we recommend planting seeds soon after collection with and without the fleshy fruit wall in order to provide the range of conditions under which seeds appear to germinate naturally; seeds sown this way will germinate the next spring (del Tredici 1984; Dirr and Heuser 1987). Dirr and Heuser (1987) reported finding a number of young plants under a mature plant growing in a landscaped area, indicating that it might be possible to obtain some small seedlings from these situations. The growth rate of seedlings under open conditions is not documented. In its natural habitat, seedlings grow to a height of 20 to 30 cm in 5 to 10 years.

There has been little or no success in stimulating rooting in stem cuttings (Dirr and Heuser 1987). Layering occurs under natural conditions, suggesting that air-layering is a potential option for propagating leatherwood. However, Hendricks (1985) reported that air-layered stems did not produce roots or callus during an 8-week period. Our observations of layering of branches and the main stem under natural conditions suggest that it might take longer than 8 weeks for rooting to occur.

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E

Fabaceae—Pea family

Ebenopsis ebano (Berl.) Barneby & Grimes

Texas-ebony

Franklin T. Bonner

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Synonyns. *Pithecellobium flexicaule* (Benth.) Coult., *P. ebano* (Berl.) C.H. Muller, *Mimosa ebano* Berl., *Acacia flexicaulis* Benth.

Other common names. ebony blackbead, ape's earring.

Growth habit, occurrence, and use. *Ebenopsis* is a small genus, with only 2 species found in the United States. Texas-ebony occurs in Mexico and southern Texas and is the most valuable tree in the Rio Grande Valley. The species was formerly placed in the genus *Pithecellobium*; nomenclature of these species is discussed briefly in the *Pithecellobium* chapter of this book. The wood of Texas-ebony is used for furniture and fence posts, and the seeds can be used as a coffee substitute (they are boiled when green or roasted when ripe) (Vines 1960).

Flowering and fruiting. Texas-ebony flowers are yellow or cream-colored umbels about 4 cm in length borne in paniculate clusters on the end of twigs. They appear from June to August (Vines 1960). The legumes (pods) turn from green to dark brown or black as they mature in the fall. They are flat, about 13 cm long, and 2.5 cm wide (figure 1). The legumes are also indehiscent and may remain on the trees for a year or more. The seeds are reddish brown, bean-shaped, and about 1.5 cm long (figures 2 and 3). Weights range from 1,550 to 1,990 seeds/kg (700 to 900/lb) (Walters and others 1974).

Collection, extraction, and storage. Legumes are usually picked by hand from the trees and air-dried in the sun. Seeds can be extracted by hand-flailing or by using mechanical macerators. Legume fragments can by removed with screens. There are no long-term storage data for Texas-ebony, but it is a typical hardseeded legume with orthodox storage behavior. Storing seeds for several years should be easy at low moisture contents (<10%) and temperatures of 2 to 5 °C (Walters and others 1974).

Figure 1— *Ebenopsis ebano*, Texas-ebony: legume.

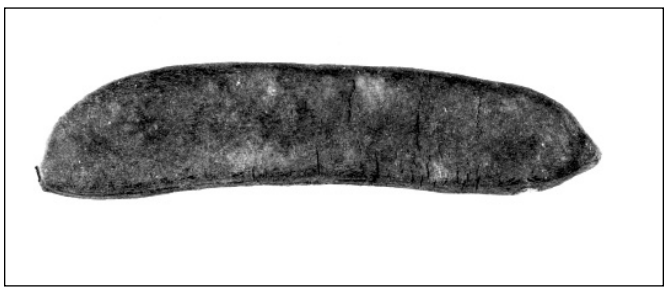
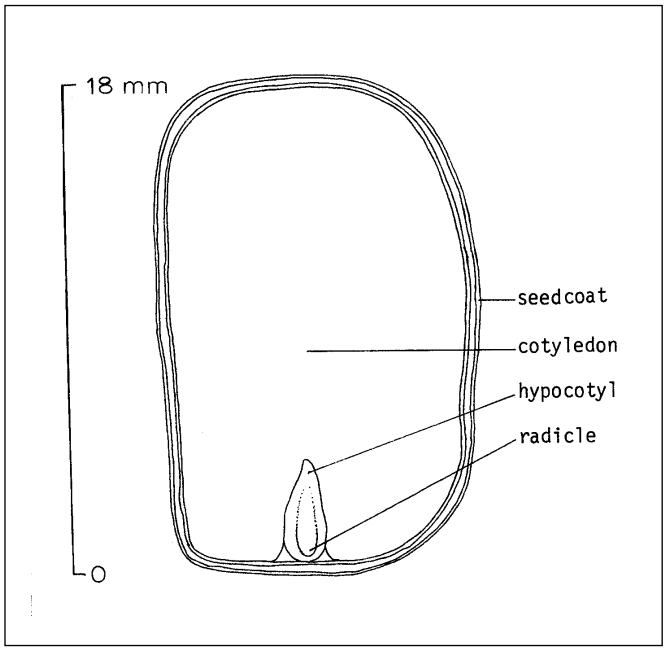


Figure 2— *Ebenopsis ebano,* Texas-ebony: seeds.

Germination. The seedcoats of Texas-ebony are very hard, and few seeds will germinate without scarification. Soaking in sulfuric acid for 30 to 150 minutes has yielded germination of 78 to 88% (Alaniz and Everitt 1978; Vora 1989). This wide variation in soaking times suggests considerable variation in hardness of the seedcoats. In such cases, time trials should be carried out with small samples to choose the optimum soaking period for a given seedlot. Official seed testing organizations do not include Texas-ebony in their prescriptions for testing, but alternating temperatures of 15 and 30 °C have been quite successful following acid scarification (Alaniz and Everitt 1978).

Figure 3— *Ebenopsis ebano*, Texas-ebony: longitudinal section through a seed.



Nursery practice. There is little information on nursery practices for Texas-ebony. Nurserybed densities of 160 to 215/m^2 (15 to 20/ft^2) appear to be suitable for raintree (*Albizia saman* (Jacq.) F. Muell.), a similar species (Walters and others 1974), and the same is suggested for Texas-ebony. Optimum planting depth in a greenhouse was reported to be 1 cm (0.4 in) (Alaniz and Everitt 1978). Direct seeding in old fields in Texas was improved by mulching the seeds with a commercial straw blanket (Vora and others 1988), and either mulching or shading would seem to be beneficial in nursery beds in that region.

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Elaeagnaceae—Oleaster family

Elaeagnus L.

elaeagnus

David F. Olson, Jr., and Jill R. Barbour

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Growth habit, occurrence, and use. The genus *Elaeagnus* includes about 40 species of shrubs and trees, but there are only 3 species that are valuable for planting and for which reliable information is available (table 1). Although these deciduous trees and shrubs are grown often as ornamentals, they also produce edible fruits and serve as a source of wildlife food and as honey plants. Russian-olive is grown widely and has escaped from cultivation in many river lowland areas, particularly in the Great Plains, where it was extensively planted for shelterbelts (Olson 1974). In many areas, it has become invasive.

Flowering and fruiting. The fragrant, small, perfect flowers are borne in late spring (table 2) and are pollinated by insects (Mowry 1971). The fruit is a dry and indehiscent achene that is enveloped by a persistent fleshy perianth and hence is drupaceous (Jack 1969) (figures 1–3). The color of ripe fruit varies with the species (table 3). Seeds are often distributed by birds following consumption of the ripe fruits (Turcek 1961).

Collection of fruits; extraction and storage of seeds. Ripe fruits are collected by picking them from the plants by hand or by beating or stripping them from the branches onto canvas or plastic sheets, usually from September to December (Olson 1974). Fruits may be spread out to dry or run through a macerator with water and the pulp floated off or screened out (Heit 1968; Olson 1974). Accordingly, commercial seedlots may consist of either dried fruits or cleaned stones. Dried fruits or cleaned stones at a moisture content from 6 to 14% can be stored successfully in sealed containers at 1 to 10 °C (Heit 1967; Mickelson 1968; Olson 1974; Peaslee 1969). Under ordinary storage conditions, seeds of silverberry remain viable for 1 to 2 years and those of Russian-olive up to 3 years (Olson 1974). The number of cleaned seeds (stones) per weight and other important yield

Table 1—*Elaeagnus*, elaeagnus: nomenclature and occurence

Scientific name & synonym(s)	Common name(s)	Occurrence
***E. angustifolia* L.** *E. hortensis* Bieb.	**Russian-olive,** oleaster, narrow-leafed oleaster	S Europe, W & Central Asia; Pacific Northwest to Minnesota, S through Great Plains to Mexico
***E. commutata* Bernh. ex Rydb.** *E. argentea* Pursch, non Moench	**silverberry,** wolfberry	Quebec to Yukon, S to New Mexico, E to Nebraska
***E. umbellata* Thunb.** *E. crispa* Thunb.	**autumn-olive,** autumn elaeagnus	China, Korea, & Japan; Maine to New Jersey & Pennsylvania, W to SW Minnesota, occasionally S to South Carolina

Sources: Fernald (1950), Harrington (1954), Olson (1974), Rehder (1940), Small (1933).

Table 2—*Elaeagnus*, elaeagnus: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal	Seed size (mm)
E. angustifolia	—	June	Aug–Oct	All winter	12–13
E. commutata	Black Hills, South Dakota	June–July	Aug–Sep	Sep–Nov	8–9
E. umbellata	—	May–June	Aug–Oct	Sep–Nov	6–8

Source: Borell (1962), Dietz (1969), Hora (1981), McDermand (1969), Radford and others (1964), Rehder (1940).

Figure 1—*Elaeagnus angustifolia*, Russian-olive: fruit.

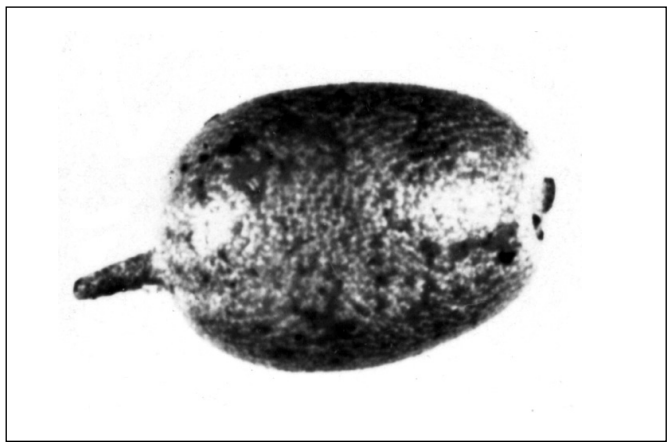
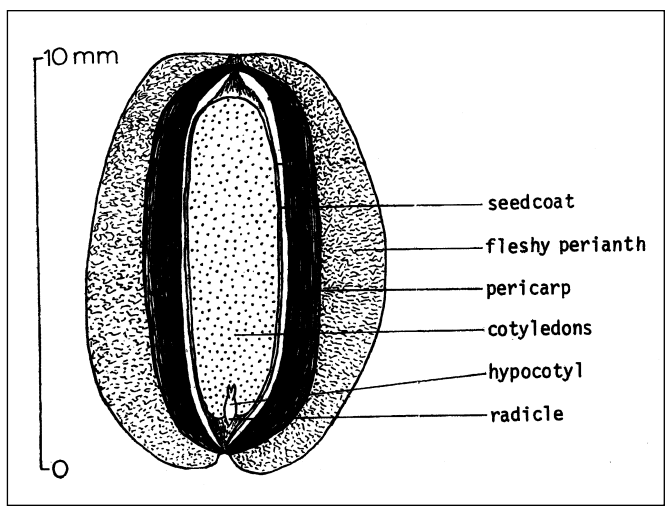


Figure 2—*Elaeagnus*, elaeagnus: achenes with fleshy perianth removed of *E. angustifolia*, Russian-olive (**left**) and *E. commutata*, silverberry (**right**).

Figure 3—*Elaeagnus angustifolia,* Russian-olive: longitudinal section through an achene enclosed in the fleshy perianth.



data are presented in table 4. From 4.5 kg (10 lb) of fruit, about 0.45 kg (l lb) of cleaned seeds can be extracted. Fresh fruits of Russian-olive lost about 16 to 20% of their initial weight when air dried. The number of dried fruits per weight ranged from 3,970 to 9,900/kg (1,800 to 4,500/lb), with an average of 6,400/kg (2,900/lb). Purity of commercial seedlots for all 3 species has been high, ranging from 95 to 100% (Mickelson 1968; Olson 1974; Zarger 1968).

Pregermination treatments. Several pregermination treatments have been tested to overcome embryo dormancy in elaeagnus seeds. The most effective treatment is cold stratification at 1 to 10 °C for 10 to 90 days (Carroll 1971; Heit 1967, 1968; Lingquist and Cram 1967; Molberg 1969; Olson 1974). Stratification for less than 60 days is less effective than for longer periods (Carroll 1971). Intact autumn-olive seeds stratified at 5 °C from 2 to 6 weeks germinated less than 50% after 12 weeks at 25 °C, whereas seeds stratified for 10 to 14 weeks germinated completely in 12 weeks (Hamilton and Carpenter 1976). Allan and Steiner (1965) found that a 24-hour water soak followed by 45 days at 2 to 3 °C was sufficient to break dormancy in seeds of autumn-olive.

Russian-olive stones sometimes exhibit hard-seededness, and then should be soaked for $^1/_2$ to 1 hour in sulfuric acid before germinating (Heit 1967). The optimum length of after-ripening for Russian-olive was reached at 12 weeks (Hogue and LaCroix 1970). Belcher and Karrfalt (1979) found that snipping off 2 mm at the radicle end, after 7 days of water soaking, resulted in 96% germination. Snipping 2 mm at the cotyledon end only resulted in 50% germination. When 2 mm was snipped off both ends of the seeds, however, germination was 100%.

Seeds of Russian-olive that were not given a cold treatment but were soaked in Ethrel (2-chloroethyl phosphonic acid) germinated significantly better than seeds soaked in distilled water (Hamilton 1972). Concentrations of 300 and 600 ppm of Ethrel gave the maximum germination of 100 and 90%, respectively (Hamilton 1972). Germination was not further stimulated by giving the seeds 45 days of cold treatment before soaking in Ethrel (Hamilton 1972).

Gibberillic acid (GA_3) applied to autumn-olive seeds at concentrations of 500 and 900 ppm decreased the time of cold stratification and increased the total germination percentage (Hamilton and Carpenter 1976). A coumarin-like inhibiting substance was found in all parts of the dormant and fully chilled seeds of Russian-olive (Hamilton and Carpenter 1976). Gibberillic acid at concentrations of 100 and 500 ppm and kinetin at 100 ppm appear to reverse the action of the inhibitor (Hamilton and Carpenter 1976).

Silverberry seeds, with endocarps removed, reached 85 to 100% germination within 10 days (Corns and Schraa

Table 3—*Elaeagnus*, elaeagnus: height; seed-bearing age, seedcrop frequency, and fruit ripeness criteria

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yr)	Years between large seedcrops	Fruit ripeness criteria	
					Preripe color	Ripe color
E. angustifolia	46–9	Long cultivated	≥3	3	Whitish to silvery l	Silver-gray outer; emon-yellow inside
E. commutata	1.8–4.6	1813	—	1–2	Silvery green	Silver
E. umbellata	0.9–3.7	1830	6	—	Silvery, with	Red-pink brown scales

Sources: Borell (1962), Dietz (1969), Fernald (1950), Rehder (1940).

Table 4—*Elaeagnus*, elaeagnus: seed yield data

Species	Seed wt/fruit wt ratio	Cleaned seeds/weight				Samples
		Range		Average		
		/kg	/lb	/kg	/lb	
E. angustifolia	15–60	7,650–15,400	3,470–6,990	11,380	5,160	15
E. commutata	—	5,950–10,140	2,700–4,600	8,380	3,800	5
E. umbellata	5–10	46,525–84,670	21,100–38,400	62,180	28,200	30

Sources: Belcher and Washburn (1965), Carroll (1971), Harrington (1954), Heit (1970), Hinds (1967), McDermand (1969), Mickelson (1968), Molberg (1969), Mowry (1971), Olson (1974), Schumacher (1968), Zarger (1968).

1962). After intact seeds were stratified at 5 °C for periods of 40 to 110 days, the germination ranged from 23 to 75%, respectively (Corns and Schraa 1962). Supplemental treatments such as hot water soaks, gibberillic acid, and potassium nitrate (KNO_3) soaks did not affect the germination of silverberry (Corns and Schraa 1962).

Germination tests. Some germination test results on stratified seeds are listed in table 5. Germination is epigeal. Silverberry had the best total germination (95 to 96%) and speed of germination after 60 to 90 days of stratification at 4 °C (Morgenson 1990). Seeds of silverberry used for strip mine reclamation yielded the highest germination (80%) after a 2-day warm (50 °C) water soak (Fung 1984). Results for autumn-olive seeds indicated that the optimum germination was achieved with cold stratification at 5 °C for 16 weeks and a night/day temperature of 10/20 °C (Fowler and Fowler 1987). Tests on excised embryos of Russian-olive have been completed in a very short time (Heit 1955). Belcher and Karrfalt (1979) found that it took 1 hour to completely excise the embryo from the seed and it resulted in 100% germination after 3 days incubation at 20 to 30 °C. Viability testing with 2,3,5-triphenyl tetrazolium chloride stain yielded 86% viable seeds for Russian-olive and 68 % viable seeds for autumn-olive (Olson 1974). Rules of the International Seed Testing Association (ISTA 1993) call for the use of tetrazolium staining for elaeagnus. Seeds should be soaked in water for 18 hours, then cut transversely at both ends to open the embryo cavity. After 48 hours of soaking in 1% tetrazolium chloride, the seeds should be cut longitudinally to expose the embryos. The radicle tips and as much as one-third of the distal cotyledons can be unstained, and the seeds still considered viable. A secondary procedure calls for longitudinal cuts at the beginning.

Nursery practice. Seeds may be sown 13 to 25 mm ($^1/_2$ to 1 in) deep in the late summer or fall without stratification, or in the spring after 10 to 90 days of cold stratification (Baker 1969; Growl 1968; Hinds 1967; Jack 1969; McDermand 1969; Mickelson 1968; Molberg 1969; Olson 1974; Zarger 1968). July seeding after 90 days of stratification gave excellent germination of Russian-olive in southeast Saskatchewan (Cram and Elliott 1966). In Michigan, autumn-olive is seeded by broadcasting 1.7 kg of fresh fruit/10 m^2 of bed area (1 lb/25 ft^2) (Carroll 1971). At the Los Lunas Plant Material Center, Russian-olive is sown at a rate of 200 seeds, or 40 g (1.4 oz) of clean seeds/m, which yields 150 usable plants. In areas with a large population of mice, the pulp should be removed and cleaned seeds used for sowing (Carroll 1971). Russian-olive seedlings are susceptible to damage from rabbits and must be protected if these rodents are a problem.

Soil splash, which coats the pubescent leaves of newly emerged seedlings, is an important cause of mortality, and consequently, nursery beds should be mulched to cover the soil and prevent rain spattering (Carroll 1971; Growl 1968;

Table 5—*Elaeagnus*, elaeagnus: germination test conditions and results for stratified seedlots*

Species	Germination test conditions: Medium	Temp (°C): Day	Temp (°C): Night	Days	Germinative energy: Amt (%)	Germinative energy: Days	Germinative capacity: Average	Germinative capacity: Samples
E. angustifolia	Sand	30	20	60	7–76	10–32	7–79	32
	Sand	—	—	21–40	—	—	54–90	11
	Moss	—	—	28	27	10	30	1
	Kimpak	30	20	28			68	19
E. commutata	Sand	30	20	50	52	13	60	1
E. umbellata	Kimpak	30	20	28			41	57
E. umbellata	—	30	10	—	—	—	93	—

Sources: Belcher and Washburn (1965), Heit (1968), Molberg (1969), Olson (1974).

* Seeds were stratified for 10 to 90 days at 1.1 to 10 °C.

Hinds 1967; Mickelson 1968; Molberg 1969; Olson 1974; Zarger 1968). A seedling density of 130 to 320/m² (12 to 30/ft²) is desirable (Baker 1969; Molberg 1969; Zarger 1968). Stock usually is field planted as 1+0 or 2+0 seedlings, and grows well in most soils, including limestone or alkaline soils (Stoeckeler 1946).

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E

Asteraceae—Aster family

Encelia Adans.

encelia

Jane E. Rodgers and Carol Miller

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Other common names. brittlebush, bush-sunflower.

Growth habit, occurrence and uses. The brittlebush genus—*Encelia*—includes 14 species of low branching shrubs native to western America. The plants are suffrutescent, often with a pungent odor (Benson and Darrow 1954). Ray flowers (sometimes absent) are yellow, usually conspicuous when present, and produce neither pollen or fertile seeds. Disk flowers are yellow or purple (Benson and Darrow 1954). Species frequently hybridize, especially in disturbed areas. Species commonly found in the southwestern United States are listed in table 1.

The brittle wood secretes a clear resin used by Native Americans as a glue. In some parts of Mexico, the resin has been burned as incense for religious ceremonies (Benson and Darrow 1954). The Cahuilla of the southwestern United States have used gum from this plant as a medicine; the gum was heated and applied to the chest to relieve pain (Bean and Saubel 1972).

Flowering and fruiting. Flowering can begin in February and continue through July, weather conditions permitting. Most encelia flowerheads are yellow or a brown- or yellow-purple. The achenes are densely compressed, obovate or wedge-shaped, with edges that are long-ciliate and faces that are glabrous or short-hairy (figures 1 and 2) (Jepson 1993).

Collection, extraction, and storage. Timing of seed collection is critical, as the achenes are easily blown from the plant after maturity (Kay and others 1977). Seeds may be hand-harvested and stored successfully for several years. Cleaning is difficult, for seeds are often mixed with dry flower and plant parts of similar size and weight. Studies on long-term storage of seeds of rayless encelia and Acton brittlebush showed good germination after 4 and 14 years, respectively (Kay and others 1988). Seeds of both species that were stored under 4 conditions (–15 °C, 4 °C, room temperature, and warehouse temperatures) also showed significantly poorer germination rates in the warehouse after 3 years. Storage conditions studied by Padgett and others (1999) showed that seedlots stored for 6 months in a stan-

Figure 1—*Encelia farinosa*, brittlebush: achenes.

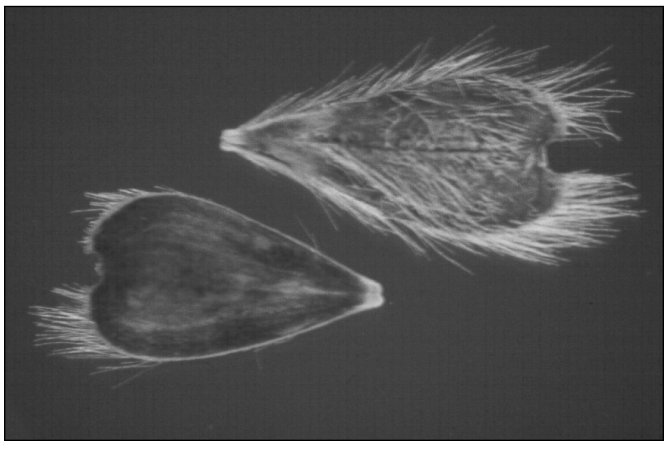
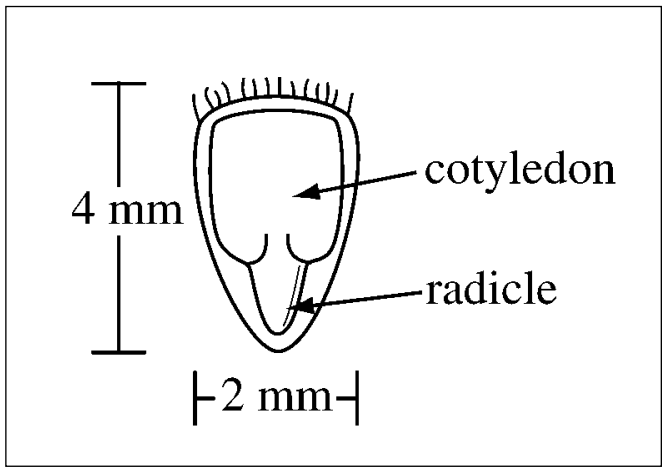


Table 1— *Encelia,* encelia: nomenclature and occurrence

Scientific name	Common names	Occurrence
***E. californica* Nutt.**	**California brittlebush**	Coastal California scrub to Baja California
***E. farinosa* Gray ex Torr.**	**brittlebush,** *incienso*, goldenhills	Deserts of SW Utah, Arizona, & NW Mexico
***E. frutescens* (Gray) Gray**	**rayless encelia**, green brittlebush	Deserts of S Nevada, W Arizona, & Baja California
***E. virginensis* A. Nels.**	**Virgin River encelia,** brittlebush	E Mojave to SW Virgin River, Utah, & NW Arizona
***E. virginensis* var. *actonii* (Elmer) B.L. Turner**	**Acton brittlebush**	SW California, SW Nevada to N Baja California

Source: Jepson (1993).

Figure 2— *Encelia farinosa,* brittlebush: longitudinal section through a seed.



dard refrigerator held at about 5 to 10 °C exhibited 2 to 3 times greater germination percentages than those stored at room temperature.

Pregermination treatment and germination tests. No seed treatment is necessary (Emery 1988). Some research has been done to test dormancy in encelias, especially in brittlebush. At Joshua Tree National Park (JTNP), germination of brittlebush was tested with direct sowing and with the following seed treatments: 24 hours of cold water soaking, 6 hours of cold water soaking, and 24 hours of leaching, with all seeds sown on moist blotter paper (CALR 1993). Results showed very low germination rates (<1%). Research at the University of California at Riverside (UCR) has shown that the most significant cause of poor germination is lack of viable embryos in nearly half of the seeds tested for viability and germination behavior (Padgett and others 1999). Pre-soaking appears critical, and gibberellic acid (GA) has enhanced germination rates 2 to 3-fold (Padgett and others 1999). Treatment tests subjected seeds to warm water soaking for 30 minutes, followed by soaking in 100 ppm GA in water for 30 minutes. These treated seeds were then sown on or in 3 different media: UCR soil mix, vermiculite, and germination paper. All seeds were incubated in low light at 25 to 30 °C. Two general trends were observed: seed treatment with gibberellic acid for 30 minutes significantly increases germination rates, and sowing into vermiculite followed by transplantation into sterile potting medium appears to be the best method for seedling germination and survival. The vermiculite is pre-soaked, and misted every 2 days to avoid drying out. Seeds sown into the UCR soil mix had severe damping-off problems, and results from the germination paper are thus far inconclusive. From the vermiculite, seedlings were successfully transplanted to larger containers and maintained in greenhouse conditions.

Work with Acton brittlebrush has correlated temperature and germination rates (Kay and others 1997):

Temperature (°C)	2	5	10	15	20	25	30	40
Germination (%)	0	1	47	65	55	5	7	0

Seeds were collected in late June 1973, yielding 1.96 kg of material of 24% purity. Cleaned seeds were 86% pure and had a pure fruit weight of 477,000 achenes/kg (216,721/lb). Emergence testing of encelia seedlots planted at 1-cm depth over a 10-day period showed a total emergence of 57%. Emergence at a 2-cm ($^3/_4$ in.) depth was somewhat reduced and delayed, whereas no plants emerged from a 4-cm ($^1/_2$ in) depth (Kay 1975).

Nursery practice. Both cuttings and seedlings of brittlebush and Virgin River encelia have been successfully planted into 76-cm (30-in) tall and 15.2-cm (6-in) diameter tubes at JTNP using a mixture of sand, perlite, and mulch with a slow-release fertilizer. Both species were also grown in 3.8-liter (1-gal) pots, 15.1-liter (4-gal) pots, and plant bands, with the greatest outplanting success being the 76-cm (30-in) tubes or "tall pots" (CALR 1993). Plants in the nursery require a hardening-off period of 1 to 2 weeks and may be subject to aphid predation. Seedlings must be transplanted with care, for branches break off easily (CALR 1993).

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E

Fabaceae—Pea family

Enterolobium cyclocarpum (Jacq.) Griseb.

guanacaste or earpod-tree

John K. Francis

Dr. Francis retired from the USDA Forest Service's International Institute of Tropical Forestry

Growth habit, occurrence, and use. At maturity, the fast-growing *guanacaste* is a huge, spreading tree with feathery, bipinnately compound leaves. The trunks of open-grown trees are short and thick, tipped with an inverse cone-shaped crown; trunks of trees growing in closed stands have much longer boles. Guanacaste grows in both acid and alkaline soils (Bauer 1982) in forests and savannas from central Mexico (23°N) through Central America to about the Equator in northern Brazil (Little and others 1974; Pennington and Sarukhan 1968). However, the species has been widely planted in tropical and subtropical areas, including Puerto Rico, the U.S. Virgin Islands, Florida, and Hawaii (Francis 1988). Guanacaste is recommended for planting in areas that receive from 750 to 2,000 mm of mean annual precipitation (Bauer 1982; Fournier and Herrera 1977). Dry seasons of 1 to 6 months are normal in the native range (Bauer 1982; Janzen 1983). Guanacaste is principally used as an ornamental and shade tree in parks, estates, and broad avenues. It is also valued as a pasture shade tree, especially in Central America. Cattle, horses, and goats feed heavily on its sweet legumes (pods). The heartwood has a rich brown color and is in demand for cabinetry, furniture, crafts, and construction (Chudnoff 1984; Guridi 1980).

Flowering and fruiting. Small white flowers are borne in clusters or heads at the base of leaves (Little and others 1974; Pennington and Sarukhan 1968). Flowering takes place in March and April during the regrowth of new leaves after the leafless dry season (Hughes and Styles 1984; Janzen 1983). There is no indication in the literature as to the age at which flowers first appear; however, trees in a 26-year-old plantation in Puerto Rico had not yet flowered. The fruits are shiny, dark brown legumes that curve around one edge, giving them a shape that resembles a human ear (figure 1). Legumes are 7 to 12 cm in diameter and contain 8 to 18 seeds (Holdridge and Poveda 1975; Janzen 1983; Pennington and Sarukhan 1968); they mature the year they are formed and fall in March and April.

Collection, cleaning, and storage. Seeds can be collected in quantity by picking up the legumes after they have fallen to the ground. They can be separated by macerating the legumes and then washing them to remove the sticky syrup or by picking the seeds from the tough legumes with the point of a knife (Francis 1988). One thousand to a few thousand seeds are produced per tree. The 1.3- to 1.9-cm ($^1/_2$- to $^3/_4$-in) seeds (figure 2) number 1,100/kg (500/lb) (Janzen 1983; Neal 1965). The seeds store well according to Bauer (1982).

Germination. Without scarification, a moderate percentage of the seeds germinate over a span of several

Figure 1—*Enterolobium cyclocarpum*, guanacaste: seeds and legume.

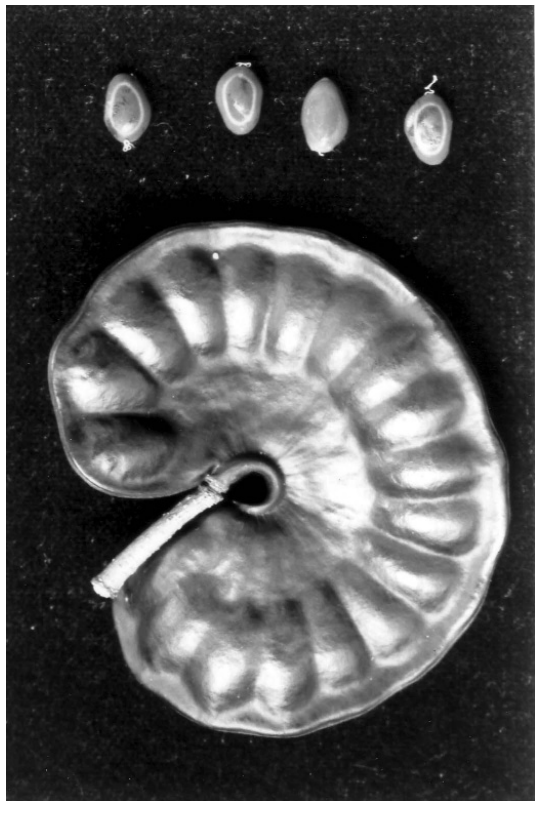
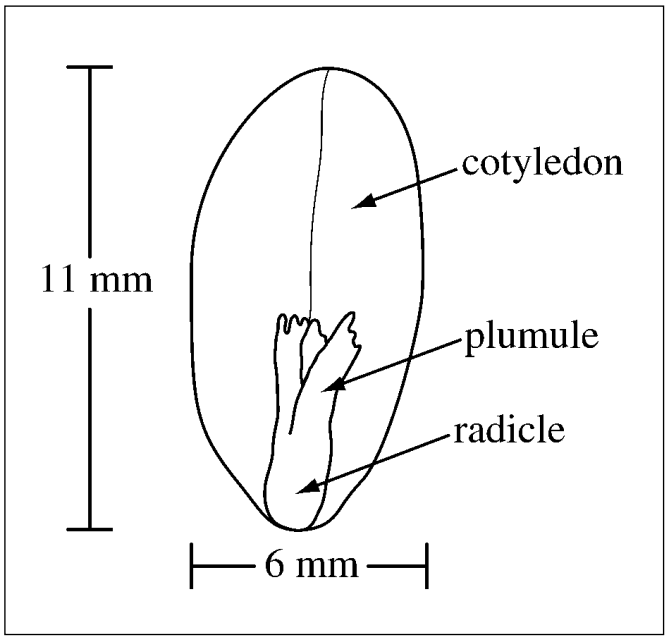


Figure 2—*Enterolobium cyclocarpum*, guanacaste: longitudinal section through a seed.



months. Scarified seeds in most kinds of soil germinate in 3 to 7 days. Germination values of 79 and 84% were observed in tests in Puerto Rico (Francis and Rodríguez 1993) and Costa Rica (Salazar 1985). A seed can be scarified by nicking it on a grindstone, by cracking it with a pair of pliers, or by immersing it briefly in boiling water. In nature, seeds are scarified and disseminated primarily when the legumes are eaten by domestic and wild ungulates or when they are nicked by rodents (Janzen 1983). Germination is epigeal (Francis 1988).

Nursery practice. Seeds may be sown in nursery beds, germination trays, or directly in pots. They should be covered with about 1 cm (.4 in) of soil or potting mix. Seedlings develop rapidly in full sunlight, reaching plantable size of about 0.5 m (20 in) in about 6 months (Francis 1988). The seedlings are very drought hardy and generally, good survival at outplanting can be obtained with potted seedlings and stump plants (Bauer 1982). A test of container seedlings in southeastern Mexico yielded an average of 77% survival (Beroni and Juarez 1980).

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E

Ephedraceae—Ephedra family

Ephedra L.

ephedra or Mormon-tea

Susan E. Meyer

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Growth habit, occurrence, and uses. The genus *Ephedra*—known in much of North America as Mormon-tea—comprises about 40 shrubby species that are found throughout the arid and semiarid regions of the Northern Hemisphere. Ephedras are gymnosperms that are characterized by their greatly reduced, bractlike leaves and their evergreen, broomlike photosynthetic stems. They are common plants in the semiarid region of western North America (table 1) and are often locally codominant with creosotebush (*Larrea tridentata* (Sessé & Moc. ex DC.) Coville), blackbrush (*Coleogyne ramosissima* Torr.), shadscale saltbush (*Atriplex confertifolia* (Torr. & Frem.) S. Wats.), and various species of sagebrush (*Artemisia* spp.). Species of ephedra are often the dominant vegetation on sand hills at middle elevations, where they perform an important role as sand-binders. They provide a significant source of browse for domestic livestock, especially sheep, and for wild ungulates such as mule deer (*Odocoileus hemionus*) and pronghorn antelope (*Antilocapra americana*). The seeds provide food for rodents and birds. The twigs, especially those of green Mormon-tea, are used to make a reputedly refreshing tea, although ephedrine, the pharmaceutically active compound found in the Old World species *E. sinica* Stapf., has not been detected in any North American species. Ephedras are attractive and interesting plants, with considerable potential for landscape use, and green Mormon-tea can now be readily obtained from commercial nurseries.

Flowering and fruiting. Ephedras are dioecious, with male and female cones occurring on separate plants. The cones are borne singly or in pairs or whorls at the branch nodes. The seeds are borne singly or in pairs in the axils of the female cone scales. The inner cone scales are modified to enclose the seed and form integuments that mimic the angiosperm pericarp. Flowering usually takes place in March through May, and seeds ripen from June through September, depending on elevation and species. The plants are wind-pollinated. Ephedra plants do not flower every year; their reproductive pattern could be described as mast fruiting, where most individuals in the population flower synchronously in a year with ample rainfall, and large quantities of seeds are produced. The population does not flower again for several years, whether or not a high-rainfall year occurs. The seedcrop may be damaged by late frosts, late spring drought, or infestations of pentatomid bugs.

The distribution of male and female ephedra plants is not random; individuals on dry slopes are overrepresented by males, whereas those growing on run-on surfaces are 4 times as likely to be females as males (Freeman and others

Table 1—*Ephedra,* ephedra: habit, habitat, and geographic distribution of some species used in revegetation

Scientific name	Common name(s)	Habit	Habitat	Distribution
***E. nevadensis* S. Wats.**	**Nevada Mormon-tea,** gray Mormon-tea, gray ephedra, gray Nevada joint-fir	Sprawling, gray-green, leaves in pairs, bases	Creosote bush shrubland to pinyon–juniper woodlands	W US
***E. torreyana* S. Wats.**	**Torrey Mormon-tea,** Torrey ephedra, Torrey's joint-fir	Sprawling, gray-green, leaves in whorls of 3, bases gray	Creosote bush shrub to pinyon-juniper woodlands	Colorado Plateau, Chihuahuan Desert
***E. viridis* Coville**	**green Mormon-tea,** Brigham tea, green ephedra, Mormon-tea	Erect, broomlike, bright green, leaves in pairs, bases black	Blackbrush shrub land to mountain brush	W US

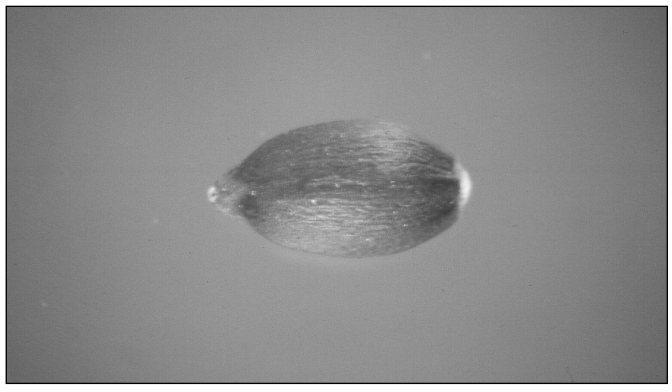
Sources: Welsh and others (1987).

1976). The genetic basis for sex differentiation in *Ephedra* is not known, but the spatial arrangement of males and females functions to maximize reproductive output, as it places males where their pollen can be easily wind-dispersed early in the season and females where they are more likely to have resources later in the season to ripen a seedcrop.

North American ephedra species fall into 2 groups characterized by differences in seed size and dispersal ecology (table 2). The large-seeded species (for example, green and Nevada Mormon-teas) are dispersed by scatter-hoarding rodents such as kangaroo rats (*Dipodomys* spp.), which deposit them in shallowly buried caches and later return to eat most of the seeds or sprouts. The cone scales in these species are small. In small-seeded species (for example, Torrey Mormon-tea) the outer cone scales are large and membranous, and the intact cones are often seen windrowed at some distance from adult plants. The seeds are apparently wind-dispersed, as they have long, awnlike points that probably make them unattractive to rodents. Cones with seeds intact may remain on the surface for many months.

Fruit collection, cleaning, and storage. Ephedra seeds (figures 1–3) are easily collected when fully ripe by beating the branches over a hopper or pan; in mast years, large quantities can be collected in a short time. The collection window is narrow and crops must be watched carefully, as ripe seeds can be dislodged by wind or rain in a single day. Seed fill is usually high (table 2), but it is a good idea to check fill in the field before harvesting, as late drought can prevent filling of seeds that otherwise look normal. After the seeds are thoroughly dried, they may be broken free of the cone scales in a barley de-bearder if necessary and then cleaned in an air-screen cleaner (fanning mill). The seeds are usually long-lived in warehouse storage if initially of high quality, and storage times of 15 years may result in little viability loss (Stevens and others 1981). In a warehouse storage experiment, seedlots stored from 10 to 20 years had an average viability of 80% (n = 3), whereas seedlots stored from 20 to 30 years had an average viability of 31% (n = 12). The vigor of the older lots was low, however, as evidenced by their low germination in response to chilling (<5% for lots >20 years old). It is doubtful whether seedlots >20 years old could be field-seeded successfully. The ability to remain highly viable for many years (orthodox storage behavior) facilitates stockpiling of ephedra seeds collected in mast years for use over the period when few seeds are produced.

Figure 1—*Ephedra nevadensis*, Nevada Mormon-tea: seed.



Seed germination and testing. Ephedra seeds are sometimes dormant at harvest, but this dormancy usually disappears through after-ripening after a few months in storage (Kay and other 1977). The dormancy also disappears after short periods (2 to 4 weeks) of chilling; this chilling also hastens the subsequent germination of nondormant seeds (Kay and others 1977; Meyer and others 1988). In experiments with 6-month-old seedlots, 7-day germination for unchilled seeds at 10 to 20 °C was 10% for 1 lot of green Mormon-tea, 49 to 54% for 2 lots of Nevada Mormon-tea, and 95 to 100% for 3 lots of Torrey Mormon-tea. The 7-day germination after 2 weeks of chilling at 1 °C was over 90% for all seedlots. Germination is generally highest at temperatures of 15 to 20 °C, except in more dormant lots, which show higher percentages of germinatation in temperature regimes that include a temperature in the chilling range (Young and others 1977). Germination is suppressed by higher temperatures, which probably prevent the

Table 2—*Ephedra*, ephedra: seed weight and viability data

Species	Seed weight				% viability	
	Range		Mean			
	/g	/oz	/g	/oz	Range	Mean
E. nevadensis	33–57	935–1,615	43	1,220	84–94	89
E. torreyana	108–128	3,060–3,630	118	3,345	76–91	83
E. viridis	28–62	790–1,760	47	1,330	46–100	89

Sources: Belcher (1985), Kay and others (1977), Meyer (1995), Meyer and others (1995), Monsen (1995).

Figure 2—Ephedra viridis, Torrey Mormon-tea: seeds (**outer**) and cone (**center**) with single seed.

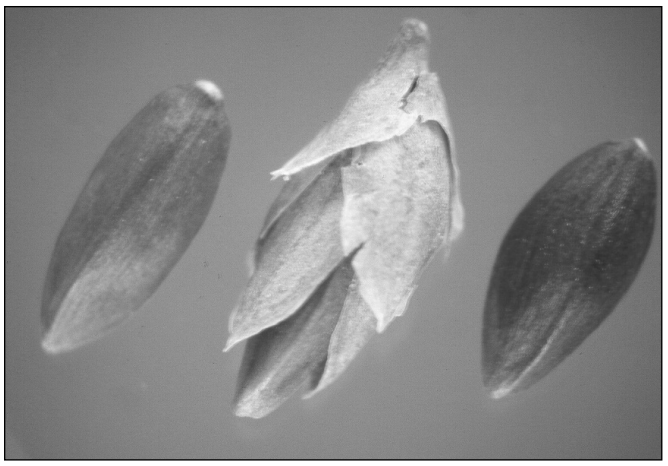
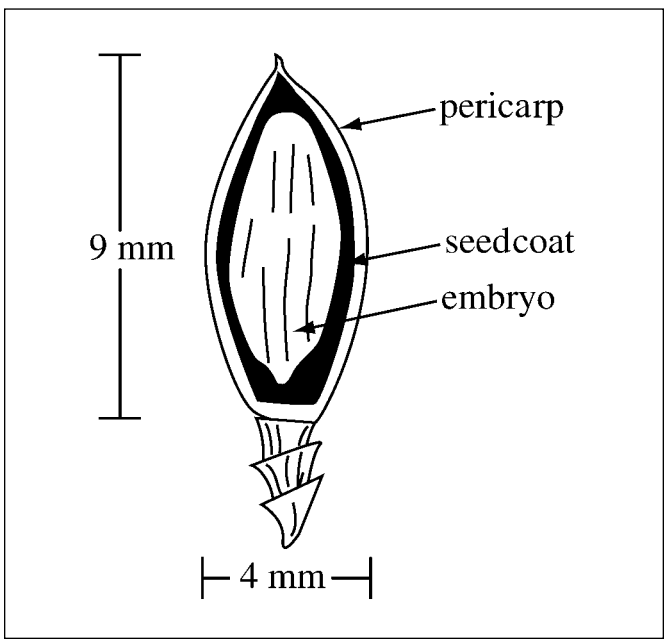


Figure 3—*Ephedra nevadensis*, Nevada Mormon-tea: longitudinal section through a seed.



otherwise nondormant seeds from precocious summer germination. Ephedra seeds germinate readily during prolonged chilling. Kay and others (1977) reported 76% germination during a 30-day stratification at 2 °C for a Mojave desert collection of Nevada Mormon-tea. In chilling experiments with the 6 seedlots mentioned above, weeks to 50% germination at 1 °C varied from 6 to 7 weeks for the Torrey Mormon-tea collections and from 8 to 9 weeks for collections of the other 2 species. All viable seeds germinated during chilling within 12 weeks.

Official rules for testing green Mormon-tea call for a 4-week test at 15 °C, with the option of a 4-week prechill for more dormant lots (AOSA 1993; Meyer and others 1988). Ungerminated seeds should be scored for viability using tetrazolium staining, which is also an acceptable substitute for a germination test. Seeds should be allowed to imbibe water, then clipped or slit on the cotyledon end and immersed in 1% tetrazolium solution for 8 hours. Seeds are then bisected longitudinally for evaluation.

Nursery and field practice. Large-seeded species of ephedra have been successfully established from direct seeding using drilling or with a seed dribbler or thimble seeder. If seeds are distributed aerially, a method for covering them with soil must be provided, as the seeds must be planted for successful establishment. Seedlings emerge and establish quickly and can withstand considerable drought once established. Emergence is best from depths of 1 to 2 cm (4/10 to 8/10 in) (Kay and others 1977). Emergence in green Mormon-tea is epigeal and the seedlings resemble those of conifers, whereas emergence in Nevada Mormon-tea is reported to be hypogeal (Kay and others 1977). Late-fall-seedings have been successful in the northern part of the range, where most effective precipitation comes in winter; whereas early-summer-seedings are recommended in the southern part of the range, where rainfall comes in the summer.

Ephedra planting stock may be produced either in bareroot or container culture. Plants do best in a coarse well-drained medium. Roots are fragile, so stock must be handled very carefully to avoid damage. The root systems of container stock are often too small to bind the root plug together, and those of bareroot stock are also usually poorly developed, resulting in low root–shoot ratios. Outplanting success rates are generally quite low (<50%).

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Ericaceae—Heath family

Epigaea repens L.

trailing-arbutus

Franklin T. Bonner

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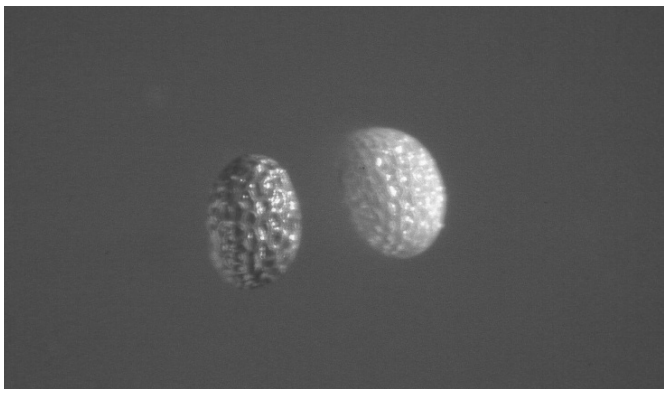
Other common names. mayflower, ground-laurel, gravel weed, mountain-pink, winter-pink, crocus, gravel plant.

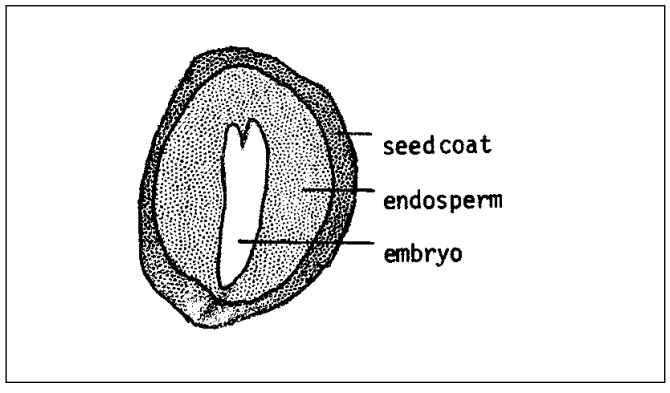
Growth habit, distribution, and use. Trailing-arbutus is an evergreen, prostrate, creeping shrub that grows in patches up to 60 cm in diameter (Bailey 1949). It is found growing in woodlands on acid, sandy soils from Florida to Mississippi, north to New England, southeast to New York, Pennsylvania, West Virginia, and Ohio. The variety *glabrifolia* Fern. ranges north from the higher parts of the Appalachian Mountains to Newfoundland, Nova Scotia, and Labrador and west to Saskatchewan (Fernald 1950). Although it is difficult to grow, trailing-arbutus has been planted as an ornamental since 1736 (Barrows 1936; Lemmon 1935). In some parts of its range it has become locally rare (Clay 1983). The blossoms are quite fragrant, and the fruits are sometimes eaten by small game. An infusion of the above-ground parts was used by the Cherokees to treat diarrhea in children (Jacobs and Burlage 1958).

Flowering and fruiting. The flowers are spicy smelling, pink to white in color, and bloom from March to May, although specimens have been known to bloom as early as January at low elevations in the southern part of its range (Stupka 1964). Flowering usually begins when plants are 3 years old (Steffek 1963). Flowering is normally dioecious, but perfect flowers may occasionally be found (Bailey 1949; Barrows 1936; Fernald 1950). Double-flowered forms and fall-blooming forms have been reported (Fernald 1950). The fruit is a 5-lobed, hairy, dehiscent capsule about 6 mm in diameter (Bailey 1949; Fernald 1950; Steffek 1963). The seeds are embedded in a sticky, white, fleshy pulp within the capsule (Barrows 1936; Clay 1983; Steffek 1963). A sample of 155 wild fruits contained an average of 241 (range: 29 to 415) tiny, shiny, brown, hard seeds per capsule (figures 1 and 2). In June and July, as the capsules ripen, the sutures split open and many of the seeds are ejected with some force (Blum and Krochmal 1974). As the sutures begin splitting, ants will commonly enter the fruits and rapidly remove all seeds (Clay 1983).

Collection of fruits; extraction and storage of seeds. Capsules should be collected after they are mature and before they eject their seeds. Small collections of capsules can be air-dried in open containers until seeds are ejected. The empty capsules can be separated by screening. One sample of cleaned seeds contained 22,700 seeds/g (643,750/oz) (Blum and Krochmal 1974). Storing seeds for more than 1 year is not recommended, but short-term storage at room temperature or in a refrigerator is satisfactory (Barrows 1936).

Figure 1— *Epigea repens*, trailing-arbutus: seeds (**top**) and longitudinal section through a seed (**bottom**).





Germination tests. Germination is epigeal and has been reported to require no pretreatment (Blum and Krochmal 1974). To secure complete germination on moist filter paper in petri dishes; however, Lincoln (1980) found it necessary to stratify seeds for 30 days at 5 to 8 °C and then germinate them at alternating temperatures of 15 to 25 °C or 20 to 30 °C with light at the higher temperature. This procedure yielded germination values of 92 and 90%, respectively.

Nursery and field practice. The seeds of trailing-arbutus are so small that sowing in small pots or trays filled with acid soil, sand, and peat moss or leaf mold mixtures is recommended (Blum and Krochmal 1974). The seeds should be scattered on top of the mixture, and the container should be covered with a glass plate or plastic bag to maintain a high humidity. With this method, germination takes place over a period of 22 to 66 days, with most germination occurring in 30 days (Barrows 1936). There are other reports of good germination within 3 to 5 weeks of time (Dirr and Heuser 1987).

When the seedlings have 3 to 5 leaves above the cotyledons, they may be transplanted to individual pots. High humidity should be maintained until the plants are well established (Barrows 1936). In 1 year, the plants develop into rosettes about 10 cm (4 in) in diameter (Blum and Krochmal 1974). Plants will tolerate a fairly wide range of acidity. Wild plants in Connecticut grew on soils ranging in pH from 7.67 to 4.65, but the larger plants occurred on the more acid soils (Barrows 1936; Coville 1911; Lemmon 1935; Steffek 1963).

Trailing-arbutus thrives best in association with mycorrhizal fungi. Including soil that was collected near healthy wild plants in soil mixtures will introduce the necessary fungus (Barrows 1936; Coville 1911, 1915). The mycorrhizal fungus also appears to be essential for propagation from cuttings (Barrows 1936). Stem cuttings taken in August have given 94% rooting in a sand–peat mixture without any treatment (Dirr and Heuser 1987).

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Asteraceae—Aster family

Ericameria parishii (Greene) Hall

Parish goldenweed

Raymond D. Ratliff and Franklin T. Bonner

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Synonyms. *Haplopappus parishii* (Greene) Blake, *Aplopappus parishii* (Greene) Blake, *Bigelovia parishii* Greene, *Chrysoma parishii* Greene.

Other common names. Parish goldenrod, Parish goldenbush, Parish heathgoldenrod.

Growth habit, occurrence, and uses. An erect shrub, Parish goldenweed has a mature height of 1 to 2.5 m (Jepson 1951). Plants 15 years old have attained heights of 2 m and crown spreads of 1.2 m (Everett 1957). Parish goldenweed occurs in the lower parts of the chaparral belt between 460 and 2,130 m of elevation in the mountains of southern California and Baja California (Munz and Keck 1959). Frequently, it is found on outwash fans and exposed hillsides. The primarily value of this species is for erosion control on dry slopes (Ratliff 1974). Since the final writing of this manual, several sections of the genus *Chrysothamnus* (see table 1) have been transferred to the genus *Ericameria*.

Flowering and fruiting. Parish goldenweed will flower and bear seeds at 2 years of age and produce seeds each year thereafter (Everett 1957). Flowering takes place from July to October (Munz and Keck 1959), and ripe seeds may be collected in October and November (Mirov and Kraebel 1937). The fruit of Parish goldenweed is a single-seeded achene (figure 1) that is handled as a seed. The achenes are about 2 mm long (figure 2), and there are about 3,600 cleaned achenes/g (101,900/oz) (Mirov and Kraebel 1937).

Collection, cleaning, and storage. Achenes are usually collected by hand and separated from their bristles by rubbing and blowing (Ratliff 1974). There are no known studies of storage, but the seeds are probably orthodox and can be easily stored at low temperatures and moisture contents.

Figure 1—*Ericameria parishii*, Parish goldenweed: achene with pappus removed.

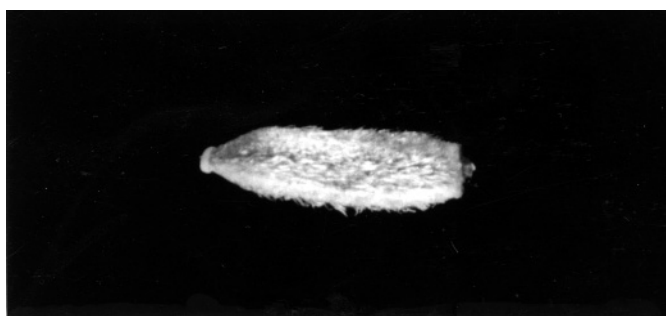
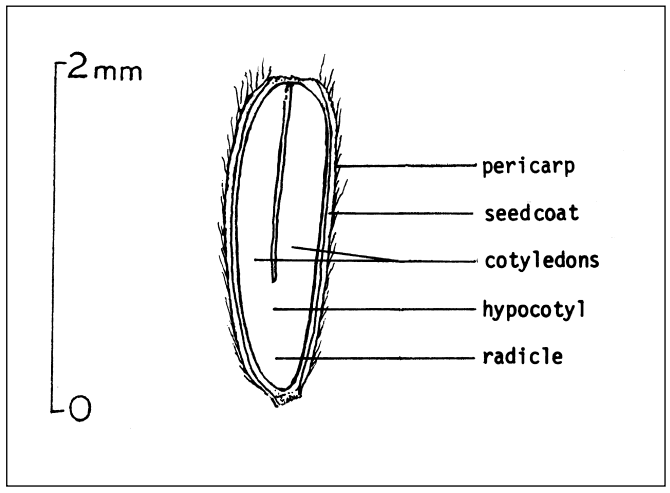


Figure 2—*Ericameria parishii*, Parish goldenweed: longitudinal section through an achene.



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Germination. Parish goldenweed seeds are not dormant, and no pretreatments are required to stimulate germination (Emery 1964). Seeds sown on sand began germinating in 4 days, and a maximum of 95% was obtained (Mirov and Kraebel 1937). Germination is, however, usually much lower (about 20%) because of a high percentage of defective seeds (Ratliff 1974). Parish goldenweed may also be propagated by cuttings (Jepson 1951).

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Polygonaceae—Buckwheat family

Eriogonum Michx.

wild-buckwheat, buckwheatbrush

Susan E. Meyer

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Growth habit, occurrence, and uses. The North American genus *Eriogonum*—wild-buckwheat, also buckwheatbrush—is made up of about 200 species of annual and perennial herbs and shrubs, most of which are found in the West. About half are woody, at least at the base. The habit of the woody species may be either (a) truly shrubby, (b) subshrubby, with annual renewal of upper shoots, or (c) pulvinate (mat-forming), with the woody shoots condensed into an above-ground caudex. The usually evergreen leaves are borne alternately and may be predominantly basal or borne along the stems. There may be whorls of leaves on the flowering stalks. The leaves are usually tomentose, at least below, and the stem nodes are often tomentose as well. The often-flat-topped inflorescences are usually borne above the leafy part of the plant and are conspicuous and characteristic even after seed dispersal.

Most plant communities in the West contain at least 1 species of woody wild-buckwheat (table 1). Some species are widely distributed and of wide ecological amplitude (for example, sulfurflower buckwheat brush), whereas others are narrowly restricted geographically and often edaphically as well (for example, pretty buckwheat brush). Wild-buckwheat species are often important pioneer plants after natural disturbance, and their presence may facilitate the establishment of later-successional species. This makes them useful for erosion control and for revegetation of anthropogenically disturbed sites such as mined land and highway rights-of-way (Ratliff 1974; Zamora 1994). Some species are important as browse plants for wild ungulates, particularly in the early spring when their evergreen habit makes them more highly nutritive than many other spring browse species (Tiedemann and Driver 1983; Tiedemann and others 1997). Some wild-buckwheat species are important bee plants. In California, Mojave buckwheatbrush has been rated third in importance for honey production, exceeded only by 2 native *Salvia* species (Kay and others 1977). Many wild-buckwheat species also have tremendous potential as easily grown, drought-tolerant ornamentals. Their interesting forms and leaf textures combined with masses of showy, long-lasting flowers make them excellent candidates for home xeriscapes. Named varieties that have been released are 'Sierra' sulfurflower wild-buckwheat (Stevens and others 1996) and 'Umatilla' snow wild-buckwheat (Tiedemann and others 1997).

Flowering and fruiting. The small, usually perfect flowers of wild-buckwheat are borne in clusters within cup-like or cylindrical involucres that are variously solitary or arrayed in capitate, cymose, or paniculate inflorescences. Each flower consists of a perianth with 9 stamens inserted at its base and a superior 1-celled and 1-seeded ovary. The perianth is made up of 6 fused segments in 2 whorls of 3. The ovary ripens in fruit into a usually 3-angled achene (figures 1 and 2). This achene is held more or less tightly within the perianth, depending on the species. For example, in snow wild-buckwheat the achenes fall free of the perianth at dispersal, whereas in Shockley wild-buckwheat the woolly perianth with the achene enclosed is the dispersal unit. The ovule within the seed is anatropous, so that the radicle end is pointing outward and upward. This makes it possible for germination and emergence to take place with the perianth still attached.

Wild-buckwheat species may flower at any time from early spring to fall, depending on species and habitat. Within a given habitat, species may bloom in succession. For example, at mid-elevation in central Utah, cushion wild-buckwheat blooms in spring, followed by James wild-buckwheat in early to midsummer, and finally by lace buckwheatbrush in late summer and fall. The bloom time for any species usually lasts well over a month, and the plants are almost as showy in fruit as in flower. The flowers are insect-pollinated.

Seed collection, cleaning, and storage. The window of opportunity for seed collection of wild-buckwheats is often rather wide, as the fruits usually persist on the plant for 2 to 3 weeks after maturity (Stevens and others 1996). When achenes are mature, the perianths dry and often change color, turning brown or rusty. At this point, the achenes can be harvested by hand-stripping or by beating them into hop-

Table 1— *Eriogonum*, wild-buckwheat: habit, habitat, and geographic range

Species	Common name(s)*	Habitat	Range
SHRUBS			
***E. corymbosum* Benth.**	**lace buckwheatbrush,** buckwheatbrush, crisp-leaf buckwheat	Desert shrub, pinyon juniper, mostly on shales	Colorado Plateau, Uinta Basin, & adjacent areas
***E. fasciculatum* Benth.**	**Mojave buckwheatbrush,** California buckwheatbrush, flat-top buckwheatbrush	Warm desert shrub, coastal sage scrub, chaparral, pinyon-juniper	Mojave & Colorado Deserts & coastal & cismontane S California
***E. heermannii* Dur. & Hilg.**	**Heermann buckwheatbrush,** molecule model plant	Warm desert shrub, mostly on rock outcrops	Mojave Desert
SUBSHRUBS			
***E. brevicaule* Nutt.**	**shortstem wild-buckwheat**	Open, barren hills, mountain brush to alpine	Central Rocky Mtns of Wyoming, Utah & Idaho
***E. heracleoides* Nutt.**	**Wyeth wild-buckwheat,** parsnipflower buckwheat	Sagebrush–grassland to aspen & Douglas-fir	N Rocky Mtns from BC to central Utah
***E. jamesii* Benth.**	**James wild-buckwheat**	Desert shrub to mountain brush & ponderosa pine	S Rocky Mtns S into N Mexico
***E. niveum* Dougl. ex Benth.**	**snow wild-buckwheat**, snow eriogonum	Sagebrush–grassland	Columbia River Plateau
***E. umbellatum* Torr.**	**sulfurflower wild-buckwheat,** sulfur wildbuckwheat	Sagebrush–grassland to spruce–fir	Widespread in W North America
PULVINATE/ MAT-FORMING			
***E. bicolor* M.E. Jones**	**pretty buckwheatbrush**	Cold desert shrub, on Mancos Shale	Central Utah
***E. ovalifolium* Nutt.**	**cushion wild-buckwheat,** roundleaf buckwheat	Wide range, from cold desert to alpine	Widespread, W North America
***E. shockleyi* S. Wats.**	**Shockley wild-buckwheat,** mat buckwheat	Desert shrub to pinyon–juniper	Idaho & Colorado to SE California, Arizona, & New Mexico

Source: Meyer and Paulsen (2000).
Note: The genus *Eriogonum* is not that of the true, domesticated buckwheat, hence the common names of wild-buckwheat and buckwheatbrush.

Figure 1—*Eriogonum fasciculatum*, Mojave buckwheatbrush: achene in calyx (**left**) and achene without calyx (**right**).

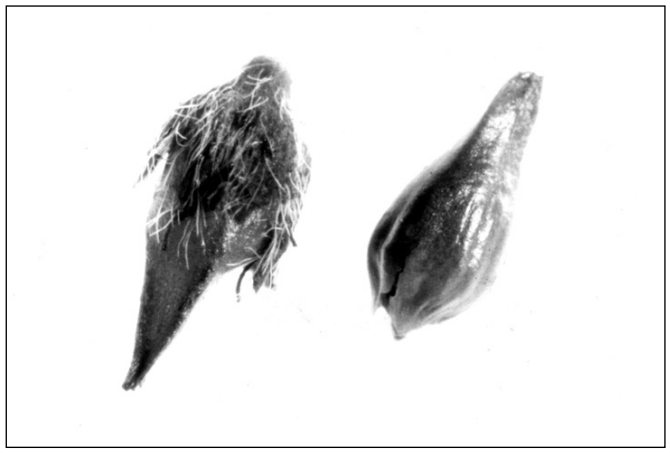
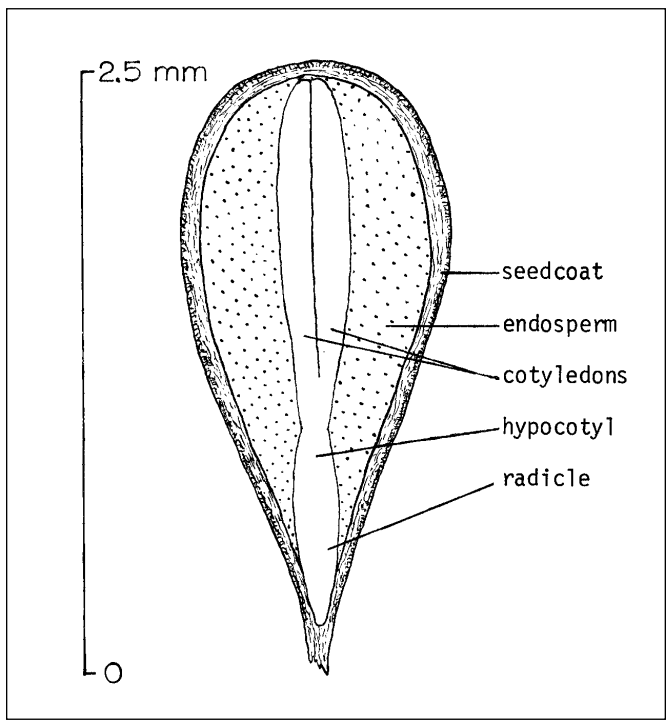


Figure 2—*Eriogonum fasciculatum*, Mojave buckwheatbrush: longitudinal section through a seed excised from an achene.



pers or other containers. Combine harvesting has proven successful for sulfurflower wild-buckwheat in seed production fields (Stevens and others 1996). The harvested material will include achenes, perianths, involucres, and inflorescence branches. After the material is dried thoroughly, it may be threshed in a barley de-bearder and cleaned with a fanning mill. Species with tightly held achenes may require hand-rubbing through screens or on a rubbing board, which is also an alternative cleaning method for small seedlots of any species. The material should not be handled too roughly, as the radicle end of the achene is often slender and easily damaged. Achene weights vary both among and within species but are usually in the range of 350 to 1,360/g (10,000 to 39,000/oz) (table 2). Seed quality is also variable (table 2).

There are few published reports of viability evaluation beyond germination percentages obtained without pretreatment, which may underestimate viability if there is a dormant fraction. Stevens and others (1996) report that viabilities of >90% may be expected from sulfurflower and Wyeth wild-buckwheats in an agronomic setting if seeds are harvested when fully mature; these values are comparable to those for wild-collected lots of many species (table 2). Insects may damage 10 to 35% of the fruits prior to harvest, but damaged seeds are normally eliminated in cleaning. Post-harvest damage from insect infestations is also possible (Stevens and others 1996). There is little information on maintenance of viability during storage for species of wild-buckwheat. Stevens and others (1996) report high viability for sulfurflower and Wyeth wild-buckwheats during 10 to 15 years in warehouse storage, which would indicate orthodox storage behavior. Other species are perhaps comparable.

Seed germination and testing. Germination is epigeal (figure 3). Seedlots of many species of wild-buckwheats contain at least a fraction that will germinate without any pretreatment (tables 2 and 3) (Young 1989). The size of this fraction depends on species and on the particular lot involved. Stevens and others (1996) report that seeds of sulfurflower and Wyeth wild-buckwheats lose dormancy during short periods of dry storage, and Mojave buckwheatbrush seeds are also reported to dry after-ripen (Kay and others 1977). Dormant seeds of most species we have examined lose dormancy during chilling at 1 °C for periods of 8 to 12 weeks (table 3).

To date there are no formal procedures for evaluating the seed quality of wild-buckwheat species, and tetrazolium (TZ) staining is probably the procedure most commonly employed. To evaluate using TZ, achenes are soaked overnight in water, clipped through both pericarp and seed coat at the cotyledon end (the wide end or hilum), and placed in 1% TZ solution for several hours at room temperature. Achenes are bisected longitudinally for evaluation (Belcher 1985).

Field seeding and nursery practice. Wild-buckwheats are generally readily established from direct seeding (Ratliff 1974; Stevens and others 1996; Tiedemann and Driver 1983; Zamora 1994). They establish best when seeded at a depth of 2 to 5 mm ($^1/_{16}$ to $^3/_{16}$ in), either by drilling or by broadcasting followed by covering (for example, raking). Seeding should take place before the season of maximum precipitation, which is generally fall or early winter in

Table 2—*Eriogonum,* wild-buckwheat: achene weights and typical viability percentages

Species	Achenes/weight /g	Achenes/weight /lb	Viability %	Viability Test
SHRUBS				
E. corymbosum	900	410,000	93	Post-chilling cut test
	2,000	900,000	—	—
E. fasciculatum	1,330	600,000	4–34	Germination %, no pretreatment
	520–1,085	236,000–490,000	20–46	Germination %, no pretreatment
E. heermannii	660	300,000	95	Post-chilling cut test
SUBSHRUBS				
E. brevicaule	700	320,000	84	Post-chilling cut test
E. heracleoides	350	160,000	95	Post-chilling cut test
	310	141,000	87	Post-chilling cut test
E. jamesii	350	160,000	—	—
E. niveum	1,290–1,360	585,000–620,000	52–72	Germination %; no pretreatment
E. umbellatum	470	213,000	86	Post-chilling cut test
	265	120,000	—	—
PULVINATE/MAT-FORMING				
E. bicolor	960	436,000	47	Post-chilling cut test
E. ovalifolium	990	450,000	95	Post-chilling cut test
E. shockleyi	750	340,000	86	Post-chilling cut test

Sources: Belcher (1985), Kay and others (1977), Meyer and Paulsen (2000), Stevens and others (1996), Tiedemann and Driver (1983).

* Post-chilling cut tests (AOSA 1996) are considered accurate for recently harvested seedlots; however, tetrazolium staining (TZ) is required for seedlots stored for more than 2 years.

Table 3—*Eriogonum,* wild-buckwheat: germination percentages

Species	Samples	Germination* (% of total viable seeds) No chill	4 weeks	8 weeks	12 weeks	16 weeks
E. brevicaule	2	3	28	65	86	96
E. corymbosum	3	28	79	100	100	100
E. heracleoides	3	4	11	30	55	77
E. jamesii	2	54	79	91	94	100
E. ovalifolium	2	22	74	98	98	100
E. umbellatum	4	7	30	74	99	100

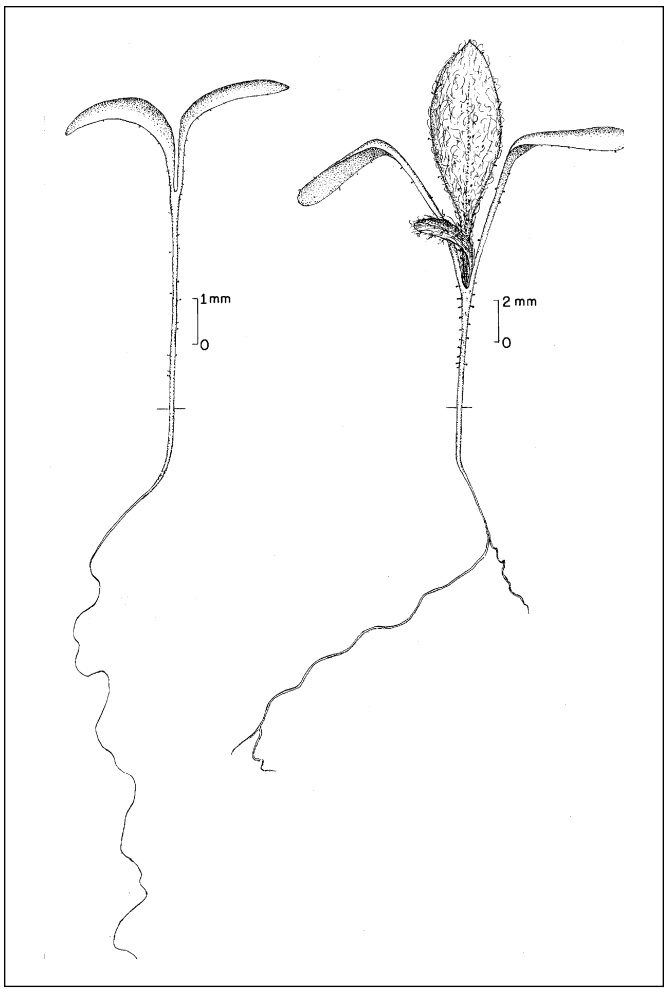
Source: Meyer and Paulsen (2000).

* Germination percentage determined after 0 to 16 weeks of chilling at 1 °C followed by 4 weeks of incubation at 10/20 °C

northern rainfall regions and midsummer in southern rainfall regions. Most wild-buckwheats are early seral and do not compete well with heavy stands of perennial grasses. Wild-buckwheats planted for field seed production are reported to reach 30 to 50% of maximum production, 200 to 400 kg/ha (180 to 360 lb/ac), the second year after planting (Stevens and others 1996).

Most species of wild-buckwheat are also easily propagated in a nursery setting. Shaw (1984) reported that Wyeth wild-buckwheat may be successfully produced as 1+0 bareroot stock. Because of the taprooted habit, plants must be lifted carefully. Other woody wild-buckwheats could probably be produced as bareroot stock, but no published information is available. Wild-buckwheats may also be produced as container stock; book planters or tube containers such as those used for producing conifer seedlings are most appropriate. Nondormant lots may be direct-sown, whereas seedlots requiring chilling may be sown as chilled seed or as young germlings (Landis and Simonich 1984). Seedlings of many species grow rapidly and should not be held in small containers for more than a few months. Many species flower the first year and may even form flowering stalks while still in small tube containers.

Figure 3—*Eriogonum fasciculatum*, Mojave buckwheat-brush: very young seedling (**left**) and older seedling (**right**).



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E

Myrtaceae—Myrtle family

Eucalyptus L'Her.

eucalyptus

Stanley L. Krugman and Craig D. Whitesell

Dr. Krugman retired from the World Bank and from the USDA Forest Service's Washington Office;
Dr. Whitesell retired from the USDA Forest Service's Pacific Southwest Research Station

Growth habit, occurrence, and use. The genus *Eucalyptus* comprises more than 523 species and 138 varieties, and new species and varieties are still being described (Blakely 1955; Johnston and Marryatt 1965; Penford and Willis 1961). Some are very tall trees, whereas others are woody shrubs (Jacobs 1979). Eucalypts are mainly native to Australia, but a few species are also native to the Philippines, New Guinea, and Timor (Hall and others 1963). Eucalypts are among the most widely cultivated forest trees in the world for ornamental use, shade, soil and site protection, wood production, and pulp making (Chippendale and others 1969). They are planted in southern Europe, the Middle East, Africa, India, Pakistan, China, North and South America—especially in Brazil, Uruguay, Chile, and Argentina (Jacobs 1979; Penford and Willis 1961).

This genus was first introduced into the United States with plantings in California and the Hawaiian Islands about 1853 (LeBarron 1962; Penford and Willis 1961). Eucalypts have also been planted, but to a limited extent, in Arizona, Florida, Georgia, Mississippi, and Texas (Geary and others 1983; Hunt and Zobel 1978; Metcalf 1961). About 250 species have been introduced into the United States and most of them are grown in California and Hawaii as ornamentals because of their decorative flowers and pleasing shapes (Jacobs 1979). Bluegum eucalyptus has been the most extensively planted eucalyptus in the United States, mainly in California, for the last 100 years (Metcalf 1961). It was initially grown for timber production but now is rarely used for this purpose. However, it is still widely used for fuel, shelterbelts, windbreaks, and has promise as a low-cost source of hardwood fiber (Krugman 1970). Among the other species that are promising for California conditions are river redgum, manna, mountain-gum, shining, and rosegum eucalyptuses (Ledig 1989). A number of other species are still being tested in California for their general landscape value (Hamilton 1979). In Florida, rosegum, robust, and river redgum eucalyptuses have been widely tested and are most promising as a source of wood fiber (Geary and others 1983; Uhr 1976). In Hawaii, several species, including rosegum, robust, red-ironbark, saligna, and bluegum eucalyptuses, have been planted as windbreaks and for watershed protection, as well as for timber and biofuel production (LeBarron 1962; Whitesell and others 1992). There are numerous other species that hold promise for future fiber production, windbreaks, and for environmental forestry purposes (Fujii 1976; King and Krugman 1980) (table 1).

Geographic races and hybrids. Many eucalypts have an extensive natural distribution, and members of the same species often grow under very different environmental conditions (Boden 1964; Eldridge 1978; Hall and others 1963; Jacobs 1979). Although detailed scientific information as to the development of geographic races is lacking for most species, there is considerable genetic variation in those species with wide natural distribution and it can be assumed that numerous races do exist (Jacobs 1979; Miles 1990). For planting eucalypts in the United States, geographic origin must be considered in selecting a suitable seed source from species wtih extensive natural ranges, such as the widely grown river redgum eucalyptus (Eldridge 1975; Karschon 1967; Pryor and Byrne 1969). As a general rule, seed source selection should at least be based on a knowledge of the absolute minimal and maximal temperatures under which the species grows in its native range (Zon and Briscoe 1911). Differential low temperature tolerance has been demonstrated for different sources of broadleaf sallee (*E. camphora* R.T. Baker) and brown-barrel, lemon-gum, and manna eucalyptuses (Boden 1964; Hunt and Zobel 1978). Precipitation appears to be of less importance, but must also be considered in selecting the proper seed source.

Under natural conditions, hybridization between species of the same subgeneric group will take place. It is relatively common in some cases, for example, brown-barrel × narrow peppermint eucalyptus (*E. fastigata* × *radiata* Seibert ex DC.) and robusta × rosegum eucalyptuses (Boden 1964;

Table 1—*Eucalyptus*, eucalyptus: nomenclature and natural and extended ranges

Scientific name & synonym(s)	Common name(s)	Natural range	Extension
***E. camaldulensis* Dehnhardt** *E. rostrata* Schldl.	**river redgum eucalyptus,** red-gum, long-beak eucalyptus	Australia	California, Hawaii, & Arizona
***E. citriodora* Hook.**	**lemon-gum eucalyptus,** lemon eucalyptus, lemon-gum	Central & N Queensland, Australia	California & Hawaii
***E. dalrympleana* Maiden**	**mountain-gum eucalyptus,** white-gum, dalrymple eucalyptus	SE Australia	California & Hawaii
***E. delegatensis* R.T. Baker** *E. gigantea* Hook. f.	**alpine-ash eucalyptus,** delegate eucalyptus	SE Australia	California
***E. fastigata* H. Deane & Maiden**	**brown-barrel eucalyptus**, cuttail eucalyptus	SE Australia	California
***E. glaucescens* Maiden & Blakey**	**tingiringy-gum**	SE Australia	California
***E. globulus* Labill.**	**bluegum eucalyptus**, bluegum, Tasmania bluegum, Tasmanian blue eucalyptus	SE Australia	California, Hawaii, & Arizona
***E. grandis* W. Hill ex Maiden**	**rosegum eucalyptus,** tooler eucalyptus.	E Australia	California, Florida, & Hawaii
***E. microcorys* F. Muell.**	**tallowwood eucalyptus**	E Australia	California
***E. nitens* (H. Deane & Maiden) Maiden**	**shining eucalyptus,** silver-top shining-gum	SE Australia	California & Hawaii
***E. obliqua* L'Her.**	**messmate stringybark eucalyptus**	SE Australia	California
***E. paniculata* Sm.**	**gray ironbark eucalyptus,** ironbark	E Australia	California & Hawaii
***E. pilularis* Sm.**	**blackbutt eucalyptus**	E Australia	California & Hawaii
***E. regnans* F. Muell.**	**mountain-ash eucalyptus,** swamp-gum giant eucalyptus	SE Australia	California
***E. robusta* Sm.** *E. miltiflora* Poir.	**robusta eucalyptus,** swamp-mahogany, beakpod eucalyptus	E Australia	California, Florida, Hawaii, & West Indies
***E. rudis* Sm.**	**desert eucalyptus,** moitch eucalyptus, desert-gum	W Australia	California & Florida
***E. saligna* Sm.**	**saligna eucalyptus,** Sidney bluegum eucalyptus, flooded-gum	E Australia	California & Hawaii
***E. sideoxylon* A. Cunningham**	**red ironbark eucalyptus,** mulga ironbark eucalyptus, red-ironbark	SE Australia	California & Hawaii
***E. viminalis* Labill.**	**manna eucalyptus,** ribbon eucalyptus, white-gum, ribbongum	SE Australia	California & Hawaii

Sources: Chippendale and others (1969), Johnston and Marryat (1965), Krugman (1974).

Jacobs 1979; Penford and Willis 1961; Pryor 1979). A number of hybrids have been described, but their value for planting in the United States must still be demonstrated. When grown under plantation conditions outside their natural habitat, species hybridization will occur more often, and seed collections from small plantations of closely related species should be discouraged if hybrid seeds are not desired (Boden 1964).

Flowering and fruiting. The flower clusters develop enclosed within an envelope formed by 2 bracteoles—small leafy structures. These bracteoles split and are shed during development, revealing the flower buds (Boland and others 1980; Penford and Willis 1961). The perfect flowers are white, yellow, or red, often in axillary umbels, corymbose, or paniculate clusters (Blakely 1955). In a few cases, the flowers develop singly as with bluegum eucalyptus, but most often they are in 5- to 10-flowered axillary umbels as with river redgum and manna eucalyptuses (Blakely 1955). Sepals and petals are united to form a cap in the bud, which drops off at anthesis. The stigma is receptive within a few days after the cap drops (Barnard 1967) and pollination is mainly carried out by insects. The ovary has 3 to 6 locules with many ovules. There is a wide range in flowering times for the eucalypts (King and Krugman 1980). In California, some species such as manna eucalyptus may flower all year; other species, such as river redgum and gray ironbark eucalyptuses, flower in the spring; tingiringy-gum and mountain-gum eucalyptus in the summer; rosegum eucalyptus in the

fall; and tallowwood eucalyptus in winter (table 2) (King and Krugman 1980; Krugman 1970, 1974).

The fruit is a hemispherical, conical, oblong, or ovoid hard woody capsule 6 to 25 mm in diameter, that is loculicidally dehiscent at the apex by 3 to 6 valves (Blakely 1955; Boland and others 1980). The seeds are numerous and extremely small in most species (table 3; figure 1). The size of fertile seeds within a given seed collection varies widely. Usually only a few seeds are fertile in a single capsule, and capsule size may influence seed size (Blakely 1955). When more than 1 seed ripens in a locule, the seeds are variously shaped and angular (figure 1). When solitary, the seed will be ovate or orbicular-compressed (Blakely 1955). The seedcoat is most often thin and smooth, but it can be ribbed, pitted, or sculptured in various ways (Blakely 1955; Penford and Willis 1961). Usually the seedcoat is black or dark brown in color as in manna eucalyptus or pale brown as with alpine-ash eucalyptus (table 3).

The embryo consists of bipartite or 2-lobed cotyledons that are folded or twisted over the straight radicle (Blakely

Table 2—*Eucalyptus,* eucalyptus: height at maturity and phenology of flowering and fruiting of trees grown in California

Species	Height at maturity (m)	Flowering	Fruit ripening	Seed dispersal
E. camaldulensis	18–36	Feb–Apr	July–Oct	Begins 8–9 months after flowering
E. citriodora	24–39	Nov–Jan	May–Aug	—
E. dalrympleana	18–36	June–Aug	Aug–Oct	Oct–Nov
E. delegatensis	30–83	Apr–June	Apr–July	May–July
E. fastigata	18–60	Apr–May	July–Aug	—
E. glaucescens	4–12	July–Aug	May–Sept	Nov–Feb
E. globulus	45–54	Nov–Apr	Oct–Mar	Oct–Mar
E. grandis	42–54	Sept–Nov	—	—
E. microcorys	30–45	Dec–Feb	—	—
E. nitens	30–90	Apr–July	May–June	May–June
E. obliqua	15–75	Apr–July	May–Aug	—
E. paniculata	24–42	Feb–May	—	—
E. pilularis	36–60	Dec–Mar	Jan–April	All year
E. regnans	52–105	Apr–July	June–Sept	—
E. robusta	24–27	Jan–Mar	—	—
E. rudis	9–15	Jan–Mar	—	—
E. saligna	15–45	Apr–June	Oct–Dec	—
E. sideroxylon	12–30	June–Sept	—	—
E. viminalis	15–45	All year	12 months after flowering	20–22 months after flowering

Source: Krugman (1970).

Table 3—*Eucalyptus,* eucalypus: description of viable seeds and chaff

Species	Seed size (mm)		Seed color	Chaff color
	Length	Width		
E. camaldulensis	0.75–1.75	0.5–1.0	Yellow-brown	Yellow-brown to orange
E. citriodora	4.25	2.5	Black	Brownish red
E. delegatensis	1.25–3.75	1.0–1.75	Pale brown or brown	Pale brown or brown
E. fastigata	1.25–3.25	0.5–1.25	Pale brown or brown	Pale brown or brown
E. glaucescens	1.25–2.5	1.0–1.75	Black or dark brown	Pale red-brown
E. globulus	2.25	1.75	Dark brown	Brownish red
E. nitens	1.25–2.5	1.0–1.75	Black or dark brown	Pale red-brown
E. obliqua	1.0–2.0	0.75–1.25	Dark brown	Orange-brown or brown
E. regnans	1.25–2.5	0.5–1.25	Pale brown or brown	Pale brown or brown
E. robusta	1.5	0.75	Dark brown	Brownish red
E. saligna	1.25	1.0	Black	Brownish red
E. sideroxylon	1.0–2.0	0.75–1.5	Dark brown or black	Orange-brown
E. viminalis	1.25–2.5	1.5	Black or dark brown	Pale red-brown

1955; Krugman 1974). There is no endosperm (Blakely 1955; Krugman 1974) (figure 2). Fruits ripen at various times during the year, depending on the species (table 2). Dispersal is largely by wind within a month or two after ripening for most species, for example, bluegum and shining eucalyptuses. For other species, such as manna eucalyptus, dispersal may not take place until 10 months after ripening (table 2). Good seeds are produced by most species by 10 years of age (Grose 1969). For mature trees the interval between large seedcrops is from 2 to 5 years.

Collection of fruits. Collecting mature eucalyptus fruits should present no serious problems, other than reaching the fruit in very tall trees, because for most species there is a relatively long interval between seed ripening and opening of the capsule (table 2). However, it is important to take care to collect only well-developed, closed capsules, because capsules at different stages of maturity—as well as buds, flowers, and empty capsules—will be found on a single branch (Boland and others 1980; Krugman 1974). The capsules should be spread in a thin layer to permit rapid drying and to prevent mold formation (Boland and others 1980; Grose and Zimmer 1958b). The most common method is to air-dry the capsules for a few hours to a few days, depending on the maturity of the capsules (Boland and others 1980; Grose and Zimmer 1958b). Drying temperatures should not exceed 37.7 °C for prolonged periods, because high temperature may strengthen the dormancy of species such as alpine-ash, brown-barrel, shining, and mountain-ash eucalyptuses and tingiringy-gum (Grose 1969; Grose and Zimmer 1958b). Capsules can also be kiln-dried for relatively short periods (Boland and others 1980; Grose 1969). Fruit drying schedules for some of the common species are listed in table 4.

Figure 2—*Eucalyptus rudis*, desert eucalyptus: longitudinal section thorough a seed.

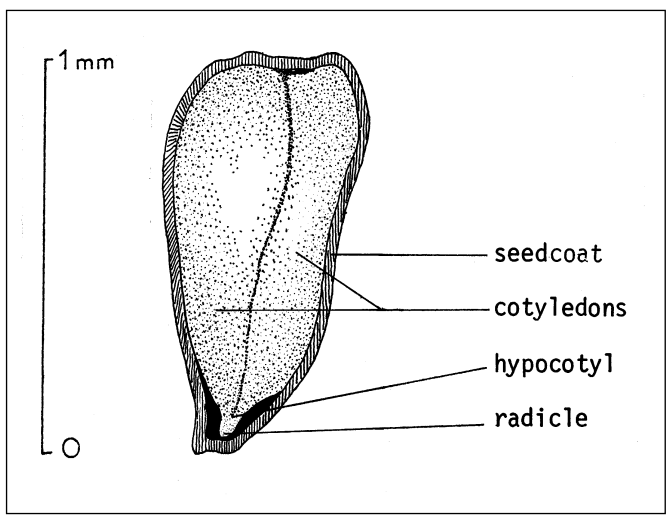
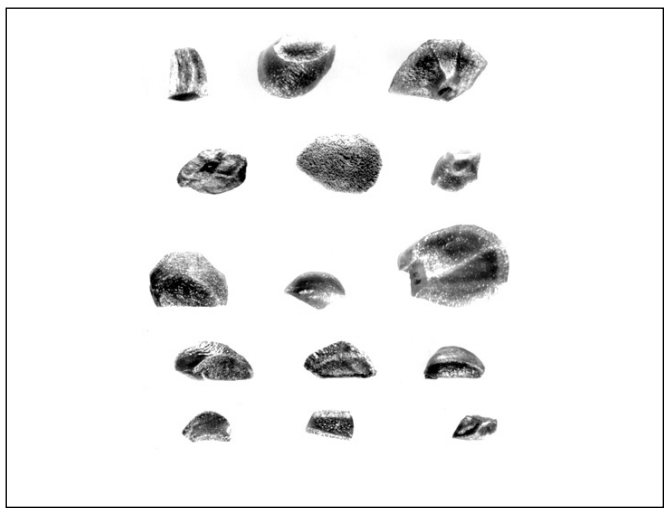


Figure 1—*Eucalyptus*, eucalyptus: seeds (**from left to right**) of *E. camaldulensis*, river redgum eucalyptus; *E. delegatensis*, alpine-ash eucalyptus; and *E. fastigata*, brown-barrel eucalyptus (**top**). *E. grandis*, rosegum eucalyptus; *E. microcorys*, tallowwood eucalyptus; *E. nitens*, shining eucalyptus (**second row**). *E. obliqua*, messmate stringybark eucalyptus; *E. paniculata*, gray ironbark eucalyptus; and *E. pilularis*, blackbutt eucalyptus (**third row**). *E. regnans*, mountain-ash eucalyptus, *E. robusta*, robusta eucalyptus; and *E. rudis*, desert eucalyptus (**fourth row**). *E. saligna*, saligna eucalyptus; *E. sideroxylon*, red ironbark eucalyptus; and *E. viminalis*, manna eucalyptus (**bottom row**).



Extraction and cleaning. Once the capsules are open, they should be vigorously shaken to remove the seeds. Shaking is especially important if the capsules are somewhat immature, because viable seeds may not have separated completely from the capsule's placenta. Thus, unless the capsules are shaken, only infertile seeds will be extracted (Boland and others 1980; LeBarron 1962). When examined, immature capsules may appear empty after the aborted seeds are removed, because viable seeds are normally attached at the base of the capsule (LeBarron 1962). Viable seeds are extracted along with the unfertilized or aborted ovules, which are known collectively as "chaff" (Boland and others 1980; Grose and Zimmer 1958b). Large impurities such as the remains of twigs, capsules, and leaves can be removed by screening. Smaller impurities can be removed by specific-gravity separators such as the one used in the air-column method (Boland and others 1980; Grose 1969). For a few species, viable seeds can be separated from the remaining chaff by employing sieves of the appropriate mesh size (Boland and others 1980). Because viable seeds and chaff of

Table 4—*Eucalyptus*, eucalyptus: fruit drying schedules

Species	Air-drying Temp (°C)	Air-drying Time (days)	Kiln-drying Temp (°C)	Kiln-drying Time (hrs)
E. camaldulensis	32	1	59	3
E. delegatensis	32	3	59	6
E. globulus	21	5	—	—
E. obliqua	32	3	59	5
E. regnans	32	3	59	6
E. sideroxylon	21	4	—	—
E. viminalis	21	6	—	—

most species cannot be separated by the usual methods, commercial seed suppliers sell chaff along with the fertile seeds. The proportion by weight of chaff to viable seeds is in the range of 5:1 to 30:1 (Grose and Zimmer 1958b). For some species, such as mountain-ash eucalyptus, the seeds and chaff are identical in size and color; for others, such as river red-gum eucalyptus, the seeds and chaff are similar in color but different in size (table 3). For most species, there are some differences in color and size, so that viable seeds can be separated from chaff to some extent if necessary. Because of their very small size, seeds of eucalyptus species are normally sold by weight with the chaff. The average number of viable seeds plus chaff per weight ranges from 770/g (21,900/oz) for river redgum eucalyptus to 35/g for blackbutt eucalyptus (1,000/oz) (table 5). There may be as many as 2,100 seeds/g (59,500/oz) for river redgum eucalyptus or as few as 7 seeds/g (200/oz) for blackbutt eucalyptus.

Storage. Eucalyptus seeds are orthodox in storage behavior. They should be stored in air-tight containers that are as completely filled as possible to reduce the amount of air (Boland and others 1980). Prior to storage, the seeds should be treated to kill insect pests, by either fumigation or placing paradichlorbenzene crystals in the container (Boland and others 1980).

Eucalypts seeds have germinated after 30 years of storage at room temperature, but the germination was very low (Penford and Willis 1961). Most seeds can be successfully stored for periods up to 10 years in air-tight containers at moisture contents of 4 to 6% and temperatures of 0 to 5 °C (Boland and others 1980; Grose 1969; Grose and Zimmer 1958b). It should be possible to store these seeds successfully for even longer at temperatures below 0 °C (Krugman 1970).

Pregermination treatments. Most eucalyptus seeds need no pretreatment to ensure adequate germination if fresh seeds are used (Boland and others 1980; Grose and Zimmer 1958b). A few species—such as tingiringy-gum and alpine-ash, brown-barrel, shining, and mountain-ash eucalyptuses—are normally dormant at the time of collection and will require pretreatment. Stratification of moist seeds stored in a plastic bag at temperatures of 3 to 5 °C for a period of 3 weeks will break the dormancy of these 5 species, except for alpine-ash eucalyptus, which should be stratified for 4 weeks (Boland and others 1980; Grose 1969). Longer stratification periods of 6 to 8 weeks are often recommended.

Dormancy between different seedlots of the same species can vary considerably. In addition, different methods of extraction and storage can induce dormancy in nondormant seed or strengthen primary dormancy in normally dormant seeds (Krugman 1970). If the seeds fail to germinate after the recommended shorter stratification periods, then a longer period should be tried before the seeds are considered nonviable. Because most seeds are stored before they are used, stratification for 3 to 4 weeks at a temperature of 3 to 5 °C is recommended for all eucalyptus seeds to ensure faster and more uniform germination (Hinkle 1968; Krugman 1970).

In a few cases, chemicals have been employed to overcome seed dormancy. The germination of unstratified and dormant seeds of alpine-ash, brown-barrel, and mountain-ash eucalyptuses was improved by germinating the seeds in a solution of gibberellic acid (Bachelord 1967). However, not all seedlots of the same species responded to gibberellic acid (Krugman 1970).

Germination tests. Standard methods for testing germination in other seeds are not used for eucalyptus seeds because of their small size and the presence of so much chaff, which can exceed the weight of viable seeds. Instead, samples for germination are of equal weight, not number (Boland and others 1980; Grose and Zimmer 1958b; ISTA 1993; Turnbull and Doran 1987). Such methods as the excised-embryo and tetrazolium tests are impractical (Boland and others 1980; Grose and Zimmer 1958b). The

Table 5—*Eucalyptus*, eucalyptus: seed yield data

Species	Viable seeds/(weight of seeds + chaff) Range /g	Range /oz	Average /g	Average /oz	Samples #
E. camaldulensis	65–2,100	1,800–59,500	770	21,900	41
E. citriodora	80–220	2,200–6,200	140	4,000	15
E. dalrympleana	65–285	1,800–8,100	195	5,500	7
E. delegatensis	40–125	1,100–3,500	75	2,100	13
E. fastigata	90–210	2,500–5,900	150	4,300	6
E. glaucescens	40–120	1,000–3,000	35	2,000	2
E. globulus	20–70	500–9,100	150	2,500	10
E. grandis	200–1,200	5,600–34,000	700	20,000	13
E. microcorys	530–900	1,500–25,600	85	6,800	22
E. nitens	230–550	6,600–15,700	385	10,900	7
E. obliqua	20–160	500–4,500	85	2,400	18
E. paniculata	65–340	1,800–9,600	75	5,000	8
E. pilularis	7–85	200–2,400	35	1,000	28
E. regnans	20–530	600–15,000	315	8,900	11
E. robusta	220–700	6,200–20,000	390	11,000	12
E. rudis	270–1,100	7,600–31,000	600	17,000	9
E. saligna	85–915	2,400–26,000	460	13,000	9
E. sideroxylon	65–440	1,800–12,500	240	6,800	16
E. viminalis	265–445	7,500–12,600	350	10,000	6

Sources: Grose and Zimmer (1958b), Larsen (1965).

International Seed Testing Association (1993) recommends a sample unit of 0.10 to 1.0 g of seeds, depending on the species. Seeds are placed on 1 or more layers of moist paper and germinated at a constant temperature of 15 to 35 °C, depending on the species (Grose 1969; Scott 1972). Some species may require alternating temperatures of 20 °C for 16 hours and 30 °C for 8 hours (ISTA 1993). The tests are normally conducted under lights, although lights are not necessary for all species. Recommendations for individual species are listed in table 6. Official rules (ISTA 1993) provide recommendations for many more species. Immature seeds of mountain-ash eucalyptus should be tested under lights (Penford and Willis 1961).

If an approximate estimate of viability is desired, a known weight of dry seeds can be soaked in water and then squashed systematically. All seeds that show a firm white embryo can be recorded as viable (Grose and Zimmer 1958b).

Soundness of eucalyptus seeds is highly variable. Seeds collected from individual trees of bluegum eucalyptus in California showed from 2 to 80% germination after 30 days (Krugman 1970). Germination of from 11 to 98% has been reported for other species (table 7).

Nursery practice. On the United States mainland, eucalyptus seeds are rarely sown directly in the nursery, a practice once common in Hawaii. The most common practice for growing eucalyptus seedlings is to germinate the

Table 6—*Eucalyptus*, eucalyptus: germination test conditions

Species	Daily light exposure (hrs)	Temp (°C)	Days
E. camaldulensis	24	35	14
E. citriodora	0	25	14
E. dalrympleana	24	25	14
E. delegatensis†	0	20	14
E. fastigata‡	0	25	14 or 21
E. glaucescens‡	24	20	14 or 21
E. globulus	24	25	14
E. grandis	0	25	14
E. microcorys	24	20§	28
E. nitens‡	24	20	14 or 21
E. obliqua	0	20	14
E. paniculata	24	20§	28
E. pilularis	0	20	14
E. regnans‡	24	25	21
E. robusta	24	20	28
E. rudis	24	35	14
E. saligna	24	25	28
E. sideroxylon	24	20	14
E. viminalis	24	25	14

Sources: Grose (1969), ISTA (1966, 1993).
* Seeds germinated on 2 layers of moist, filter paper in a petri dish (Grose 1969).
† Prechilled for 28 days at 3.3 to 5 °C (Grose 1969).
‡ Prechilled for 21 days at 3.3 to 5 °C (Grose 1969).
§ Treated at 20 °C for 16 hours, then 30 °C for 8 hours.

Table 7—*Eucalyptus,* eucalyptus: germination test results

Species	% Germination	Duration (days)
E. citriodora	51	15
E. grandis	98	29
E. microcorys	76	24
E. pilularis	11	29
E. robusta	84	18
	100	21
E. sideroxylon	69	49

Sources: Floyd (1964), Ganguli (1966), Krugman (1974), Scott (1972).

Table 8—*Eucalyptus,* eucalyptus: seedlings produced per weight of seeds

Species	Seedlings produced/seed weight /g	/oz
E. camaldulensis	175	5,000
E. citriodora	60	1,700
E. glaucescens	99	2,830
E. globulus	28	800
E. microcorys	7	180
E. paniculata	6	160
E. robusta	14	400
E. viminalis	111	3,160

Sources: Zon and Briscoe (1911).

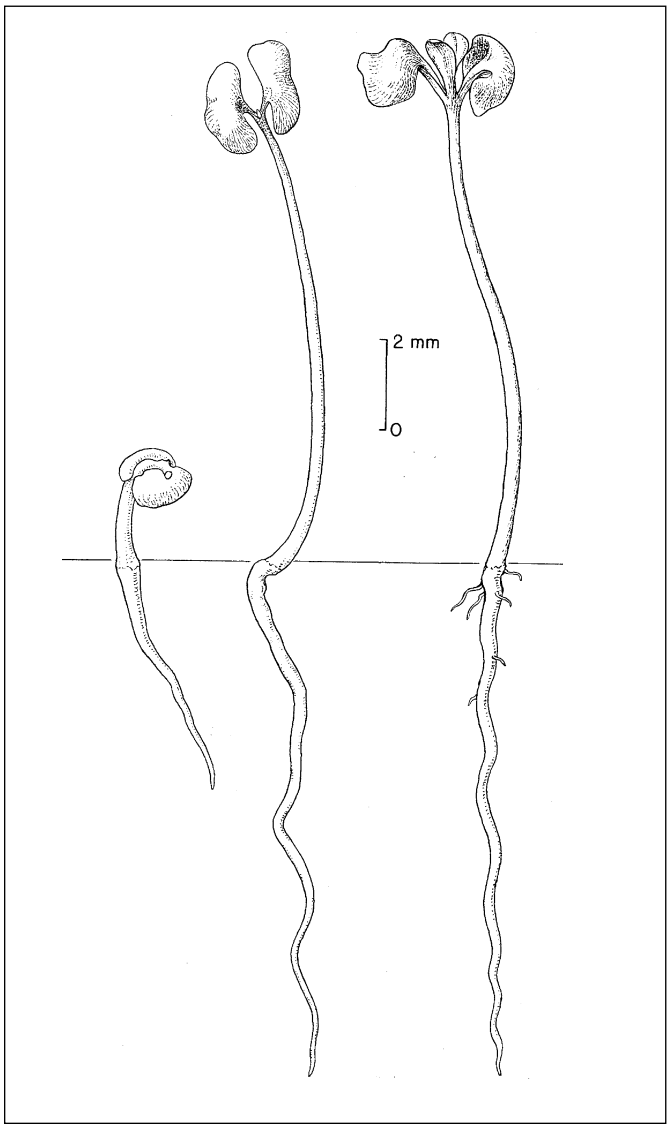
seeds in small pots, boxes, or wooden flats. Commonly used containers are wooden flats or plastic containers 45 to 50 cm (18 to 20 in) long and 40 to 50 cm (16 to 20 in) wide, and 10 to 12.5 cm (4 to 5 in) deep with good bottom drainage (Hinkle 1968; Jacobs 1955). The planting medium should be porous, friable, and light textured, such as a light, sandy loam (Hinkle 1968; Holmes and Floyd 1969; Willan 1985). The medium must permit good drainage and should not cake or become hard on the surface after watering. Because of possible weed and disease problems, the soil should be sterilized. Various mixtures are also used, with the most common consisting of equal parts (by volume) of sand, soil, and organic matter. The flats are filled to a depth of 7.5 to 10 cm (3 to 4 in) and the soil surface is leveled.

Because of their small size, the seeds are mixed with a little sand, and the mixture then is spread evenly over the soil surface (Hinkle 1968; Jacobs 1955; Penford and Willis 1961). The seeds are covered with 3 mm of fine sand, peat, or sphagnum moss to prevent surface drying.

A newer method to ensure more precision in sowing eucalyptus seeds is to coat them and form a mini-pellet (Geary and Millier 1982; Willan 1985). The seed dressing is usually an inert material serving as a sticker on which other materials can be added. One successful method involves a coating of fine silica sand filler and a polyvinyl alcohol binder (Geary and Millier 1982). In addition, fungicides and insecticides can also be added.

Enough seeds should be sown to raise between 500 and 2,000 plants/flat (table 8). Depending on seed size, this should represent about 7 g ($^1/_4$ oz) of seed/flat (Krugman 1970). The flats should be well watered and drained just before planting and should be protected from wind, heavy rains, and excessive heat. The emerging seedlings may require protection from birds and rodents in some locations.

Figure 3—*Eucalyptus*, eucalyptus: seedling development for manna eucalyptus at 1 day (**left**) and 8 days (**center**) and desert eucalyptus at 42 days (**right**).



Seedling care. Germination is epigeal (figure 3), begins in 7 to 10 days, and is completed in 3 to 4 weeks (Boland and others 1980; Jacobs 1955; Krugman 1974). Because the seeds are small and the seedlings very delicate, overhead watering should be with a fine spray and care must be taken to maintain adequate soil moisture.

When the seedlings are about 6 to 8 weeks old and have developed 2 pairs of leaves and a third pair is just visible above the cotyledons, they can be transplanted into suitable containers for further growth (Hinkle 1968; Jacobs 1955).

In transplanting, the seedlings should be lifted by the tip of a sturdy leaf, and not by the soft delicate stem. A dibble should be used to protect the fibrous root system. Prior to lifting, the seedlings should be hardened off by exposure to the open air away from full sunlight and strong winds for a few days to a week. A variety of different containers, from Jiffy™ pots to tin cans, have been used with success (Holmes and Floyd 1969; Jacobs 1955). The containers should be large enough to permit the development of strong plants, but small enough to permit ease of transportation. Tubes should be at least 4 cm (1.5 in) in diameter and 15 to 30 cm (6 to 12 in) long (Jacobs 1955). When metal tubes are employed, they are made so that they can be readily opened in the field and then later cleaned and reused. After transplants are placed in containers, care must be taken to prevent damage to them. Seedlings should be well watered and shaded from full sunlight. Fine gravel can be placed on the surface of the container to restrict slime molds. After several weeks the transplants can be placed in the open so that they can become hardy. They should be ready for outplanting in 4 to 5 months, depending on the species and growing conditions (Jacobs 1955).

Because of the rapid growth of eucalyptus seedlings, care must be taken lest they become pot-bound. Seedlings should not be permitted to grow in small containers for extended periods before outplanting.

Seeds can be sown directly in a standard 1.2-m-wide (4-ft-wide) nurserybed. The soil should be first fumigated to kill weed seeds and pathogens, then watered well and drained before sowing. Because seeds are small, even distribution is difficult when they are broadcast sown. Seeds should be sown in narrow strips or rows, covered with a thin layer of sand or peat, and watered thoroughly (Penford and Willis 1961). Under very hot conditions the nursery beds should be shaded. Young eucalyptus seedlings need a great amount of light, so only moderate shade is recommended. If bareroot stock is desired, the seedlings are left in the beds for about 6 to 12 months. More commonly, the seedlings are lifted after 5 to 10 weeks and planted in individual containers. Because of differences in seed size and purity among species seedlots, the variation in number of seedlings produced, by a given weight of seeds, will vary widely (Zon and Briscoe 1911).

Vegetative propagation. Vegetative propagation by rooting and grafting has been successful in some of the eucalypts. The following species have been rooted successfully: lemon-gum, red-ironbark, river redgum, mountain-ash, robust, desert, mountain-gum, blue-gum, rosegum, and manna eucalyptuses (Blomstedt and others 1991; Jacobs 1979; Linnard 1969; Penford and Willis 1961). But in the main, only shoots with juvenile leaves have been rooted, and these most often from trees younger than 5 years (Jacobs 1979; Penford and Willis 1961). Eucalyptus can also be propagated by grafting. At the present time, vegetative propagation appears to be a practical method for producing eucalypts in large numbers only in countries where labor is inexpensive, for example, Brazil (Jacobs 1979). The production of possibly useful cultivars is both difficult and expensive, for cuttings from mature eucalyptus trees do not readily root (Chippendale and others 1969).

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Celastraceae—Bittersweet family

Euonymus L.

euonymus, spindletree

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Growth habit, occurrence, and use. The genus *Euonymus* includes about 170 species of deciduous or evergreen shrubs and small trees, sometimes creeping or climbing, native to North and Central America, Europe, Asia, Madagascar, and Australia (Krüssmann 1960; Rehder 1940). The majority of species are native to east Asia from 52°N latitude to the Tropics (Nikolaeva 1967). Because of their attractive fruits and foliage, the euonymus species are planted widely for ornamental purposes. Winged spindletree, described by Dirr (1990) as "one of the finest landscape plants for American gardens," has brilliant red foliage in the fall (it is commonly known as burning-bush) and prominent corky wings on the stem that add variety to the winter landscape. Euonymus species show a large amount of variability: for example, Dirr (1990) listed about 70 cultivars recognized by horticulturists. At least one of these introduced species—European spindletree—has become naturalized and is considered invasive in the Northeast; other species do not appear to be as aggressive (Dirr 1990; Fernald 1950; Gleason and Cronquist 1963; Voss 1985). The deciduous and evergreen euonymus used as ornamentals in Britain have been described by Lancaster (1981). They also have value for wildlife food, shelterbelts, and minor wood products; at least 1 species is a source of gutta (Nikolaeva 1967). Eight species that have been used for conservation plantings are described in tables 1 and 2.

The 3 native species (table 1) described by Fernald (1950) occur in sites generally described as "rich" and with a mesic to wet soil water regime. In Wisconsin, eastern wahoo is most common in southern wet forests that are

Table 1—*Euonymus*, eunoymus: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***E. alata* (Thunb.) Sieb.** *Celastris alatus* Thunb.	**winged spindletree,** winged euonymus, corkbush, burning-bush	Central China, Manchuria, E Siberia, Korea, Japan, & Sakhalin
***E. americana* L.**	**American strawberry-bush,** bursting-heart, hearts-a-bustin, brook euonymus	New York to Illinois to Texas to Florida
***E. atropurpurea* Jacq.**	**eastern wahoo,** burning-bush, wahoo	W New York to S Ontario, central Michigan & Minnesota, SE North Dakota, S to NW Nebraska, central Kansas, & E Texas, E to Arkansas, Tennessee, & N Alabama
***E. bungeana* Maxim.**	**winterberry euonymus**	N China, Manchuria, & Korea
***E. europaea* L.**	**European spindletree,** European euonymus	Europe to W Asia (to 900 m in mtns)
***E. hamiltoniana* spp. *maackii* (Rupr.) Komarov**	**Maack euonymus**	N China & Korea
***E. obovata* Nutt.**	**running strawberry-bush,** running euonymus	W New York & S Ontario to central Michigan, Illinois, S to West Virginia, Kentucky, & Missouri
***E. verrucosa* Scop.**	**warty-bark euonymus,** warty spindletree	S Europe & W Asia

Sources: Dirr (1990), Rudolf (1974).

Table 2— *Euonymus,* euonymus: height and year first cultivated

Species	Height at maturity (m)	Year first cultivated
E. alata	0.9–3.1	1860
E. americana	0.9–1.8	1697
E. atropurpurea	1.8–6.2	1756
E. bungeana	4.0–6.2	1883
E. europaea	3.1–7.1	Long ago
E. hamiltoniana ssp. *maackii*	1.5–5.2	1880
E. obovata	0.3–0.6	1820
E. verrucosa	0.9–2.2	1763

Sources: Dirr (1990), Fernald (1950), Lancaster (1981), Rehder (1940).

dominated by silver maple (*Acer saccharinum* L.), black willow (*Salix nigra* Marsh.), and other trees characteristically found on wet sites (Curtis 1959); in Michigan, it is described as a floodplain species (Voss 1985). European spindletree, the naturalized exotic, is generally found on moist to wet sites, and floodplains in central Europe where it occurs naturally (Lee and others 1991). Historically, the roots, bark, and seeds were used for medicinal purposes with the warning that products of each may be poisonous to some individuals (Foster and Duke 1990; Snow and Snow 1988).

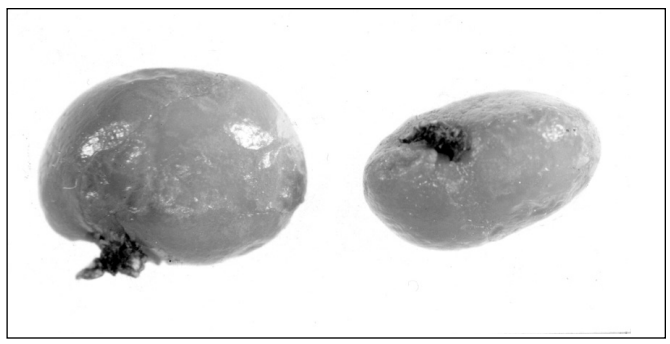
Flowering and fruiting. The usually perfect flowers, borne in clusters, bloom in the spring. The fruit, which ripens in late summer or fall, is a 4- to 5-celled (occasionally 2- to 3-celled) capsule that is usually lobed and sometimes winged (figure 1). Ostrobuka and Bencat (1987) found that winged spindletree pollen germinated in sucrose concentrations of 15, 20, and 25%, with 20% giving best results. Each fruit cell contains 1 or 2 seeds enclosed in a fleshy, usually orange aril (figure 2). Natural seed dispersal usually occurs soon after the fruits are fully ripe. Seed dispersal of European spindletree is primarily by birds, with robins (*Erithacus rubecula*) being a principal disperser in Britain. Some species ingest the entire aril, whereas others carry it to a perch and remove the pulp and drop the seeds (Snow and Snow 1988). Fruits of European spindletree have some of the highest lipid and protein contents reported for plants (Snow and Snow 1988). The flowering and fruiting habits of 8 species are summarized in tables 3 and 4.

Fruits are generally available annually. Flower bud differentiation occurs from early June to mid-August and weather conditions during this period will affect fruit production potential (Tomita and Uematsu 1978).

The fruit of European spindletree contains 1 to 5 seeds. Dry weight of the fruit is 0.17 g, with the seed accounting for about 45% of the dry weight. At maturity the water content is about 50% (fresh weight basis) (Lee and others 1991; Nielsen and Iroquoian 1988). Lee and others (1991) described the seeds of European spindletree as poisonous and little used by birds; however, Snow and Snow (1988) document a substantial use of fruits by birds, stating that the seeds are not consumed.

Figure 1—*Euonymus*, euonymus: top views of open capsules of *E. americana*, American strawberry-bush (**left**) and *E. atropurpurea*, eastern wahoo (**right**).

Figure 2—*Euonymus americana*, American strawberry-bush: seeds enclosed in their fleshy arils.



Collection of fruits. Seeds may be collected in late summer or fall by picking the ripe fruits from the bushes or trees by hand or by shaking them onto an outspread canvas. They should then be spread out to dry for several days in a warm room but need not be completely dry to be cleaned (Myatt and others 1991).

Extraction and storage of seeds. Seeds can be processed with a macerator (Stein and others 1974). The plate on the separator should be set slightly larger than the seeds and adjusted as necessary to prevent too many seeds from being lost with the pulp (Myatt and others 1991).

Smaller seedlots can be extracted by beating the fruits in a canvas bag and then rubbing them through a coarse, round-hole grain screen. The fruits may be macerated in water and the seeds extracted by flotation (Rudolf 1974). Following dry extraction, the chaff can be removed by

Table 3—*Euonymus,* euonymus: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
E. alata	New England & Japan	May–June	Sept–Oct
E. americana	Carolinas	May–June	Sept–Oct
E. atropurpurea	—	May–June	Sept–Oct
E. bungeana	NE US	June	Sept–Oct
E. europaea	NE US & Europe	May–June	Aug–Nov
E. hamiltoniana ssp. *maackii*	NE US	June	Oct
E. obovata	—	April–June	Aug–Oct
E. verrucosa	NE US & Germany	May–June	Aug–Oct

Sources: Fernald (1950), Lancaster (1981), Radford and others (1964), Rehder (1940), Sus (1925), Snow and Snow (1988), Voss (1985), Wappes (1932), Wyman (1947).

Table 4—*Euonymus,* euonymus: fruit form and color of flowers, fruits, and seeds

		Color			
Species	Fruit form	Flower	Ripe fruit	Seed	Aril
E. alata	Divided nearly to base in 4 separate pods (sometimes 1–3)	Yellowish	Reddish-purplish	Brown*	Orange-red
E. americana	3- to 5-lobed	Reddish green–greenish purple	Pink-rose	Yellowish white	Scarlet
E. atropurea	Smooth, deeply 3- to 4-lobed, 4-celled	Purple	Pink–purple	Light brown	Scarlet
E. bungeana	Deeply 4-lobed & 4-angled	Yellowish	Yellowish–pinkish white	Whitish or pinkish	Orange
E. europaea	Smooth, 4-lobed, 3 to 5–celled	Yellowish green	Rose red-pink†	White	Orange
E. hamiltoniana ssp. *maackii*	4-lobed	Yellowish	Pink	Red	Orange
E. obovata	Usually 3-lobed	Greenish purple	Crimson	Tan	Orange-scarlet
E. verrucosa	Deeply 4-lobed	Brownish	Yellowish red	Black	Orange-red‡

Sources: Bailey (1939), Dirr (1990), Fernald (1950), Rehder (1940), Snow and Snow (1988).
* Black, in one variety.
† Whitish, in one variety.
‡ Seed not wholly covered by aril.

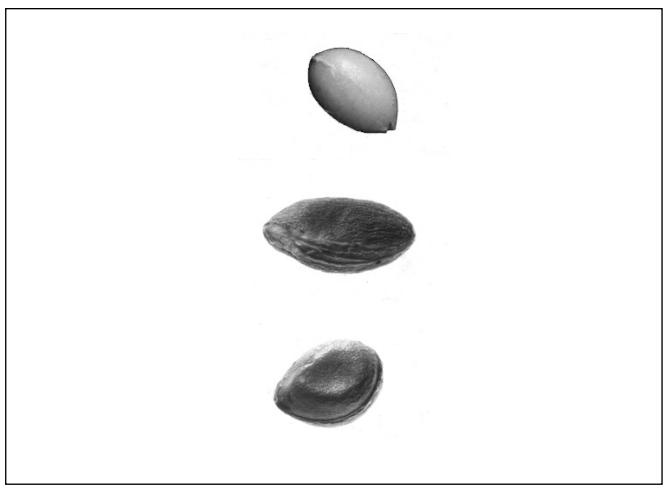
winnowing. The pulpy arils can be removed (figure 3) by rubbing the seeds through coarse-mesh wire cloth after they have dried several weeks, but this is difficult to do without breaking the relatively thin seedcoats (Lee and others 1991) and injuring the seeds. If the arils (which are sometimes oily) are not removed, the seeds may not store as well. As a result, commercial seeds are treated rather gently in extraction and seedlots usually contain seeds with parts of the arils still attached, along with completely clean seeds (figure 4).

The numbers of seeds per weight cleaned to this variable degree are shown in table 5. Forty-five kilograms (100 lb) of ripe fruits will yield about 4.5 to 9.1 kg (10 to 20 lb) and an average of 7.1 kg (16 lb) of cleaned seeds, based upon data for American strawberry-bush, eastern wahoo, European spindletree, and warty-bark euonymus (Gorshenin 1941; Rudolf 1974; Swingle 1939).

Seed weights can vary significantly within a population. Nielsen and Iroquoian (1988) reported that the variation in the dry weight of 1,000 seeds ranged from about 28 to 40 g among 8 individual European spindletree plants. Mature seeds from different positions in the plant varied significantly in seed weight; seeds from the top and shaded parts of the crown were 5% greater and 7% less than mean seed weight, respectively (Nielsen and Iroquoian 1988).

Seeds of European spindletree and warty-bark euonymus can be kept satisfactorily for 2 years in ordinary dry storage (Gorshenin 1941; Sus 1925), or in dry cold storage in sealed containers at 1 to 2 °C (Heit 1967). However, more recent Russian reports have shown high viability maintained for at least 7 years under moist conditions at constant temperatures, either warm (15 to 20 °C) or cold (Nikolaeva 1967). Any drying in storage reduced viability (Nikolaeva

Figure 3—*Euonymus*, euonymus: seeds with arils removed of *E. americana*, american strawberry-bush (**top**); *E. atropurpurea*, eastern wahoo **(middle)**; and *E. obovata*, running euonymus (**bottom**).



1967). Moist cold storage may be the most practical and effective way of retaining high viability of euonymus seeds for extended periods (table 6).

Pregermination treatments. Seeds of most euonymus species have dormant embryos. Cold stratification is adequate to break dormancy for some species, but warm stratification followed by a cold period is needed for maximum germination for other species (table 7) (Dirr 1990; Dirr and Heuser 1987; Nikolaeva 1967; Singh 1985; Yu and others 1976). The length of the warm period should be adjusted, depending on the temperature used for cold stratification. For example, Nikolaeva (1967) suggests a 2- to 3-month period of warm stratification if cold stratification is at 0 to 3 °C. Table 7 provides the range of temperatures for warm and cold stratification that have been effective for breaking dormancy. Nikolaeva (1967) provides a thorough discussion of the effects of temperature, water availability, seed maturation, and storage alone and in combination on germination. There may also be some variation in germination among European spindletree seeds formed under different climatic conditions (Dawidowicz-Grezgorzewska and Beranger-Novat 1989).

Variation in dormancy can be significantly different among plants. Nielsen (1988), for example, reported that germination of European spindletree seeds collected from 10 different plants varied from 0 to 30% following stratification

Table 5—*Euonymus,* euonymus: seed yield data

Species	Place collected	Cleaned seeds/weight: Range /kg	Range /lb	Average /kg	Average /lb	Samples
E. alata	NE US	41,110–69,620	18,600–31,500	55,250	25,000	2+
E. americana	Durham Co., North Carolina	63,300–100,113	30,000–45,300	77,571	35,100	3+
E. atropurpurea	Carver Co., Minnesota; Cole Co., Missouri; & rangewide	19,227–88,400	8,700–40,000	37,349	16,900	8
E. bungeana	US	—	—	29,835	13,500	1+
E. europaea	Russia, Netherlands, & NE US	18,785–35,360	8,500–16,000	29,393	13,300	32+
E. obovata	Clinton Co., Michigan	—	—	49,725	25,500	1
E. verrucosa	Russia	35,950–58,870	16,300–26,700	45,084	20,400	10+

Sources: Barnes (1969), Gorshenin (1941), Heit (1968a), NBV (1946), Nielsen and Eriksen (1988), Rudolf (1974), Sus (1925), Swingle (1939).

Table 6—*Euonymus,* euonymus: seed storage conditions

Species	Seed storage conditions: Seed moisture	Temp (°C)	Viable period (yrs)
*E. atropurpurea**	Air-dry	–1.1–3.3	—
E. europaea	Dry	—	1–2
	Moist	15–20 or 2.8	7
*E. obovatas**	Air-dry	1.1–3.3	—
E. verrucosa	Air-dry	20	2
	Moist	15–20 or 2.8	7

Sources: Gorshenin (1941), Heit (1967), NBV (1946), Nikolaeva (1967), Rudolf (1974), Sus (1925), Swingle (1939).

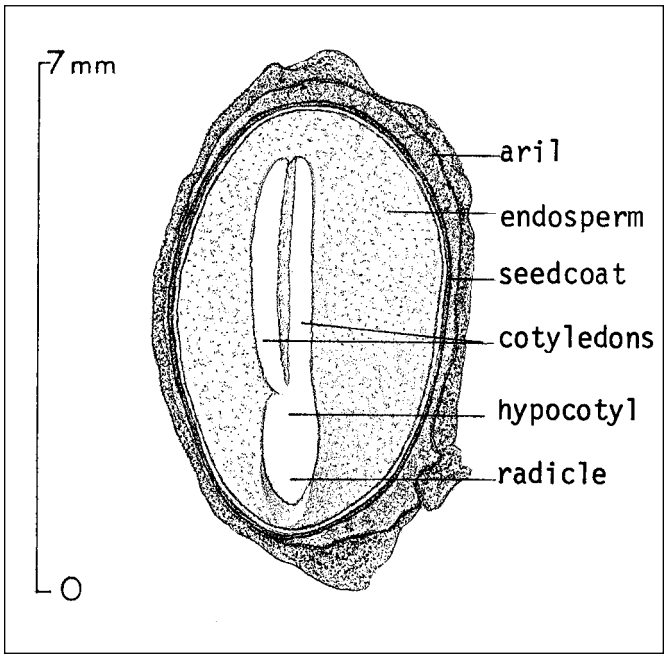
* Seed stored in closed containers.

Table 7—*Euonymus,* euonymus: stratification treatments

Species	Moisture-holding medium	Warm period		Cold period	
		Temp (°C)	Days	Temp (°C)	Days
E. alata	Sand or peat	—	0	0–10	90–100
E. americana	Perlite–peat mix	—	0	5	139
E. atropurpurea	Sand	20–30	60	5	60
	Sand	—	0	2.8–5	60–180
E. bungeana	Sand, peat, or filter paper	—	0	2.8–10	61–120
E. europaea	Sand, peat, or filter paper	20–25	60–90	32–50	60–120
		—	—	2.8–5	60–120
E. hamiltoniana ssp. *maackii*	Sand or filter paper	—	0	0–10	60–90
E. obovata	Sand	—	0	2.8–5	60–150
E. verrucosa	Sand or filter paper	15–20	60–90	0–10	120–150

Sources: Heit (1968a), Nikolaeva (1967), Rudolf (1974), Shumailina (1949), Swingle (1939).

Figure 4—*Euonymus europaea,* European spindletree: longitudinal section through a seed.



at 4 to 6 °C. This variation may have been significantly different if seeds had been subjected to warm stratification before cold stratification (table 7) (Nikolaeva 1967).

The morphological changes that occur during pretreatment are important indicators of the adequacy of the pregermination treatment. An increase in seed volume, cracking of the seedcoat, and protrusion of the tip of the hypocotyl occur during warm stratification or warm stratification hastens these changes when seeds are moved to cold stratification. Completeness of germination depends on these changes in seed morphology (Nikolaeva 1967).

There seems to be little information on the natural germination pattern of euonymus seeds. Untreated seeds of European spindletree germinated mainly in the second year after sowing (Lee and others 1991), suggesting that the alternation of warm and cold stratification also regulates germination under field conditions. Although birds are important in the dispersal of European spindletree seeds, the seeds may (which can cause some degree of scarification) or may not pass through the digestive tract of birds, depending on the species taking the seeds (Snow and Snow 1988).

Germination tests. Germination is epigeal (figure 5). Germination tests on stratified seeds can be run in sand flats, germinators, or petri dishes. ISTA (1993) recommends 45 days of stratification at 3 to 5°C, then a 28-day test at 20/30 °C for European spindletree. Viability can also be estimated by the embryo excision method (Heit 1966) or tetrazolium staining (ISTA 1993). Germination test conditions are summarized in table 8.

X-radiography has been used to assess viability in fresh European spindletree seeds. However, stored seeds should be stained with tetrazolium to determine viability (Smirnova and Tikhomirova (1980).

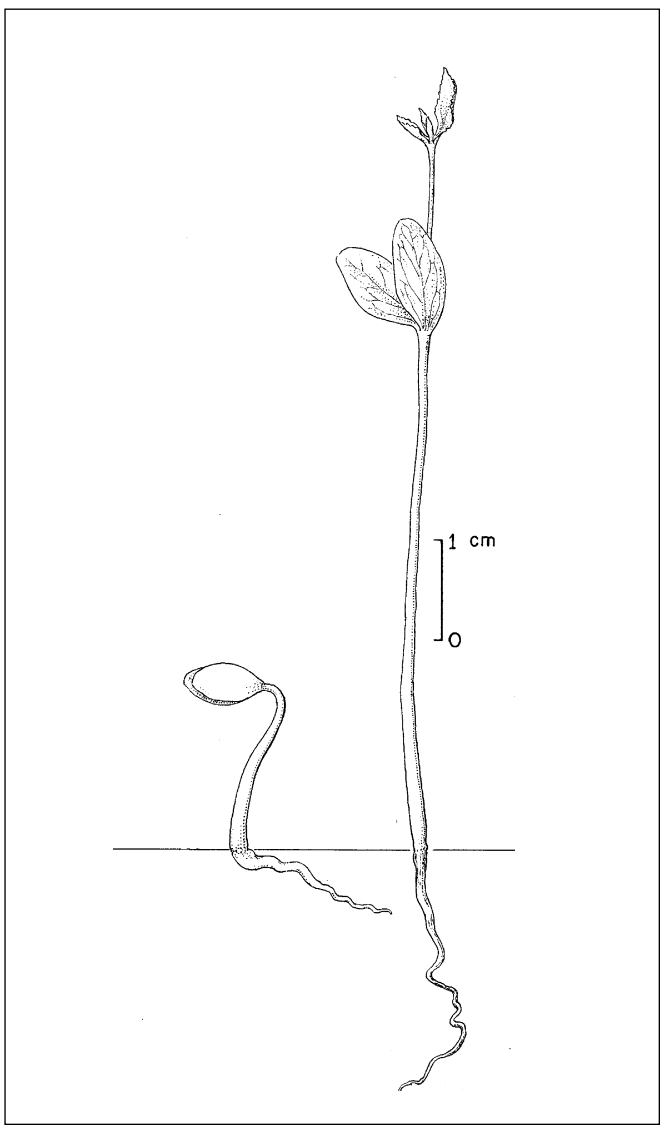
Nursery practice. Seedlings can be grown in containers or nurserybeds. For best results, cleaned euonymus seeds should be sown in the fall soon after collection, before the seeds have dried out (Heit 1968a&b; NBV 1946). If sowing after seeds have been collected is not feasible, stratified seeds can be planted (table 6) early the next spring or the next fall (NBV 1946). Details for most species are lacking, but for European spindletree, recommendations are to sow the seeds 6 mm ($^1/_4$ in) deep at a density to produce 422 seedlings/m^2 (40/ft^2) of nurserybed (NBV 1946). The beds should be mulched with pine straw (NBV 1946). Tree percentages range from about 10% for winterberry euonymus to 20% for eastern wahoo and 25% for European spindletree (Swingle 1939).

Table 8—*Euonymus,* euonymus: germination test conditions and results on stratified seeds

Species	Germination test conditions: Medium	Temp (°C): Day	Temp (°C): Night	Days	Avg germ capacity (%)	Purity (%)	Soundness (%)	Samples
E. americana	Filter paper	21.1	21.1	14	15	—	—	1
E. atropurpurea	Sand flats	30	20	61	40	75	88	2
E. bungeana	Germinator	10	0	60	20	—	—	1
E. europaea	Sand flats, germinators	25	20	60	71	75	96	22+
E. hamiltoniana ssp. *maackii*	Germinators	20	15	60	75	—	—	3+
E. verrucosa	Sand flats, filter paper	20	12	60	70	75	96	7+

Sources: NBV (1946), Nikolaeva (1967), Rudolf (1974), Swingle (1939).

Figure 5—*Euonymus europaea*, European spindletree: seedlings 1 and 12 days after germination.



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F

Fagaceae—Beech family

Fagus L.

beech

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Growth habit, occurrence, and use. The beeches—the genus *Fagus*—includes 10 species of medium-sized, deciduous trees native to the temperate regions of the Northern Hemisphere (Rehder 1940). Only 1 species, American beech, is native to North America, although another, the European beech, has been widely planted as an ornamental in the Northeast (table 1). Some authorities have argued that there are separate northern and southern species of American beech, but this view is not widely supported (Tubbs and Houston 1990). Beeches that grow in northeastern Mexico are now classified as a variety of American beech—*F. grandifolia* var. *mexicana* (Martinez) (Little 1965). There is some evidence of geographic races of European beech in that species' native range (Rudolf and Leak 1974). Beech wood is used for flooring, furniture, veneer, plywood, ties, charcoal, and many specialty products. The trees are highly valued for ornamental plantings, and the mast is widely utilized by numerous birds and animals (Tubbs and Houston 1990).

Flowering and fruiting. Beech flowers are monoecious. The minute male and female flowers appear in the spring when the leaves are about one-third grown (table 2). The staminate flowers occur in densely clustered, drooping heads 8 mm wide, whereas the pistillate flowers are generally paired on stout stalks about 2.5 cm long (Brown and Kirkman 1990). Flowers of European beech are quite vulnerable to late spring frosts (Matthews 1955). The fruit is a prickly bur approximately 2 cm long, which opens soon after maturity in the fall (figure 1).

Each fruit contains 2 or 3 yellowish-brown or chestnut-brown, unevenly triangular nuts, 1 to 1.5 cm long (figures 2 and 3). Times of flowering, fruiting, and seed dispersal for the 2 species are listed in table 2. Natural seed dispersal is chiefly by gravity and by animals such as rodents and blue jays (*Cyanocitta cristata*) (Johnson and Adkisson 1985; Tubbs and Houston 1990). Information on height at maturity, minimum seed-bearing age, and interval between good seedcrops is shown in table 3.

Table 1—*Fagus*, beech: nomenclature and occurrence

Scientific name	Common name	Occurrence
***F. grandifolia* Ehrh.**	**American beech,** beech	Nova Scotia to S Ontario & N Michigan, S to N Florida & E Texas
***F. sylvatica* L.**	**European beech**	Europe; planted in NE US

Source: Little (1979).

Table 2—*Fagus*, beech: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
F. grandifolia	March–May	Sept–Nov	Sept–Nov (after frost)
*F. sylvatica**	Apr–May	Sept–Oct	Oct–Nov (after frost)

Sources: Brown and Kirkman (1990), Rudolf and Leak (1974), Tubbs and Houston (1990).

* Dates are similar for western Europe and the northeastern United States.

Figure 1—*Fagus grandifolia*, American beech: nuts enclosed in a partially opened husk.

Figure 2—*Fagus sylvatica*, European beech: nut.

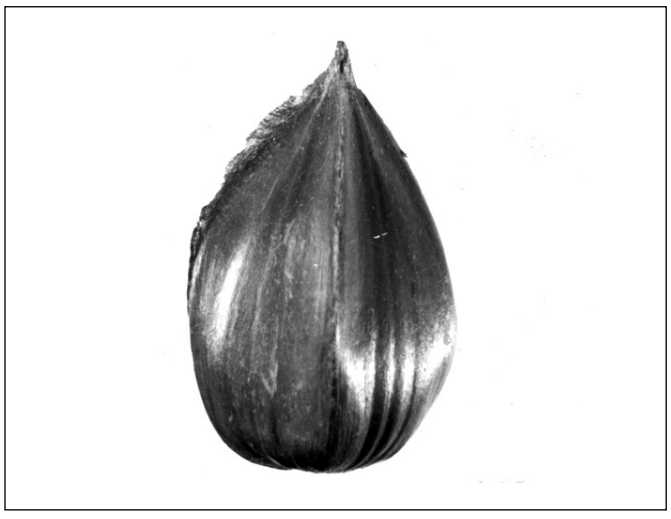
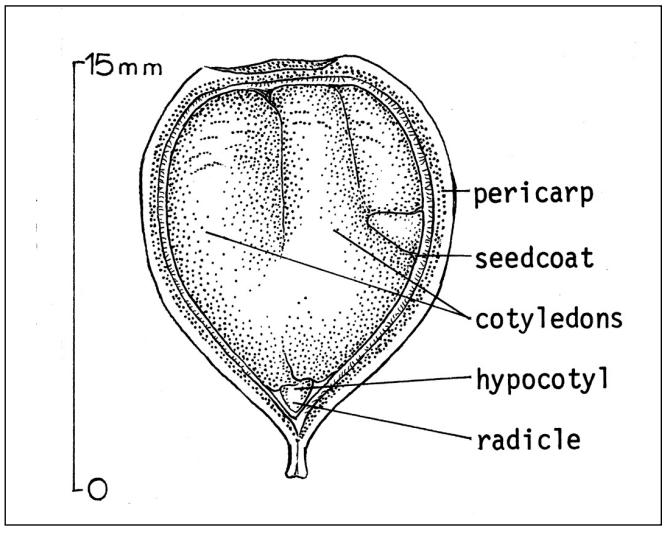


Figure 3—*Fagus grandifolia*, American beech: longitudinal section through a seed.



Long-term studies of seed production of European beech in England show widespread variation among trees and crop years (Harmer 1994). A positive correlation between size of the seedcrop and air temperature and amount of sunshine in July has also been recorded (Matthews 1955). A study in Hungary found that production of viable seeds was increased 3.5 times by fertilization of the stand with 200 kg/ha of N and 240 kg/ha of P_2O_5 (Fuhrer and Pall 1984). Predispersal destruction of seeds in Sweden by a moth—*Cydia fagiglandana* Z.—was found to range from 3 to 38% of the total crop, depending on crop size (Nilsson and Wastljung 1987). Studies in New England documented higher losses in American beech from insects, rodents, and birds combined (Gruber and Leak 1992; Leak and Gruber 1993). Records of seed production by American beech have shown that there is a great amount of natural variation, but no geographic or elevational patterns (Gysel 1971; Sain and Blum 1981; Stalter 1982). Like many other species, the better producers in any particular year will usually produce good seedcrops in other years (table 3) (Grisez 1975).

Collection and extraction. Beech nuts may be raked from the ground after they have fallen or shaken from the trees onto canvas or plastic sheets after the fruits open naturally (table 2). There is some evidence that seeds of European beech caught by nets suspended above the ground have less fungal infection than seeds raked from the ground (Dubbel 1989). Closed fruits also can be picked in the fall from trees recently felled in logging operations. Seed maturity is indicated by a completely brown fruit, and care should be taken to ensure that the seeds are fully mature when collecting unopened fruits. After the fruits are stripped from the branches, they should be spread to dry in a thin layer until they open and the seeds (also called nuts) can be shaken out. The seeds can be separated from empty fruits, leaves, and other large trash by screening. European beech seeds collected in Germany are sometimes separated from leaves, twigs, and fruit capsules with a tractor-mounted cleaning machine at the collection sites (Gottfriedsen 1991). Data on seed yields and weights are given in table 4.

In a good seed year, in France, a 150-year-old European beech high forest yielded 50 hl/ha (57 bu/ac) of seeds, whereas in Germany, a beech forest yielded 900 to 1,680 kg/ha (800 to 1,500 lb/ac) of seeds (Rudolf and Leak 1974).

Storage and pregermination treatments. Seeds of European beech can be stored for at least 6 years without loss of viability by drying the seeds to a moisture content of 8 to 10% at room temperature and holding them in sealed containers at temperatures from –5 to –15 °C (Muller and

Table 3—*Fagus*, beech: height, seed-bearing age, and seedcrop frequency

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yrs)	Years between large seedcrops	
				Time	Location
F. grandifolia	21–37	1800	40	2–3	—
	—	—	—	4–5	Wisconsin
F. sylvatica	20–30	Long ago	40–80*	5–8	Mtn areas
	—	—	—	9–12	Great Britain
	—	—	—	3–10	—
	—	—	—	15–20	—

Source: Rudolf and Leak (1974).

* 40 to 50 years for open-grown trees and 60 to 80 years for trees in stands.

Table 4—*Fagus*, beech: seed yield data

Species	Fruit wt/vol		Seed wt/fruit vol		Cleaned seeds/weight				Samples
					Range		Average		
	kg/hl	lb/bu	kg/hl	lb/bu	/kg	/lb	/kg	/lb	
F. grandifolia	—	—	12	9	2,850–5,110	1,290–2,320	3,500	1,600	10
F. sylvatica									
Fresh fruits	50–53	39–41	—	—	4,000–6,200	1,800–2,800	4,630	2,100	24+
Air-dried fruits	39–45	30–35	—	—	—	—	—	—	—

Source: Rudolf and Leak (1974).

Bonnet-Masimbert 1982; Suszka 1974). Poulsen (1993) recommends that drying should be done at temperatures below 20 °C. This behavior would seem to put beeches into the orthodox class of storage behavior, although there is evidence that beeches fit somewhere between the orthodox and recalcitrant classes (Gosling 1991) or in the sub-orthodox class (Bonner 1990). The high lipid content of 40.7% reported for kernels of European beech (Prasad and Gulz 1989) would seem to support the sub-orthodox classification. The seeds are basically orthodox, however, and 5 years of storage is long enough for operational storage. There are no comparable data for American beech, but there are no reasons to suspect that this species cannot be treated in the same way. Beech seeds require cold stratification (prechilling) for prompt germination, and current practices with European beech have combined stratification and storage into a coordinated procedure. The first step is to determine how much stratification is needed to overcome dormancy (Suszka and Zieta 1977). Samples of fresh seeds are brought to maximum moisture content or mixed with moist sand and stored at 3 °C until about 10% of the seeds have started germination (radicles are visible). This period is assumed to be the amount of time required to overcome dormancy in that particular lot. The remainder of the seeds are adjusted to a moisture content of 28 to 30% and prechilled in plastic containers (without media) at 4 °C for this amount of time, plus 2 more weeks. At this level of moisture, dormancy is overcome, but germination does not begin (Muller and Bonnet-Masimbert 1983). The seeds are then brought to room temperature, or no higher than 20 °C (Poulsen 1993), without heating, dried to a moisture content of 8%, and stored in sealed containers at –5 °C (Muller and Bonnet-Masimbert 1989). The effect of stratification is retained, and germination is prompt when the seeds are sown. Moisture level is the key to successful stratification. Treatment without media can lead to excessive seed moisture; it should not exceed 30% (Muller and Bonnet-Masimbert 1983).

Long-term storage of beech seeds for germplasm conservation may be possible with cryopreservation techniques. Intact seeds may not survive the temperatures of liquid nitrogen (–196 °C) (Ahuja 1986), but excised embryos have survived the same conditions for at least 24 hours (Jorgensen 1990).

Germination testing. The prescribed testing method for European beech is to germinate stratified seeds on the top of moist blotters at 3 to 5 °C. Test duration varies according to degree of dormancy (see above) but may run up to 24 weeks, which includes 140 days of stratification at

the same 3 to 5 °C (Suszka 1975). Some laboratories also test stratified beech seeds with the common alternating regime of 30 °C (day) and 20 °C (night) with acceptable results (table 5). Because of the lengthy tests, viability estimation by tetrazolium staining is recommended as an alternate method (ISTA 1993). Both tetrazolium and indigo carmine staining (Suszka 1991) are commonly used in Europe. North American testing rules (AOSA 1993) do not include either of these beech species, but the same methods should work for both. Germination is epigeal (figure 4).

Nursery practice. Beech seeds can be sown in the fall as soon after collection as possible, or stratified seeds can be sown in the spring. In the stratification/storage procedure described earlier for European beech, seeds can be removed from storage and planted at any time in the spring without additional treatment. This procedure eliminates the uncertainty over when to start stratification in time for spring-sowing and is favored by nurserymen in Europe (Gosling 1991). Sowing density should be 700 viable seeds/m^2 (65/ft^2) for European beech, which, on the average, should produce about 325 seedlings/m^2 (30/ft^2) (Aldhous 1972). Seeds should be covered with 12 mm ($^1/_2$ in) of soil. Fall-sown beds should be mulched until midsummer and given special protection against rodents (Rudolf and Leak 1974). Some seedbeds may require half-shade until past mid-summer. Vegetative propagation by cuttings is very difficult, but some successes have been reported for stem cuttings taken in late summer. Grafting is more common for ornamental selections (Dirr and Heuser 1987).

Figure 4—*Fagus grandifolia*, American beech: seedling development at 2, 5, and 7 days after germination.

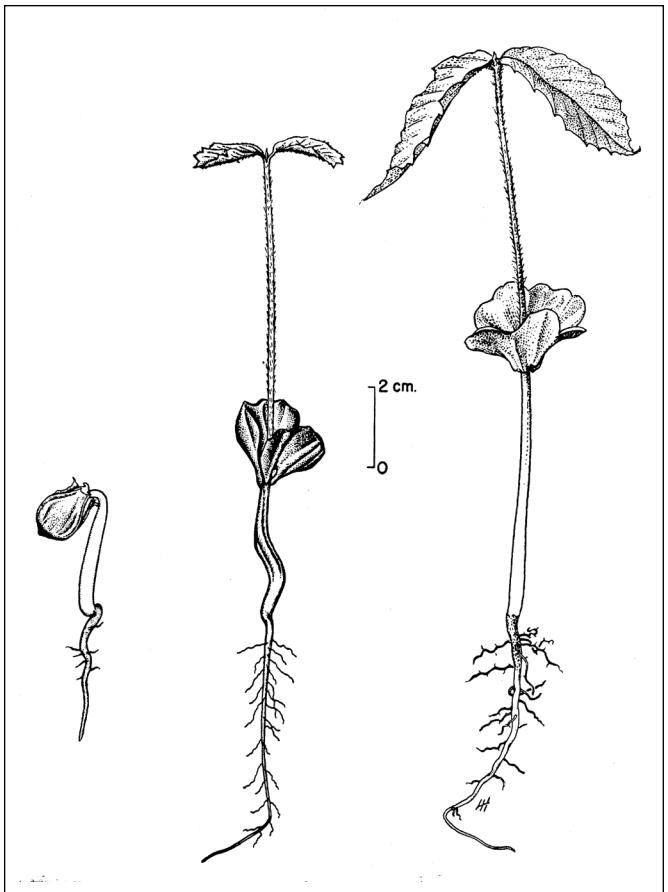


Table 5—*Fagus*, beech: germination test conditions and results

Species	Cold stratification (days)	Test conditions			Germination rate		Germination (%)
		Medium	Temp (°C) Day	Temp (°C) Night	Amount (%)	Period (days)	
F. grandifolia	90	Sand	30	20	84–47	85	—
F. sylvatica	42	Sand, paper	30	20	—	—	81
F. sylvatica							
Fresh seeds	140	Sand + peat	1	1	56–120	100	—
Stored seeds	150	Sand + peat	5	5	60–110	100	—

Source: Rudolf and Leak (1974).

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Rosaceae—Rose family

Fallugia paradoxa (D. Don) Endl. ex Torr.

Apache-plume

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Growth habit, occurrence, and use. The genus *Fallugia* contains a single species—Apache-plume, *F. paradoxa* (D. Don) Endl. ex Torr.—found throughout the southwestern United States and northern Mexico. It occurs mostly on coarse soils on benches and especially along washes and canyons in both warm and cool desert shrub communities and up into the pinyon–juniper vegetation type. It is a sprawling, much-branched shrub from 1 to 2.5 m in height that can root-sprout to produce extensive patches (Shaw and Monsen 1983). It has white to straw-colored, flaking or scaly bark and fascicles of small wedge-shaped leaves that are deeply divided into 3 to 7 lobes and are rusty-tomentose on the undersides. Apache-plume is reported to be evergreen in the warmer portions of its range (Shaw and Monsen 1983). It can be an important browse plant for both domestic and wild ungulates on some ranges and is also valuable for erosion control (Deitschman and others 1974). It is somewhat fire-tolerant, with the ability to resprout after burning (Shaw and Monsen 1983). Because of its handsome habit and showy flowers and fruits, it is used extensively for landscape plantings in the Southwest. It is hardy in areas far north of its natural range (Deitschman and others 1974; Shaw and Monsen 1983) and has potential for use in revegetation or as an ornamental over a wide geographic area.

Flowering and fruiting. Apache-plume has large, white, 5-petaled, roselike flowers borne singly or in small groups on elongate peduncles. In spite of the typical rose appearance, most plants of Apache-plume have been found to be functionally dioecious or sometimes monoecious (Blauer and others 1975). Each flower has a set of both stamens and pistils, but one or the other fails to develop completely, resulting in functionally unisexual flowers. The male flowers have numerous stamens, whereas the female flowers have 20 to 30 separate pistils borne on a hypanthium. These develop into hairy achenes with long, plumose styles. The clusters of styles are shining-pink and very showy in fruit, giving the plant its name.

Apache-plume flowers mostly in late spring to early summer, and flowers are usually not damaged by late frosts (Shaw and Monsen 1983). Summer rains may extend the season of flowering. The flowers are insect-pollinated and attract a wide variety of colorful insects (Blauer and others 1975). The single-seeded achenes (figures 1–3) ripen in midsummer and are detached and dispersed by wind. Good seedcrops are generally produced every 2 to 3 years (Deitschman and others 1974).

Seed collection, cleaning, and storage. The window of opportunity for harvest of Apache-plume is generally quite short because ripe fruits do not persist on the plants. When the achenes turn from greenish to reddish and the pink color of the styles starts to fade, the fruits may be collected by stripping or beating them into a hopper or other container or with a vacuum-harvester. Achenes comprise only 15 to 20% of collected material by weight. Unless the plumes are removed by chopping or rubbing or with a barley de-bearder or similar device, the collected material remains in a thick, entangled mass that cannot be handled or seeded. Once the styles are broken up, the material can be cleaned in a conventional fanning mill.

The seeds are held tightly within the achene and cannot be threshed out, so the achene is considered to be the seed

Figure 1—*Fallugia paradoxa*, Apache-plume: achene with style (tip broken).

Figure 2—*Fallugia paradoxa*, Apache-plume: achene with style removed.

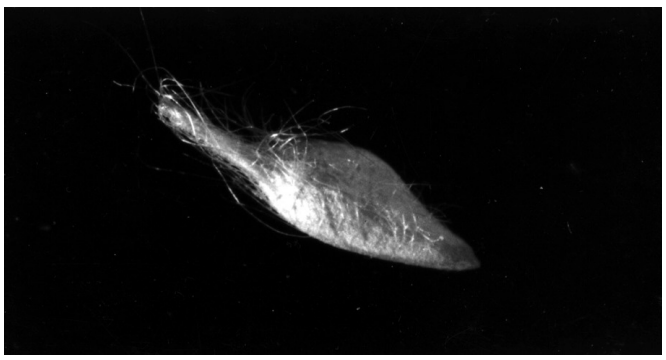
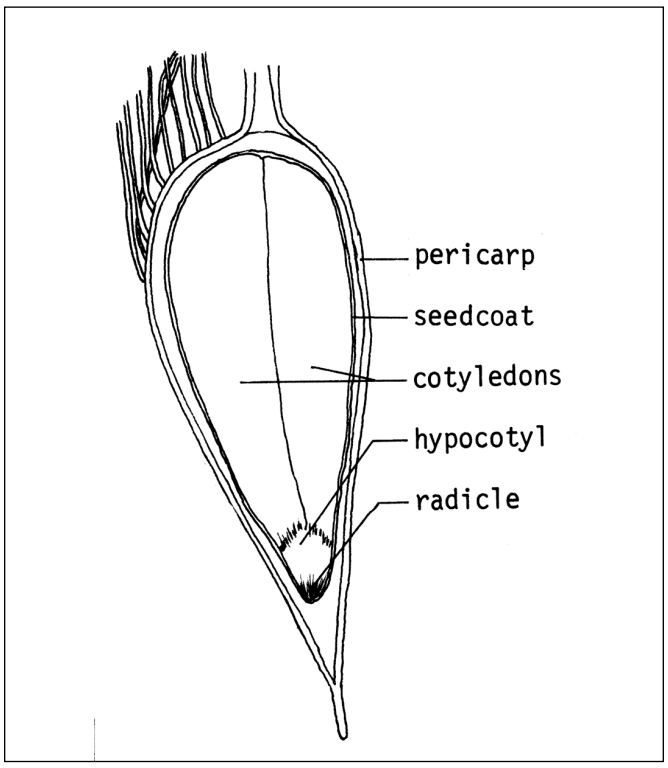


Figure 3—*Fallugia paradoxa*, Apache-plume: longitudinal section through an achene.



unit. Reported weights are 925 to 1,280 achenes/g (420,000 to 580,000/lb) (Deitschman and others 1974; Belcher 1985; Link 1993). Fill is sometimes quite low—for example, Link (1993) reported 30 to 40%—and unfilled fruits cannot be detected or removed in cleaning; it is therefore a good practice to check fill in the field before harvest. Seeds of Apache-plume apparently are orthodox in storage behavior, but they have a more limited shelf life in warehouse storage than those of related genera. Serious loss of viability commences after as little as 3 years, even if seeds are held at optimum moisture content (7 to 12%) (Belcher 1985; Deitschman and others 1974; Link 1993).

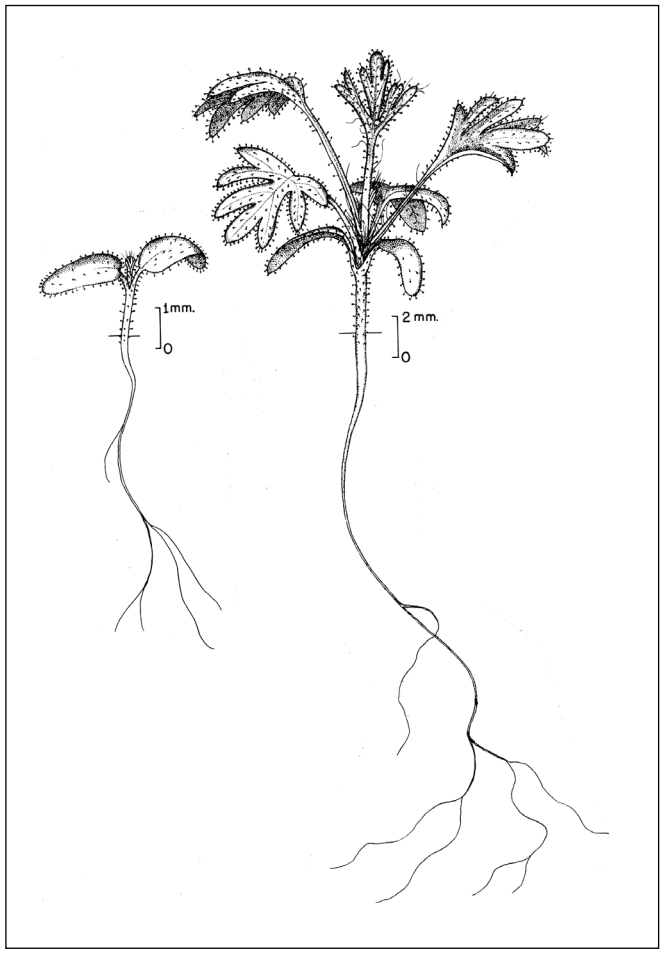
Germination and seed testing. Most workers report that seeds of Apache-plume germinate readily without pretreatment, at least when freshly harvested (Belcher 1985; Deitschman and others 1974; Link 1993; Veit and Van Auken 1993). Veit and Van Auken (1993) reported better germination for a seedlot from west Texas at lower light levels and with the styles removed, the latter possibly because of better seed–substrate contact. They also found that germination was better at higher incubation temperatures (85% at 20 to 25 °C vs. 51% at 5 to 10 °C after 60 days), in contrast to the results of Deitschman and others (1974), who reported that seeds of 2 lots from central Utah germinated to 60 and 73% (that is, to maximum viability) during 60 days at 0 to 3 °C. These differences may represent ecotypic differentiation between northern populations that emerge in response to winter precipitation and southern populations that emerge in response to summer rains. Chilling-responsive secondary dormancy that is induced during dry storage (Link 1993) may also represent an adaptive response, in that seeds that do not germinate in response to summer rains may develop a short chilling requirement that prevents them from germinating too late in the fall.

Belcher (1985) recommends 14 days of testing at 20 or 22 °C for evaluating the viability of Apache-plume seeds and states that 30 days of chilling at 3 to 5 °C may be helpful for some lots. Viability may also be evaluated using tetrazolium (TZ) staining. Achenes are soaked overnight in water, clipped at the cotyledon end, immersed for several hours in 1% TZ solution, and bisected longitudinally for evaluation (Belcher 1985).

Field seeding and nursery practice. Although Apache-plume has been successfully established via direct-seeding in the fall or spring in the northern part of its range and during summer rains in the southern part (Deitschman and others 1974), it is somewhat difficult to establish this way. Despite of their small size, the seeds must be covered in order for seedlings to establish, but planting them too deep can also prevent establishment. Veit and van Auken (1993) reported maximum emergence from seeds planted 1 to 2 mm ($^3/_{64}$ to $^5/_{64}$ in) deep in greenhouse trials, whereas planting depths of 3 to 6 mm ($^1/_8$ to $^1/_4$ in) have been recommended for seeding into nursery beds (Deitshman and others 1974). The seedlings are quite drought hardy but do not survive in competition with an understory of annual grass weeds or perennial grasses. Young seedlings are depicted in figure 4.

Apache-plume plants can be readily produced from seeds in either bareroot or container systems. They grow rapidly with irrigation, often flowering their first growing

Figure 4—*Fallugia paradoxa*, Apache-plume: seedling with primary leaves only (**left**); seedling with primary and secondary leaves (**right**).



season. For bareroot production, seeding into a firm seedbed prior to the season of most dependable moisture is recommended. When grown in the North, the seedlings are deciduous and can be safely lifted and transplanted once they lose their leaves. The stems are brittle and the roots often poorly developed, necessitating careful handling. For container production, direct-sowing without pretreatment is the usual practice, though some workers prefer to chill or cold-stratify the seeds for 30 days, either before or after planting, to ensure rapid and complete germination (Link 1993). A well-drained growing medium is required. Container-grown plants tend to be evergreen and must be hardened off carefully to minimize transplant losses.

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F

Rutaceae—Rue family

Flindersia brayleyana F. Muell.

Queensland-maple

Herbert L. Wick and John A. Parrotta

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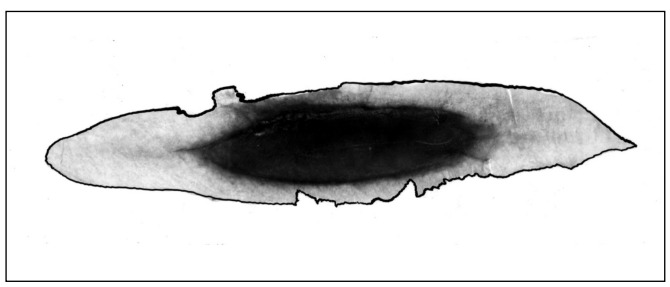
Synonym. *Flindersia chatawaiana* F.M. Bailey.

Growth habit, occurrence, and use. Queensland-maple (*Flindersia brayleyana* F. Muell.)—also known as Brayley flindersia, maple-silkwood, red-beech, and silkwood—is a native of Queensland, Australia, that was introduced to Hawaii in 1935 (Francis 1951; Wick 1974). It is a broadleaf, tropical hardwood tree that attains a height of 20 to 30 m at maturity. Queensland-maple ranks with mahogany, walnut, cedar, and blackwood as one of the best cabinet timbers of the world and is one of the most valuable species on the Australian market. The sapwood is pink and the heartwood a lustrous pale brown, often with interlocked and wavy grain (Little and Skolmen 1989). The heartwood is also used for veneer, plywood, and laminated panels and doors (Boas 1947). It is a medium-dense wood with an average specific gravity of 450 to 540 kg/m^3. Plantings in Hawaii have not, as yet, been commercially harvested.

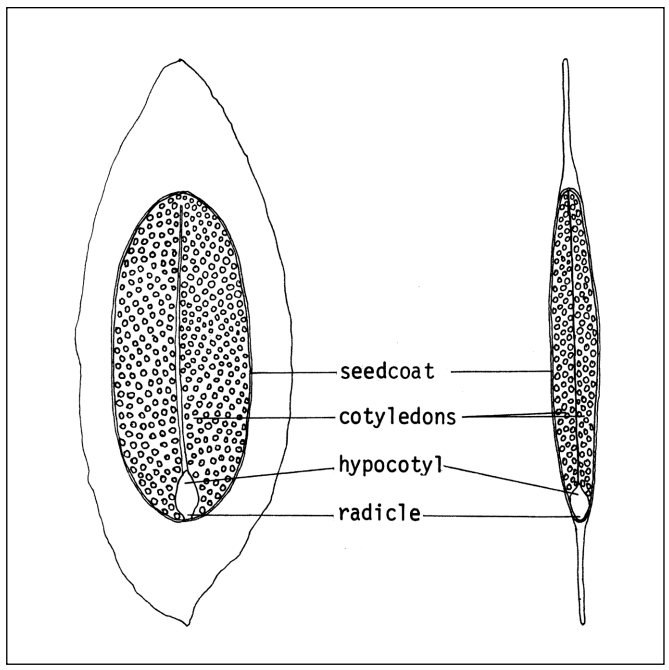
Flowering and fruiting. Queensland-maple has small (3 mm long), white, fragrant, 5-petaled bisexual flowers that generally form large panicles from August to September. The fruit is a cylindrical, hard-shelled, warty, 5-valved dehiscent capsule, about 6 cm long and 2.5 cm in diameter (Little and Skolmen 1989). In Hawaii, it generally ripens from June to July and releases its several flat, winged seeds (measuring 5 by 1 cm) from July through September (figures 1 and 2) (Little and Skolmen 1989; Neal 1965; Wick 1974). A tree usually starts bearing seeds at 8 years of age and produces an abundant crop annually (Wick 1974).

Figure 1—*Flindersia brayleyana*, Queensland-maple: seed.



Collection, extraction, and storage. When the capsules turn from green to brown, they are ripe and should be picked. In Hawaii, the capsules are picked from felled or standing trees. The fruits are spread on trays for air-drying or are oven-dried. As the capsules dry, they open, releasing the seeds. In Hawaii, there are between 9,800 and 11,700 seeds/kg (4,400 to 5,300 seeds/lb), or an average of about 10,500 seeds/kg (4,800 seeds/lb) (Wick 1974). In Queensland, Swain (1928) reported a range of 6,600 to 11,000 seeds/kg (3,000 to 5,000 seeds/lb). In Hawaii, the seeds are stored in airtight containers at 2 °C. The seeds do not store well and lose their viability within a year. Because seeds are easily damaged, they must be handled gently. The seeds are also very sensitive to chemicals used in storage or fumigation (Wick 1974).

Figure 2—*Flindersia brayleyana*, Queensland-maple: longitudinal section through two planes of a seed.



Germination. In Hawaii, good germination was obtained without any pregermination treatment (Wick 1974). In a test in Queensland, germination rates were 70% in 7 days and 90% in 20 days (Swain 1928).

Nursery and field practice. In Hawaii, Queensland-maple seeds are sown as soon as they are collected, at a rate of 150 to 200/m^2 (14 to 18/ft^2) and at a sowing depth of 0.6 to 1.2 cm ($^1/_4$ to $^1/_2$ in). Young seedlings should be provided overhead shade for about the first 2 months. Seedlings may be outplanted as 1+0 seedlings (Wick 1974).

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F

Rhamnaceae—Buckthorn family

Frangula P. Mill.

buckthorn

Andrew Youngblood

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Growth habit, occurrence, and use. The buckthorn genus—*Frangula*—and the closely related genus *Rhamnus* have until recently been treated as a single genus (*Rhamnus*) consisting of more than 125 species of evergreen or deciduous shrubs and trees with alternate branches and simple leaves with prominent pinnate veins (Hickman 1993). Kartesz and Gandhi (1994), however, used floral morphology and leaf venation, as well as anatomical features of xylem vessels, to support segregation of *Frangula*. Under their treatment, *Frangula* species lack winter bud scales, the pinnate leaf nerves are almost straight rather than arcuate, and thorns are absent. Both *Rhamnus* and *Frangula* are native to the temperate region of North America, Europe, and Asia and also occur in the Neotropics and southern Africa as shrubs and trees up to 1.5 m dbh and over 60 m tall (Johnston and Johnston 1978; Krüssmann 1985). The common name, buckthorn, is probably misapplied and is based on European species of *Rhamnus* that are thorny (Mozingo 1987; USDA 1937). At least 16 species and subspecies are distributed within the United States (table 1) (USDA NRCS 2001).

Glossy buckthorn, which is native to Europe, North Africa, and western Europe, also is naturalized in northeastern and central United States and southern Canada, where it grows to a height of 6 m and is often used for hedges. The fruits are eaten by American robins (*Turdus migratorius*), Bohemian waxwings (*Bombycilla garrulus*), cedar waxwings (*B. cedrorum*), rose-breasted grosbeaks (*Phencticus ludovicianus*), and starlings (*Sturnus vulgaris*). Dispersal of seeds by birds and subsequent germination and establishment represents a rapidly increasing problem; for example, this non-native invasive shrub has replaced natural open and semi-open wetland communities in southern Ontario (Catling and Porebski 1994).

Beechleaf buckthorn is a low-growing shrub with dark green leaves found in rock crevices, hanging gardens, and desert shrub communities in the Southwest (Welsh and others 1990).

Within North America, the largest assemblage of *Frangula* species in the genus is in the West, especially California and northern Mexico. Six subspecies of California buckthorn are recognized (Kartesz and Gandhi 1994), yet the extent to which published seed handling characteristics apply equally within this complex is unknown. California buckthorn is an evergreen shrub that reaches maximum heights of 2 to 6 m. The fruits were gathered historically by Native Americans for culinary as well as medicinal purposes and are a preferred food of birds and bears (Conrad 1987). California buckthorn var. *californica,* which was introduced on Mauna Kea on the island of Hawaii in 1940 to provide food for introduced game birds, is now well established and shows signs of becoming an invasive pest (Conrad 1996). Regeneration of California buckthorn is primarily by stump-sprouting after fire (Keeley 1981; Martin 1982; Conrad 1987).

Carolina buckthorn, native to eastern North American, is a deciduous shrub or small tree with maximum height of about 10 m. It often occurs over basic rock in moist deciduous woods (Radford and others 1968).

Cascara, or Pursh buckthorn, native to the coniferous forest zone in northwestern United States and British Columbia, is a deciduous tall shrub or tree that grows to a height of 12 m. The bark of cascara is harvested for its cathartic properties. According to Heiser (1993), cascara is northern North America's principal wild plant in terms of the number of drug products and the cascara derivative is considered the world's most widely used cathartic. The Spanish common name *cascara sagrada* means "holy bark" and may be derived from its use by Franciscan missionaries in California (Arno and Hammerly 1977). The low-growing and spreading variety *arbuscula* occurs on serpentine slopes in the Wenatchee Mountains of Washington and may tolerate open and dry sites (Kruckeberg 1982). Cascara regenerates primarily by stump-sprouting after fire (Leege 1979). It is an alternate host for crown rust—*Puccinia coronata* Corda—which causes yellow leaf spot in the aecial stage; economic

Table 1—*Frangula,* buckthorn: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***F. alnus* P. Mill.** *Rhamnus frangula* L. *R. frangula* L. var. *angustifolia* Loud.	**glossy buckthorn**	Europe, W Asia, & N Africa: naturalized in Nova Scotia, S Quebec & S Ontario to Minnesota, S to Illinois, Ohio, Tennessee, West Virginia, W to Colorado, & Wyoming
F. betulifolia* (Greene) V. Grub. ssp. *betulifolia *R. betulifolia* Greene	**beechleaf buckthorn,** birchleaf buckthorn	Nevada, Utah, Arizona, New Mexico, Texas, & Mexico
***F. betulifolia* (Greene) V. Grub. ssp. *obovata* (Kearney & Peebles) Kartesz & Gandhi**	**obovate buckthorn**	Nevada, Arizona, & New Mexico
F. californica* (Eschsch.) Gray ssp. *californica *R. californica* Eschsch.	**California buckthorn**	California; naturalized on the Island of Hawaii
***F. californica* (Eschsch.) Gray ssp. *crassifolia* (Jepson) Kartesz & Gandhi**	**California buckthorn**	California
***F. californica* (Eschsch.) Gray ssp. *cuspidata* (Greene) Kartesz & Gandhi** *R. californica* Eschsch. ssp. *cuspidata* (Greene) C.B. Wolf *R. tomentella* Benth. ssp. *cuspidata* (Greene) J.O. Sawyer	**California buckthorn**	California
***F. californica* (Eschsch.) Gray ssp. *occidentalis* (T.J. Howell) Kartesz & Gandhi** *R. californica* (Eschsch.) ssp. *occidentalis* (T.J. Howell) C.B. Wolf *R. californica* (Eschsch.) ssp. *occidentalis* (T.J. Howell) Jepson	**California buckthorn**	Serpentine soils of SW Oregon & N California
***F. californica* (Eschsch.) Gray ssp. *tomentella* (Benth.) Kartesz & Gandhi** *R. californica* Eschsch. ssp. *tomentella* (Benth.) C.B. Wolf *R. tomentella* Benth.	**California buckthorn**	California
***F. californica* (Eschsch.) Gray ssp. *ursina* (Benth.) Kartesz & Gandhi** *R. californica* Eschsch. ssp. *ursina* (Greene) C.B. Wolf *R. tomentella* Benth. ssp. *ursina* (Greene) J.O. Sawyer	**California buckthorn**	California, Nevada, Arizona, & New Mexico

damage by crown rust is confined to heavy damage in fields of oats grown in close proximity to plant communities containing cascara (Ziller 1974).

Red buckthorn is a low-growing deciduous shrub with reddish branchlets found on dry open slopes in chaparral and montane zones of California and Nevada.

The earliest know cultivation of species native to North America includes 1727 for Carolina buckthorn and the mid-1800s for California buckthorn and cascara (Krüssmann 1985).

Flowering and fruiting. The inconspicuous perfect flowers are either borne in small umbels or fascicles or are solitary. The flowers are bisexual and mostly 5-merous. White to greenish white petals (brown in beechleaf buckthorn) are equal to the sepals in number and alternating, or lacking. There are 5 stamens. The ovary has 2 or 3 cells. When Orme and Leege (1980) followed phenological changes in cascara in northern Idaho for 3 years, they found that flowering occurred in late May to mid-June and that fruits began developing 1 week later.

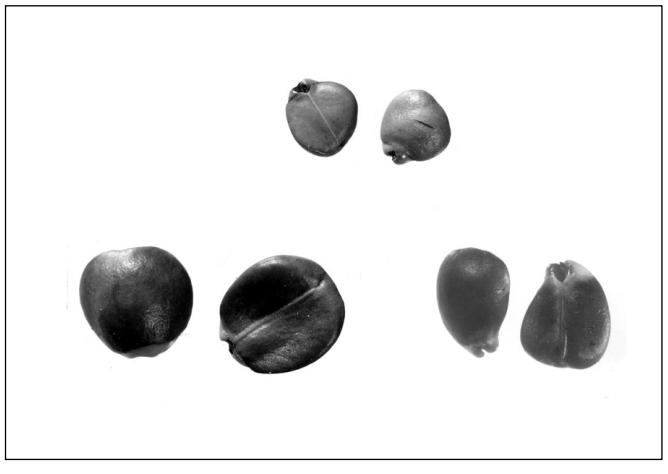
Fruits are drupaceous, the berrylike pulpy mesocarp embedding 2 or 3 smooth-sided stones (Johnston and Johnston 1978; Kartesz and Gandhi 1994) (figure 1). Fruits, which are generally black or reddish black, average 5 mm in diameter for Carolina buckthorn, 10 mm for cascara, 12 mm for red buckthorn, and up to 15 mm for California buckthorn. Dispersal is mostly by birds. Cascara begins to produce fruit when it is 5 to 7 years old (Hubbard 1974); comparable information for other species is lacking. Good seedcrops for all species are likely to occur in most years.

Table 1—*Frangula*, buckthorn: nomenclature and occurrence (continued)

Scientific name(s)	Common name(s)	Occurrence
***F. caroliniana* (Walt.) Gray** *R. caroliniana* Walt. *R. caroliniana* Walt. var. *mollis* Fern.	**Carolina buckthorn,** yellow buckthorn, yellowwood	New Jersey S to Florida, W to Missouri, Kentucky, Arkansas, & Texas
F. purshiana (DC.) Cooper *R. purshiana* DC.	**cascara,** *cascara sagrada,* Pursh buckthorn, chittam, coffeetree	British Columbia, Washington, Oregon, N California, also N Idaho & W Montana
***F. rubra* (Greene) V. Grub. ssp. *modocensis* (C.B. Wolf) Kartesz & Gandhi** *R. rubra* Greene ssp. *modocensis* C.B. Wolf	**Modoc buckthorn**	California
***F. rubra* (Greene) V. Grub. ssp. *nevadensis* (A. Nels.) Kartesz & Gandhi** *R. rubra* Greene ssp. *nevadensis* (A. Nels) C.B. Wolf	**Nevada buckthorn**	Nevada
***F. rubra* (Greene) V. Grub. ssp. *obtusissima* (Greene) Kartesz & Gandhi** *R. rubra* Greene ssp. *obtusissima* (Greene) C.B. Wolf	**obtuse buckthorn**	California & Nevada
F. rubra* (Greene) V. Grub. ssp. *rubra *R. rubra* Greene	**red buckthorn,** Sierra buckthorn, coffeeberry	California & Nevada
***F. rubra* (Greene) V. Grub. ssp. *yosemitana* (C.B. Wolf) Kartesz & Gandhi** *R. rubra* Greene ssp. *yosemitana* *C.B. Wolf*	**Yosemite buckthorn**	California

Figure 1—*Frangula purshiana*, cascara: fruit.

Figure 2—*Frangula*, buckthorn: seeds of *F. alnus*, glossy buckthorn (**top**); *F. californica*, California buckthorn (**left**); and *F. purshiana*, cascara (**right**).

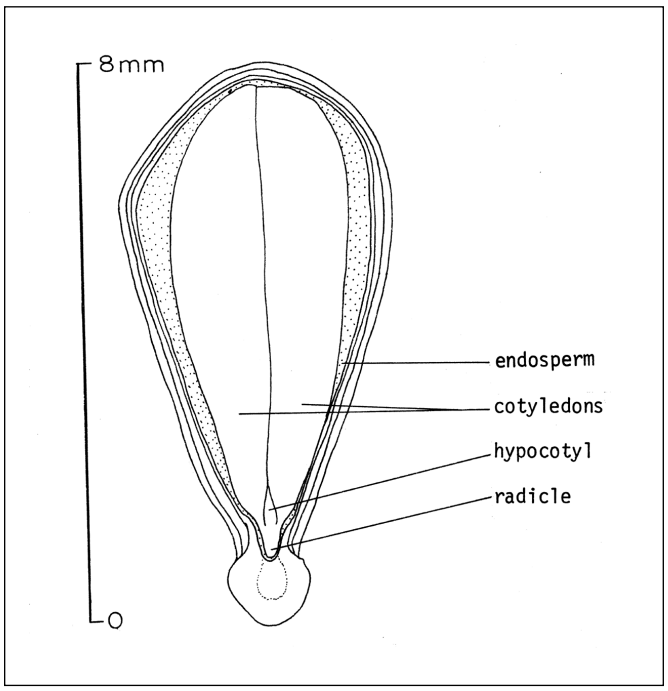


Collection, extraction, and storage. Fruits can be collected from the shrubs and trees when ripe; collecting fruits about 2 weeks before they are fully ripe may limit losses to birds (Hubbard 1974). Fruits can be run through a macerator with water soon after collecting and full seeds can be cleaned of other material by repeated decantation (Radwan 1976). Seeds typically are small, rounded, with one slightly flattened side, and a terminal knob (figure 2). Seeds may contain relatively little endosperm (figure 3). Data on yield of seeds are scant and based on limited samples: yields are about 11 seeds/g (312/oz) for California buckthorn and 6 seeds/g (170/oz) for cascara (Piper 1986).

Seed storage guidelines have not been developed for *Frangula* species, but it appears that seeds can be stored adequately for several years if they are kept in sealed containers at low temperatures (Hubbard 1974). Seeds of California buckthorn are relatively short lived (< 9 months) if allowed to dry to room conditions (Keeley 1987).

Pregermination treatment. Fresh seeds of California buckthorn apparently have no innate germination require-

Figure 3—*Frangula californica*, California buckthorn: longitudinal section through a seed.



ments (Hubbard 1974; Keeley 1981, 1987). During laboratory tests involving 1 month of stratification at 5 °C, however, more than 75% of the total germination occurred after 7 days of incubation at 23 °C in the dark. Germination increased to 90% when seeds were incubated with an initial heat treatment of 100 °C for 5 minutes and then placed on soil containing 0.5 g powdered charred wood (charate) of the chaparral shrub chamise—*Adenostoma fasciculatum* Hook. & Arn. This treatment is designed to simulate conditions after a chaparral fire (Keeley 1987). Seeds of cascara germinated best when stratified in the dark for 112 days at 5 °C, then incubated for 28 days at 30 °C for 10 hours under cool-white fluorescent light followed by 14 hours of darkness at 20 °C (Radwan 1976). Dormant seeds responded favorable to applications of 500 ppm of potassium gibberellate (K-GA_3) when light was available during germination and may represent a practical alternative to artificial cold stratification for breaking dormancy (Radwan 1976). Clean seeds of glossy buckthorn have been treated with sulfuric acid (H_2SO_4) for 20 minutes to break dormancy; the acid treatment should be done carefully because soaking the seeds of other buckthorns was harmful (Hubbard 1974).

There are no officially prescribed germination tests procedures for buckthorns. Viability tests by tetrazolium staining have been suggested for European species (Enescu 1991). Seeds should be soaked in water for 24 hours, cracked open in a vise, then re-soaked overnight. Staining should take place in a 1% tetrazolium solution for 24 hours at 30 °C (Dirr 1990). To be considered viable, the embryos must be completely stained, with the exception of the extreme third of the distal ends of the radicle and cotyledons.

Nursery and field practice. Detailed nursery techniques have not been developed for most *Frangula* species. The available information suggests that for most of the species, the seeds should be sown in the spring at a depth of 10 to 40 mm (0.4 to 1.6 in) after they have been treated to break dormancy (Hubbard 1974). In contrast, cascara seeds may germinate faster and produce more vigorous plants when seeds are sown at a depth of 3 mm (0.1 in) (Radwan 1976). Germination is epigeal, with thick, straight cotyledons (Kartesz and Gandhi 1994). Cascara has also been propagated by cuttings, and glossy buckthorn by grafting (Hubbard 1974).

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Theaceae—Tea family

Franklinia alatamaha Bartr. ex Marsh.

Franklin tree

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Synonyms. *Gordonia alatamaha* (Bartr. ex Marsh.) Sarg.; *Gordonia pubescens* L'Hér.

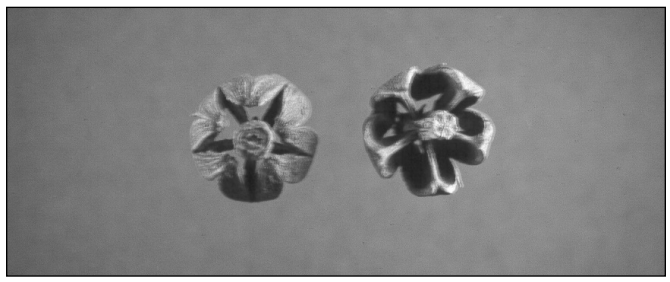
Other common names. franklinia, lost camellia, lost gordonia.

Growth habit, occurrence, and uses. Franklin tree—*Franklinia alatamaha* Bartr. ex Marsh.—was discovered by Bartram in 1765 on 0.8 to 1.2 ha of sandhill bogs near the mouth of the Altamaha River in Georgia, but the species has not been found in a native setting since 1803. Currently, it exists only in cultivation in USDA Hardiness Zones 5–9 (Everett 1981; Jacobson 1996; Wildman 1996). Franklin tree is a deciduous small tree or large multi-stemmed shrub reaching a height of 9 m (LHBH 1976). Upright spreading branches with leaves clustered at the tips give the plant a tightly rounded exterior appearance and its open interior reveals striated bark that adds year-round interest (Elias 1989; Wildman 1996).

Valued for ornamental characteristics, Franklin tree produces large, showy white flowers appearing from July to the first frost of autumn (Elias 1989; Schneider 1988; Wildman 1996). Lustrous dark green leaves turn "a blazing red in fall" before abscising to reveal an attractive smooth gray bark that is broken by lighter colored fissures (Wildman 1996). These attributes clearly make the species a superb specimen tree or small flowering tree in a mixed planting.

Flowering and fruiting. Perfect flowers, 7 to 9 cm in diameter, appear in July and are borne solitary in the axils of the leaves. Each flower consists of a 1.3-cm-diameter center, filled with golden yellow stamens, surrounded by 5 white petals (1 remains cupped). Flowering persists until the first frost (Elias 1989). Seeds are produced in 1.3- to 2.0-cm-diameter, 5-valved, subglobose, dehiscing, woody capsules that split alternately from above and below (figure 1) (LHBH 1976). Capsules persist through the winter, providing an excellent feature for identification (Wildman 1996). Each cell of a capsule contains 6 to 8 wingless seeds, 12- to 14-mm-long, that are angled due to mutual pressure during development (figures 2 and 3) (Sargent 1949; Small 1933).

Figure 1—*Franklinia alatamaha*, Franklin tree: capsules after seed release.



Collection of fruits, seed extraction, cleaning, and storage. Capsules should be collected in October to November, before they split, and then allowed to dry and open indoors. Seeds can then be shaken from the capsules and sown immediately (Dirr and Heuser 1987). Currently, no information regarding long-term storage of seeds of Franklin tree has been published.

Pregermination treatments. Seeds that are collected when the capsules split and sown immediately will germinate without any pretreatment (Dirr and Heuser 1987). Best germination, however, occurs after stratification (moist-prechilling) for 1 to 2 months (Dirr and Heuser 1987; Farmer and Chase 1977). If seeds are stored and allowed to dry, stratification becomes necessary (Hartmann and others 1997).

Germination tests. Farmer and Chase (1977) studied the influence of stratification, temperature, and light on seed germination of Franklin tree. Seeds were stratified at 3 °C for 0, 4, 8, or 12 weeks followed by germination at 14-hour day/10-hour night thermoperiods of 16/7 °C, 24/16 °C, or 29/24 °C. At each thermoperiod, seeds were maintained in darkness or subjected daily, during the high temperature portion of the cycle, to a 14-hour photoperiod of 2.2 klux provided by incandescent and fluorescent light sources. Results indicated the seeds have an obligate light requirement.

Figure 2—*Franklinia alatamaha*, Franklin tree: seeds.

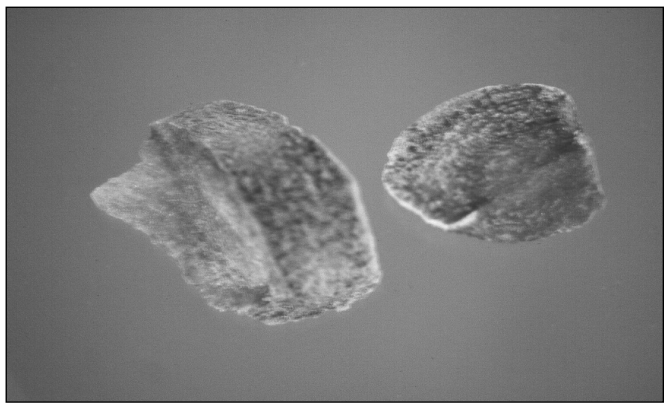
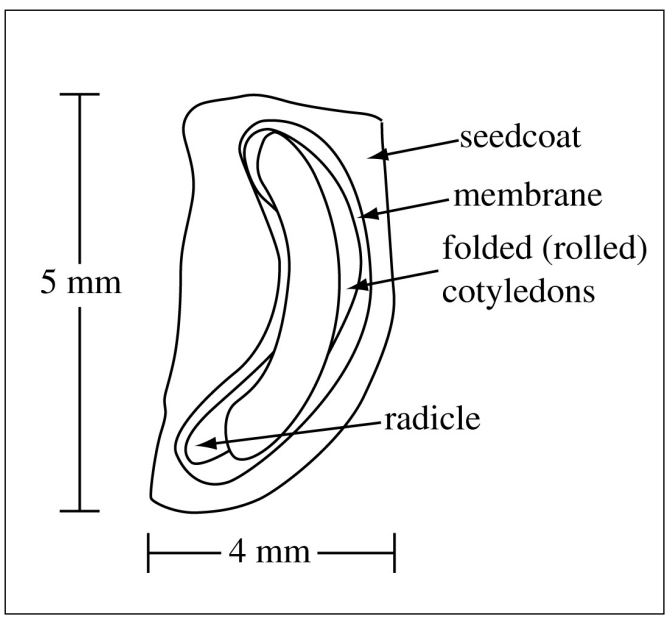


Figure 3—*Franklinia alatamaha*, Franklin tree: longitudinal section of a seed.



Regardless of temperature, germination in the dark was negligible for nonstratified seeds. However, in the presence of light, cumulative germination at 16/7 °C, 24/16 °C, or 29/24 °C was 2, 75, and 61%, respectively. Stratification enhanced germination by accelerating the rate of germination and reducing sensitivity of the seeds to light. After 4 weeks of stratification, total germination in the presence of light at 16/7 °C, 24/16 °C, and 29/24 °C was 5, 87, and 91%, respectively, in comparison to 2, 31, and 85%, respectively, for seeds in darkness. Germination following stratification for 8 weeks was similar to that of 4 weeks of stratification. Additional stratification for 12 weeks resulted in an increase in dark germination at 24/16 °C to 53% and a large increase in germination at 16/7 °C with dark and light germination of 32 and 52%, respectively.

Nursery practice. For field production, seeds sown in late winter to early spring will result in seedlings that grow quite vigorously, attaining heights of about 30 cm (12 in) by fall (Judd 1930). If container production is desired, Farmer and Chase (1977) recommend 8 to 16 weeks of stratification, after which seeds are sown to a 5-mm (0.2-in) depth in flats containing a medium of peat and perlite. Shoot emergence occurs in about 2 weeks at day/night germination temperatures of 27/21 °C. Seedlings should remain in flats until they reach a height of 3 to 5 cm (1 to 2 in), when they should be transplanted to 10-cm (4-in) pots containing a medium of finely ground peat moss. Plants are maintained in these pots under natural photoperiods for a period of 4 to 8 weeks and fertilized monthly with a complete soluble fertilizer. At this point, seedlings will have attained a height of 15 to 20 cm (6 to 8 in) and are ready for sale. Like many native ornamentals, Franklin tree prefers a moist, acidic soil (pH 5.5 to 6.5) that must be well drained (Schneider 1988). Although Franklin tree is relatively pest free, seedlings will often suffer from a root rot caused by *Phytophthora cinnamomi* Rands if soil conditions are too wet (Wildman 1996).

The species can also be propagated easily by stem cuttings taken from June to August. Treatment of cuttings with a solution of 1,000 ppm (0.1%) indolebutyric acid (IBA) will result in 90% rooting (Dirr and Heuser 1987). Although sexual propagation is possible as mentioned previously, seeds are usually quite expensive, making propagation by cuttings more economical (Schneider 1988).

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Oleaceae—Olive family

Fraxinus L.

ash

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Growth habit, occurrence, and uses. The genus *Fraxinus*—the ashes—is a large genus of deciduous trees whose members are valued for many reasons. In addition to the 9 native ash species, 2 European species that have been widely planted as ornamentals in North America (European and flowering ashes) are included in this manual (table 1). Practically all ashes have been planted to some extent for landscaping and in parks. Ashes make excellent shade trees in residential areas, and numerous selections of European and flowering ashes are in cultivation today (Dirr and Heuser 1987). Native favorites for landscaping are white and green ashes for the eastern and central United States and velvet ash for arid situations in the Southwest.

Geographic races and hybrids. Both green and white ashes exhibit ecotypic variation, but no patterns have been consistent enough to firmly establish geographic races (Kennedy 1990; Schlesinger 1990). White ash and Texas ash—*F. texensis* (Gray) Sarg.—intergrade in Texas (Schlesinger 1990). Oregon ash becomes very similar to velvet ash south of the Kern River in California (Owston 1990), which suggests intergrading of these 2 species. There is also some evidence that pumpkin ash is a true-breeding natural hybrid of white ash and green ash (Kennedy 1990). Several large provenance tests are underway with white ash (Clausen 1984; Clausen and others 1981) and green ash (Hendrix and Lowe 1990; Steiner and others 1988; Van

Table 1—*Fraxinus*, ash: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***F. americana* L.**	**white ash,** Biltmore white ash, Biltmore ash	Cape Breton Island, Nova Scotia, W to SE Minnesota, & S to Texas & Florida
***F. caroliniana* P. Mill.**	**Carolina ash,** swamp ash, water ash, pop ash	NE Virginia S to S Florida, W to Texas & Arkansas
***F. dipetala* Hook. & Arn.** *F. trifoliolata* (Torr.) Lewis & Epling	**two-petal ash,** flowering ash, foothill ash	SW Utah, W to Nevada, California, & Mexico
***F. excelsior* L.**	**European ash**	Europe & Asia Minor; widely planted in US
***F. latifolia* Benth.**	**Oregon ash**	Puget Sound in Washington to S California
***F. nigra* Marsh.**	**black ash,** basket ash, brown ash, hoop ash, swamp ash, water ash	Newfoundland to SE Manitoba S to Iowa & Delaware
***F. ornus* L.**	**flowering ash**	S Europe & W Asia; widely planted in US
***F. pennsylvanica* Marsh.** *F. pennsylvanica* var. *lanceolata* (Borkh.) Sarg.	**green ash,** red ash, Darlington ash, white ash, swamp ash, water ash	Cape Breton Island to Alberta, S to Texas & NW Florida
***F. profunda* (Bush) Bush**	**pumpkin ash,** red ash	S Maryland & Illinois, S to Louisiana & N Florida
***F. quadrangulata* Michx.**	**blue ash**	S Ontario and Wisconsin, S to NE Oklahoma & NW Georgia
***F. uhdei* (Wenzig) Lingelsh.**	**Shamel ash,** tropical ash, *fresno*	W-central Mexico through Guatemala; planted in Hawaii & Puerto Rico
***F. velutina* Torr.**	**velvet ash,** desert ash, leatherleaf ash, smooth ash, Modesto ash, Arizona ash, Toumey ash	Utah & Nevada, S to S California & SW Texas

Source: Little (1979).

Deusen and Cunningham 1982), and their results should provide more information about the variation in these species.

Flowering and fruiting. The small, usually inconspicuous flowers of most ash species appear in the spring (table 2) with or just before the leaves in terminal or axillary panicles (compound racemes). The flowers may be greenish yellow, greenish purple, or even greenish red (white ash) (Brown and Kirkman 1990; Vines 1960). Flowering ash is an exception, with showy, white flowers appearing after the leaves (Dirr and Heuser 1987). Flowering habit varies by species and may be dioecious, perfect, or polygamous (table 2). Ash fruits are elongated, winged, single-seeded samaras that are borne in clusters (figures 1–3). Samara length ranges from 2.5 to 7.5 cm, depending on species. In white ash, fruit size increases as latitude increases (Winstead and others 1977). Fruits mature by late summer or fall and are dispersed by wind shortly afterward (table 2). Samaras of pumpkin ash, which is found in swamps and river bottoms, are reported to remain viable in water for several months (Harms 1990). Samaras of black and blue ashes have a characteristic spicy odor. Fruiting data are summarized in table 3.

Collection of fruits. Ash fruits are usually collected in the fall when their color has faded from green to yellow or brown (Bonner 1974; Vines 1960). Soljanik (1961) recommended collecting the fruits of European and flowering ashes in Europe when the samaras are still slightly green and sowing can be done immediately. The aim of this strategy is to avoid the deep dormancy that is common in these species when they are fully mature. Other good indices of maturity are a firm, crisp, white, fully elongated seed within the samara (Bonner 1974; Soljanik 1961); minimum samara moisture content (Cram and Lindquist 1982); and maximum samara dry weight (Bonner 1973). There are several good chemical indices of maturity in green ash as well (Bonner 1973), but these are not practical for collection operations.

Clusters of samaras can be picked by hand or with pruners and seed hooks. Fully dried samaras may be shaken or whipped from limbs of standing trees onto sheets spread on the ground. Samaras can also be swept up from paved streets or other hard surfaces after they fall (Bonner 1974).

Local seedcrops of white and green ashes are often seriously damaged by ash seed weevils—*Thysanocnemis bischoffi* Blatchley, *T. helvola* Leconte, and *T. horridulus* (Casey) (Barger and Davidson 1967; Solomon and others 1993). The greatest reported losses have been in the Northeast and the Great Plains, with smaller amounts of damage in the South. The female deposits 1 egg per seed, and mature larvae exit the seeds from fall until the following spring. Direct control measures are rarely justified (Solomon and others 1993).

Figure 1—*Fraxinus americana*, white ash: cluster of samaras.

Table 2—*Fraxinus*, ash: flowering habit and phenology of flowering and fruiting

Species	Location	Flowering	Flowering habit	Fruit ripening	Seed dispersal
F. americana	—	Apr–May	Dioecious	Oct–Nov	Sept–Dec
F. caroliniana	—	Feb–Mar	Dioecious	Aug–Oct	—
F. dipetala	California	Apr–May	Perfect	July–Sept	—
F. excelsior	—	Apr–May	Polygamous	Aug–Sept	Winter–early spring
F. latifolia	—	Apr–May	Dioecious	Aug–Sept	Sept–Oct
F. nigra	—	May–June	Polygamous	June–Sept	July–Oct
F. ornus	NE US	May–June	Polygamous	—	—
F. pennsylvanica	—	Mar–May	Dioecious	Sept–Oct	Oct–spring
F. profunda	—	Apr–May	Dioecious	Sept–Oct	Oct–Dec
F. quadrangulata	—	Mar–Apr	Perfect	June–Oct	—
F. uhdei	Hawaii	Mar–May	Dioecious	July–Sept	July–Sept
	Puerto Rico	Nov–Jan	—	Aug	—
F. velutina	—	Mar–Apr	Dioecious	Sept	—

Sources: Bonner (1974), Francis (1990), Harms (1990), Kennedy (1990), Owston (1990), Rehder (1940), Schlesinger (1990), Vines (1960), Wright and Rauscher (1990).

Figure 2—*Fraxinus*, ash: single samaras of *F. americana,* white ash (**top left**); *F. caroliniana*, Carolina ash (**top center**); *F. dipetala*, two-petal ash (**top right**). *F. latifolia*, Oregon ash (**middle left**); *F. nigra*, black ash (**middle center**), *F. pennsylvanica*, green ash (**middle right**). *F. profunda*, pumpkin ash (**bottom left**), *F. uhdei*, tropical ash (**bottom right**), *F. velutina*, velvet ash (**lower right**).

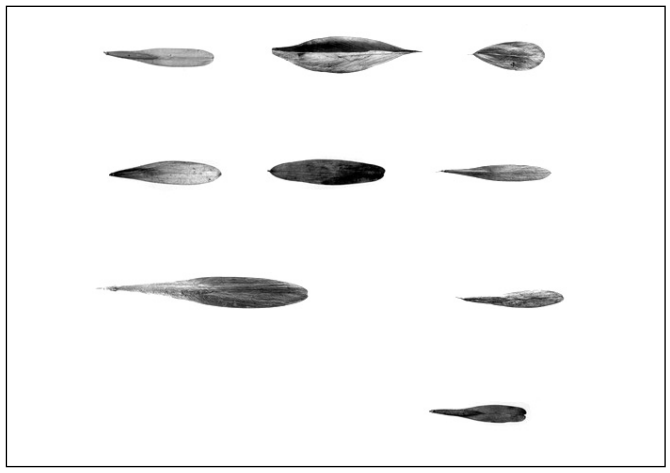


Figure 3—*Fraxinus pennsylvanica*, green ash: longitudinal section through the embryo of a samara.

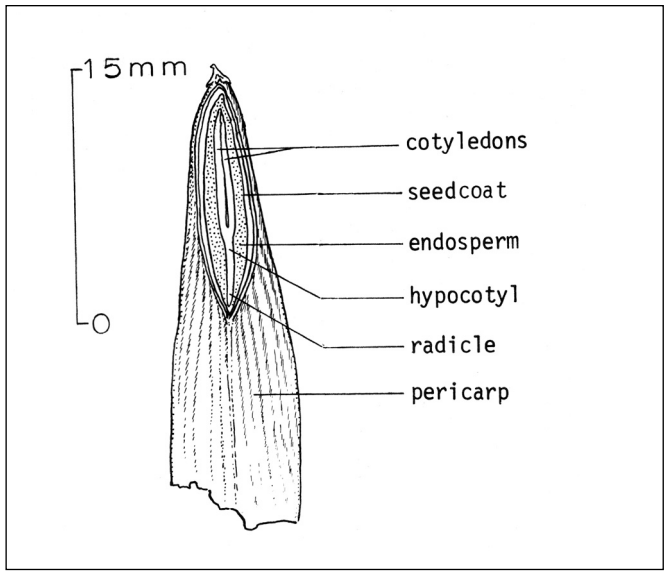


Table 3—*Fraxinus,* ash: height, seed-bearing age, and seedcrop frequency

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yr)	Years between large seedcrops
F. americana	21–24	1724	20	3–5
F. caroliniana	6–12	—	—	—
F. dipetala	2–6	—	—	—
F. excelsior	29–38	Long ago*	15	1–2
F. latifolia	18–24	—	30	3–5
F. nigra	12–24	1800	—	—
F. ornus	6–20	pre-1700	20	—
F. pennsylvanica	21+	1824	—	1
F. profunda	37	—	9	—
F. quadrangulata	4–9	1823	25	3–4
F. uhdei	37	1900	15	1
F. velutina	15	1900	—	—

Sources: Bonner (1974), Krinard (1989).
* Cultivated for many centuries (Rehder 1940).

Extraction and storage of seeds. Samaras should be spread in shallow layers for complete drying, especially when collected early. Dried clusters may be broken apart by hand, by flailing sacks of clusters, or by running the clusters through macerators or brush machines dry (Bonner 1974). Stems and trash can then be removed by fanning or with air-screen cleaners. Screen openings of 1 by 1 cm are good for white and green ash. De-winging of samaras is not necessary for storage or sowing, but many nurseries prefer to do so. Large amounts of samaras can be de-winged by dry maceration in a macerator or in brush machines (Karrfalt 1992), but they must be completely dry for the process to be successful. Smaller seedlots, such as those used for research or testing, can be de-winged in laboratory blenders operated at low speeds about half-full of water. Seed yield data for ashes are summarized in table 4.

Long-term storage studies with seeds of the ashes are few, but these seeds are definitely orthodox in their storage characteristics. Studies by Barton (1945) showed no loss in viability for 7 years for green and European ash seeds stored in sealed containers at 5 °C with seed moisture contents of 7 to 10%. Similar conditions have proved successful for flowering ash (Heit 1967) and Shamel ash (Bonner 1974).

Table 4—*Fraxinus*, ash: seed yield data

Species	Place fruit collected	Seeds/vol kg/hl	Seeds/vol lb/bu	Cleaned seeds/weight Range /kg	Range /lb	Average /kg	Average /lb	Samples	Seed moisture (%)
F. americana	Midwest	16*	12.4	12,220–40,100	5,540–18,185	28,930	13,120	7	—
	Mississippi	16*	12.5	12,600–24,900	5,712–11,288	18,680	8,470	2	11
F. caroliniana	Arkansas	—	—	—	—	13,660	5,744	1	13
F. dipetala	California	—	—	11,025–19,400	5,000–8,800	—	—	3+	—
F. excelsior	Europe	18	14	10,470–15,430	4,750–7,000	—	—	—	7–8
	USA	—	—	8,800–15,430	4,000–7,000	13,000	5,900	10+	—
F. latifolia	—	—	—	22,000–31,000	10,000–14,060	—	—	—	—
F. nigra	Great Lakes region	—	—	13,450–20,950	6,100–9,500	17,860	8,100	4	—
F. pennsylvanica	Midwest & Great Lakes region	—	—	24,250–54,250	11,000–24,000	38,850	17,260	51	—
	Arkansas & Mississippi	9†	7.2	35,060–74,150	15,900–35,630	46,200	20,950	9	10
F. profunda	Mississippi	—	—	6,830–7,270	3,000–3,300	7,050	3,200	5	—
F. quadrangulata	—	—	—	13,000–15,430	5,900–7,000	—	—	2+	—
F. uhdei	Hawaii	—	—	34,200–38,600	15,500–17,500	36,380	16,500	10	—
F. velutina	—	—	—	28,850–61,740	13,000–28,000	45,420	20,600	6	—

Sources: Bonner (1974), Owston (1990).

* Number of seeds per volume Midwest = 394,500/hl (139,000/bu); Mississippi = 326,540 (115,000/bu). † Number of seeds per volume Arkansas–Mississippi = 416,620/hl (146,800/bu).

Pregermination treatments. Most species of ash exhibit a complex dormancy that is due to both seedcoat and internal factors. The seedcoat effect apparently is based on restriction of moisture and oxygen uptake, and scarification or removal of pericarp, seedcoats, or both will lead to quick germination of several species of ash (Arrillaga and others 1992; Bonner 1974; Gendel and others 1977; Marshall 1981). Karrfalt (1992) reported that de-winging white ash seeds with a brush machine led to quicker germination, apparently because the brushes scarified the seedcoats.

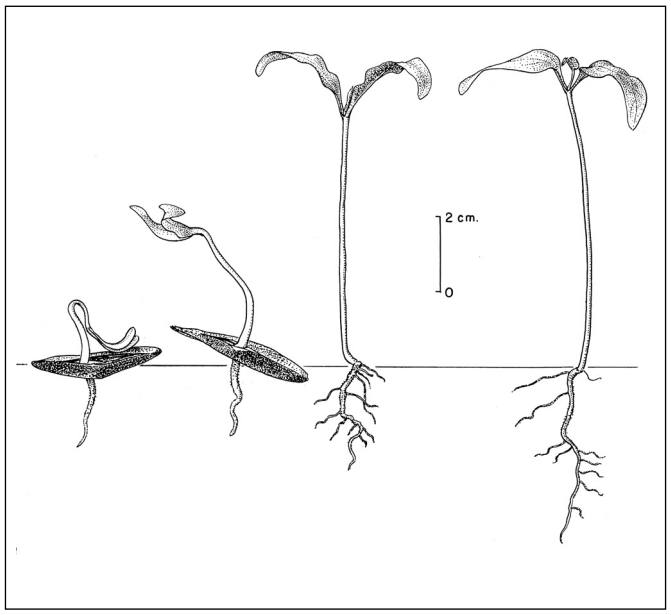
Internal dormancy appears to be related to germination inhibitors or their balance with germination promoters (Kentzer 1966; McBride and Dickson 1972; Sondheimer and others 1974; Stinemetz and Roberts 1984; Tinus 1982; Tzou and others 1973). European and black ashes also have immature embryos that must complete development during after-ripening for good germination (Nikolaeva 1967; Suszka and others 1996; Vanstone and LaCroix 1975; Walle 1987). This condition has led to the use of warm incubation of imbibed seeds prior to cold stratification for overcoming dormancy in these species. For European ash, Tylkowski (1990, 1993) has recommended 16 weeks at 15 or 20 °C, followed by 16 weeks at 3 °C. Seed moisture content should be from 55 to 60% during this period, and a 1-hour re-soak in water should be carried out weekly in the warm phase and every 2 weeks in the cold phase. The warm phase can be less than 16 weeks if periodic examinations of longitudinal cuts of seeds show the embryo to have reached 80 to 90% of the seed length (Suszka and others 1996). In many cases, the same warm/cold treatment approach has been beneficial to green and white ashes from the northern portions of their ranges (Bonner 1974; Cram 1984; Tinus 1982).

Cold stratification alone is usually sufficient for sources of these 2 species from the southern portion of their ranges (Bonner 1973, 1975). The degree of dormancy also seems related to seed age: older stored seeds appear more dormant than freshly collected ones (Bonner 1974; Tinus 1982).

Shamel ash does not require pretreatment for prompt germination (Francis 1990). Pretreatment recommendations for dormant ashes are summarized in table 5. Germination is epigeal (figure 4) and may occur the spring following seedfall, or seeds may lie dormant in the litter for several years before germinating.

Germination tests. Official germination recommendations for ashes call for either 56 days (ISTA 1993) or 28 days (AOSA 1993) with stratified seeds on blotter paper with diurnally alternating temperatures of 30 °C in light and 20 °C in the dark. Prescriptions for individual species and some representative results of tests with stratified seeds

Figure 4—*Fraxinus nigra*, black ash: seedling development at 1, 2, 8, and 14 days after germination.



under or near these conditions are given in table 6. Recent research in Italy with European and flowering ashes suggests that alternating temperatures of 25 °C for 8 hours and 5 °C for 16 hours (both in the dark) are better than 30/20 °C because of the greater amplitude of temperature change (Piotto 1994).

Because of the dormancy encountered with seeds of this genus, rapid viability tests by embryo excision or tetrazolium staining are preferred over actual germination tests for all except green ash (AOSA 1993; ISTA 1993). Staining with indigo-carmine has been popular and successful with European ash (Suszka and others 1996). Rapid testing with x-rays is also possible, but relating the images to seed quality is reported to be difficult with white ash (Houston 1976).

Nursery practice. Ash seeds may be sown in the fall without stratification, especially in the northern United States. Seeds should be planted as soon as collected, preferably by mid-October (Eliason 1965). European ash is usually sown unstratified in August or September or stratified for 16 to 18 months and sown in March or April in England. Fall-sown seeds of this species will germinate the following spring, but yield is erratic (Aldhous 1972). Seeds treated with warm incubation, followed by cold stratification, as described earlier, can be stored non-dormant at –3 °C for up to 8 weeks before sowing, or dried up to 8 to 10% moisture at 20 °C and stored for up to 2 years before sowing (Suszka and others 1996). Fall-sown beds should be mulched with burlap or straw, and the mulch removed as soon as germination starts in the spring. For spring-sowing, stratified seeds should always be used. Seeds of most species should be drilled in rows 15 to 30 cm (6 to 12 in) apart at rates of 80 to 100 seeds/m (25 to 30/ft), or broadcast to achieve a bed density of 105 to 160 seedlings/m^2 (10 to 15/ft^2) (Bonner 1974; Williams and Hanks 1976).

Table 5—*Fraxinus*, ash: stratification treatments to promote germination

Species	Medium	Warm period		Cold period	
		Temp (°C)	Days	Temp (°C)	Days
F. americana	Sand	20–30	30	5	60
	Plastic bag*	—	—	3	56–84
F. caroliniana	Plastic bag*	—	—	3	60
F. dipetala	Sand, peat	—	—	2–5	90
F. excelsior	Sand†	—	—	Cool‡	480–540
	Sand, peat, or plastic bag*	20	60–90	4–5	60–90
F. nigra	Sand	20–30	60	5	90
	Peat	21	126	4	90
F. ornus	Soil	Warm‡	30	Cold‡	90
F. pennsylvanica	Moist substrate	20	60	0–5	210
	Plastic bag*	—	—	2–5	60–150§
F. profunda	Moist paper	—	—	5	60
F. quadrangulata	Sand	20–30	60	5	90
F. uhdei	—	—	0	—	0
F. velutina	Sand, soil	—	—	2–5	90

Sources: Bonner (1974), Bonner (1975), Francis (1990), Mirov and Kraebel (1939), Soljanik (1961), Steinbauer (1937), Vanstone and LaCroix (1975), Walle (1987).
* Naked stratification in plastic bags.
† In outdoor pits.
‡ Exact temperatures not given.
§ For seeds from southern sources, 2 or 3 months is enough, but for seeds from northern sources, 5 months is needed. The warm period is helpful but not essential for southern sources (Bonner 1974; Eliason 1965).

Table 6—*Fraxinus*, ash: germination test conditions and results for stratified seed

Species	Germination test conditions: Daily light period (hrs)	Medium	Temp (°C): Day	Temp (°C): Night	Days	Germination rate: Amt (%)	Germination rate: Days	Germination percentage: Avg (%)	Germination percentage: Samples
F. americana	—	Sand	30	20	24–40	49	24	54	3
	8	Paper	25	15	56	—	—	68	1
F. caroliniana	8	Kimpak	30	20	60	54	14	61	3
F. dipetala	—	—	—	—	—	—	—	71	2
F. excelsior	—	—	—	—	—	—	—	61	4
F. nigra	—	Sand	30	20	40	7	18	20	6
F. ornus	—	Soil	—	—	—	—	—	49	3
F. pennsylvanica	8	Paper	30	20	30–34	70	20	76	6
	16	Paper	30	20	42	71	21	80	3
	NDL	Sand	—	—	30	—	—	89	3
F. profunda	NDL	Soil	30	16	45	32	20	48	1
F. quadrangulata	—	Sand	30	20	56	43	40	44	1
F. uhdei	8	Kimpak	30	20	40	66	21	69	4
F. velutina	—	Sand	30	20	—	—	—	33	5

Sources: Bonner (1974), Bonner (1975), Cram (1984), Mirov and Kraebel (1939), Soljanik (1961), Tinus (1982).
NDL = Natural daylength in a greenhouse.

Recommendations for Shamel ash are 215 to 320 seedlings/m^2 (20 to 30/ft^2) (Bonner 1974). Seeds should be covered with 6 to 19 mm ($^1/_4$ to $^3/_4$ in) of soil, and shading of the beds for a short time after germination may be desirable. Some ash species are subject to severe defoliation by a fungus—*Marssonina gloeodes* (H.C. Greene) H.C. Greene—especially in northern nurseries, and control measures may be necessary. The normal outplanting age for North American ashes is 1+0, or in some cases 2+0. European ash stock is ordinarily outplanted as 1+1 or 2+0.

Shamel ash coppices readily, and shoot tip cuttings from these sprouts can be rooted (Francis 1990). Cuttings of green ash from 1+0 seedlings or 1-year-old coppice shoots root easily, but older material is extremely difficult to propagate (Kennedy 1990). Air-layering of green ash limbs on 5-year-old trees in Mississippi was 22% successful (Bonner 1963). Other ash species are not easily rooted, but ornamental selections are commonly propagated by budding and grafting (Dirr and Heuser 1987).

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F

Sterculiaceae—Sterculia family

Fremontodendron Coville

fremontia, flannelbush

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Growth habit, occurrence, and use. The genus *Fremontodendron* is endemic to California and adjacent areas of Arizona and Baja California. It includes 2 common and 1 rare species (table 1) (Kelman 1991). Fremontias are shrubs or small trees with evergreen leaves that are alternate, entire to lobed, and covered with characteristic stellate hairs. They are components of chaparral vegetation and are able to resprout abundantly after fire. The resprouts are valuable forage for deer and domestic livestock (Nord 1974). Fremontias are handsome plants that are used extensively in California for roadside and residential landscaping and are becoming known as native garden plants (Holmes 1993). Interspecific hybrids such as *F. mexicanum* × *F. californicum* 'California Glory' have been developed for horticultural use. Fremontias are drought-tolerant and have been successfully planted for watershed protection in wildland settings (Nord 1974).

Flowering and fruiting. The large, perfect, yellow to copper-colored flowers appear on the plants from April through June. They have a single perianth series that is fused into a saucer shape, 5 stamens fused into a staminal column, and a superior ovary. The flowers produce abundant nectar and are pollinated mostly by large native bees (Boyd 1994). Much of the seedcrop may be destroyed by insect larvae prior to dispersal, at either the flower bud or the immature fruit stage (Boyd and Serafini 1992). The large, bristly, 4- to 5-chambered capsules ripen from July to September and split open at the tip. The numerous reddish brown to black seeds are cast from the capsules by wind, hail, or animal disturbances (Nord 1974). The seeds have a more or less well-developed caruncle or elaiosome at the micropylar end (figure 1), and there is good evidence of dispersal by harvester ants, at least for eldorado fremontia (Boyd 1996). In that species, the testa is much thicker under the elaiosome than at other positions on the seed (figure 2), apparently as a protection from the ant dispersers that eat the elaiosomes. These ants act as predators on seeds that do not possess an elaiosome "bribe."

Seed collection, cleaning, and storage. Fremontias grow rapidly and reach reproductive age the second season

Figure 1—*Fremontodendron californicum*, California fremontia: seeds.

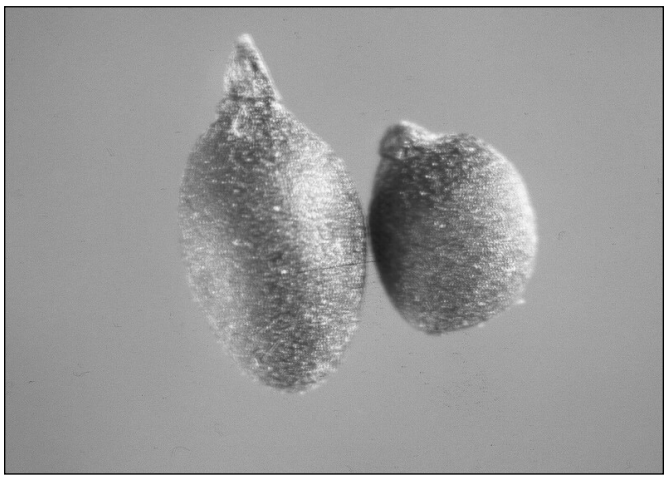
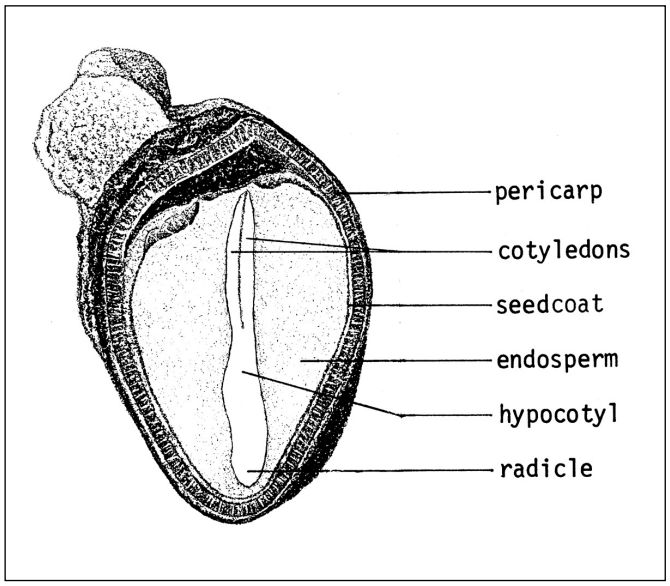


Table 1—*Fremontodendron,* fremontia: common names and occurred

Scientific name	Common name(s)	Distribution
***F. californicum* (Torr.) Coville**	**California fremontia,** flannelbush	N to S California & central Arizona
***F. decumbens* R. Lloyd**	**eldorado fremontia,** California flannelbush	One location in Eldorado Co., California
***F. mexicanum* A. Davids.**	**Mexican fremontia,** Mexican flannelbush	San Diego Co., California & N Baja California

Source: Kelman (1991).

Figure 2—*Fremontodendron californicum*, California fremontia: longitudinal section through a seed



after emergence. Seed production is reportedly better in cultivated than in naturally occurring individuals (Nord 1974). The ripened seed may be retained in the capsule for up to a month, but it is best to collect seeds when the first capsules begin to split open (Nord 1974). Capsules are collected by hand stripping or beating into containers. Gloves are recommended to protect hands against the irritating capsule bristles. Capsules that do not open soon after collection should be soaked in water for a few minutes, then dried before extraction. Capsules may be broken up in a hammermill or other threshing device, and the seeds cleaned out by screening and fanning (Nord 1974). Seed weight varies among and within species (table 2). Fremontia species form persistent seed banks in the field and are probably long-lived in storage (orthodox). In field seed bank experiments with eldorado fremontia, there was little loss of viability over a 7-year period (Boyd and Serafini 1992).

Germination and seed testing. Fremontia seeds are not permeable to water and must be scarified, either mechanically or by heat, in order for them to imbibe the water (Boyd and Serafini 1992; Emery 1988; Nord 1974). For nursery propagation, the seeds are given a hot water treatment, that is, immersion in hot water (85 to 95 °C) that is then allowed to cool for 12 to 24 hours. In nature, wildfire provides the heat stimulus. Most, if not all, recruitment of new plants takes place after fire. Seedlings from plantings into mature chaparral using artificially scarified seed were destroyed by herbivores or succumbed to drought (Boyd and Serafini 1992). Although scarification is a requirement for imbibition, it may not be sufficient to induce germination. Seed collections of California fremontia and some collections of Mexican fremontia may also require a 2- to 3-month chilling treatment at 5 °C (Emery 1988; Nord 1974). In a study by Keeley (1987), a collection of California fremontia responded only minimally to heat shock treatments, perhaps because the chilling requirement was not fully met. For eldorado fremontia, scarification with chilling produced no significant increase in seedling emergence over scarification alone, whether the scarification was mechanical or heat-induced (Boyd and Serafini 1992). A heat treatment of 5 minutes at 100 °C plus incubation with charate from chamise (*Adenostoma fasciculatum* Hook. & Arn.) charcoal produced significantly higher emergence than heat shock scarification alone (72 vs. 58%). Charate-stimulated germination has been reported for other chaparral species and represents an adaptation for detecting the occurrence of fire (Keeley 1987, 1991).

Seed quality evaluation for fremontia may be carried out using tetrazolium staining (Boyd and Serafini 1992). The testa is first nicked and the seeds allowed to imbibe water overnight. They are then immersed in 1% tetrzolium chloride for 6 hours and bisected longitudinally for evaluation. The embryo is linear and is embedded in abundant endosperm (Nord 1974). Germination testing is difficult

Table 2—*Fremontodendron*, fremontia: seed yield data

Species	Seeds/weight /kg	Seeds/weight /lb	Maximum Fill %	Maximum germination %
F. californicum	30,870–55,125	14,000–25,000	53	50
F. decumbens	26,460	12,000	100	72
F. mexicanum	44,100–66,150	20,000–30,000	100	55

Sources: Boyd (1966), Keeley (1991), Nord (1974).

because the period of germination is apparently relatively long even for scarified and chilled seeds (Boyd and Serafini 1992; Nord 1974).

Field seeding and nursery practice. Direct-seeding in the fall using hot-water scarified seed has been successful for California fremontia (Nord 1974). Because of the relatively large seed size, spot-seeding or drilling with a rangeland drill at a depth of 10 to 25 mm (0.4 to 1 in) gave much better results than hydroseeding or broadcasting. Successful spring seedings required the use of chilled seed.

Fremontia species have been produced as container stock using the hot water soak plus chilling protocol for seed germination described above (Emery 1988; Nord 1974). They are also readily produced from stem cuttings (Nord 1974).

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Garryaceae—Silktassel family

Garrya Dougl. ex Lindl.

silktassel

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Growth habit and occurrence. The genus *Garrya*—silktassel—consists of 14 New World species ranging from the Pacific Northwest to Panama (Dahling 1978). Only those in the United States and Mexico are considered here. *Garrya* is a highland genus occurring in chaparral and coniferous forests above lowland deserts, in semiarid regions, or in coastal or near-coastal conditions. Species may vary in size from low shrubs to trees (table 1). First discovered by David Douglas in the Pacific Northwest in 1826, Garrya was named in honor of Nicholas Garry, the first secretary of the Hudson Bay Company (Dahling 1978). Alternatively classified in Garryaceae and Cornaceae by various taxonomists, the genus will be classified as Garryaceae in this manual, after Dahling (1978) and Kartesz (1994).

Use. Wavyleaf and canyon silktassels and bearbrush are planted as ornamentals in many areas of the world (Dahling 1978). The graceful catkins and stately shape of these species make them desirable landscape shrubs. Introduced into cultivation between 1842 and 1902, silktassels have also been used for erosion control (Rehder 1940; Reynolds and Alexander 1974). Native plants are browsed by domestic livestock, deer (*Odocoileus* spp.), and bighorn sheep (*Ovis canadensis*) (Reynolds and Alexander 1974). Wavyleaf silktasssel will tolerate arid conditions, low fertility, sandy soils, and a wide range of pH values (Ridgeway 1973).

Although known to be toxic, stem extracts of laurel-leaf silktassel are used as an antidiarrhetic throughout rural Mexico, and bark extracts were reportedly used by Native Americans to treat fever (Dahling 1978). Ashy silktassel was used as a laxative and to treat colds, stomach aches, and gonorrhea by Kawaiisu Indians (Moerman 1986). Whole-plant extracts of ashy and wavyleaf silktassel plants native to Arizona have been found to contain gutta-percha, a natural rubber. This is the first reported occurrence in Garryaceae (Roth and others 1985).

Flowering and fruiting. Flowers are dioecious. Both appear in axillary or terminal catkinlike racemes in the spring (Reynolds and Alexander 1974); however male flowers are minute (Dahling 1978). Silktassels are well adapted for wind pollination. Several species hybridize, most notably bearbrush with ashy silktassel and eggleaf silktassel with laurel-leaf silktassel (Dahling 1978; Mulligan and Nelson 1980).

Silktassel fruits are persistent, 2-sided berries that appear green and fleshy when young but become dry and brittle at maturity (Dahling 1978) (figures 1–3). The fruit is globose to ovoid and relatively uniform among the species included here, averaging 7.2 mm long by 6.2 mm wide and producing from 1, 2, or (rarely) 3 seeds that are 2 to 3 mm in diameter (Dahling 1978).

Collection of fruits. Ripe fruits may be gathered by stripping them from the branches onto canvas, or hand-picking them from the bushes. Because the fruits may be infested with insect larvae, care must be taken to collect only sound fruits (Reynolds and Alexander 1974).

Extraction and storage of seeds. After twigs, leaves, and other debris have been sifted out, fruits are run through a macerator and the pulp and empty seeds floated off or screened out. Seeds may also be extracted by rubbing the fruits over a fine-mesh screen and floating off the pulp and empty seeds in water (Reynolds and Alexander 1974). Fifty kilograms (110 lb) of dry bearbrush berries yield about 25 kg (55 lb) of cleaned seeds. Cleaned seed densities range from 37,500 to 72,800 seeds/kg (17,000 to 33,000/lb). About 85 to 99% of the seeds will normally be sound (Reynolds and Alexander 1974). Storage methods suitable for most shrub species should also apply to silktassel seeds.

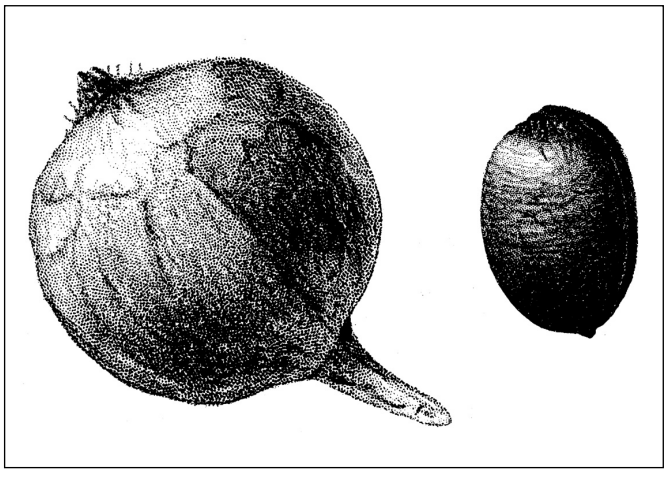
Pregermination treatments. Seeds of ashy silktassel and bearbrush will not germinate without pretreatment because of embryo dormancy (Mirov and Kraebel 1937; Reynolds and Alexander 1974). Some seeds of Wright silktassel exhibit embryo dormancy, whereas others germinate

Table 1—*Garrya,* silktassel: occurrence, elevational range, and growth form

Scientific name	Common name	Occurrence	Elevation (m)	Growth form
***G. buxifolia* Gray**	**dwarf silktassel**	N California, S Oregon chaparral, associated with pine at higher elevations	60–2,133	Brushy shrub
***G. elliptica* Dougl. ex Lindl.**	**wavyleaf silktassel**	Central Oregon to Santa Cruz Island, California; coastal & higher elevations inland	3–840	Shrub (< 6 m)
***G. flavescens* S. Wats.**	**ashy silktassel**	Pacific Coast states, SW US, Baja California; canyons, deserts, mtns	450–2,740	Shrub (< 6 m)
***G. fremontii* Torr.**	**bearbrush**	S Washington to central California; Sierra Nevada & Cascades	150–2,740	Shrub
***G. glaberrima* Wangerin**	—	Scattered locations in mtns of Coahuila, Neuvo Leon, & Tamaulipas; between lowland deserts & highland conifer forests	1,487–2,740	Small tree
***G. grisea* Wiggins**	—	Baja California; upper Sonoran & transition communities	1,370-2,423	Shrub (2–4.6 m)
***G. laurifolia* Benth.**	**laurel-leaf silktassel**	Central Mexico to Central America; semiarid shrub communities	610–3,566	Tree (< 11 m)
***G. longifolia* Rose**	—	S Mexico on volcanic slopes	1,280–2,650	Small tree
***G. ovata* Benth.**	**eggleaf silktassel**	Arizona, New Mexico, Texas, N Mexico; mtns above lowland deserts	610–2,560	Clumped shrub (2–4.6 m)
***G. salicifolia* Eastwood**	—	S Baja California; sandy loam soils	1,554–1,830	Small tree
***G. veatchii* Kellog**	**canyon silktassel**	S California, Baja California; lower mtn chaparral & riparian communities	230–2,600	Shrub
***G. wrightii* Torr.**	**Wright silktassel**	Arizona, W Texas, N Mexico; arid Sonoran & transition communities	914–2,133	Shrub

Source: Dahling (1978).

Figure 1—*Garrya fremontii*, bearbrush: berry (**left**) and seed (**right**).



well without pretreatment (Reynolds and Alexander 1974). Because of this variability, seeds of Wright silktassel should also be pretreated before testing or sowing. Recommended pretreatments for these species include stratification at 2 to 5 °C in moist sand, vermiculite, or sphagnum moss for 30 to 120 days (Reynolds and Alexander 1974; Mirov and Kraebel 1937), followed by soaking for 17 hours at room temperature in a 100-ppm solution of gibberellin. However, germination of bearbrush was also improved by stratification in moist sand for 90 days at greenhouse temperatures followed by 90 days at 5 °C (Reynolds and Alexander 1974).

Germination tests. Germination tests have been done on pretreated seeds placed in sand, vermiculite, Kimpak™, and sphagnum moss under light for 30 to 60 days, and at temperatures alternating diurnally from 25 to 13 °C, or from 30 to 20 °C (Reynolds and Alexander 1974). Seeds of Wright silktassel had germination capacities of 47 to 86%.

Figure 2—*Garrya wrightii*, Wright silktassel: berry (**left**) and seed **(right)**.

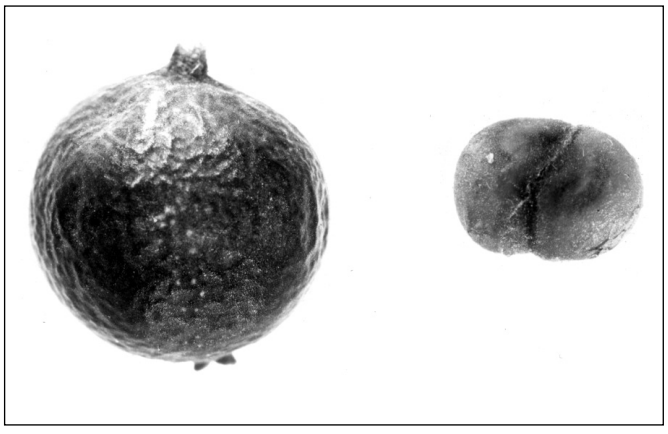
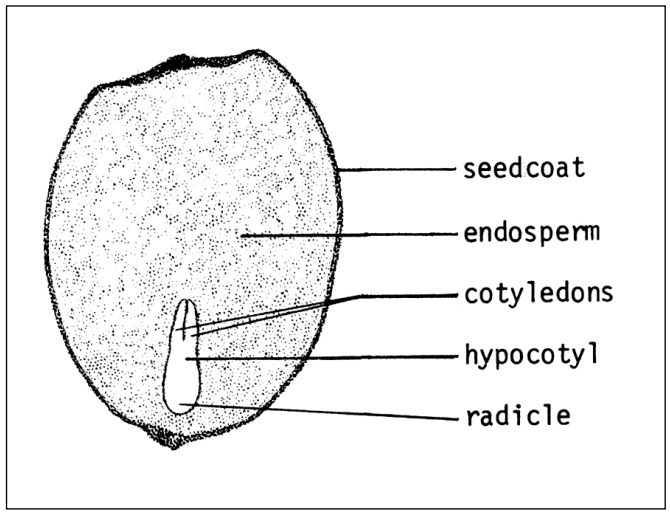


Figure 3—*Garrya fremontii*, bearbrush: longitudinal section through a seed.



Seeds of ashy silktassel germinated best at temperatures between 10 to 15 °C, but poor at 23 to 27 °C. Low-temperature stratification alone does not always result in satisfactory germination of bearbrush (Reynolds and Alexander 1974).

Nursery practice. Seeds of Wright silktassel should be sown in the late winter after 90 days of stratification in moist sand. Sufficient viable seeds should be sown to produce about 100 seedlings/m^2 (9 seedlings/ft^2). They should be covered with about 1.2 cm ($^1/_2$ in) of soil and a light mat mulch. Seedlings are ready for outplanting at age 2 years (Reynolds and Alexander 1974).

Silktassels can also be vegetatively propagated in the nursery. Tip nodal cuttings of wavyleaf silktassel 8 to 18 cm (3 to 4 in) long that were collected in late summer through November, then basally treated with 0.8% indole butyric acid (IBA) and bottom-heated at 20 to 21 °C, successfully rooted within 6 to 8 weeks (Ridgeway 1973). The growth medium should be well drained and only misted during the day. Silktassels are sensitive to root disturbance when actively growing, so dormant potting is recommended (Ridgeway 1973); however, they will not tolerate high fertility in the potting compost. It is difficult to achieve economic rooting percentages unless selection of cutting material, and porosity and hygiene of the rooting medium are carefully controlled (Ridgeway 1985).

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G

Ericaceae–Heath family
Gaultheria L.
wintergreen

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Growth habit, occurrence, and uses. Of the 100 to 150 species of the genus *Gaultheria*, commonly called wintergreen, most are found in Asia, Australia, and South America. Only 6 species—creeping snowberry, alpine wintergreen (*G. humifusa* (Graham.) Rydb.), *G. miqueliana* Takeda, *G. ovatifoli*a A. Gray, checkerberry, and salal—occur in North America north of Mexico (Abrams 1951; Chou 1952; Hitchcock and others 1959; Viereck and Little 1972). The 3 species considered here (table 1) are evergreen shrubs. Both creeping snowberry and checkerberry have a prostrate or creeping form (Fernald 1950) and have been described as semi-herbaceous or almost herbaceous (Fernald 1950; Rosendahl 1955). Salal has a distinctly woody stem and grows 1 to 3 m tall.

Over its wide range in the United States and Canada, creeping snowberry is most common in bogs and wet forested conditions (Curtis 1959; Gleason 1952; MacKinnon and others 1992). Checkerberry tolerates site conditions ranging from dry to poorly drained and grows well on many acidic soil types, including peat, sand, sandy loam, and coal mine spoils (Robinette 1974). Salal also grows on a variety of sites, including shallow rocky soils, sand dunes, glacial till, and peat (Haeussler and Coates 1986). It is most common on well-drained slopes and ridges in coastal Oregon and Washington, on lowland sites in British Columbia, and on low-productivity timber sites in southeast Alaska (Fraser and others 1993; Hemstrom and Logan 1986; Minore and Weatherly 1994; Viereck and Little 1972).

Both creeping snowberry and checkerberry are low cover species valued for wildlife habitat and ornamental use (Dirr 1990; Hitchcock and others 1959; Robinette 1974; Stiles 1980; White and Stiles 1992). Animals known to feed on fruits, buds, or leaves of checkerberry include migratory birds; grouse, including blue (*Dendragapus obscurus*), spruce (*Canachitea canadensis*), and ruffed (*Bonasa umbellus*) grouse; bobwhite quail (*Colinus virginianus*); wild turkey (*Meleagris gallopavo*); ring-necked pheasant (*Phasianus colchicus*); as well as black bear (*Ursus americanus*); white-tailed deer (*Odocoileus virginianus*); and others. Checkerberry is a favorite food of the eastern chipmunk (*Tamias strictus*) (Martin and others 1951; Robinette 1974; Stiles 1980; Van Dersal 1938). Leaves of this species contain oil of wintergreen, which has been extracted for pharmaceutical use, and the edible fruits have been marketed (Dimock and others 1974).

Within the plant communities in which they grow, creeping snowberry and checkerberry occupy a far less

Table 1—*Gaultheria,* wintergreen: nomenclature, and occurrence.

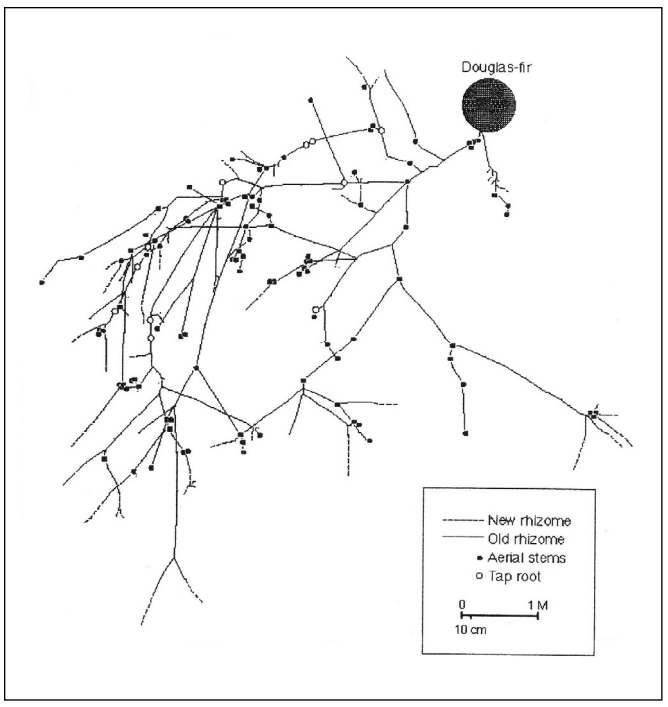
Scientific name & synonym	Common name(s)	Occurrence
***G. hispidula* (L.) Muhl. ex Bigelow** *Chiogenes hispidula* (L.) Torr. & Gray	**creeping snowberry,** creeping pearlberry, moxieplum	Labrador to British Columbia; S to Newfoundland, Nova Scotia & Pennsylvania; higher elevations to North Carolina; W through Michigan, Wisconsin & Minnesota; Idaho
***G. procumbens* L.**	**checkerberry,** wintergreen, mountain-tea	Newfoundland to Manitoba; S through Minnesota & Wisconsin, to Alabama & Georgia
***G. shallon* Pursh**	**salal,** Oregon wintergreen	Pacific Coast from S Alaska to S California inland into the Cascades & Sierra Nevada

Sources: Abrams (1951), Fernald (1950), Gleason (1952), Hitchcock and others (1959).

prominent niche than their Pacific Coast relative—salal. Common to the point of invasiveness, salal is a dominant shrub that lends watershed protection wherever it thrives. Because it rapidly forms dense rhizome mats (figure 1), salal is recommended for sand dune stabilization along the northern Pacific Coast (Brown and Hafenrichter 1962; Huffman and others 1994a&b). Under open canopied forests, salal often forms a dense, vigorous cover that dominates understory plant communities. Sala shoots bearing its glossy, evergreen leaves are highly prized nationwide by the floral industry and marketed as "lemon leaf" in the eastern United States (Sabhasri 1961; Schlosser and others 1991). Harvesters look for dark green sprays, free of discoloration and defect. These are sold as short-stemmed bunches ("tips") or regular bunches 60 to 75 cm long. Salal leaves range from 7 to 21 cm^2 in area, depending on light conditions (Huffman and others 1994b; Messier 1992) and persist on the plant from 2 to 4 years (Haeussler and Coates 1986). A handsome ornamental, salal responds well to cultivation, both domestically and abroad (Fraser and others 1993); wild transplants have been a commercial product (Douglas 1970).

The leaves, buds, and fruits of salal are dietary staples for several game bird species, blue (*Dendragapus obscurus*), ruffed (*Bonasa umbellus*), and spruce (*Falcipennis canadensis*) grouse and band-tailed pigeon (*Patagioenas fasciata*) including (Dimock and others 1974; Martin and others 1951; Van Dersal 1938). Mammals that use its leaves or fruit include black bear, black-tailed deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), Douglas squirrel (*Tamiasciurus douglasi*), Townsend chipmunk (*Tamias* spp.), and mountain beaver (*Aplodontia rufa*) (Hayes and others 1995; Martin 1971; Martin and others 1951; Van Dersal 1938). Salal berries were eaten either fresh or dried by Native Americans; leaves were smoked with bearberry (kinnikinnick)—*Arctostaphylos uva-ursi* (L.) Spreng.—and used in various medicinal preparations (Gunther 1945; Pojar and Mackinnon 1994). The fruit can also be used for jam or preserves (Brown and Hafenrichter 1962; Pojar and Mackinnon 1994).

Figure 1—*Gaultheria shallon, salal*: diagram of a typical clone comprised of 78 aerial stems and 91 m of interconnected rhizomes growing under an open canopied forest (Huffman and others 1994a).



Flowering and fruiting. The perfect, white to pinkish flowers are borne either solitary and axillary, or in axillary (creeping snowberry) or terminal racemes (figure 2). The number of flowers per inflorescence is 1 to 4 for checkerberry and 5 to 15 for salal (Fraser and others 1993; Reader 1977). Stamens number either 8 (creeping snowberry) or 10 (checkerberry and salal), and ovaries are either 4- or 5-celled, with many ovules (Abrams 1951; Hitchcock and others 1959; Rehder 1940). Flowering dates range from early spring to late summer (table 2). In forest conditions, flowering shoots of salal over 4 years old had greater growth and leaf production than non-flowering shoots the year preceding flowering (Bunnell 1990). Shoot growth and leaf production the same year as flowering was less for flowering shoots than for others. Stems less than 4 years old and those under overstory canopies greater than 33% mean crown cover did not flower (Bunnell 1990). In the nursery, 2nd-year stems produced from rhizome cuttings flowered under light levels as low as 20%, whereas seedlings did not flower

Figure 2—*Gaultheria shallon*, salal: racemes bearing pinkish white flowers.

Table 2—*Gaultheria,* wintergreen: phenology of flowering and fruiting

Species	Flowering	Fruit ripening & dispersal
G. hispidula	Apr–Aug	Aug–Oct*
G. procumbens	May–Sept	Aug–June†
G. shallon	Mar–July	July–Dec

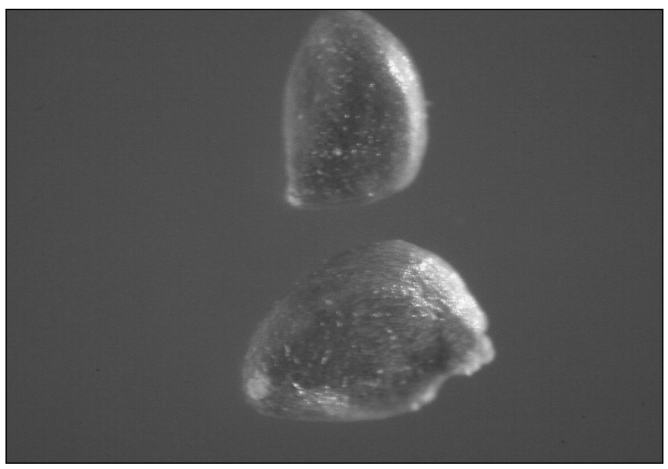
Sources: Fernald (1950), Gleason (1952), Hitchcock and others (1959), McMinn (1951), Robinette (1974), Rosendahl (1955), Van Dersal (1938).

* Actual ripening time uncertain.

† Fruit of this species notably persistent and reportedly increase slightly in size during winter (Van Dersal 1938).

Figure 3—*Gaultheria shallon*, salal: the ripe fruit is a purplish black, somewhat-fuzzy pseudo-berry.

Figure 4—*Gaultheria shallon*, salal: the seeds are very small.



under the same conditions (Huffman and others 1994b). Bumble bees are important pollinators of wintergreen (Pojar 1974; Reader 1977). Autogamy also occurs; all 3 species appear self-compatible.

The fruit of wintergreen is a many-seeded capsule surrounded by a persistent, thickened and pulpy calyx that forms a fleshy pseudoberry (Hitchcock and others 1959) (figure 3). The distinctly colored fruits of the 3 species range from 3 to 10 mm in diameter (table 3). Fruits ripen from mid-summer on and are persistent on the plants into winter, thus providing food for birds and mammals, the main dispersers (Stiles 1980; Van Dersal 1938). Checkerberry fruits remain on the plant throughout the winter and are present after snowmelt. Good seedcrops are frequent.

Collection of fruits. Fruits of wintergreen are sufficiently persistent after ripening to permit collection over an extended period (table 2). Depending upon species, they may be combed, stripped, or picked individually from the plant. Refrigeration at temperatures just above freezing minimizes molding if fruits must be stored before processing. Dried fruits of checkerberry vary from 6,250 to 6,600/kg (2,835 to 3,000/lb) (Dimock and others 1974; Swingle 1939) and contain 35 to 81 seeds each (Mirick and Quinn 1981). Dried fruits of salal vary from 8,333 to 1,1494/kg (3,750 to 5,180/lb) (Huffman and others 1994b), averaging 8.5 per cluster (Sabhasri 1961) and containing from 80 to 140 seeds each (Huffman and others 1994b; Zasada 1996). Seeds per fruit averaged 98.7 (range, 79.0 to 125.9) in samples of 20 to 25 fruits collected from widely separated sources (Sabhasri 1961; Zasada 1996). In a nursery study, seed production (seeds per fruit) and fruit dry weight (0.89 to 0.12 g/fruit) were highest for plants growing under 70% light (Huffman and others 1994b).

Extraction and storage of seeds. Either dry or wet seed extraction is possible. Fruits of checkerberry and salal can be dried until they are brittle and powdery, then rubbed through a 30-mesh screen to separate the seeds from the pulp (Dimock and others 1974; Zasada 1996). Seeds of salal can also be separated from dry pulp fragments by using a South Dakota–type seed cleaner (Zasada 1996). Maceration of fresh salal fruits followed by repeated washings to separate seeds and pulp also is effective (Dimock and others 1974). Wintergreen seeds are very small (table 4; figures 4 and 5). Seed weight is a small fraction of fresh fruit weight; for example, 100 lbs of fresh salal fruits produced 2.3 to 4.0 lbs of cleaned seeds (Dimock and others 1972).

Table 3—*Gaultheria,* wintergreen: growth form, height at maturity, and fruit characteristics

Species	Growth habit	Height at maturity (cm)	Fruit diameter (mm)	Color of ripe fruit
G. hispidula	Prostrate*	20–40*	3–10	Clear–white
G. procumbens	Creeping	5–20	5–10	Scarlet–bright red
G. shallon	Tall shrub	25–300	6–10	Dark purple to bluish black

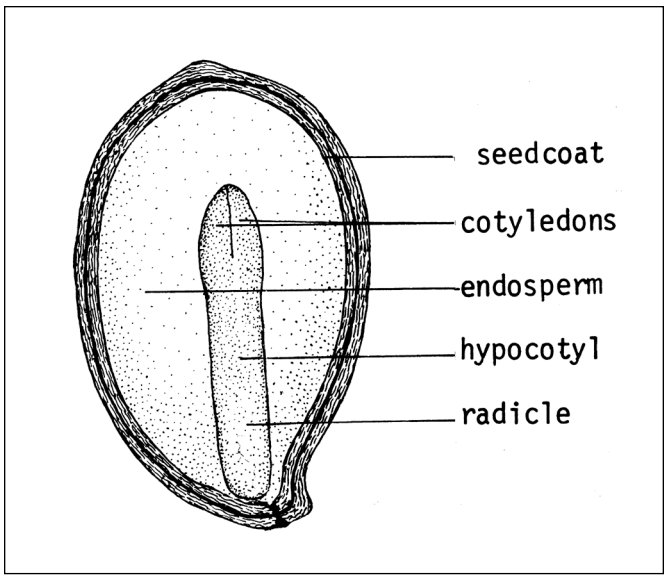
Sources: Fernald (1952), Gleason (1952), Hitchcock and others (1959), Rehder (1940), Rosendahl (1955), Stein (1995).
* Length.

Table 4—*Gaultheria,* wintergreen: seed yield data

	Cleaned seeds (x millions)/weight			
	Range		Average	
Species	/kg	/lb	/kg	/lb
G. hispidula	6.75–6.89	3.06–3.13	6.82	3.09
G. procumbens	6.33–10.67	2.87–4.84	8.50	3.86
G. shallon	5.67–8.33	2.57–3.78	7.14	3.24

Sources: Dimock and others (1974), McKeever (1938), Sabhasri (1961).

Figure 5—*Gaultheria procumbens*, checkerberry: longitudinal section through a seed.



Based on limited evidence, viability of wintergreen seeds may be maintained for 5 years or longer in cool, dry storage; storing seeds at temperatures below freezing has not been studied. Untested seeds of checkerberry stored for 2 years at 5 °C in sealed bottles showed 16% germination (Dimock and others 1974). McKeever (1938) obtained as high as 83% germination of salal seeds stored dry in paper bags at 21 °C for 159 days and 49% for seeds stored at the same conditions for 525 days. Salal seeds declined in germinative capacity from 31 to 21% after 1 year of storage at 4 °C (Sabhasri 1961). Another seedlot showed 73 and 27% germination, respectively, after 3 years of storage at 4 °C or room temperature (Mirov and Kraebel 1937). Some seedlots stored for 3 to 4 years at 1 °C showed 70 to 80% germination and did not differ in germination characteristics from fresh seedlots (Zasada 1996).

Pregermination treatments and germination tests. Very limited data indicate that creeping snowberry and checkerberry require cold stratification to substantially improve seed germination; however, salal does not (table 5). For seeds of creeping snowberry collected in New Hampshire, germination was completed after 98 days in a greenhouse when preceded by winter stratification outdoors for 83 days; unstratified seeds kept in a greenhouse did not germinate (Nichols 1934). Low germination of checkerberry was doubled with stratification (table 5). Salal seeds germinate as well without stratification as with it, but stratification tends to increase the rate and widen the range of temperatures at which germination can occur (table 5). Seeds stratified for 120 days began to germinate in 4 to 12 days at temperatures of 21 to 10 °C, respectively (Zasada 1996). Germination was complete in 18 days at 10 °C; germination was complete in 27 days at 21 °C. Seeds stratified for 150 days began to germinate during stratification. Germination is epigeal (figure 6).

Nursery practice and natural regeneration. Untreated seeds of checkerberry, and perhaps of creeping snowberry, can be sown from fall through early winter, or

stratified and sown in the spring (Dimock and others 1974; Rogers 1994). Salal seeds can be sown in the fall or spring without stratification, but stratification will increase germination at lower temperatures.

Surface-sowing is recommended in either glass- or poly-covered flats, in open beds under tacked down loose-weave cheesecloth or muslin (which seedlings penetrate after germination), or under shade cloth (Huffman and others 1994b; McKeever 1938; Rogers 1994). Even without such measures, up to 73% germination has been obtained in soil-filled flats (Mirov and Kraebel 1939). Light for 8 hours/day is recommended. Some propagators expose seeds to an additional 2 hours of light during the dark period (Rogers 1994). A potted plant of checkerberry can be propagated from seeds in 4 months (Rogers 1994). Salal seedlings raised in outdoor nursery beds grew 11 to 17 cm (4.3 to 6.7 in) tall in 2 years (Huffman and others 1994b). They exhibited poor apical dominance, however, developing 6 to 12 aerial stems. Light shade (70% light) produced seedlings with greater biomass, greater canopy size, and more aerial stems compared to those under 20 or 50% or full sun. Under all light intensities, some seedlings produced rhizomes in 2 years.

All 3 species are readily propagated vegetatively from layers, suckers, division of plants, stem or root cuttings, stolons, or rooting at the nodes (Brown and Hafenrichter 1962; Dimock and others 1974; Huffman and others 1994b; Rogers 1994; Sabhasri 1961; Van Dersal 1938). In the Northwest, salal is presently propagated almost entirely by rhizome cuttings (Dimock and others 1974). Cultured rhizome cuttings can produce 5 or more new rhizomes and over 7 aerial shoots/year under light shade during the first 2 years after planting (Huffman and others 1994b). Moist, acid conditions under partial shade are beneficial for young plants of all 3 species raised from either cuttings or seed.

Figure 6—*Gaultheria shallon*, salal: seedling development 2, 8, 15, and 33 days after germination

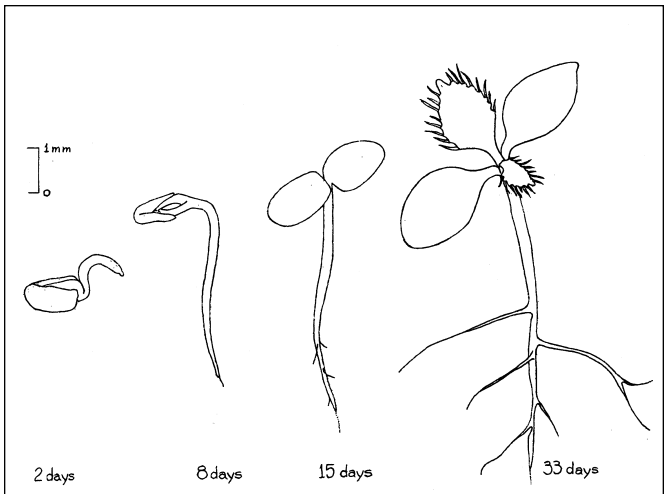


Table 5—*Gaultheria,* wintergreen: stratification, germination test conditions, and results

Species	Cold stratification (days*)	Germination test conditions: Moist medium	Temp (°C): Day	Temp (°C): Night	Germination rate: Days	Germination rate: %	Total germination: Days	Total germination: %
G. hispidula†	83	Soil	—	—	98	—	—	—
G. procumbens	0	Peat	30	20	213	7	59	8
G. shallon	60	Peat	30	20	56	16	15	16
	0	Paper	30	20	61	28	27	38
	30–120	Paper	30	20	55	26	37	31
	0	Sand/soil	21	21	28	74	22	76
	0	Paper/pads	21	16	60	42	30	51
	0‡	Paper/pads	16	10	60	28	30	51
	0‡	Paper/pads	10	4	60	0	30	41
	60‡	Paper/pads	21	16	60	39	30	45
	60‡	Paper/pads	16	10	60	31	30	40
	60‡	Paper/pads	10	4	60	23	30	50
	150‡	Paper/pads	21	16	60	55	30	59
	150‡	Paper/pads	10	4	60	32	30	40

Sources: Dimock and others (1974), Zasada (1996).
* Stratification temperature was 5 °C for *G. procumbens* and 3 °C for *G. shallon.*
† An unknown number of seeds were stratified outdoors during the winter and 147 seeds subsequently germinated in a greenhouse.
‡ Data are for 1 western Oregon seed source; 2 other seed sources had similar responses (Zasada 1996).

Seeds of wintergreen appear to have little innate dormancy under field conditions. No evidence of delayed emergence of salal was observed in 2 replicated studies subsequent to sowing test plots (Huffman and others 1994a; Tappeiner and Zasada 1993). Salal seedlings establish most readily on rotten logs and stumps under partial shade (Huffman and others 1994a; Huffman and Tappeiner 1997). There is evidence that this is also true for checkerberry (Matlack and Good 1989). Forest floor disturbance that exposes mineral soil enhances survival of salal seedlings (Huffman and others 1994a; Tappeiner and Zasada 1993). Predation of seeds did not appear to be a significant factor in a seedling establishment study in the Oregon coastal range (Tappeiner and Zasada 1993). Under field conditions, growth of salal seedlings is slow; they attained average heights of 2 to 4 cm (.8 to 1.6 in) in 2 years but can grow to 20 cm (7.9 in) (Huffman and others 1994a). Seedlings begin vegetative expansion in 4 to 6 years (Huffman and others 1994a). Young seedlings are susceptible to late spring frost (Sabhasri 1961).

Most field regeneration of wntergreen is vegetative (Bunnell 1990; Huffman and others 1994a; Huffman and Tappeiner 1997; Matlack and Good 1990; Matlack and others 1993; Sabhasri 1961). Checkerberry expands by growth of rhizomes and layering of creeping stems where conditions permit (Matlack and others 1993; Robinette 1974). Maximum expansion rates can be 10 cm (3.9 in) per year or more (Sobey and Barkhouse 1977). Clones of creeping snowberry develop as a result of layering of prostrate stems; maximum expansion rates range from 2 to 7 cm (.8 to 2.8 in) per year (Sobey and Barkhouse 1977). Rhizome expansion rates of 44 cm (17 in) per year have been reported for salal; the maximum observed was 93 cm (37 in)/year (Huffman and others 1994a). Individual clones of salal can occupy areas up to 29 m^2 (312 ft^2)with up to 218 m (715 ft) of interconnected rhizomes (figure 1) (Huffman and others 1994a). Salal populations rapidly recover after logging (Halpern 1988; Messier 1992; Messier and Kimmins 1991; Stein 1995) and can severely compete with commercially important tree species (Price and others 1986; Weetman and others 1990; Messier and Kimmins 1990). Clonal assemblages persist by vegetative regeneration of aerial shoots that replace older, dying stems (Huffman and others 1994a). Although shade-tolerant, salal loses vigor with increasing overstory density and clones disintegrate into smaller fragments (Huffman and others 1994a). An estimated minimum light requirement for salal survival ranges from 0.3 to 3.3% of full sunlight (Messier and others 1989).

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Ericaceae—Heath family

Gaylussacia baccata (Wangenh.) K. Koch

black huckleberry

Franklin T. Bonner

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Synonym. *Gaylussacia resinosa* (Ait.) Torr. & Gray.

Other common names. highbush huckleberry, black-snap, huckleberry.

Growth habit, occurrence, and use. Black huckleberry—*Gaylussacia baccata* (Wangh.) K. Koch—is a small deciduous shrub found from Louisiana east to Florida and north to Maine, Iowa, and Manitoba. It is upright and highly branched and reaches heights of 0.3 to 1.2 m at maturity (Vines 1960). The berries are an important food for wild animals (Van Dersal 1938) and are sometimes eaten by humans. The shrub was cultivated as early as 1772 (Bonner and Halls 1974).

Flowering and fruiting. The small, perfect, pinkish flowers appear in May to June, and the berrylike, drupaceous fruits mature in July to September. They are dark reddish to purple when immature and black when mature. Fruits are 6 to 10 mm long and contain 10 one-seeded, bone-colored nutlets that are 1.5 to 2.0 mm in length (Radford and others 1968; Vines 1960) (figures 1 and 2).

Collection, extraction, and storage. Black huckleberry fruits ("berries") may be stripped from the branches by hand or with blueberry rakes any time after they thoroughly ripen. They often persist for several weeks. Seeds may be extracted by macerating the fruits in water and allowing the pulp and empty seeds to float away. Some samples have been reported to have less than 50% filled seeds. Seed yields of 30 g of cleaned seeds/kg ($^1/_2$ oz/lb) of fruits have been reported (4 samples), with an average of 780 cleaned seeds/g (22,100/oz) (Bonner and Halls 1974). No seed storage studies have been reported with this species, but the seeds appear to be orthodox in storage behavior. This assumption is supported by a report that seeds stored in sealed bottles at 5 °C for over 2 years did not lose viability (Bonner and Halls 1974).

Figure 1—*Gaylussacia baccata*, black huckleberry: exterior view of seed in 2 planes.

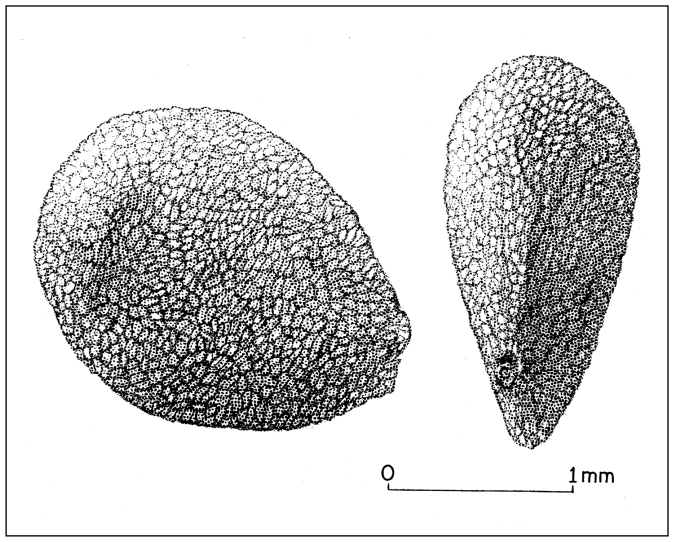
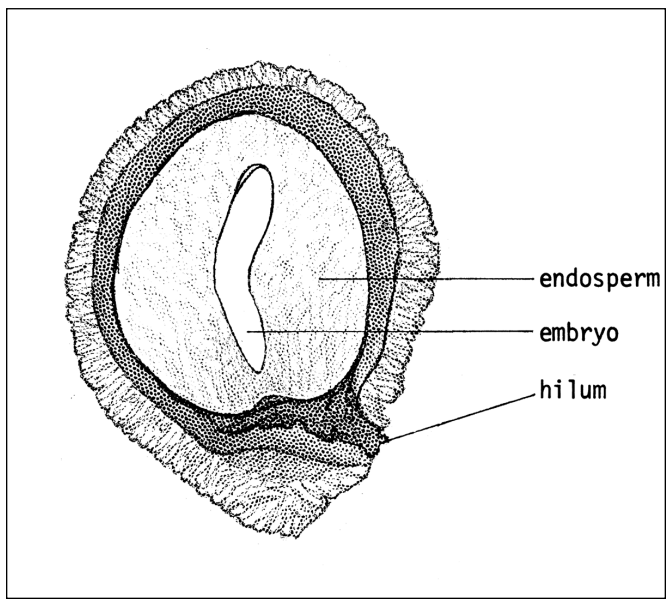
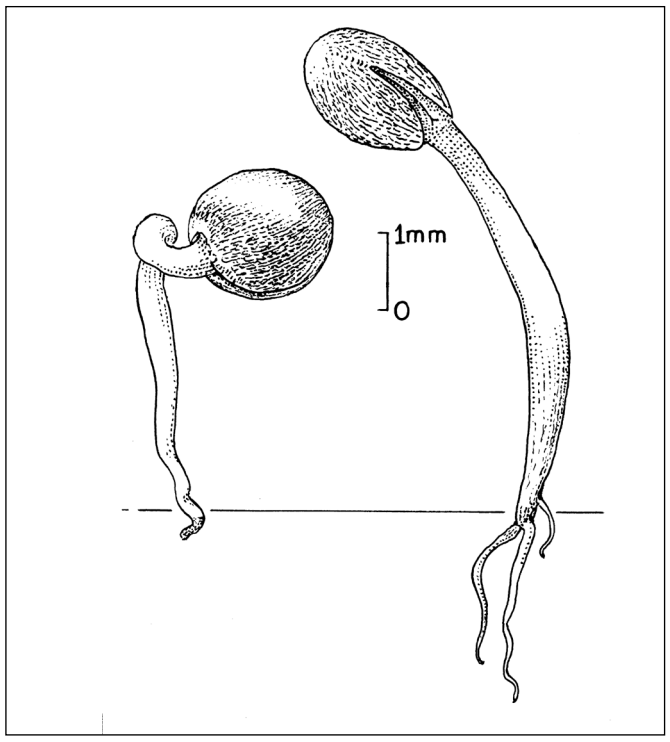


Figure 2—*Gaylussacia baccata*, black huckleberry: longitudinal section through a seed.



Germination. Black huckleberry seeds are dormant and require treatment for good germination. In one test, samples from a 2-year-old seedlot were subjected first to warm stratification in moist peat at diurnally alternating temperatures of 20 to 30 °C for 30 days. Then the temperature was lowered to 10 °C, and 80% of the seeds germinated after 27 days and 96% after 47 days (Bonner and Halls 1974). Germination is epigeal (figure 3).

Figure 3—*Gaylussacia baccata*, black huckleberry: seedling development at 3 and 9 days



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Ginkgoaceae—Ginkgo family

Ginkgo biloba L.

ginkgo

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Other common names. maidenhair-tree, Kew-tree.

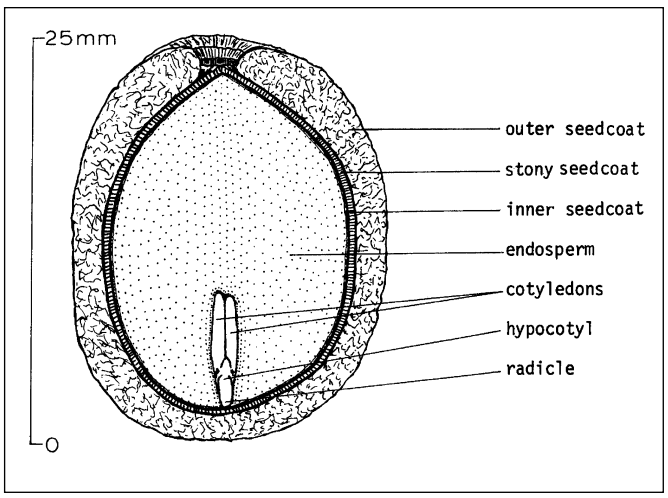
Growth habit, occurrence, and use. *Ginkgo* is a monotypic genus native to China, the sole survivor of the ancient family of Ginkgoaceae (Bailey 1923; Dallimore and Jackson 1948; Seward and Gowan 1900). Geologic records indicate that ginkgos have grown on Earth for 150 million years (AGINFO 1994). This tall (<35 m) deciduous, sparsely branched, long-lived tree has been cultivated extensively in the Far East and Europe (AGINFO 1994; Bailey 1923, 1947; Seward and Gowan 1900). The foliage of this broad-leaved gymnosperm consists of alternate, simple, fan-shaped, leathery leaves 2 to 5 cm long, with forking parallel veination. Ginkgo trees grow in an upright pyramidal form, becoming broader and regular with age (AGINFO 1994). Ginkgo was introduced into North America in 1784 and has generally been successful on good sites in the moist temperate zone of the midwestern and eastern United States and along the St. Lawrence River in Canada (Bailey 1947; Rehder 1940). Ginkgo trees prefer full sunlight and well-drained conditions and are adaptable to many soils, but they are slow to recover from transplanting (AGINFO 1994). The male of the species is valued as an ornamental and shade tree, particularly as a park and street tree (Bailey 1947). Ginkgo is highly resistant to air pollution and can be grown in areas within its introduced range where air pollution damages other species. The cooked seeds are used for food by the Chinese, but the fleshy layer can cause dermatitis (AGINFO 1994; Porterfield 1940).

Flowering and fruiting. The species is dioecious. The catkin-like male flowers appear in late March or early April, and the pistillate flowers appear later in April before leafout (Sakisaka 1927). A single naked ovule ripens into a drupe-like seed with a fleshy outer layer smelling of rancid butter and a thin, smooth, cream-colored, horny inner layer (figures 1 and 2). The fleshy coated seeds are frequently called fruits. They are cast in the fall after the first frost, but at this time a larger percentage of the seeds have immature embryos and cannot be germinated under normal test conditions (Alexander 1974; Eames 1955; Willan 1985). Embryo development continues while seeds on the ground are exposed to temperatures normally encountered during fall and early winter. Embryo maturation is usually complete about 6 to 8 weeks after the seeds drop (Lee 1956; Maugini 1965). Because of the offensive odor of the outer layer of the seeds, only male clones are recommended for landscape use (AGINFO 1994).

Ginkgo is also capable of reproducing vegetatively. Del Tredici (1992) describes the origin and development of basal chichi, tuber-like callus growths on the lower trunk that originate from superficial meristematic buds (located in the cotyledonary axils of all ginkgo seedlings) that allow clonal regeneration. Within 6 weeks of germination, these buds become embedded in the cortex of the stem and develop below the bark surface. If a traumatic event damages the tree, these buds grow down from the trunk to form basal

Figure 1—*Ginkgo biloba*, ginkgo: seeds enclosed in their fleshy outer layers (**far left and right**) and cleaned seeds with fleshy layers removed (**center**).

Figure 2—*Ginkgo biloba*, ginkgo: longitudinal section through a seed



chichi from which both aerial shoots and adventitious roots can grow. Up to 40% of mature trees Del Tredici observed at 1 location in China were multi-stemmed, with 2 or more secondary stems originating from 1 or more basal chichi. This form of vegetative regeneration may have played a role in the remarkable survival of ginkgo since the Cretaceous Period.

Collection, extraction, and storage. Ginkgo trees begin bearing seeds when they reach 30 to 40 years of age (Hadfield 1960; Ponder and others 1981). The flesh-coated seeds may be collected on the ground as they ripen or picked by hand from standing trees from late fall through early winter. Seeds may be prepared for cleaning by covering them with water for several days until the flesh begins to soften (Munson 1986). Food processing blenders can be used to macerate the softened fruits after their metal blades are replaced with plastic tubing propellers. Fruits should be covered with water, then macerated thoroughly in a blender cup using short bursts of the motor. The pulp is then floated away by slowly adding additional water and allowing filled seeds to sink to the bottom of the cup (Munson 1986). About 12.5 kg (27.5 lb) of cleaned seeds can be obtained from 50 kg (110 lb) of seeds with fleshy layers (Swingle 1939). Cleaned seed density varies from 400 to 1,150 seeds/kg (180 to 520 seeds/lb) (Alexander 1974; Swingle 1939). Cleaned seeds have been kept in ordinary dry storage in both open and closed containers at 5 to 21 °C without any apparent adverse effects (Davis and Henery 1942; Hatano and Kano 1952; Swingle 1939).

Germination. Recommended germination test conditions for ginkgo call for the placement of the seeds, with their coats removed, on the top of or between moist blotters at alternating day/night temperatures of 30 and 20 °C for 30 days (ISTA 1993). Germination tests conducted in moist sand for 60 days using 20 °C nights and 30 °C days ranged from 46% germination for seed collected in October to 90% germination for seed collected in December (Alexander 1974). Germination of untreated seed planted in a soil medium varied from 32 to 85% (Davis and Henery 1942; Swingle 1939). A stratification period of 30 to 60 days at 5 °C before planting has been recommended (Ponder and others 1981), however 1 to 2 months of warm stratification before cold stratification is also advised to allow seeds to fully mature (Dirr and Heuser 1987; Willan 1985).

Nursery practice. Seeds should be sown in the late fall (November), preferably in furrows, and covered with 5 to 8 cm (2 to 3 in) of soil and a sawdust mulch (Alexander 1974; Heit 1967). About half of the viable seeds that are sown will produce usable 2+0 seedlings (Alexander 1974). Ginkgo seedlings grown in artificial growth chambers were able to grow continuously for 20 weeks under a 32 to 25 °C day/night regime (16-hour day-length). This regime produced similar-sized plants as those grown under a 24/17 °C regime for 40 weeks (Flesch and others 1991).

Ginkgo can also be propagated in the nursery from cuttings, although rooted cuttings are slow growing. Cuttings 10 to 15 cm (4 to 6 in) long should be collected from mature trees in midsummer, treated with 8,000 ppm indole-butyric acid (IBA) in solution or in talc, and misted for 7 to 8 weeks (Dirr and Heuser 1987).

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G

Fabaceae—Pea family

Gleditsia L.

honeylocust

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Growth habit and uses. There are 12 species of *Gleditsia,* but only the 2 North American species and their natural hybrid are considered here (table 1). Honeylocusts are deciduous trees that are useful for windbreaks, shelterbelts, erosion control, wildlife food, and local wood products (posts and railroad ties) (Blair 1990). There are numerous ornamental selections; the most notable is a thornless variety—*G. triacanthos* var. *inermis*—that is widely planted in this country and in Europe (Blair 1990; Dirr and Heuser 1987). Honeylocust has also become highly valued as an agroforestry species in other parts of the world (Davies and Macfarlane 1979; Felker and Bandurski 1979).

Flowering and fruiting. The polygamo-dioecious flowers of honeylocusts are borne in single or densely clustered axillary racemes. Those of waterlocust and honeylocust are greenish in color, whereas flowers of their hybrid are orange-yellow (Vines 1960). Honeylocust fruits are flat, indehiscent, often twisted legumes (pods) 15 to 41 cm in length (Blair 1990) (figure 1). The small, flat, brownish seeds, 8 to 12 mm in length, are embedded in a sweet pulp, the feature that attracts livestock and wildlife to the fruits. Waterlocust legumes are smaller (2.5 to 8 cm), oval-shaped, and pulpless (Vines 1960). Their legumes contain 1 to 3 seeds each, whereas honeylocust legumes may have up to 12. These legume and seed characteristics are the best way to distinguish between the species where both occur together (Brown and Kirkman 1990).

Figure 1—*Gleditsia*, honeylocust: legumes of *G. triacanthos*, honeylocust (**top left**), *G. aquatica*, water honeylocust (**bottom left**), and *G.* × *texana*, Texas honeylocust (**right**).

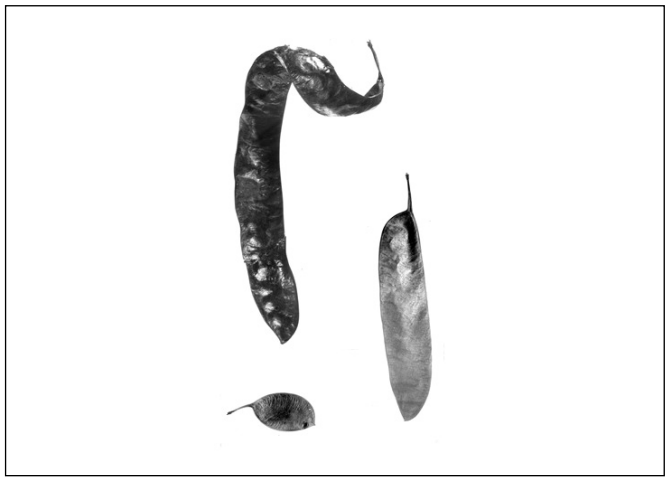


Table 1—*Gleditsia,* honeylocust: nomenclature, occurrence, height at maturity, and year first cultivated

Scientific name	Common name(s)	Occurrence	Height (m) at maturity	Year first cultivated
***G. aquatica* Marsh.**	**waterlocust,** swamp honeylocust.	Coastal plain from South Carolina to Texas,N in Mississippi Valley to Missouri, Illinois, & Indiana	12–18	1723
***G.* × *texana* Sarg.**	**Texas honeylocust,** Texas locust	Mississippi to E Texas, N in Mississippi Valley to Arkansas & SW Indiana	40	1900
***G. triacanthos* L.**	**honeylocust,** sweet-locust, thorny-locust	W Pennsylvania to SE South Dakota, S to E Texas & NW Florida; widely planted & naturalized E of Appalachian Mtns from South Carolina to New England	21–43	1700

Sources: Little (1979), Vines (1960).

The seeds are close to the same size (figure 2) and contain a thin, flat embryo surrounded by a layer of horny endosperm (figure 3). Phenology of flowering and fruiting is summarized in table 2. Seedbearing starts at about age 10, with optimum production between 25 and 75 years (Blair 1990). Good crops are borne almost every year (Bonner and others 1974).

Collection of fruits. Fruit color changes from green to a deep reddish brown, or even brownish black at maturity (Brown and Kirkman 1990; Gordon 1966). Legumes may be picked from the trees after they dry or from the ground after natural dissemination, which may last into late winter (Blair 1990). Collection from the ground should be completed early to avoid losses to wildlife and to disintegration of the legumes in late winter or spring. Moist legumes should be spread for thorough drying before extraction. Tree shakers have been used to collect honeylocust fruits in Russia, with as much as 90 to 100% of the crop recovered (Kiktev and others 1977).

Extraction and storage. Dried legumes may be run through macerators or other mechanical threshers to extract the seeds; hand flailing will also work. The Forest Service macerator can extract 180 to 270 kg (400 to 600 lb) of clean seeds per day (Bonner and others 1974). Small trash can be removed with fans, air-screen cleaners, or water flotation, which will also remove empty, insect-damaged, and incompletely developed seeds. Seeds can be separated from large trash, such as legume fragments, with screens.

A seed yield of 44 to 77 kg/100 kg (20 to 35 lb/100 lb) of honeylocust legumes and a purity of 95% and soundness of 98% have been reported (Bonner and others 1974). In 36 seed samples of this species, there was an average of 6,100 seeds/kg (2,800/lb) with a range of 3,800 to 9,000 (1,750 to 4,050). Seeds of Texas honeylocust are generally larger, with 4,000 seeds/kg (1,830/lb) in 1 sample (Bonner and others 1974).

Seeds of honeylocust species are orthodox in storage characteristics. Their viability can probably be maintained for many years if seeds are stored at low temperatures with moisture contents below 10%, although no long-term storage studies have been done. The food reserves in the seeds are primarily carbohydrates and proteins (Felker and Bandurski 1977; Mazzini and Cerezo 1979).

Figure 2—*Gleditsia*, honeylocust: seeds of *G. aquatica*, waterlocust (**top**); *G.* x *texana*, Texas honeylocust (**middle**); *G.triacanthos*, honeylocust (**bottom**).

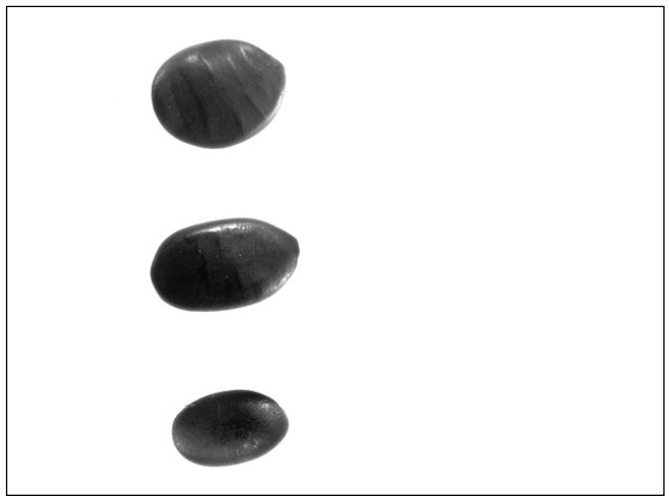
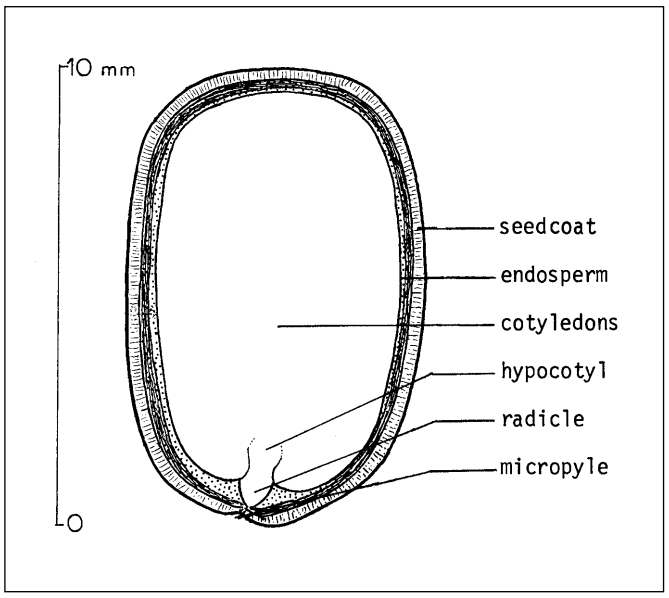


Figure 3—*Gleditsia*, honeylocust: longitudinal section through a seed.



Pregermination treatments. The hard seedcoats of honeylocusts must be treated to make them permeable before germination can occur. Soaking the seeds in either concentrated sulfuric acid or hot water has been used, but

Table 2—*Gleditsia,* honeylocust: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
G. aquatica	May–June	Aug–Oct	Sept–Dec
G. × texana	Apr–May	Aug–Sept	Sept–Dec
G. triacanthos	May–June	Sept–Oct	Sept–late winter

Source: Bonner and others (1974).

the acid treatment has been much more effective. Soaking time in acid must be determined for each seedlot because of variation in seedcoat hardness due to genetic or developmental differences. Several studies have shown that anywhere from 1 to 2 hours is ideal for acid scarification of fully matured honeylocust (Heit 1942; Liu and others 1981). Seeds collected while they are slightly immature will have thinner seedcoats and may be damaged by the acid treatments that work for fully mature seeds. In fact, seeds collected when legumes still show some green areas can often be germinated without any pretreatment. This practice is not recommended, however, because the immature seedcoats are not effective barriers against disease. When the hot water treatment is used, the seeds are placed in 3 to 4 times their volume of water at 85 to 90 °C. Seeds and water are allowed to cool to room temperature or until the seeds swell. The imbibed seeds should be sown promptly, as they will not store well in this imbibed condition.

For pretreatment of small seedlots, as in germination testing, nicking with a knife or burning with a heated needle are both excellent methods (Singh and others 1991). Tests with other legumes (Stubsgard 1986) have indicated that seeds treated with a hot needle can be returned to storage without any problems, and this may be true with honeylocust seeds as well.

Germination tests. Recommendations for official tests call for testing scarified seeds at a constant 20 °C on moist blotter for 21 days (AOSA 1993). Alternating temperatures of 20 and 30 °C also have been used with great success on moist blotters (Singh and others 1991). In 22 tests in other media, pretreated seeds of honeylocust were germinated in a mixture of sand, peat, and soil at 30 °C under light for about 8 hours each day and at 21 °C during the dark period of each 24 hours. Germination ranged from 45 to 99% after 9 and 20 days and averaged 75% in 40 days (Bonner and others 1974).

Nursery practice. Pretreated seeds can be drilled in rows 15 to 25 cm (6 to 10 in) apart and covered with soil to a depth of 12 to 19 mm ($^1/_2$ to $^3/_4$ in). A sowing rate of 33 to 49 seeds/linear m (10 to 15/ft) is recommended (Bonner and others 1974). Mechanical broadcasting of seeds is also feasible. With either method, a desirable seedbed density is 160 to 215 seedlings/m^2 (15 to 20/ft^2) (Williams and Hanks 1976). Seedlings should reach suitable size for field planting in 1 year. Vegetative propagation by hardwood cuttings is extremely difficult, but root cuttings have been quite successful. Budding is also practiced successfully on ornamental varieties (Dirr and Heuser 1987).

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Theaceae—Tea family

Gordonia lasianthus (L.) Ellis

loblolly-bay

Franklin T. Bonner

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Other common names. holly-bay, gordonia, bay, tan bay, black laurel.

Growth habit, occurrence, and use. Loblolly-bay—*Gordonia lasianthus* (L.) Ellis—is a small to medium-sized evergreen tree that occurs on swampy sites on the Atlantic Coastal Plain from Albermarle Sound in North Carolina south to central Florida, with separate populations in southern Alabama and Mississippi (Gresham and Lipscomb 1990; Little 1979). This relatively slow-growing tree can attain a height of 23 m on rich sites but is shrubby on poorer ones. Although its bark was once used locally for tanning leather, loblolly-bay has little commercial value now except as an ornamental (Brown and Kirkman 1990).

Flowering and fruiting. The perfect, showy, white flowers open for 2 to 3 days in May to August; 7 to 8 cm wide, they are borne singly on long stalks in axillary clusters. Pollination is primarily by insects. The fruits are ovoid, woody capsules 12 mm in diameter and 20 mm long (figure 1); they contain from 10 to 40 small, square, winged seeds about 1.5 mm long (figures 2 and 3). The capsules turn brown as they mature in September or October, and most seeds are disseminated by wind by mid-December (Brown and Kirkman 1990; Gresham and Lipscomb 1990; Vines 1960).

Collection, extraction, and storage. Capsules should be collected when they turn brown in the fall. They can be opened with air-drying, and the seeds are then easily extracted by shaking. There are 264,550 to 332,895 dry seeds/kg (120,000 to 151,000/lb) (Gresham and Lipscomb 1990). No storage data are available for this species, but the nature of the seeds suggests that they are orthodox and can be stored easily at low temperatures and low seed moisture contents.

Germination and nursery practices. Loblolly-bay seeds have no dormancy and will germinate readily when sown (Dirr and Heuser 1987). There are no published recommendations for germination testing, but the ease of germination suggests that the common alternating regime of 20/30 °C would suffice. Germination of 70 to 80% within 10 days in petri dishes in sunlight has been reported (Gresham and Lipscomb 1990). Germination is epigeal. This species is also very easy to propagate vegetatively. Cuttings taken in June through August rooted 90 to 100% in peat–perlite and mist with 3,000 ppm of IBA applied (Dirr and Heuser 1987).

Figure 1—*Gordonia lasianthus,* loblolly-bay: capsules.

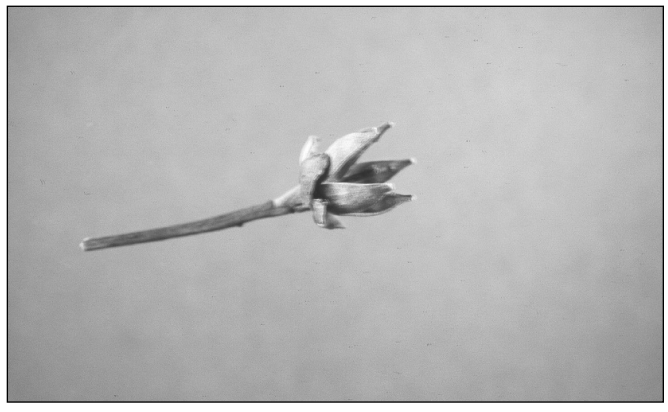


Figure 2—*Gordonia lasianthus*, loblolly-bay: seeds.

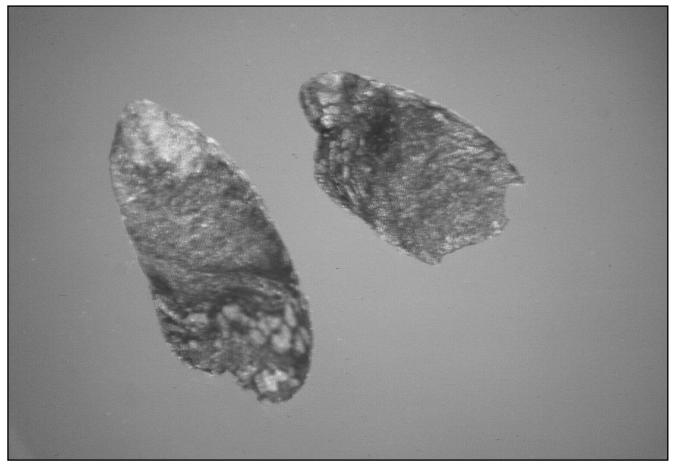
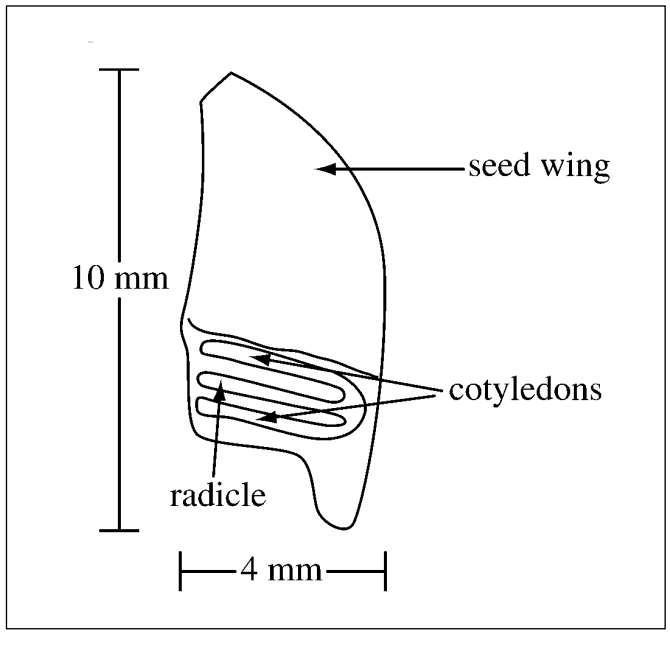


Figure 3—*Gordonia lasianthus*, loblolly-bay: longitudinal section of a seed.



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Chenopodiaceae—Goosefoot family

Grayia spinosa (Hook.) Moq.

spiny hopsage

Nancy L. Shaw, Marshall R. Haferkamp, and Emerenciana G. Hurd

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Growth habit, occurrence, and use. The genus *Grayia* Hook. & Arn., named for the American botanist Asa Gray, contains a single species—spiny hopsage (table 1). Plants are erect to rounded, summer-deciduous shrubs 0.3 to 1.2 (1.5) m tall. Branches are divergent and thorn-tipped, with whitish gray to brownish bark that exfoliates in long strips. Leaves are gray-green, alternate, entire, and fleshy, sometimes turning bright red before abscising. Pubescence of young twigs and leaves consists of simple or stellate hairs. Prominent globose, gray-green overwintering leaf buds develop prior to summer leaf fall.

Widely distributed in the western United States (table 1), spiny hopsage is a common associated species in Wyoming big sagebrush, salt desert shrub, pinyon–juniper, Mojave Desert, and Great Basin–Mojave Desert transition communities, but it rarely grows in monocultures (Welsh and others 1987). The species occurs at elevations ranging from 160 to 2,130 m on soils that are silty to sandy, neutral to strongly basic, and often high in calcium. It also grows on sand dunes. Growth and nutrient content of vegetation growing near spiny hopsage are enhanced by the accumulation of litter rich in potassium and other cations (Rickard and Keough 1968).

Spiny hopsage provides cover for birds and other small animals; spring and early summer forage for big game and livestock, and soil stabilization on gentle to moderate slopes (McCullough 1969; USDA SCS 1968). The species was first cultivated in 1897 (Rehder 1940).

Geographic races and hybrids. Spiny hopsage is tetraploid (4x = 36) (McArthur and Sanderson 1984). Natural hybridization between spiny hopsage and related members of the Chenopodiaceae has not been observed. However, Drobnick and Plummer (1966) were successful in fertilizing female flowers of fourwing saltbush—*Atriplex canescens* (Pursh) Nutt.—with spiny hopsage pollen and obtaining viable progeny.

Flowering and fruiting. Plants are monoecious or dioecious, with the percentage of each varying among populations (Goodrich and Neese 1986; McArthur and Sanderson 1984). Inflorescences develop on floral shoots that die back following fruit dispersal. Flowers are inconspicuous. Staminate flowers, each consisting of a 4- or 5-lobed perianth and 4 or 5 stamens, develop in glomerate spikes. Pistillate flowers develop in dense bracteate spikes, racemes, or panicles with 1 to several flowers in the axil of each bract. Some flowers are commonly vestigial. Each flower

Table 1—*Grayia spinosa*, spiny hopsage: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***G. spinosa* (Hook.) Moq.** *Chenopodium spinosum* Hook. *G. polygaloides* Hook. & Arn. *Eremosemium spinosum* Greene *Atriplex grayii* Collotzi *A. spinosa* (Hook.) Collotzi	**spiny hopsage**, applebush, grayia, Gray's saltbush, hopsage, horsebush, saltbrush, spiny-sage, wintersage	E-central & SE Washington, E Oregon, S & central Idaho, S Montana, Nevada, Utah, W Wyoming W Colorado, E & S California, & N Arizona

Sources: Collotzi (1966), Dayton (1931), Hitchcock and Cronquist (1973), Kay (1977), Shaw (1992a&b), Smith (1974), Welsh and others (1987).

consists of a single pistil enclosed in 2 cordate to orbicular bracteoles united along their length except for a minute apical opening. Bracteoles enlarge in fruit, forming a papery, dorsally wing–margined sac 9 to 15 mm in diameter (Shaw and others 1996) (figure 1). Mature bracteoles are white, green, or parchment-colored and are sometimes suffused with pink or red.

Fruits are utricles with the thin, papery pericarp free from the seed (Shaw and others 1996) (figure 2). Seeds are vertical, disk-shaped, and 1 to 2 mm in diameter (figure 3). The seedcoat consists of a thin, dark brown outer layer and a tough, elastic inner layer. A well-developed embryo with pale yellow cotyledons and an elongate, inferior radicle encircles the perisperm (figure 4).

During a prolonged drought, spiny hopsage shrubs developing from a southern Idaho seeding began flowering in the 4th year (Shaw 1992b). Flowering occurs in late winter or early spring (table 2) and may be triggered by photoperiod (Ackerman and Bamberg 1974). Flowers are wind-

Figure 1—*Grayia spinosa*, spiny hopsage: bracted utricle

Figure 2—*Grayia spinosa*, spiny hopsage: utricle.

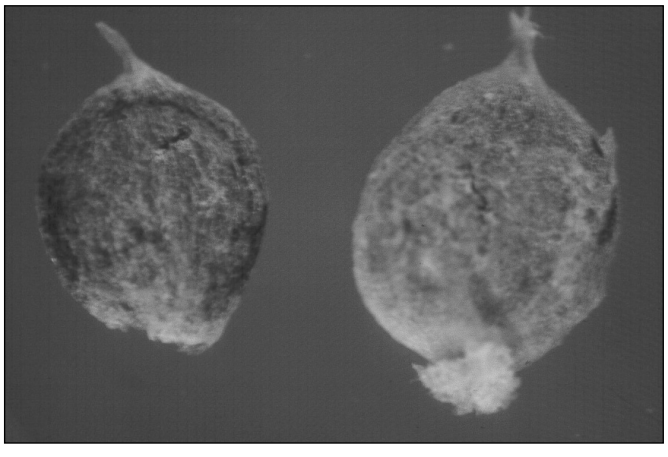


Figure 3—*Grayia spinosa*, spiny hopsage: seeds.

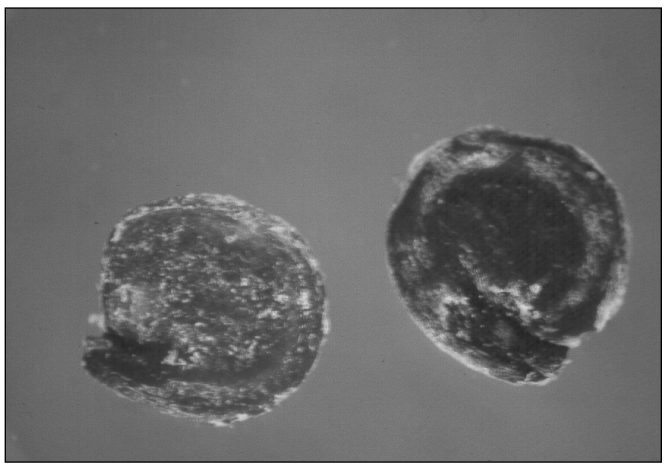
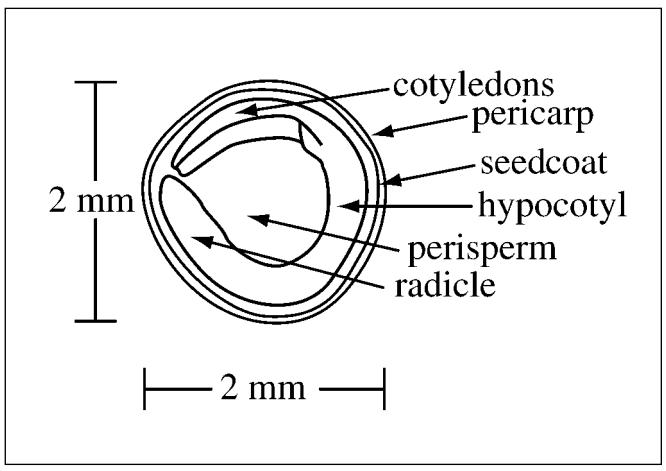


Figure 4—*Grayia spinosa*, spiny hopsage: longitudinal section through a seed.



pollinated. Fruits mature in late spring or early summer and are usually dispersed within 1 or 2 weeks. High winds accompanying summer storms can rapidy remove all mature fruits. Herbage, flower, and fruit production are dependent upon the availability of soil water and other environmental factors and vary widely among years (Rickard and Warren 1981; Wallace and Romney 1972). In dry years, plants may remain dormant, producing neither leaves nor flowers.

Collection of fruits. Size and quality of the developing seed crop at prospective collecting sites should be estimated prior to the harvest season. Mature utricles can be harvested by hand-stripping or by beating the shrubs with paddles or tennis rackets. Freshly harvested utricles should be spread in a thin layer over drying racks or screens in an enclosed area with good ventilation. Utricles dried outdoors or in open buildings must be covered with netting or wire screens as they are easily scattered by light breezes. The

hygroscopic bracts absorb water rapidly if exposed to environments with increased humidity.

Seed extraction and cleaning. Preliminary separation of harvested seedlots with an air-screen machine removes twigs, large leaves, and other coarse material. Some empty bracts can also be separated by this process. Bracteoles may be removed, if necessary, by threshing them with a hammermill (King 1947) or a barley de-bearder (Jorgensen 1992). A seed scarifier, seed de-winger, or rubbing board may be used to thresh small collections (Shaw and Haferkamp 1990). Threshing generally results in complete removal of bracteoles and partial to complete removal of the pericarp, leaving seeds as the product. Some embryos may be damaged during threshing as the radicle tip is vulnerable to abrasion (figure 4).

Threshed seeds may be separated from chaff using an air-screen machine or a seed blower. Removing the chaff is necessary only when it is desirable to reduce bulk for storage or shipping. Otherwise, the chaff can serve as a diluent for the small seeds as it will feed through most seeding mechanisms when dry. Smith (1974) obtained 1.2 kg (2.6 lb) of cleaned seeds from 45.4 kg (100 lb) of fruits. Number of bracted utricles and seeds per weight and seed fill data are provided in table 3.

Storage. Kay (1976) and Kay and others (1977, 1984, 1988) found that total germination percentage of seeds dried to a water content of 5.1% and stored at –15 or 4 °C or room temperature in sealed glass containers containing a silica gel desiccant did not decline from the initial value of 42% after 14 years (Kay 1976; Kay and others 1977, 1984, 1988). Germination of air-dried seeds stored in cloth bags in a warehouse decreased to about 20% after 1.5 years and to 0% after 7 years. All germination tests were conducted at 15 °C. Thus, for long-term storage, it is recommended that seeds be dried to a water content below 10% and kept in sealed containers.

Pre-germination treatments and germination tests. Dormancy of freshly harvested utricles of many woody chenopods can be reduced by dry after-ripening, whereas the response to wet prechilling and temperature is regulated by the environmental conditions in which they were produced (Ansley and Abernethy 1985; Kay and others 1988; Springfield 1972). However, the response of spiny hopsage seeds to dry after-ripening is poorly known and may vary with seedlot and with seed age. Shaw and others (1994) found that field germination and seedling establishment of 2 spiny hopsage seed collections from the northern shrub steppe were similar after 2 and 4 years of dry storage at room temperature. By contrast, King (1947) found that an additional 2 years of dry after-ripening decreased the wet prechilling (5 °C) requirement for eastern Washington seeds from 12 weeks for 4-year-old seeds to 2 weeks for 6-year-old seeds.

Spiny hopsage seeds produced in the northern shrub steppe generally have a requirement for wet prechilling; seeds produced in the Mojave Desert do not (Shaw 1992a;

Table 2—*Grayia spinosa*, spiny hopsage: phenology of flowering and fruiting

Location	Flowering	Fruit ripening	Seed dispersal
Northern Mojave Desert, Nevada	Mar	Mar	Mar
Great Basin, Mojave Transition Desert, Nevada	Feb–April	Mar–Apr	Apr
Book Cliffs, Colorado	Mar–May	May	May–June
Great Basin, Nevada	April & June	May & July	May & Aug
Sagebrush steppe, Oregon & Idaho	April–May	May–June	May–June

Sources: Ackerman and Bamberg (1974), Ackerman and others (1980), Blauer and others (1976), Branson and others (1967), Everett and others (1980), Goodrich and Neese (1986), Plummer and others (1968), Shaw (1992b), Wallace and Romney (1972).

Table 3— *Grayia spinosa*, spiny hopsage: fruit and seed numbers per weight

Bracted utricles/weight		Seeds/weight			
		Range		Average	
/kg	/lb	/kg	/lb	/kg	/lb
337,000–447,000	152,900–202,800	339,000–930,000	153,800–421,800	500,000	227,000
—	—	692,600–1,031,600	314,200–468,000	1,219,500	553,200

Sources: Belcher (1985), Kay and others (1977), King (1947), Plummer and others (1968), Shaw (1992b), Smith (1974), Swingle (1939).
Note: Filled seeds (%) = 18 to 95.

Wallace and Romney 1972; Wood and others 1976). Shaw (1992a) examined the effect of 45 days of wet prechilling at 3 to 5 °C on 2 northern shrub steppe collections. Prechilled bracted utricles and cleaned seeds of each collection were incubated over a wide range of constant (10, 15, 20, 25 or 30 °C) and alternating (8/16 hours) temperatures (15/5 °C and 10/2 °C). Prechilling increased germination from 9 to 64% and reduced days required to reach 50% germination from 40 to 29. Based on these results, she recommended 1 to 2 months of wet prechilling for northern shrub steppe seedlots.

Wood and others (1976) examined the germination response of 4 Nevada (Great Basin) and 1 California (Mojave Desert) spiny hopsage seedlots at 5 constant and alternating temperatures. Prechilling was not required as the seeds were nondormant. After 1 week, germination of seedlots incubated at constant temperatures was greatest at 10 and 15 °C (66 to 74%). For a seedlot collected at Dayton, Nevada, a 5 °C low temperature alternating with high temperatures between 10 and 30 °C, inclusive (8/16 hours alternations), provided the greatest germination percentages (85 to 90%). Maximum seedling elongation for this seedlot occurred after 1 week at 5, 20/15, 20, or 25/5 °C.

Wood and others (1976) also found that the presence of bracts did not affect germination of seeds collected in Nevada and California that were exposed to favorable incubation conditions. At low water potentials, greater germination of bracted utricles compared to seeds was attributed to the presence of the hygroscopic bracteoles. Shaw (1992a) found that prechilling enhanced subsequent germination of seeds more than bracted utricles from northern shrub steppe populations when placed under favorable incubation conditions and speculated that enhancement might be due to improved oxygen uptake by the seeds.

The following techniques and criteria (with instructions) are recommended for laboratory analyses by Belcher (1985), Dueleheimer (1992), and Shaw (1992a):

Germination—Incubate seeds at 15/5 °C (8 hours/16 hours) or 15 °C. First count is taken at 7 days, last count at 14 days. Wet prechilling for 30 to 60 days at 3 to 5 °C is recommended for northern populations. Normal seedlings are epigeal, with a thin, 10- to 15-mm-long hypocotyl; small, narrow cotyledons; short epicotyl; and well-developed roots hairs (figure 5).

Embryo excision—Soak seeds in water at 28 °C for 12 hours, then drain; excise embryos with sharp needles. Spiny hopsage embryos germinate rapidly at 15/5 or 15 °C. Evaluate as described for germination of seeds.

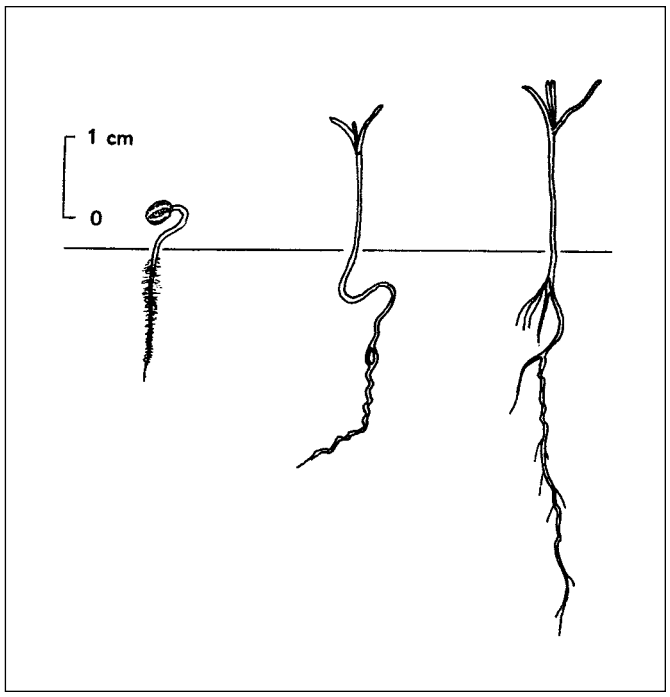
Viability testing—Soak seeds in water at 28 °C for 12 hours, then drain; pierce seeds through perisperm with a sharp probe or needle; soak in a 1% 2,3,5-triphenyl tetrazolium chloride solution for 4 to 8 hours at 28 °C. Excise embryos with sharp needles and evaluate as described by Peters (2000) for members of the Chenopodiaceae.

X-radiography—Shoot at 12 kV for 30 seconds with Kodak® AA film and Industrex® paper or at 12 kV for 60 seconds with Polaroid® film. Filled, empty, and abnormal development will be visible.

Nursery practice. Container stock can be grown using planting media as described by Augustine and others (1979), Ferguson (1980), and Ferguson and Monsen (1974). Seeds should be wet prechilled, if necessary.

Bareroot stock of northern spiny hopsage populations may be produced by fall-seeding to permit early spring germination (Shaw 1992a, Shaw and Haferkamp 1990). This treatment maximizes the period of active seedling growth prior to leaf abscission and the onset of summer dormancy. Spring seedings of prechilled seeds generally have not been successful as it is difficult to prepare and plant the nursery beds early enough in the season. Seedlings developing from fall plantings generally produce a branched shoot and a taproot system with few lateral roots during the first growing season. Plants may attain adequate size for lifting as 1+0 stock, or they may be allowed to grow for an additional sea-

Figure 5—*Grayia spinosa*, spiny hopsage: seedling development at 1, 9, and 14 days after germination.



son, during which time they develop a more extensively branched root system. Bareroot seedlings must be lifted, packed, and handled with care as stems and branches are brittle and break easily. For prolonged storage, seedlings should be stored at –2 °C in paper nursery bags packed in waxed cardboard boxes to reduce desiccation and mold problems (Beall 2000).

Dormant bareroot spiny hopsage seedlings or container stock should be planted as soon as the ground thaws and before native shrubs in the vicinity of the planting site break dormancy. Removal of competing vegetation is critical to survival of the shrub seedlings. Container stock has been established using supplemental water the first year (Ferguson and Frischknecht 1981, 1985; Frischknecht and Ferguson 1984; Hunter and others 1980; Romney and others 1971; Tueller and others 1974; Wallace and Romney 1974; Wallace and others 1980). Hunter and others (1980) recommended protecting seedlings with chicken-wire sleeves to reduce seedling predation in areas with high rodent or rabbit densities.

Direct seeding. In the commercial trade, "cleaned seeds" may mean bracted utricles from which coarse debris has been removed or seeds that have been separated from the bracteoles, pericarp, and extraneous debris. Either bracted utricles or seeds may be planted, but it is important to know which structure one is using. Bulk is considerably greater for bracted utricles, whereas purity and viability are generally greater for seeds. When bracted utricles ("fluffy" seeds) are being planted, a conventional drill seeder with an agitator or a drill with a separate seed box and agitator are needed to ensure uniformity of flow. Seeds may be planted with most conventional seeders. Regulating the seeding rate for the small seeds may be difficult unless they are sown through a drill with precision seeding regulation or mixed with either a diluent or seeds of other shrubs.

Broadcasting without covering the seeds is not recommended. However, seeds or bracted utricles can be broadcast-seeded if they are incorporated into the soil by harrowing. Wood and others (1976) found emergence from broadcast seeding on a rough seedbed was greater from bracted utricles (18%) than from seeds (0%) in a greenhouse study. However, emergence of both bracted utricles and seeds was greater and similar (50%) from a 5-mm planting depth.

Spiny hopsage has been planted in southern Idaho in late fall or winter by direct seeding or by broadcasting and covering. Seeds are thereby exposed to cool, wet seedbed environments, permitting early spring emergence when soil water conditions are favorable for growth prior to the onset of summer drought (Shaw and others 1994). Some seeds not encountering favorable soil water conditions for germination may enter secondary dormancy. Shaw and Haferkamp (1990) found seedling density was greater on rough seedbeds than on smooth seedbeds in early spring, perhaps because of improved microsite conditions. First-year establishment ranged from 0 to 24% of viable seeds planted from early fall to late spring on rough and smooth seedbeds. Seedling predators included seed harvester ants (*Pogonomyrmex salinus* Olsen) and nymphs of an unidentified plant bug (*Melanotrichus* spp.).

Microenvironmental conditions in prepared seedbeds differ sharply from those in natural seedbeds as spiny hopsage seedlings usually establish beneath nurse plants (Manning and Groeneveld 1990; Shaw and Haferkamp 1990). Consequently, spiny hopsage establishment may be enhanced by mulching or water catchment techniques that moderate soil water and temperature conditions.

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Proteaceae—Protea family

Grevillea robusta A. Cunningham ex R. Br.

silk-oak

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Synonym. *Stylurus robusta* (A. Cunn.) Deg.

Other common names. silver-oak, lacewood.

Growth habit, occurrence, and use. Silk-oak—*Grevillea robusta* A. Cunningham ex R. Br.—is a medium to large evergreen tree native to coastal regions of eastern Australia (Skolmen 1990). Silk-oak is commonly planted as an ornamental for its showy orange blossoms, and in reforestation programs in many warm–temperate, subtropical, and tropical locales worldwide. In the United States, it has been planted in Hawaii (since about 1880), California, Florida, and Puerto Rico, and has become naturalized in Hawaii and southern Florida, where it is considered by some to be a noxious weed (Skolmen 1990). The species has adapted well to Hawaii's varied climates and grows vigorously from sea level to 1,200 m (Neal 1965). Its prolific seeding, wide dissemination of the seeds by wind, and its tolerance of diverse site conditions have enhanced its ability to proliferate (Wong 1974). The tree attains heights of up to 35 m and diameters up to 0.9 m (Wong 1974).

The pale pinkish brown wood has a beautiful, well-marked silver grain, making it desirable for furniture and cabinet work (Magini and Tulstrup 1955; Skolmen 1990). However, care must be taken when machining and finishing this wood because the sawdust contains a skin irritant that produces an uncomfortable rash lasting a week or more. Hydrocyanic acid has been detected in the fruit and flowers (Wong 1974).

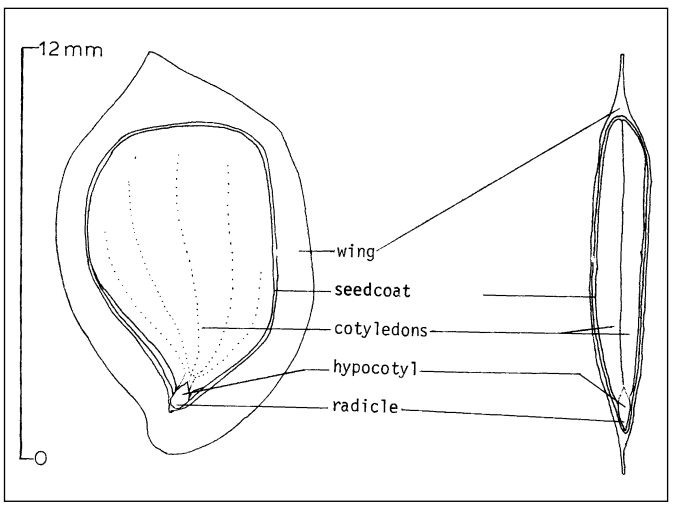
Another species—Kahili flower, *Grevillea banksii* R. Br.—is less common because reforestation attempts with it have failed in Hawaii. Only on Kauai and Maui are remnant stands of early plantings found (Wong 1974). It is a smaller tree, up to 10 m in height. The flowers and fruits of this species also contain cyanogenic compounds that produce a rash similar to that from poison-ivy (*Toxicodendron radicans* ssp. *radicans* (L.)) Kuntze; see *Rhus* (p.954) (Magini and Tulstrup 1955; Wong 1974). A white-flowered form of this species—white Kahili flower, *G. banksii* forma *albiflora*—is also found in Hawaii (Wong 1974) and is officially classified there as a noxious weed (Haselwood and Motter 1966).

Flowering and fruiting. Silk-oak is monoecious and flowers from early March through October, reaching its peak during the months of April through June in Hawaii (Little and Skolmen 1989; Skolmen 1990; Wong 1974). Trees in Hawaii usually begin producing flowers and seeds when they are 10 to 15 years old (Wong 1974). In Jamaica, trees seed profusely from 10 years of age (Streets 1962). The bright orange blossoms are borne on horizontal racemes, 8 to 18 cm long, which are on short, leafless branches arising mostly from the trunk (Little and Skolmen 1989). The fruit, which turns from green to black on maturity, is a slightly flattened, leathery, dehiscent follicle, 15 to 25 mm long, tipped with a slender, recurved, stiff style (figure 1) (Little and Skolmen 1989; Wong 1974). The follicles remain on the tree for a year or so after the seeds are dispersed (Neal 1965). Two brown, elliptical, flattened seeds—each 10 to 15 mm long with light, winged margins—are found in each follicle (figures 1 and 2). Seedcrops of Kahili flower resemble those of silk-oak. The blossoms of silk-oak are orange, those of Kahili flower are red, and those of white Kahili flower are creamy white.

Collection, extraction, and storage. The fruits of silk-oak are gathered from the tree before opening, when the first hint of brown color appears, indicating that the seeds are mature (Wong 1974). The seeds are extracted by air-drying the fruits in trays under shade for 5 or 6 days or until the follicles open and release the seeds. The seeds are then separated by means of a seed cleaner (Wong 1974). Purity has averaged 87% (Goor and Barney 1968; Magini and Tulstrup 1955). Moisture content of fresh seeds collected in Hawaii was 28.5% (ETSL 1969). The following numbers of seeds per weight have been reported for 3 locations: Hawaii, 64,700/kg (29,350 lb) (ETSL 1969); East Africa, 66,000 to 154,000/kg (29,950 to 69,850/lb) (Parry 1956); and Australia, 79,200 to 99,000/kg (35,925 to 44,900/lb) (Goor

Figure 1—*Grevillea robusta*, silk-oak: follicle and seed.

Figure 2—*Grevillea robusta*, silk-oak: longitudinal section through a seed.



and Barney 1968). Seeds of silk-oak are orthodox in storage behavior and are easy to store in cool, dry conditions (Schaefer 1991). Seeds stored for 2 years at –7 and 3 °C had germination rates ranging from 60 to 70% when seed moisture was maintained below 10% during storage in airtight containers (Jones 1967).

Germination. Testing procedures for official purposes call for 21 days of testing at alternating temperatures of 20/30 °C with no pretreatment (AOSA 1993). Two pregermination treatments have been found to increase substantially the germination of stored seeds (ETSL 1969). A 48-hour water soak and stratification at 3 °C for 30 days were equally effective. Pretreated seeds were germinated on moist Kimpak at diurnally alternating temperatures of 30 °C during an 8-hour light period and 20 °C during the dark period. The average germination rate of 8 samples was 38% after 17 days and 70% after 72 days. Germination of stored, untreated seeds, however, was only 26% (ETSL 1969). Fresh seed in Australia had a germination rate of 60 to 80% (Goor and Barney 1968). Germination of fresh, unstratified seeds require about 20 days (Skolmen 1990). Germination in silk-oak is epigeal.

Nursery practice. Nursery practices vary among countries where silk-oak is grown (Skolmen 1990). In some countries 4- to 6-week-old wildlings are lifted and potted and later replanted. Seedlings grown in Sri Lanka are outplanted when they are about 40 cm (16 in) tall, whereas those in Jamaica are outplanted when about 60 cm (24 in) tall (Streets 1962). Elsewhere, plants are grown to 45-cm (18 in) heights in large baskets so that they can compete more effectively when outplanted. In Hawaii, silk-oak seeds are sown at a depth of 1.25/cm ($^1/_2$ in) without mulch (Wong 1974). Seedbeds are treated with insecticides and fungicides before sowing. Seedling density ranges from 200 to 300 seedlings/m^2 (19 to 28/ft^2). Seedlings grown in flats are outplanted when they are about 9 months old (Wong 1974), whereas container-grown seedlings reach a plantable size of 20 cm (8 in) in height in 12 to 14 weeks (Skolmen 1990).

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Asteraceae—Aster family

Gutierrezia Lag.

snakeweed

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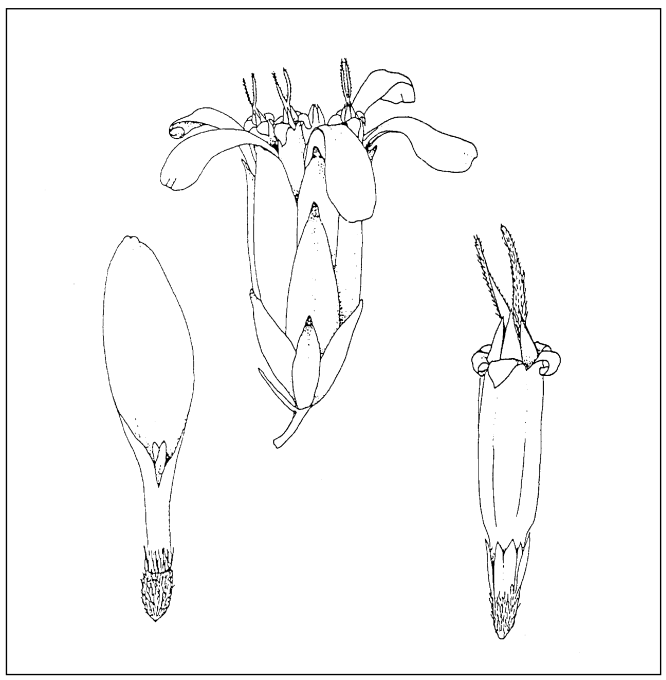
Growth habit, occurrence, and use. The genus *Gutierrezia*—commonly called snakeweed or broomweed—includes 16 annual or perennial species of low-growing woody and herbaceous plants native to the arid regions of North and South America. Shinners (1950, 1951) placed *Gutierrezia* in the genus *Xanthocephalum,* based mainly on morphological characteristics. Since that time, the generic alignment has vacillated between the 2 genera, and publications using either name can be found between 1950 and 1985. Lane (1985) authoritatively resolved the issue when she provided evidence that the name *Gutierrezia* was taxonomically more appropriate. The genus in general—and broom snakeweed (*G. sarothrae* (Pursh) Britt. & Rusby) in particular—is regarded as undesirable on grazing land in the western United States because it interferes with forage growth and is toxic to livestock (McDaniel and others 1982).

Threadleaf snakeweed—*G. microcephala* (DC.) Gray—is closely allied to broom snakeweed and collectively these 2 species are commonly referred to as perennial snakeweed or simply, snakeweed. Other common names often used to describe these species include turpentine weed, rubberweed, rockweed, stinkweed, yellowtop, matchweed, and perennial broomweed. Snakeweeds are widespread on rangeland in the southwestern United States and are rarely included in seeding mixtures.

Flowering and fruiting. Flowering heads of broom snakeweed are numerous and small (about 3.75 mm high and 1.75 mm wide) and are borne in clusters of 2 or 3 in panicles or short spikes (Lane 1985; Ruffin 1974; Solbrig 1960, 1964). The heads usually contain 2 to 7 ray flowers with yellow corollas and from 0 to 9 disk flowers (figure 1). Viable achenes are produced mainly by ray flowers and only occasionally by disk flowers. Threadleaf snakeweed usually has 2 or less flowers per capitulum, but only ray flowers produce viable seeds (Lane 1985). Flowering in southwestern deserts usually begins in August and continues until a freeze in early November. In northern latitudes, flowering begins earlier, often in June or July. Under greenhouse conditions,

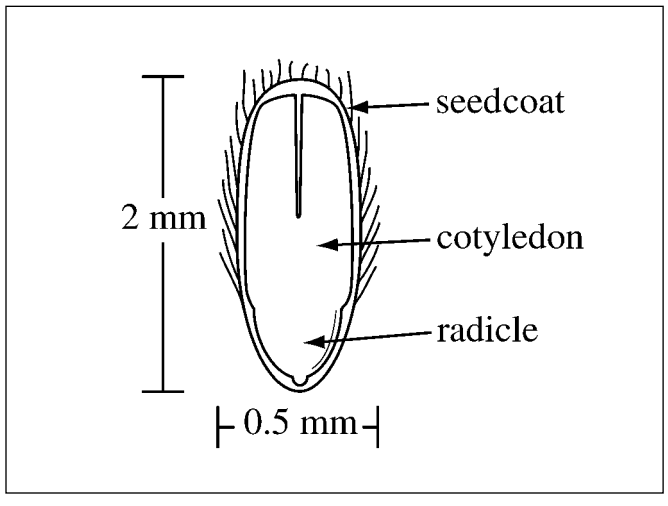
Figure 1—*Gutierrezia sarothrae*, broom snakeweed: flowering head (**center**); ray (**left**) and disk (**right**) flower with attached achene (adapted from Ruffin 1974).



flowering can occur any time of the year. Snakeweed plants may bear a few seeds the first year, but they become more productive in later years. Good crops may occur every year on some sites, but climatic factors, plant age, and insects generally cause wide fluctuations in seed production from year to year.

The achenes from ray florets are brown, roughly cylindrical (about 0.9 to 1.6 mm long and 0.2 to 0.7 mm wide), and weigh about 0.15 mg (figures 2 and 3). The often-infertile disk achenes are smaller than the ray achenes. The achenes are pubescent, with rows of white trichomes appressed to the seedcoat in the direction of the pappus. Upon imbibition, the trichomes radiate outward to draw and retain water next to the pericarp. The trichomes act to anchor the achene and enhance soil penetration (Mayeux 1983, 1989). The

Figure 2—*Gutierrezia sarothrae*, broom snakeweed: longitudinal section through an achene.



pappus consists of small white or yellowish erose scales (<1 mm length) aligned with the axis of the achene. This highly reduced pappus is unlike many members of the tribe Astereae, which usually have a well-developed pappus for wind dispersal (Solbrig 1960). Thus, snakeweed achenes are absent of any specialized structures to facilitate long-range dispersal and most fall directly below the parent on the leeward side (Oshman and others 1987; Wood and others 1997). Dispersal is highest in the autumn (about 60%) and may continue into the following summer or as long as flower bracts remain on the plant. About 91% of the achenes are independently dispersed, with the remainder falling within a portion of the capitula (Wood and others 1997).

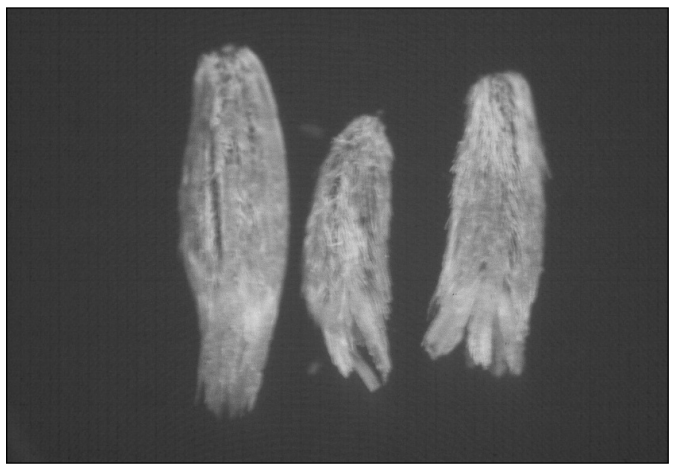
Seed collection and cleaning. A mature plant in autumn can be clipped or pulled from the soil, placed in a paper bag, and shaken to remove most achenes from the capitula. Oven-drying a plant for 48 hours at 50 °C facilitates achene removal and reduces the after-ripening period (Mayeux 1989). Contents after hand-threshing should be pulsed twice in a seed scarifier to further loosen the achenes. A pneumatic seed cleaner with 2 sieves (about 3 and 5 mm round holes) can be used to separate achenes from other flower parts by setting the air blower at 8.0 mm and turning it on twice for about 10 sec/plant (Wood and others 1997). A medium-sized snakeweed plant produces about 4,000 achenes, but this number can vary greatly by year and plant age (Ragsdale 1969).

Seed storage. Snakeweed achenes (figure 3) can be stored in paper or cloth bags under dry laboratory conditions for 3 or more years (Mayeux 1989). They are reportedly dormant at maturity and require a 4- to 6-month after-ripening period unless they are dried soon after collection (Mayeux and Leotta 1981). Under field storage, achenes contained within nylon packets and placed on the soil surface in fall were mostly inviable by the next summer (Wood and others 1997). Similarly, achenes retained in flower bracts and collected biweekly from October to May were tested as more than 50% viable; however, after May viability declined below 10%.

Germination. The after-ripening requirements of freshly collected snakeweed achenes were reduced by exposing them to a continuous temperature of 50 °C for at least 48 hours before laboratory or greenhouse germination trials (Mayeux and Leotta 1981). Dormancy-breaking treatments such as scarification, stratification, and leaching have been reported not to enhance germination (Kruse 1970). Stirring in dichloromethane for 10 minutes increased germination of newly harvested threadleaf snakeweed seeds and stirring in large volumes of distilled water for 24 hours before incubation on filter paper had the same effect (Mayeux and Leotta 1981). Tests show that optimal germination in greenhouse pots occurs when achenes are sown on the surface or pressed lightly onto the soil and maintained at a 15 to 25 °C alternate temperature regime, a minimum of 8 hours of light, and soil saturated and subsequently maintained at a soil water potential above –300 kPa for at least 5 days (Kruse 1970; Mayeux 1981; Wood and others 1997).

Field practice. Because snakeweed is toxic to livestock and sometimes to wildlife, competes with more desirable forage, and offers limited soil erosion protection, it is usually not considered a beneficial species for seeding rangelands. It might be considered for use on land under reclamation. Although we found no studies to confirm this, we anticipate that sowing seeds extensively on an exposed soil surface in early spring when daytime temperatures are near 20 °C offers the best potential for propagation.

Figure 3—*Gutierrezia sarothrae*, broom snakeweed: achenes.



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G

Fabaceae—Pea family

Gymnocladus dioicus (L.) K. Koch

Kentucky coffeetree

Franklin T. Bonner

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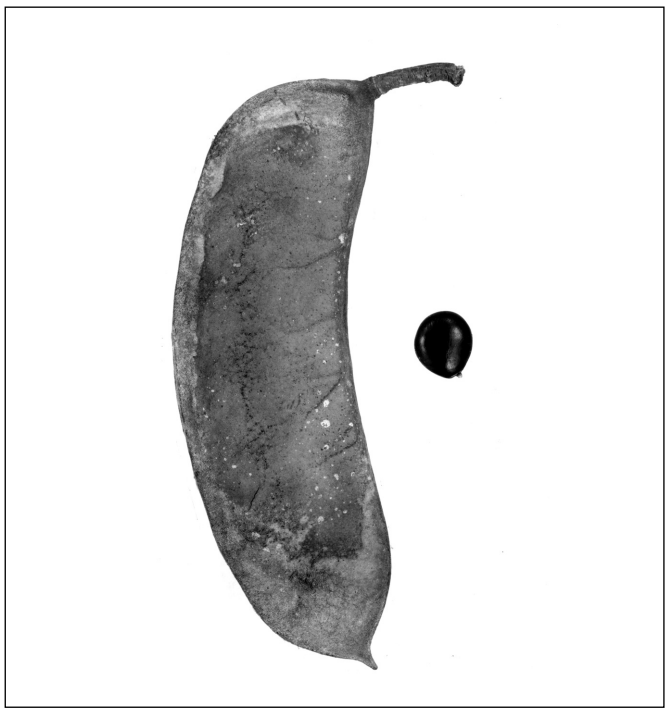
Growth habit, occurrence, and uses. Kentucky coffeetree—*Gymnocladus dioicus* (L.) K. Koch—is a medium to large deciduous tree that occurs naturally in rich bottomlands from New York, Pennsylvania, southern Ontario, and Minnesota, southward to eastern Nebraska, Oklahoma, eastern Kentucky, and Tennessee. The only other species of *Gymnocladus* is native to central China (Sargent 1965). The tree grows to heights of 23 to 34 m and bole diameters of 60 to 90 cm. Kentucky coffeetree is used chiefly as an ornamental and also to some extent for posts and crossties (Harrar and Harrar 1946). Rehder (1940) reported that the species was introduced into cultivation prior to 1748. It has been reported that early settlers of Kentucky and Tennessee used the seeds as a substitute for coffee and the pulp of the green fruit in medicines (Harrar and Harrar 1946). There has been some research into the insecticidal properties of certain unusual amino acids isolated from the seeds (Rehr and others 1973; Evans and Bell 1978).

Flowering and fruiting. The greenish white, dioecious flowers appear in May and June (after the leaves) and are borne in terminal racemose clusters. The fruit is a tardily dehiscent, flat, thick, woody legume (pod) that ripens in September or October and usually persists unopened on the tree until late winter or early spring (Van Dersal 1939). The dark brown or red brown legume is 15 to 25 cm long, 2.5 to 5 cm wide, and usually contains 4 to 8 dark brown or black oval seeds separated by a mass of dark, sweet pulp (figures 1 and 2). The seeds are about 2 cm long with a very hard and thick seedcoat. They will generally remain in the legume until it falls and is broken up by decay, a process that may take 2 years or longer (Harr 1927; Sargent 1965).

Collection of fruits; extraction and storage of seeds. The fruits can be collected at any time during the late fall, winter, or spring by picking them from the tree or from the ground. Sometimes the legumes can be dislodged by vigorously shaking or flailing the branches.

The seeds may be extracted from the fruits by hand or with mechanical macerators or threshers (see chapter 3). The

Figure 1—*Gymnocladus dioicus*, Kentucky coffeetree: legume and seed.



number of clean seeds per weight ranges from 440 to 600/kg (200 to 300/lb) and averages 500/kg (230/lb). Purity of seedlots is almost 100% and 90 to 95% of the seeds are usually sound (Sander 1974).

There are no long-term storage data for seeds of Kentucky coffeetree, but like other Fabaceae of the temperate zone, storage is not difficult. Dried seeds should be stored at near- or below-freezing temperatures. Short term storage (overwinter) has been successful under these conditions (Weisehuegel 1935), and storage for much longer periods should be possible also.

Pregermination treatments. Kentucky coffeetree's hard, impermeable seedcoat normally requires scarification for timely germination. The best results have been obtained by treating the seeds with concentrated sulfuric acid for

Figure 2—*Gymnocladus dioicus*, Kentucky coffeetree: longitudinal section through a seed.

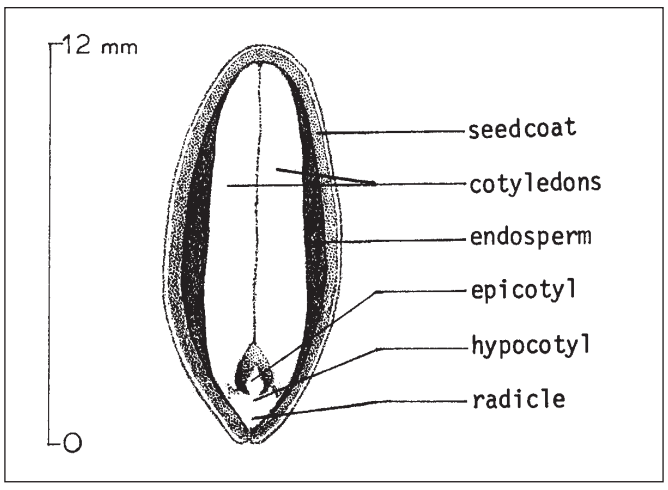
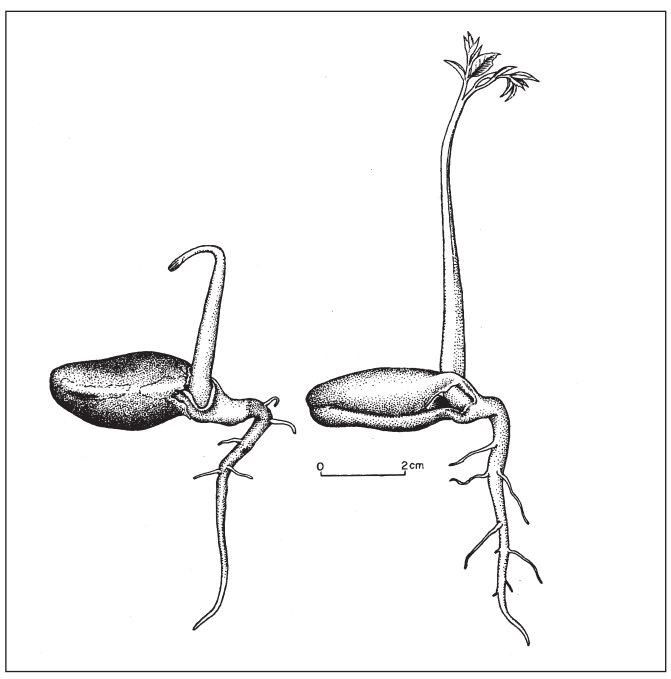


Figure 3—*Gymnocladus dioicus*, Kentucky coffeetree: seedling development at 2 and 54 days after germination.



periods of 2 to 4 hours (Liu and others 1981; Dirr and Heuser 1987). Seeds from one source in southern Minnesota germinated 80% without acid treatments, and acid did not improve that performance (Ball and Kisor 1985). When treating large lots of seeds, it is best to do time trials with small samples to determine the soaking period that gives complete imbibition without damaging the seeds. After the acid soak, the seeds should be thoroughly washed to remove any remaining acid before planting. Other precautions on the use of strong acids for seed scarification are found in chapter 5.

Germination tests. There are no official test prescriptions for Kentucky coffeetree seeds, but germination can be tested easily. Samples of scarified seeds should be incubated in flats of sterile sand or on paper media at alternating temperatures of approximately 20 °C at night and 30 °C in the daytime (Sander 1974). For such small numbers of seeds, cutting or filing through the seed coats may be used in place of acid scarification. One test in sand gave 86% germination in 30 days (Sander 1974). Dirr and Heuser (1987) reported that 93 to 100% germination should be achieved. Germination is hypogeal (figure 3).

Nursery practice. Pretreated seeds should be sown in the spring in rows spaced 45 to 75 cm (18 to 30 in) apart, depending upon irrigation and cultivation methods. Even closer spacing can be used, but rows should be no closer together than 15 cm (6 in). The sowing rate should be 40 to 60 seeds/linear meter (12 to 18/ft) with the seeds covered with about 2.5 cm (1 in) of firmed soil (Phillips 1931; Engstrom and Stoeckler 1941). In general, about 60 to 75% of the seeds sown will produce plantable seedlings. Seedlings may be planted in the field after 1 year (Sander 1974).

Kentucky coffeetree may also be propagated by cuttings taken in December to March (Dirr and Heuser 1987).

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Styracaceae—Storax family

Halesia carolina L.

Carolina silverbell

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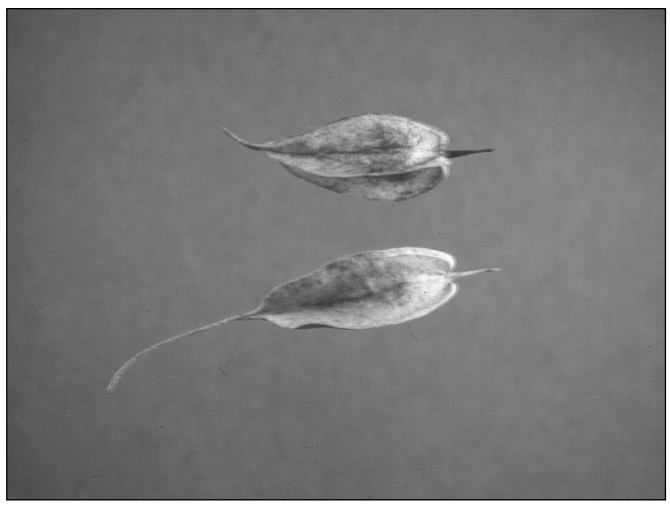
Other common names. opossum-wood, silverbell, snowdrop-tree.

Growth habit, occurrence, and uses. Carolina silverbell—*Halesia carolina* L.—is a small, deciduous tree found naturally from West Virginia and southern Illinois south to South Carolina, northwestern Florida, and Alabama, with small pockets as far west as Arkansas and Oklahoma (Sargent 1965; Sluder 1990). It has been successfully planted in Massachusetts and California and also to some extent in northern and central Europe. Carolina silverbell was first cultivated in 1756 (Bonner and Mignery 1974). It is highly valued as an ornamental, and its fruits are a source of food for wildlife.

Flowering and fruiting. The perfect, white (sometimes pink), bell-shaped, axillary flowers of Carolina silverbell are borne in fascicles of 1 to 5 in March to May (Brown and Kirkman 1990; Sluder 1990). The species is precocious and seedlings may flower when only a little over 1 m in height (Dirr and Heuser 1987). The fruit, which matures in August and September, is an oblong or oblong-ovate, dry, 4-winged, reddish brown, corky drupe 2.5 to 5 cm long. The ovary is a 4-celled ellipsoid stone, 13 to 16 mm long, usually containing only 1 seed (figures 1 and 2) (Bonner and Mignery 1974; Brown and Kirkman 1990; Sluder 1990). The fruits are persistent on the branches, and dispersal occurs well into the winter.

Collection, extraction, and storage. Carolina silverbell fruits may be collected from the trees in late fall and early winter. De-winging can be done mechanically (Thornhill 1968) and is recommended to reduce bulk and facilitate handling. Complete extraction of stones from the fruits is not necessary. Bonner and Mignery (1974) found about 2,600 to 5,500 de-winged fruits/kg (1,200 to 2,500/lb) using 2 samples. Although no data on long-term storage are available, dry cold storage of cleaned fruits has been recommended (Chadwick 1935).

Figure 1—*Halesia carolina*, Carolina silverbell: fruits.



Germination tests. The seeds are extremely dormant and they response best to warm stratification followed by cold stratification. Moist stratification at 13 °C for 60 to 120 days, then 60 to 90 days at 1 to 5 °C, has worked for seeds from many sources (Bonner and Mignery 1974), although more northern collections may require more than 90 days of cold (Dirr 1977). Other sources, however, seem to need only cold stratification (Chadwick 1935). Stratified seeds can be germinated in flats of sand or sand–peat mixtures for 60 to 90 days with 30 °C day and 20 °C night temperatures. Seven samples germinated in this manner averaged 53% germination (Bonner and Mignery 1974). Germination is epigeal (figure 3).

Nursery practice. Because of uncertain response to stratification, the most practical method of propagation from seeds may be to plant in the fall and allow 2 years for full germination (Dirr and Heuser 1987). Stratified seeds should always be used for spring-sowing. Some growers in the North have planted seeds in flats of soil and have kept them in a greenhouse during the early winter months. In January,

Figure 2—*Halesia carolina*, Carolina silverbell: longitudinal section through 2 embryos of a stone.

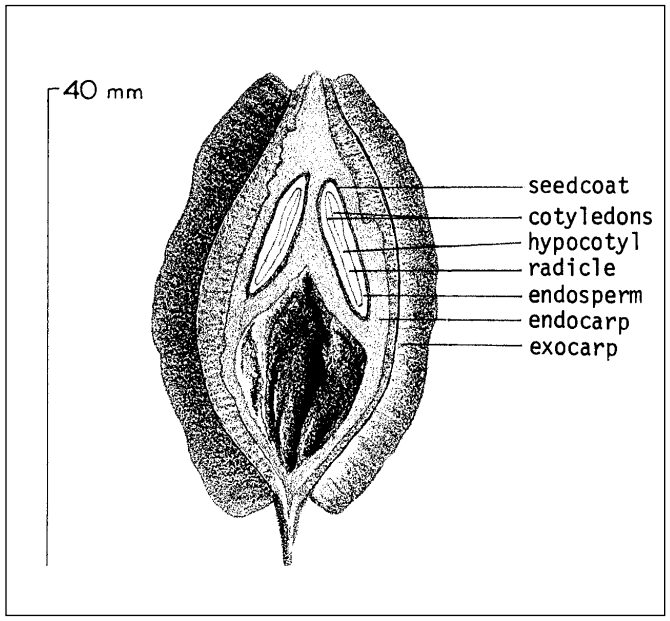
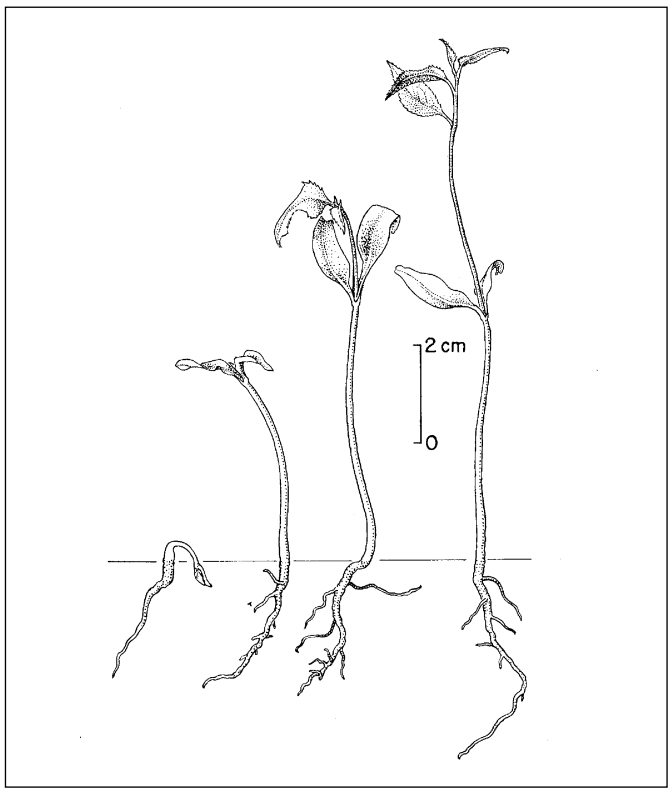


Figure 3—*Halesia carolina,* Carolina silverbell: seedling development after 1, 4, 16, and 40 days.



the flats are then moved to an outdoor cold frame for the cold part of the after-ripening treatment. The flats are protected by mulch or by board covers on the coldframes (Bonner and Mignery 1974).

Carolina silverbell can also be propagated by cuttings taken in mid-summer after shoot elongation has ceased but before fall hardening sets in. It is best to treat cuttings with 2,500 or 10,000 ppm indole butyric acid (IBA) solution and place them in peat or perlite under mist. Rooting success at levels of 80 to 100% can be expected (Dirr and Heuser 1987; Sluder 1990). Micropropagation techniques are also under study (Brand and Lineberger 1986).

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Hamamelidaceae—Witch-hazel family

Hamamelis L.

witch-hazel

Jill R. Barbour and Kenneth A. Brinkman

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Growth habit, occurrence, and use. Witch-hazels are deciduous shrubs or small trees that attain heights of 2 to 10 m (table 1). American witch-hazel is native from Nova Scotia to southeastern Minnesota, south to Missouri, southeastern Oklahoma and Texas, and east to central Florida (Little 1953). First cultivated in 1736 (Rehder 1940), American witch-hazel is used in environmental plantings largely because it flowers in late autumn. The species provides seeds for birds and browse for wildlife (Van Dersal 1938). Bark, leaves, and twigs have been used medicinally in the form of extracts. Another species—Ozark witch-hazel—is a shrub of the Ozark region of Missouri, Arkansas, and Oklahoma but is seldom planted. Japanese and Chinese witch-hazels are popular introduced ornamentals that bloom in the spring. *Hamamelis* × *intermedia* 'Arnold Promise', a hybrid of Japanese and Chinese witch-hazels, was first produced at the Arnold Arboretum (Hora 1981).

Flowering and fruiting. The spider-like yellow or rusty red flowers of American witch-hazel open in September or October, but the ovules are not fertilized until the following May. The fruits ripen early the next autumn (Rehder 1940; Van Dersal 1938). Members of the witch-hazel family have catkins for flowers and they are wind-pollinated (Johnson 1973). Ozark witch-hazel flowers from midwinter to spring (Fernald 1970). Capsules (figure 1) burst open when dry, each discharging 2 shiny black seeds (figure 2). There is limited dispersal by birds. Annual fruit production is highly variable, with abundant fruit crops occurring 1 out of 4 years (DeSteven 1982).

Developing witch-hazel seeds are the larval food of the beetle *Pseudanthonomus hamamelidis* Pierce (Curculionidae) (DeSteven 1982). Weevil eggs are laid on the fruits from mid-June to early July and the newly hatched larvae feed on the fruits from mid-July to September. Lepidopteran caterpillars may also consume the seeds. The 2 most abundant species are in the families Gelechiidae and Pyralidae, and 3 other "occasional" species are in the families Nolidae,

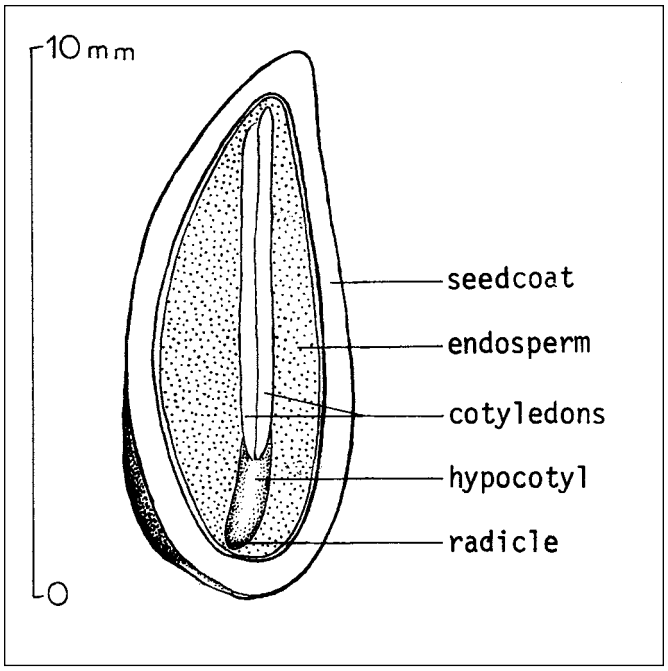
Figure 1—*Hamamelis virginiana,* witch-hazel: fruits (capsules) before and after seeds were discharged.

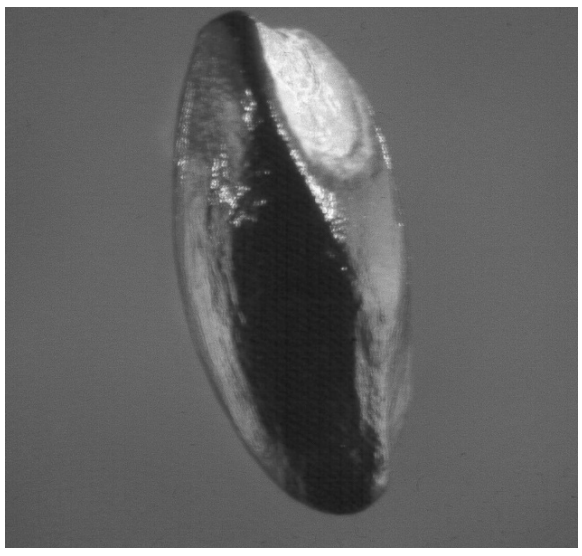
Table 1—*Hamamelis,* witch-hazel: nomenclature and occurrence

Scientific name	Common name	Occurrence	Height (m)
***H. japonica* Siebold & Zucc.**	**Japanese witch-hazel**	Japan	10
***H. mollis* D. Oliver**	**Chinese witch-hazel**	W central China	10
***H. vernalis* Sarg.**	**Ozark witch-hazel**	Ozark Mtns of Missouri & Arkansas	2
***H. virginiana* L.**	**American witch-hazel**	E US & Canada	7–10

Sources: LHBH (1976), Hora (1981).

Figure 2—*Hamamelis virginiana*, witch-hazel: longitudinal section through a seed (**top**) and exterior view (**bottom**).





Phalaenidae, and Geometridae (DeSteven 1982). Small mammals begin feeding on the seeds once they mature in the autumn. Only 14 to 16% of the seeds survive the predation by insects and mammals (DeSteven 1982)

Collection, extraction, and storage. Witch-hazel fruits should be picked in early autumn before they split open and discharge their seeds. Ripe fruits are dull orange-brown with blackened adhering fragments of floral bracts, but the seeds apparently mature as early as August before the fruit coat is fully hardened (Sandahl 1941). Fruits should be spread out to dry so the seeds may be separated from the capsules by screening. Two samples had 19,200 and 24,000 seeds/kg (8,727 and 10,909 seeds/lb) (Brinkman 1974). Fresh seeds can be stored dry in sealed containers at 5 °C for at least 1 year without loss of viability. For overwinter storage before spring-planting, seeds should be stratified in a 1:1 mixture of dampened sand and peat moss at 5 °C. The stratification medium should be 2 to 3 times the volume of seeds (Fordham 1976).

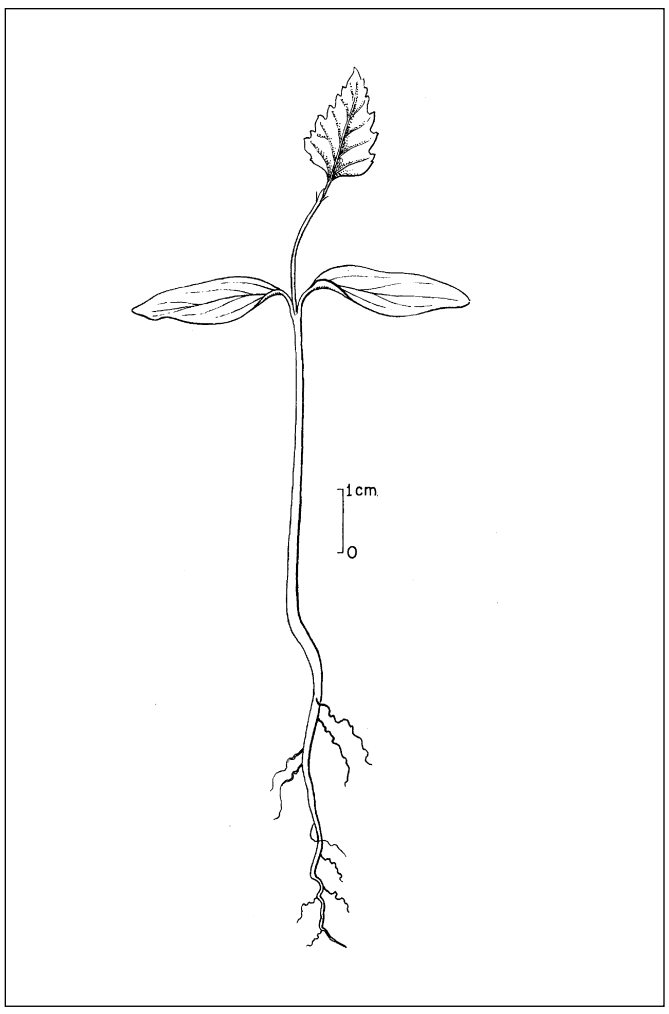
Germination and seed testing. Some stratified seeds germinate in the first spring but many remain dormant until the following year. Dormancy is due to conditions in both seedcoat and embryo, but satisfactory methods for overcoming dormancy have not been found. Rivera and others (1937) subjected witch-hazel seeds to pressures of 2,070 to 413,700 kN/m^2 (300 to 60,000 lb/in^2) at temperatures of 0, 25, and 50 °C and found that none of these conditions resulted in germination. In a series of tests, Brinkman (1974), stratified seeds for 60 days at 30 °C (day) and 20 °C (night) plus 90 days at 5 °C. When tested in sand at 30 °C (day) and 20 °C (night), 17% of these seeds germinated in 60 days.

Work in England on American witch-hazel seeds stratified for 2 months of warm and 2 months of cold, then 2 months of warm and 4 months of cold, produced 88% germination. The same seeds stratified for 2 months of warm and 1 month of cold, then $^1/_2$ month of warm and 4 months of cold, produced 84% germination. Chinese witch-hazel seeds stratified for 3 months of warm and 3 months of cold resulted in 88% germination. Ozark witch-hazel seeds germinated 70% after 3 months of cold stratification; 75% after 3 months of warm and 3 months of cold; 81% after 4 months of warm and 3 months of cold; and 85% after 5 months of warm and 3 months of cold (Dirr and Heuser 1987). A study at the Arnold Arboretum showed that Ozark witch-hazel germinated about as well after cold stratification only as it did after 2 stages of pretreatment (Fordham 1976). The Arnold Arboretum has found that 5 months of warm stratification followed by 3 months of cold treatment was satisfactory for witch-hazel seeds (Fordham 1991).

Chemical staining with 2,3,5-triphenyl tetrazolium chloride (TZ) is the preferred laboratory method for testing the viability of witch-hazel (Moore 1985). One-fourth of the seed opposite the radicle is clipped off to allow for the seed to imbibe the chemical. After staining, the seed is cut longitudinally to expose the embryo for observation. The average viability of 19 samples of witch-hazel seeds was 59% with a range of 0 to 97% (Brinkman 1974).

Nursery practice. Witch-hazel seeds may be fall-sown in the nursery as soon as collected, or stratified seeds may be sown in the spring. Limited trials show that seeds collected as early as August and sown by early October results in as much as 90% germination the following spring (Heit 1968; Sandahl 1941). Fall-sowing is recommended; the seedbeds should be mulched over winter and uncovered at germination time in the spring. For spring-sowing of stratified seeds, seedbeds should be prepared as early as soil conditions permit. Sowing in drills spaced 20 to 30 cm (8 to 12 in) apart will facilitate weeding and cultivating. Secondary leaves may develop on a seedling within 21 days after germination (figure 3). Propagation by layering also is possible.

Figure 3—*Hamamelis virginiana*, witch-hazel: seedling at 21 days after germination.



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Rosaceae—Rose family

Heteromeles arbutifolia (Lindl.) M. Roemer

Christmasberry

Susan E. Meyer

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Growth habit, occurrence, and uses. The genus *Heteromeles* has only a single species—*H. arbutifolia* (Lindl.) M. Roemer, also known as *H. salicifolia* (K. Presl.) Abrams (Phipps 1992). It is closely related to the large tropical genus *Photinia* Lindl., to which it has sometimes been referred. Christmasberry, also known as toyon, California-holly, and hollywood, is a long-lived shrub or small tree, 2 to 10 m in height, that sprouts freely after fire from a subterranean burl. It has shiny, leathery, evergreen leaves that are sharply toothed along the margins. A common constituent of chaparral vegetation throughout California and Baja California, it is usually found on less harsh, more mesic microsites. Christmasberry is useful for erosion control, is a source of honey, and has leaves and fruits that provide food for wildlife. It has also been widely planted in California as an ornamental for park, freeway, and home landscape use (Magill 1974). The attractive foliage and fruits are cut and used for their decorative value.

Flowering and fruiting. Unlike many chaparral shrubs, Christmasberry is summer-flowering (Magill 1974). The numerous, small flowers are borne in flat-topped or convex terminal inflorescences. The flowers are perigynous and have 5 separate petals, 10 stamens, and a 2- to 3-carpellate ovary. The fruits are bright red to orange, 2- or 3-seeded juicy pomes that are 6 to 10 mm in diameter. They ripen from October through January and are dispersed by birds. Good crops are reported to occur yearly (Keeley 1992).

Seed collection, cleaning, and storage. Christmasberry fruits may be clipped or stripped from the branches once they have attained a bright red or orange color (Magill 1974). They should be soaked in water and allowed to ferment slightly. (However, too-long a soaking period can damage the seeds, which have soft, pliable seedcoats.) The seeds (figure 1 and 2) may then be separated from the pulp by passage through a macerator, followed by flotation to remove the pulp. Small lots can be hand-rubbed through a large-holed screen. The seeds may then be allowed to dry. Once dry, any flat, unfilled seeds can be removed by screening.

Figure 1—*Heteromeles arbutifolia,* Christmasberry: seeds.

Christmasberry seed weight is apparently highly variable. Magill (1974) reported a mean seed weight of 19 mg and count of 52,630 seeds/kg (23,900/lb), whereas Keeley (1991) reported a seed weight of 5.5 mg and count of 181,820/kg (82,500/lb). Martineja and Bullock (1997) examined Christmasberry seed weight as a function of habitat variables. They found no correlation with latitude or annual precipitation but did find a significant increase in seed weight with increasing elevation. Overall mean seed weight for their 12 Christmasberry populations was 36 mg and seed count was 27,800 seeds/kg (12,600/lb), with weight ranges of 28 to 49 mg and counts of 20,400 to 35,700 seeds/kg (9,200 to 16,200/lb).

Christmasberry seeds have limited longevity at room temperature, but they are probably orthodox in storage behavior. Keeley (1991) reported a shelf life of less than 1 year in laboratory storage. The seeds were also damaged or killed by high temperature treatments. One hour at 70 °C reduced viability from 99 to 33%, and 5 minutes at 120 °C resulted in essentially complete mortality (Keeley 1987). Magill (1974) recommended sealed storage at low tempera-

Figure 2—*Heteromeles arbutifolia*, Christmasberry: longitudinal section through a seed.

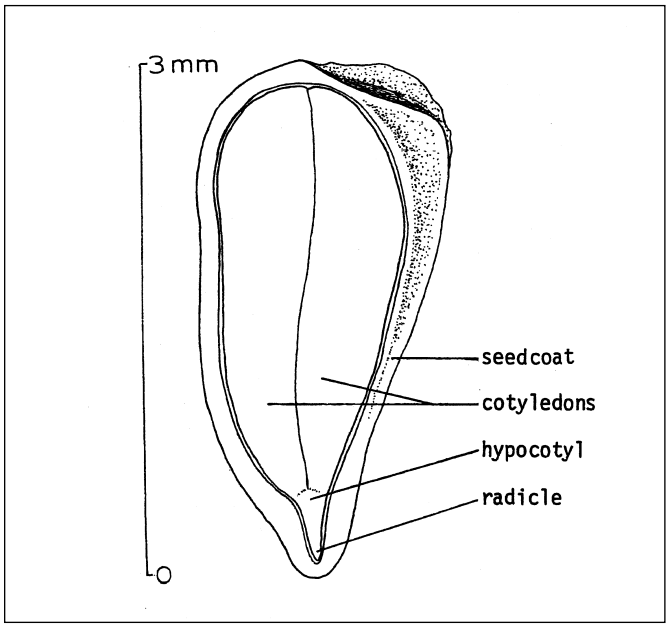
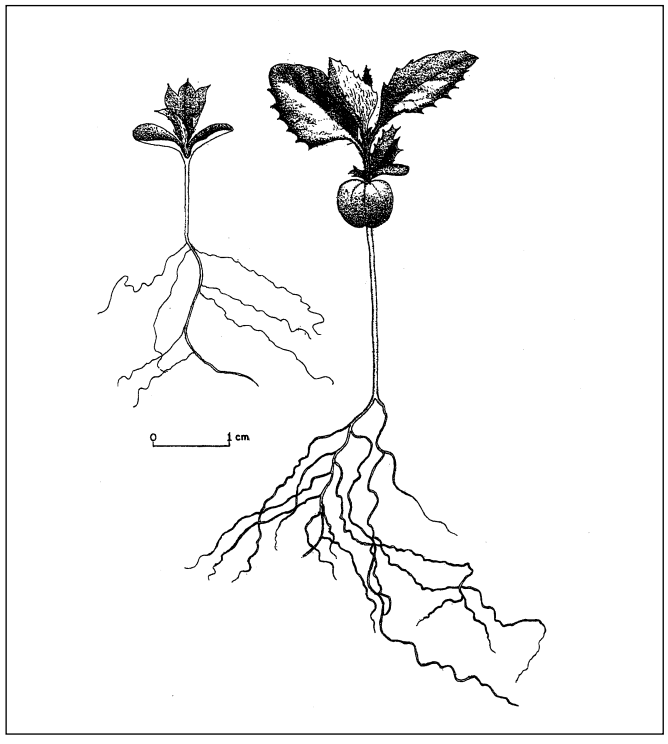


Figure 3—*Heteromeles arbutifolia*, Christmasberry: young seedling (**left**) and older seedling (**right**).



ture but did not give any data on viability retention under these conditions.

Germination and seed testing. Christmasberry seeds are reported to be nondormant at dispersal (Emery 1988; Keeley 1987; Magill 1974), whereas seeds that have been stored are rendered secondarily dormant and require 3 months of chilling at 3 to 5 °C in order to germinate. Under field conditions, Christmasberry seeds germinate within a few months of dispersal and do not form a persistent seedbank (Parker and Kelly 1989). Germination is epigeal (figure 3). Recruitment of new individuals is rarely observed. Although winter seedling emergence is a common occurrence, the seedlings almost invariably die, either from herbivory or summer drought (Parker and Kelly 1989). Because of the transient seed bank, there can be no recruitment after fire, and new recruitment is in fact restricted to chaparral stands that have been free of fire for at least 50 years (Keeley 1992). The seedlings are not very drought-tolerant and seem to need the shade and the deep litter that develops under adult shrub canopies in old stands in order to survive.

Recently harvested lots of Christmasberry seeds that are well-cleaned to remove unfilled seeds generally have high fill and high viability. Keeley (1987) reported germination of 99% at 23 °C. Such lots should be relatively easy to evaluate, either with a germination test or with tetrazolium staining. A 3-month chill at 5 °C followed by a germination test of 28 days at 20 or 25 °C should give maximum germination. Christmasberry seeds have no endosperm, and the embryo completely fills the seed cavity (figure 2). A procedure similar to that used for apple (*Malus* spp.) or bitterbrush (*Purshia* spp.) can be used for tetrazolium evaluation. The seeds should be soaked in water overnight, then clipped at the cotyledon end. The embryos can then be gently squeezed out, immersed in 1% tetrazolium chloride for 6 hours at room temperature, and examined for staining patterns. Older seedlots that have begun to lose viability and germinate sporadically will probably also have ambiguous tetrazolium staining patterns.

Field seeding and nursery practice. Christmasberry would probably be difficult to direct-seed in a wildland setting because of its establishment requirements (Keeley 1992). The seedlings require shady, moist conditions and deep litter, so they would have difficulty getting established on the open disturbances that characterize most wildland seeding projects. Christmasberry is easily propagated from seeds in a nursery setting, however. The seeds maybe planted in flats in sand or soil. If freshly harvested seeds are used, no pretreatment is necessary, and seedlings emerge over a period of 10 to 40 days (Magill 1974). Emergence of 73% has been reported in one case. The seeds may also be planted outdoors in nursery beds. Chilling before spring-planting is recommended (Magill 1974). Greever (1979) reported 100% emergence from March sowing in sand and that there was little difference in seedling size between December and March sowings by May. Propagation by grafting or cuttings is also practiced (Greever 1979; Magill 1974).

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H

Elaeagnaceae—Oleaster family

Hippophae rhamnoides L.

common seabuckthorn

Richard T. Busing and Paul E. Slabaugh

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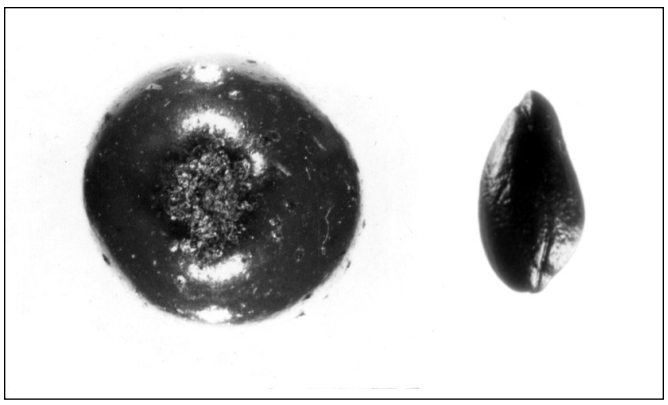
Other common names. Sandthorn, swallow-thorn.

Growth habit, occurrence, and use. Common seabuckthorn—*Hippophae rhamnoides* L.—is native to northwestern Europe through central Asia to the Altai Mountains, western and northern China, and the northern Himalayas. Of the 2 species in the genus, only common seabuckthorn is widely cultivated (Rehder 1940). A very hardy deciduous shrub or a small tree, common seabuckthorn is used primarily for ornamental purposes. In Europe and Asia, it is used to form hedges and, because of its nitrogen-fixing symbionts, serves to enrich and protect soils (Bogdon and Untaru 1967; Kao 1964; Stewart and Pearson 1967). A tendency to form thickets by root suckering limits its use in shelterbelts. In Asia, the plant has a variety of medicinal uses (Ma 1989). The berries, which are a rich source of vitamins (Stocker 1948; Valicek 1978; Zhmyrko and others 1978), have been used in making a cordial and jam in Siberia (Hansen 1931). The plant stems bear many sharp, stout thorns and provide protection, cover, and food for various birds and small rodents (Hansen 1931; Pearson and Rogers 1962).

Flowering and fruiting. The species is dioecious; its very small, yellowish, pistillate flowers appear in March or April before the leaves (Pearson and Rogers 1962; Slabaugh 1974). Orange-yellow, drupelike acidic fruits about the size of a pea (figure 1) (Rehder 1940) ripen in September or October (Hoag 1965; Hottes 1952) and frequently persist on the shrubs until the following March. Each fruit contains a bony, ovoid seed (figures 1 and 2). Seedcrops are borne annually.

Collection, extraction, and storage. Common seabuckthorn fruits are soft and cling tenaciously to the brittle twigs (Demenko and others 1983). Fruits may be picked from the bushes at any time between late fall and early spring. However, germination may vary with the time that seeds were extracted from the ripe fruits (Eliseev and Mishulina 1972). Seeds may be extracted by running the wet fruits through a macerator and floating off the pulp. Prompt cleaning and drying is advantageous because germination rate is very low for seeds left too long in the fruits (Eliseev and Mishulina 1977; Rohmeder 1942). From 45 kg (100 lb) of fruits, 4.5 to 14 kg (10 to 30 lb) of cleaned seeds may be extracted. Soundness of 85% and purity of 97% have been reported (Slabaugh 1974). The average number of cleaned seeds determined on 10 samples is 88,000/kg (40,000/lb), with a range of 55,000 to 130,000/kg (25,000 to 59,000/lb) (Slabaugh 1974). Smaller seeds, numbering 258,000 to 264,500/kg (117,000 to 120,000/lb), were reported in Romania (Enescu and Stegaroiu 1954). The seeds are orthodox and store easily at low moisture contents and temperatures. Dry seeds have been kept satisfactorily for 1 to 2 years at room temperature (Slabaugh 1974). Viabilty of 60% has been reported for seeds stored 4 to 5 years (Smirnova and Tikhomirova 1980).

Figure 1—*Hippophae rhamnoides*, common seabuckthorn: fruit and seed.



Germination. Internal dormancy in seeds of seabuckthorn can be broken by stratification in moist sand for 90 days at 2 to 5 °C (Cram and others 1960; Pearson and Rogers 1962). Stratification for 15 days is sufficient if seeds are sown in the autumn (Grover and others 1962). Germination tests may be run in 40 days on stratified seeds

Figure 2—*Hippophae rhamnoides*, common seabuckthorn: longitudinal section through a seed.

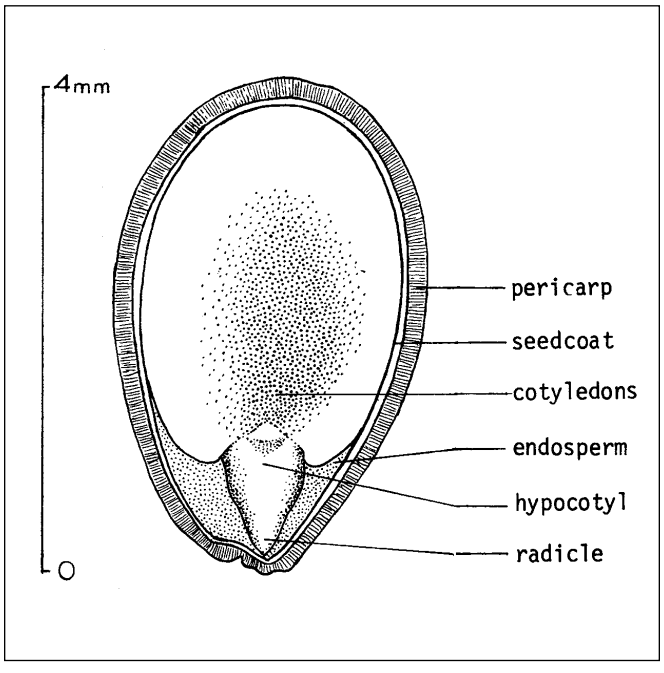
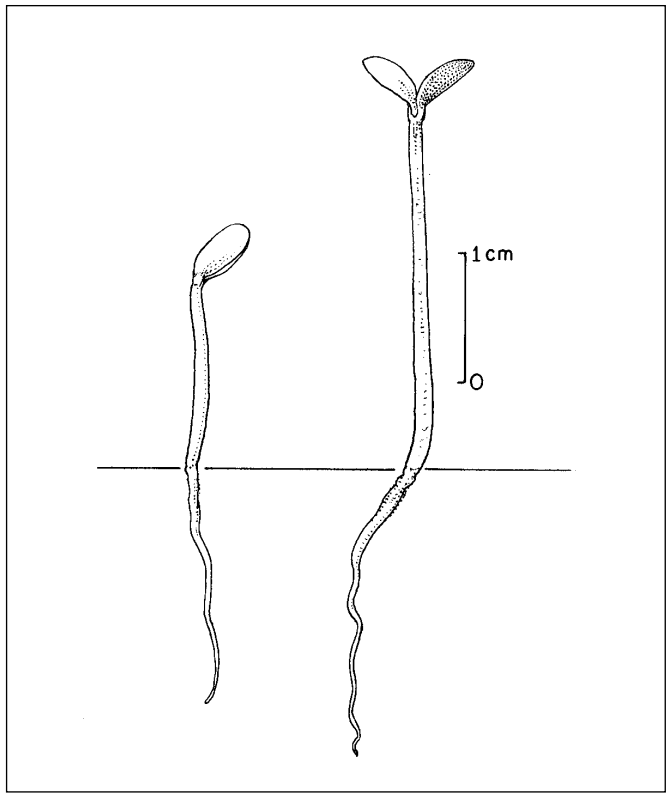


Figure 3—*Hippophae rhamnoides*, common seabuckthorn: seedling development at 1 and 7 days from germination.



in sand flats at diurnally alternating temperatures of 20 and 30 °C (Slabaugh 1974). Germination was increased slightly by exposure to light intensities up to 2,150 lumens/m^2 (Pearson and Rogers 1962). Soaking seeds in solutions of gibberellic acid, sulfuric acid, or other compounds, such as potassium iodide (KI), zinc sulfate ($ZnSO_4$), manganese sulfate ($MnSO_4$), or cobalt sulfate($CoSO_4$), may also increase germination (Avanzanto and others 1987; Eliseev and Mishulina 1972). Germination of untreated seeds ranged from only 6 to 60% after 60 days (Slabaugh 1974). Tests in Romania and England gave results of 75 to 85% and 95 to 100% (Enescu and Stegaroiu 1954; Pearson and Rogers 1962). Germination is epigeal (figure 3).

Nursery practice. Untreated seeds may be used for fall-sowing (Grover and others 1962), but stratified seeds are needed for spring-sowing (Cram and others 1960). Either broadcast or drill sowing is satisfactory if seeds are covered with about 6 mm ($^1/_4$ in) of soil. Shading during the early stages of germination is beneficial (Hansen 1927). This species can be propagated by layers, suckers, and root cuttings as well as by seeds (Avanzanto and others 1987; Papp 1982, Varga and Foldesi 1985). It grows best on moist, neutral to basic, sandy soils (Pearson and Rogers 1962).

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Rosaceae—Rose family

Holodiscus (K. Koch) Maxim.

ocean-spray

Nancy L. Shaw, Emerenciana G. Hurd, and Peter F. Stickney

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Growth habit, occurrence, and use. *Holodiscus* is a taxonomically complex genus including about 6 species of western North America and northern South America (Hitchcock and others 1961; Ley 1943). The 2 generally recognized North American species (table 1)—creambush ocean-spray and gland ocean-spray—are deciduous, multi-stemmed shrubs with simple, alternate, deciduous, toothed to shallowly lobed, exstipulate leaves.

Creambush ocean-spray grows from 1 to 6 m in height, with slender, arching branches and grayish red exfoliating bark. It is a prolific root sprouter, capable of recovering from fire, grazing, or mechanical damage by resprouting from perennating buds in the root crown. Growing at elevations from sea level to 2,150 m, it is most abundant in coastal areas from British Columbia to southwestern California. It also occurs eastward to Montana in drier conifer types of the interior Pacific Northwest. A dominant shrub in a number of forested communities, creambush ocean-spray is also common in riparian areas and on rocky talus slopes (Halversen and others 1986; Topik and others 1986). Remnant stands are found on higher peaks of Great Basin mountain ranges (Hitchcock and others 1961; USDA FS 1937).

Gland ocean-spray is a low, intricately branched shrub that is 0.1 to 3 m tall (Harrington 1954). It differs from creambush ocean-spray in its more compact growth habit, leaves with decurrent petioles, and leaf lobes or teeth without secondary teeth. Gland ocean-spray grows east of the Cascade Mountains and the Sierra Nevada, from north central Oregon to Chihuahua, Mexico, at elevations ranging from 1,400 to 3,350 m (Harrington 1954; Mozingo 1987; USDA FS 1937). Although gland ocean-spray is found in a variety of plant communities, its most characteristic habitats are talus slopes, rock outcrops, slickrock plateaus, and dry, rocky desert areas.

Palatability and forage value of both ocean-spray species vary geographically but are generally low for livestock and big game. However, in the absence of more palatable shrubs, substantial quantities are browsed by deer (*Odocoileus* spp.) and by elk (*Cervus elaphus*) on low-elevation winter ranges. In some areas, ocean-sprays are important year-round (USDA FS 1937). Both shrubs may increase on summer ranges where other forage species are browsed preferentially (Ferguson 1983). Gland ocean-spray is browsed in summer by bighorn sheep (*Ovis canadensis*) and both species are browsed by rabbits (Sutton and Johnson 1974; Todd 1975; Van Dersal 1938).

Ocean-spray has considerable potential for revegetating a variety of disturbed areas. Populations capable of growing on dry, rocky, well-drained sites may be particularly useful

Table 1—*Holodiscus*, ocean spray: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***H. discolor* (Pursh) Maxim.** *Spiraea discolor* Pursh *Spiraea ariaefolia* Smith in Rees *Schizonotus discolor* Raf. *Sericotheca discolor* Rydb.	**creambush ocean-spray,** creambush, creambush rockspirea, hardhack, Indian arrow-wood, ocean-spray	S British Columbia, Washington, Oregon, W Montana, N Idaho, NE Nevada, & California
***H. dumosus* (Nutt.) Heller** *Spiraea dumosa* Nutt. ex T. & G. *Spiraea discolor* var. *dumosa* Wats. *Schizonotus dumosus* Koehne. *Sericotheca dumosus* Rydb.	**gland ocean-spray,** bush ocean-spray, bush rockspirea, mountain-spray, rock-spirea, creambush	E & S Oregon, N central & S Idaho, NE California, Nevada, Utah, W & S Wyoming, Colorado, Arizona, New Mexico, & S to Chihuahua, Mexico

Sources: Archer (2000), Flessner and others (1991), Hitchcock and others (1971), Ley (1943), McMurray (1987b).

(Stark 1966; Sutton and Johnson 1974). Ocean-spray has been recommended for use in nonintensive highway plantings, riparian areas, windbreaks, erosion control projects, wildlife habitat improvement projects, and conservation plantings (Antieau 1987; Atthowe 1993; Flessner and others 1992). Because of their growth habits, showy inflorescences, and fall coloration, both species are attractive ornamentals. Creambush ocean-spray was first cultivated in 1827 and gland ocean-spray in 1853 (Rehder 1940).

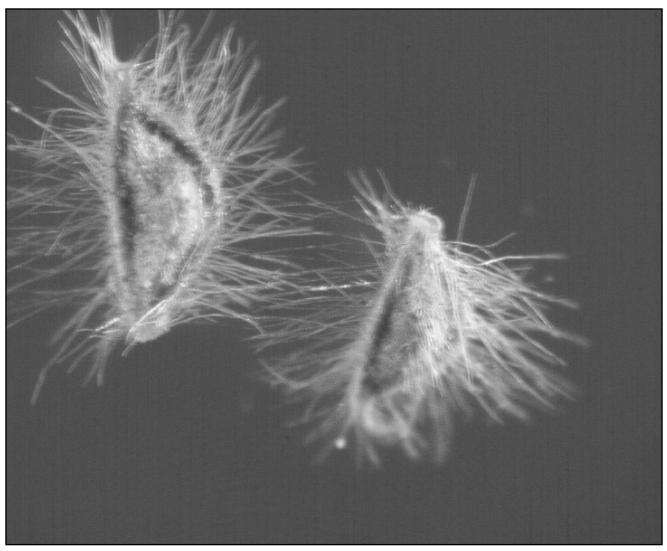
Native Americans made digging sticks and arrow shafts from the hard wood and straight branches of ocean-spray (Anderson and Holmgren 1969; Daubenmire 1970; Hopkins and Kovalchik 1983). Fruits of gland ocean-spray were eaten by Native Americans of the Great Basin, and pioneers made nails from its wood.

Both North American ocean-sprays are tetraploid, with 2X = n = 18 (Antieau 1986; Goldblatt 1979; McArthur and Sanderson 1985), and both exhibit considerable morphological variation. A genetic basis for variability in such characteristics as growth habit, growth rate, leaf morphology, and flower abundance in creambush ocean-spray is suggested by common garden studies (Flessner and others 1992).

Flowering and fruiting. Although the showy terminal panicles and floral buds of both species develop in early spring, flowering is delayed until late spring to mid-summer. Fruits ripen in late summer and are dispersed by wind and gravity through November (Hitchcock and others 1961; Stickney 1974) (table 2). The insect-pollinated flowers are small, creamy-white, perfect, and perigynous (Hitchcock and others 1961; McArthur 1984). The entire disk lining the hypanthium gives the genus its name (Greek: *holo* = whole and *diskos* = disk). Each flower produces 5 villous, light-yellow achenes that are about 2 mm long (figures 1 and 2). Seeds are broadly oblong and contain a thin endosperm and an embryo with ovate cotyledons (figure 2) (Ley 1943).

Collection, cleaning, and storage. Ocean-spray achenes are among the smallest of shrub fruits. Estimates of the number of cleaned achenes per weight exceed 11,000,000/kg (5,000,000/lb) for each species (King 1947; Link 1993). Achene collection is tedious, and supplies are

Figure 1—*Holodiscus*, ocean spray: achenes of *H. discolor*, creambush ocean-spray (**left**) and *H. dumosus*, gland ocean-spray (**right**).



rare and costly. In addition, the achenes are difficult to handle because of their pubescence and small size. Achenes are hand-stripped from inflorescences in late summer or autumn (table 2) (Monsen 1996). Large debris in air-dried collections can be removed with a fanning mill. Small lots may be cleaned by hand-rubbing and sieving (Link 1993).

Sound achenes are identified by examining imbibed achenes through a dissecting microscope for the presence of an embryo. Using this method, King (1947) found that only 7% of ocean-spray achenes collected were sound. In creambush ocean-spray from British Columbia, viability was greater for achenes collected in October or November than for those collected in August or September (Marchant and Sherlock 1984).

Storage requirements for ocean-spray have not been examined. The achenes appear to be orthodox in storage behavior and can probably be stored for several years at low water contents and temperatures.

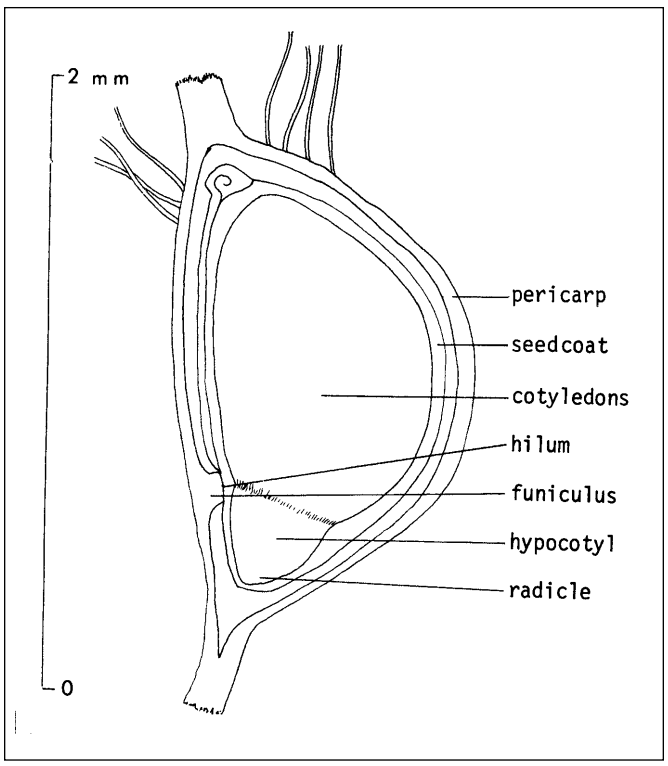
Germination. There are no official testing prescriptions for this genus. Germination of creambush ocean-spray seeds is enhanced by wet prechilling at 2 to 5 °C for 15 to 18 weeks (King 1947; Marchant and Sherlock 1984). King

Table 2—*Holodiscus*, ocean-spray: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
H. discolor	California	May–Aug	—	—
	N Idaho	July	Aug	—
	N Idaho	July	Late July–early Sept	Aug–Nov
H. dumosus	Great Basin	June–Aug	—	—
	Utah	June–Aug	—	—
	—	—	Aug	Aug

Sources: Drew (1967), Jorgensen (2004), Mozingo (1987), Munz and Keck (1973), Orme and Leege (1980), Welsh and others (1987).

Figure 2—*Holodiscus discolor*, creambush ocean-spray: longitudinal section through an achene.



(1947) obtained 84% germination in 22 days when seeds were chilled for 18 weeks before incubation at 20 to 24 °C.

Germination of gland ocean-spray has received little study. Link (1993) reported that 16 weeks of wet chilling failed to release dormancy in this species. Effective treatments have not been reported.

Viability of ocean-spray seeds may be tested by tetrazolium chloride staining. After 3 hours of imbibition in water at room temperature, seeds are excised from the achene and the seedcoat is pricked or slit near the center of the seed. Seeds are then allowed to imbibe a 1% tetrazolium chloride for 4 hours at room temperature. Stained embryos may be read in place, as the seedcoat is very thin (Hurd 1996; King 1947). Staining should be evaluated as described by Peters (2002) for Rosaceae III genera.

Nursery practice. Ocean-sprays may be propagated as bareroot or container stock (Everett 1957). Achenes should be fall-sown or artificially prechilled and spring-sown in bareroot nurseries (Flessner and others 1992). Marchant and Sherlock (1984) obtained successful plantings only by planting freshly harvested achenes in fall. Cleaned achenes of both species can be drilled at reasonably uniform spacings within rows (Shaw and Monsen 2004). They may also be broadcast and covered by dragging a lightweight chain over the seedbed. Seedlings develop slowly and may be lifted as 1+0 or 2+0 stock, depending upon size specifications and growing conditions.

Container seedlings are propagated by planting several wet-prechilled achenes in each container and thinning or by planting germinants. Kruckeberg (1982) reported that ocean-spray can be propagated by fall-sowing achenes in boxes outdoors and covering them lightly with soil. Flessner and others (1992) planted wet prechilled (4 months at 4 °C) creambush ocean-spray achenes in shallow flats in a greenhouse. Seedlings emerged after 16 to 30 days of incubation at a minimum temperature of 21 °C. Developing seedlings were fertilized and treated with a fungicide as necessary. After 2 months they were transferred to larger containers in a lathhouse and held overwinter for planting as 1+0 stock.

Kruckeberg (1982) reported that creambush ocean-spray planting stock is easily obtained by potting wildlings, which are often abundant. Morgan and Neuenschwander (1988) observed high densities of creambush ocean-spray wildlings following severe burns, but Wright and others (1979) and Stickney (1996) concluded that the species exhibits poor seedling regeneration following fire in sagebrush (*Artemesia* spp.) and conifer communities of the intermountain and northern Rocky Mountain regions.

Ocean-spray can be grown from cuttings, but rooting of both species varies widely among clones, cutting types, and propagation techniques (Antieau 1987; Link 1993). Softwood cuttings may be treated with rooting hormones and propagated in a greenhouse with a mist system (Antieau 1987; Marchant and Sherlock 1984). Success with semi-hardwood cuttings is variable (Everett and others 1978; Kruckeberg 1982). Fall-harvested hardwood cuttings are cut to 15-cm (6-in) lengths and treated with 0.8% indole-3-butyric acid (IBA) powder and a fungicide (Macdonald 1986). Hardwood cuttings stored in straw-bale bins or cold frames will develop calluses (Macdonald 1986; Marchant and Sherlock 1984). When fall-planted, these cuttings root rapidly. Layers and suckers have also been propagated successfully (Kruckeberg 1982).

Field practice. Fresh achenes broadcast over a rough seedbed in fall are covered by natural soil sloughing (Shaw and Monsen 2004; Van Dersal 1938). Achenes may be mixed with seeds of other shrub species, but they should not be sown with more competitive grasses or forbs. Planting areas should be selected carefully to make the best use of seed supplies, as seeding results are often erratic. Native creambush ocean-spray seedlings develop slowly and are poor competitors (Wright and others 1979).

Creambush ocean-spray can be established by transplanting. Youtie (1992) reported good survival of rooted cuttings on biscuit scablands in Oregon's Columbia River Gorge. Marchant and Sherlock (1984) found that planted seedlings grew slowly the first year. Low survival on western Montana roadcuts was attributed to poor soils and unhealthy planting stock (Hungerford 1984).

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Fabaceae—Pea family

Hymenaea courbaril L.

courbaril

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Other common names. jutaby, *cuapinol*, *algarrobo*.

Occurrence and growth habit. Courbaril—*Hymenaea courbaril* L.—is a large tree, about 45 m tall, relatively slow growing (about 1 m/year) with a well-formed clean trunk. It develops best on sandy, drained ridges and river banks (but not well in wetlands) and is normally found in open sites from southern Mexico, Central America, and the West Indies, to northern South America. It is found in a variety of soils, such as clay to sand, occurring predominantly in oxisols, with a pH range from 4.8 to 6.8. It grows best in areas with 1,900 to 2,150 mm of rainfall, and from sea level to about 900 m. It coppices well in cut-over areas except from large stumps and can also be propagated from cuttings. Courbaril is the most widespread of the 17 species in the genus *Hymenaea*; there is an African species and the remaining species are found in neotropical America. Courbaril readily forms forest associations in semi-deciduous, secondary, moist subtropics (Rzedowski 1981). It is also reported in nearly pure stands in Mexico (Weaver 1987).

Use. Courbaril's basic use is for timber. The wood is strong, hard, and tough; it is difficult to saw, machine, and carve but bends well after steaming. It is commercially useful for flooring, handles, sporting equipment, furniture, and railroad ties (Chudnoff 1984). Its heartwood has a specific gravity of about 0.70 g/cm^3. Although courbaril wood is resistant to white-rot fungi (less to brown-rot) and termites, it has little resistance to marine borers. It does not weather well and does require painting (Francis 1990; Longwood 1962). The tree has limited ornamental use for shade, parks, and streets because of its heavy legumes (pods) and the offensive odor of the broken legumes as seeds mature. Although it has a limited appeal, the seed pulp is a good dietetic source of sugar and high in fiber when eaten plain or toasted or drunk as a fermented beverage. It is also given to livestock. According to local folk medicine, a bark infusion is used as a laxative and the fruit pulp as an antidiarrheal (Liogier 1978).

Flowering and fruiting. Large trees with full, overhead light usually flower during spring and summer. Terminal racemes bear white flowers about 4 cm wide. Mature legumes (figure 1) measure 5 to 10 cm long, 2 to 3.5 cm wide, and 2.5 cm thick and fall during the following spring. The thick, hard legume does not open naturally, but protects 3 or 4 large seeds (figures 2 and 3) encased in a powdery, cream-colored pulp (Liogier 1978). Small animals—such as agouties (*Tayassu* spp.) and peccaries (*Dasyprocta* spp.)—open the legumes to eat the pulp and seeds. Legumes have a protective gum that delays rotting for several months, until the seeds begin to take up moisture for germination; otherwise the seeds would rot in their legumes (Jansen 1983).

Collection and storage. Seeds collected in Puerto Rico average about 253/kg (115/lb) (Francis 1990), whereas those collected in Brazil yield 475/kg (215/lb) (Pereira 1982). A single tree may produce 100 legumes per year but not necessarily each year. Because of the height of the trees, the legumes are usually picked manually from the ground, and seeds are obtained from fresh legumes that have fallen in spring (Jansen 1983). After-ripening causes an actual

Figure 1—*Hymenaea courbaril*, courbaril: legume.

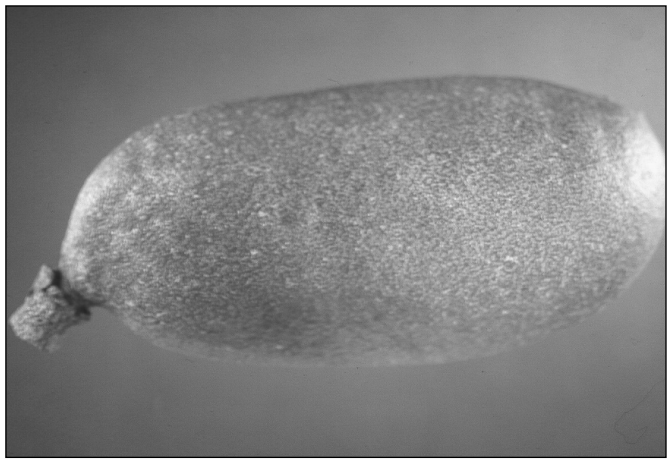


Figure 2—*Hymenaea courbaril*, courbaril: seeds.

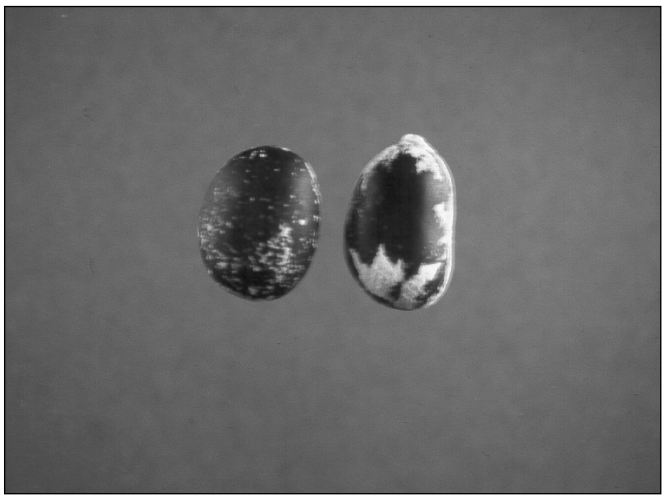
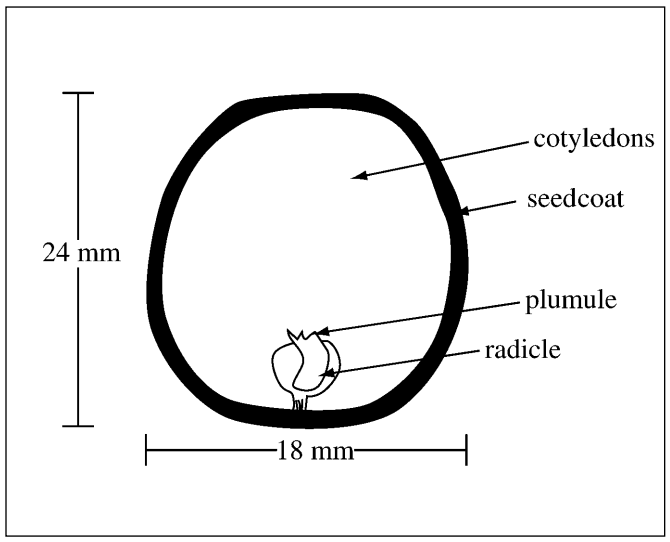


Figure 3—*Hymenaea courbaril*, courbaril: longitudinal section through a seed.



germination enhancement during the first 4 months after collection. This may also account for the long (9-month) period seeds remain in the legume on the tree before falling. Courbaril seeds are orthodox in storage behavior and store relatively well with acceptable germination for periods in excess of 1 year. However, the conditions for optimal storage changes with time. For the first year, sealed containers are preferable at ambient temperatures; after that, seeds should be refrigerated or kept in unsealed bags (Marrero 1943).

Germination. Simple scarification or an hour of soaking in sulfuric acid is necessary as a germination pretreatment (Marshall 1939). After imbibition, seeds may be germinated in potting mix for 14 to 21 days with up to 90% germination (Francis and Rodriquez 1993; Marrero 1949). Seeds can be germinated at ambient temperature in either potting mixture or sand placed in shallow trays or moistened filter or blotter paper in petri dishes.

Nursery practice. Container stock may be grown in either full sun or 50% shade. However, seedlings grown in full sun are ready for outplanting about 2 weeks earlier than seedlings grown in shade (Francis 1990; Pereira 1982). Although courbaril may be direct-seeded or underplanted, success is greater with containers unless seeds can be given greater protection. A large taproot with a well-developed fibrous net grows deeply and may or may not have associated nitrogen-fixing nodules (Allen and Allen 1981). Seeds may be infected by a bruchid beetle, *Pygiopachymerus* sp. (Decelle 1979); a weevil, *Rhinochenus* sp. (Jansen 1975); and an ant, *Atta* sp. (Jansen 1983).

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Aquifoliaceae—Holly family

Ilex L.

holly

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Growth habit, occurrence, and use. The hollies—genus *Ilex*—include almost 400 species of deciduous or evergreen shrubs and trees that occur in temperate and tropical regions of both hemispheres (Brown and Kirkman 1990). About 20 species are native to eastern North America. Of the 7 species included in this book (table 1), most are highly valued for ornamental plantings and all are good food sources for wildlife. More than a thousand cultivars of American holly have been selected for their ornamental features (Grelen 1990). This species also hybridizes with dahoon (*Ilex cassine* L.) to produce Topel holly (*I.* × *attenuata* Ashe) (Little 1979). The wood of American holly is also used in cabinetry and for construction of novelties and specialized wood products (Vines 1960).

Flowering and fruiting. The small, axillary, white or greenish white, dioecious flowers appear in the spring on the current season's growth (table 2). Holly fruits are rounded, berrylike drupes that range from 6 to 13 mm in diameter (figure 1). Each fruit contains 2 to 9 bony, flattened seeds that are botanically defined as nutlets, or pyrenes (figure 2). The fruits mature in the fall (table 2), turning from green to various shades of red, yellow, or black (table 3). The seeds contain a very small embryo in a fleshy endosperm (figure 3).

Collection, extraction, and storage. Ripe fruits may be picked by hand or flailed from the branches onto sheets spread on the ground. Seeds should be extracted by running the fruits through a macerator with water and floating or skimming off the pulp and empty seeds. For small seedlots, kitchen or laboratory blenders do a thorough job, although replacing the metal blades with plastic tubing propellers has been recommended to avoid damage to the seeds (Munson 1986). In another method, the fruits are fermented in warm water, then rubbed over a screen by hand to remove the pulp (Vines 1960). Seed yield data are summarized in table 4.

If the seeds are to be stratified immediately, drying is not necessary. If the seeds are to be stored, they should be dried to about 10% moisture content, placed in moisture-proof containers, and stored at temperatures near or below freezing. Viability of seeds after storage for more than 1 year has not been reported, but hollies are orthodox in storage behavior and should keep well at temperatures a few degrees above (or below) freezing. Storage foods in the embryo are primarily lipids and proteins (Hu and others 1979).

Table 1—*Ilex,* holly: nomenclature and occurrence

Scientific name & synonym	Common name(s)	Occurence
***I. aquifolium* L.**	**English holly**	Native to S Europe, N Africa, & W Asia to China; widely planted in SE & NW US
***I. decidua* Walt.**	**possumhaw,** deciduous holly, winterberry, swamp holly	Maryland to Florida, W to Texas, Missouri, & Illinois
***I. glabra* (L.) Gray** *I. monticola* Gray	**inkberry,** gallberry, smooth gallberry	Nova Scotia to Florida, W to Missouri & Texas
***I. montana* Torr. & Gray ex**	**Gray mountain holly,** mountain winterberry	New York to Florida, W to Louisiana
***I. opaca* Ait.**	**American holly,** holly, white holly	Massachusetts to Florida, W to Texas & Missouri
***I. verticillata* (L.) Gray**	**common winterberry,** winterberry, black alder	Newfoundland to Minnesota, S to Louisiana & Florida
***I. vomitoria* Ait.**	**yaupon,** cassena, Christmas-berry, evergreen holly	Virginia to central Florida, W to Texas & Oklahoma

Source: Little (1979).

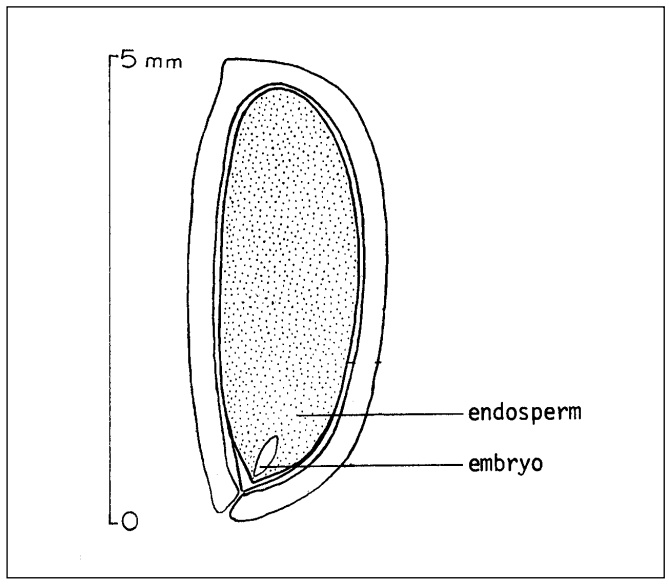
Table 2—*Ilex, holly:* phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
I. aquifolium	—	May–June	Sept	Winter–spring
I. decidua	Gulf Coastal Plain	Mar–May	Fall	Winter–spring
I. glabra	—	Mar–June	Fall	Winter–spring
I. montana	Appalachian Mtns	May–June	Sept	—
I. opaca	—	Apr–June	Sept–Oct	Mar
I. verticillata	—	June–July	Sept–Oct	Fall–winter
I. vomitoria	Gulf Coastal Plain	Apr–May	Sept–Oct	Dec

Sources: Bonner (1974), Halls (1973), Little and Delisle (1962), Stupka (1964), Vines (1960).

Figure 1—*Ilex*, holly: fruits and leaves of *I. opaca,* American holly (**top**) and *I. vomitoria*, yaupon (**bottom**).

Figure 3—*Ilex montana*, mountain holly: longitudinal section of a nutlet.



Pregermination treatment. Holly seeds exhibit a deep dormancy that is caused partly by the hard endocarp surrounding the seedcoat (figure 3) and partly by an immature embryo. In nature, germination of American holly is commonly delayed for as long as 3 years (Bonner 1974). This condition suggests that alternating warm and cold moist treatments may be the best approach. Reasonable germination of American holly has been reported after 12 months of warm treatment that is followed by 3 months of

Figure 2—*Ilex*, holly: nutlets (pyrenes) of *I. aquifolium*, English holly (**top**); *I. montana*, mountain holly (**second**); *I. opaca*, American holly (**third**); *I. verticillata,* common winterberry (**fourth**); *I. vomitoria*, yaupon (**fifth**); and *I. glabra*, inkberry (**bottom**).

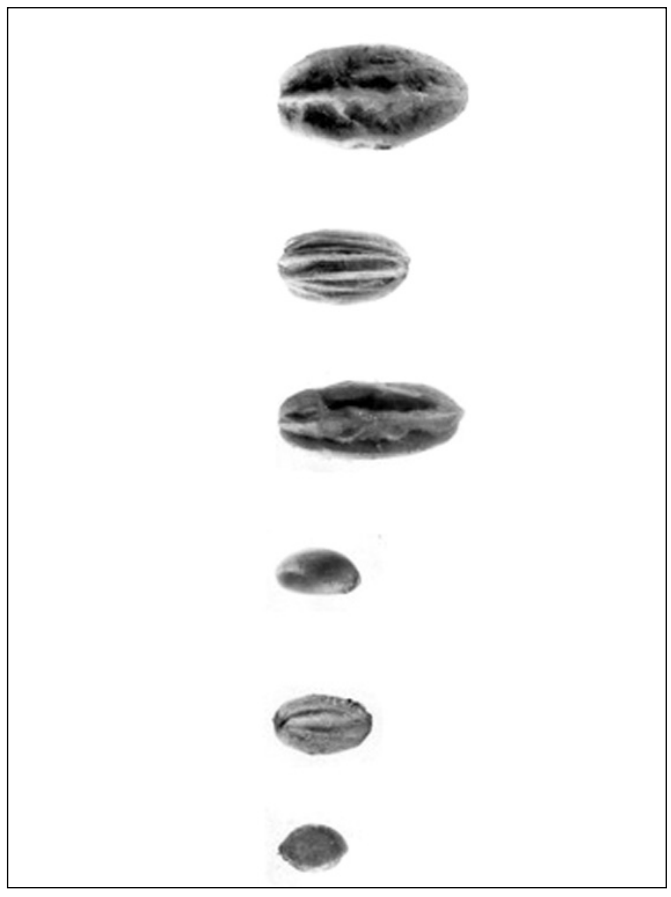


Table 3—*Ilex,* holly: height, seed-bearing age, and color of ripe fruit

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yrs)	Color of ripe fruit
I. aquifolium	15–24	Ancient times	5–12	Light red
I. decidua	6–9	—	—	Red, orange-red
I. glabra	4	1759	—	Black
I. montana	12	1870	—	Orange-red, rarely yellow
I. opaca	30	1744	5	Red, rarely orange or yellow
I. verticillata	8	1736	—	Red, orange or yellow
I. vomitoria	3–8	—	4–7	Red

Sources: Bonner (1974), Brown and Kirkman (1990), Grelen and Duvall (1966), Halls (1973), Little and Delisle (1962), Maisenhelder (1958), Rehder (1962), Vines (1960).

Table 4—*Ilex,* holly: seed yield data

	Cleaned seeds/weight				
	Range		Average		
Species	/kg	/lb	/kg	/lb	Samples
I. aquifolium	—	—	125,700	57,000	1
I. decidua	—	—	43,6000	19,800	1
I. glabra	—	—	63,900	29,000	1
I. montana	—	—	77,200	35,000	1
I. opaca	48,500–80,150	22,000–36,350	62,700	28,430	4
I. verticillata	88,200–284,450	40,000–129,000	202,860	92,000	4
I. vomitoria	—	—	83,350	37,800	1

Sources: Bonner (1974), Swingle (1939).

cold (Dirr and Heuser 1987). For common winterberry, which may have a more permeable endocarp than other hollies, some benefit may be obtained by stratifying seeds at alternating temperatures of 20 °C (night) and 30 °C (day) for 60 days, followed by 60 days at 5 °C (Giersbach and Crocker 1929).

Germination and viability tests. Because of the extremely slow germination of hollies, there is no satisfactory method for testing germination directly. Germination of 70 to 95% has been reported for inkberry in tests that ran over 300 days (Hughes 1964), and 33 to 56% for American holly in tests that ran 2 $^1/_2$ years (Barton and Thornton 1947). Test periods of this length are not practical, and indirect estimates of viability are commonly used in place of germination tests. Cutting tests give good estimates of viability for freshly collected seeds, but for most purposes, tetrazolium staining is best. Procedures recommended for English holly by the International Seed Testing Association (1993) should work well with other holly species. Seeds should be cut longitudinally through the seedcoat and into the endosperm, or cut transversely at distal or both ends into the endosperm, to allow entry of the tetrazolium solution. Incubation for 24 hours at 30 °C in a 1.0% solution should be sufficient for staining. All tissues, including the endosperm, should be fully stained in viable seeds.

Nursery practice. Holly seeds may be broadcast or sown in drills in fall or spring. Sowing immediately after collection has been recommended for American holly and inkberry (Afanasiev 1942; Hartmann and Kester 1968), but germination should not be expected until the second or even third spring (Bonner 1974). Seeds should be covered with 3 to 13 mm ($^1/_8$ to $^1/_2$ in) of soil, and fall-sown beds should be mulched (Bonner 1974; Muir 1965). In another recommended procedure, seeds are sown in a flat of moist medium that is then covered with a plastic bag and placed in a warm (15 to 27 °C) shaded room until seedlings start to emerge. When this occurs, the bag should be removed and the flat moved to a spot with normal germination conditions (Dirr and Heuser 1987). Half-shade is recommended for beds of English holly during the first 2 summers, and field planting should be with 2+2, 2+3, or 2+2+2 stock (Bonner 1974). Because of the extreme dormancy in holly seeds, most propagation is by rooted cuttings, especially for ornamental varieties and selections. All species do not root equally or with the same treatments, so a good manual on vegetative propagation should be consulted (Dirr and Heuser 1987). A considerable amount of research on embryo culture of several holly species has also taken place (Hu 1975, 1977).

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Juglandaceae—Walnut family

Juglans L.

walnut

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Growth habit, occurrence, and use. The walnuts include about 20 species of deciduous trees or large shrubs that occur in the temperate regions of North America, northwestern South America, northeastern Europe, and eastern Asia. Six are native to the United States, and 2 exotic species are also planted in this country (table 1). The wood of most species is used to some extent, and that of many species, primarily black walnut, is highly valued for furniture, cabinet work, gunstocks, and interior trim. The nuts provide food for humans as well as for wildlife, and ground shells are used as an abrasive grit for industrial cleaning. Numerous medicinal products and dyes have been made from extracts of walnut fruits (Krochmal and Krochmal 1982). English walnut is a major nut crop in many temperate regions around the world, including the United States. Of the 6 native species, black walnut is by far the most widely planted. Butternut, little walnut, and Hinds walnut have had limited utilization. Butternut is currently being killed throughout its range in North America by *Sirococcus clavigignenti–juglandacearum* Naiv. Kostichka & Kuntz, a fungus of unknown origin (Ostry and others 1994). Research is underway to identify and propagate resistant trees.

Geographic races. There is considerable genetic variation in the walnuts that are widely distributed. Three distinct geographic races of English walnut are recognized: Turkestani, Himalayan, and Central Asian—and many horti-

Table 1—*Juglans*, walnut: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***J. ailantifolia* Carriere** *J. sieboldiana* maxim.	**Japanese walnut,** Siebold walnut	Japan
***J. californica* S. Wats.**	**California walnut,** southern California walnut, black walnut	Coastal S California (Santa Barbara Co. to Orange Co.) California
***J. cinerea* L.** *Wallia cinerea* (L.) Alef.	**butternut,** oilnut, white walnut	New Brunswick to S Ontario & SE Minnesota, S to Arkansas, N Mississippi, N Georgia, & W South Carolina
***J. hindsii* (Jepson) Jepson ex R.E. Sm.** *J. californica* var. *hindsii* Jepson	**Hinds walnut,** northern California walnut, Hinds black walnut	Central California (Shasta Co. through Stanislaus Co.)
***J. major* (Torr.) Heller** *J. rupestris* var. *major* Torr. *J. microcarpa* var. *major* (Torr.) L. Benson *J. elaeopyren* Dode	**Arizona walnut,** Arizona black walnut, *nogal, nogal silvestre*	Central & SW Texas to SW New Mexico, Arizona, & mtns of northern Mexico
***J. microcarpa* Berl.** *J. rupestris* Englem. ex Torr.	**little walnut,** Texas walnut, river walnut, *nogal*, Texas black walnut	W Oklahoma, W & S Texas & SE *nogalito, namboca,* New Mexico, S to NE Mexico
***J. nigra* L.** *Wallia nigra* (L.) Alef.	**black walnut,** eastern black walnut, American walnut	W Vermont, S Ontario, & New York, W to S Minnesota & SE South Dakota; S to central Texas & NW Florida
***J. regia* L.**	**English walnut,** Persian walnut, Carpathian walnut	SE Europe to Himalayas & China

Sources: Brinkman (1974), Little (1979).

cultural varieties of English and Japanese walnuts have been developed (Brinkman 1974). Black walnut has demonstrated tremendous geographic variation in growth, wood, and fruiting characteristics (Bey 1970; Bresnan and others 1994; Rink and Kung 1995; Rink and Phelps 1989; Rink and others 1994; Williams and others 1985), and selected material has performed well (Beineke 1989; Hammitt 1989). Around 400 cultivars of this species alone have been released (Rink 1988; Williams 1990). Seed collection zones have also been recommended for black walnut (Deneke and others 1980).

Flowering and fruiting. Walnuts are monoecious. The greenish male flowers are slender catkins that develop from axillary buds on the previous year's outer nodes. They range in length from 5 to 7 cm on California walnut to 10 to 20 cm on Arizona walnut (Krochmal and Krochmal 1982; Sargent 1965). The small female flowers, usually 6 to 12 mm long, occur in short terminal spikes on the current year's shoots. The flowers appear with or shortly after the leaves in the spring (table 2). The ovoid, globose, or pear-shaped fruits ripen in the first year. The fruit is a nut enclosed in an indehiscent, thick husk that develops from a floral involucre (figure 1). The diameters range from 1 to 2 cm for little walnut to 5 to 8 cm for butternut (Krochmal and Krochmal 1982; Sargent 1965). The nut (figure 2) is incompletely 2- or 4-celled and has a bony, furrowed shell (figure 3). Available data on seeding habits of 8 species are listed in table 3.

Collection of fruits. Walnut fruits can be collected from the ground after natural dispersal in fall or early winter (table 2), or they may be dislodged from the trees by shak-

Figure 1—*Juglans*, walnut: nuts (enclosed in their husks) of *J. cinerea*, butternut (**left**) and *J. nigra*, black walnut (**right**).

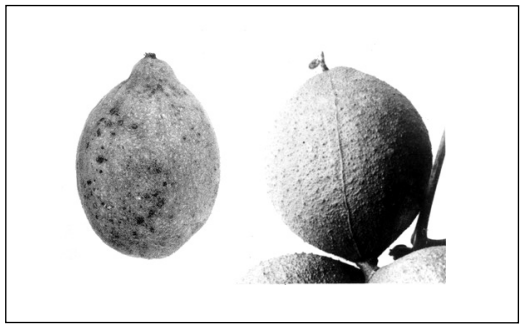


Figure 2—*Juglans*, walnut: nuts (with their husks removed) of *J. cinerea*, butternut (**top left**); *J. hindsii;* Hinds walnut (**top right**); *J. californica,* California walnut (**center left**); *J. nigra;* black walnut (**center right**); *J. microarpa*, little walnut (**bottom left**).

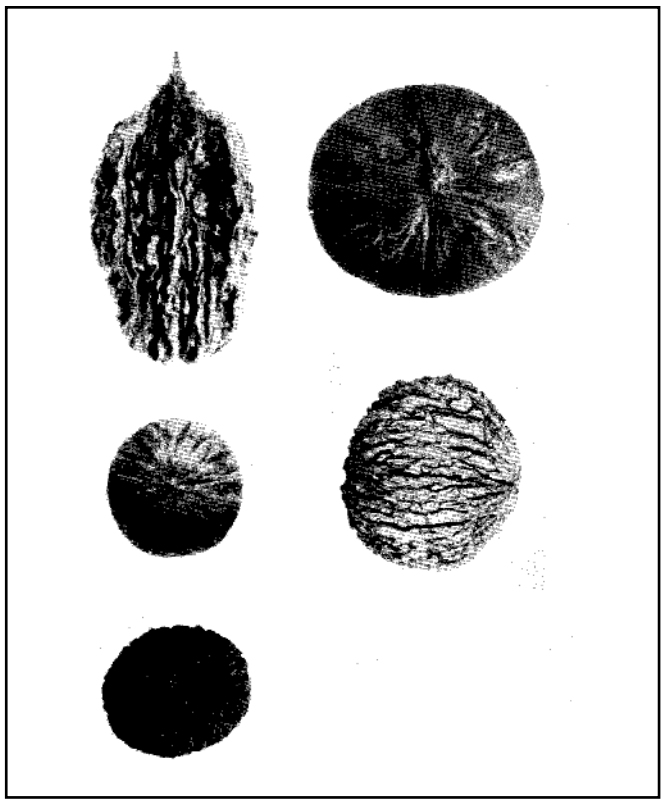


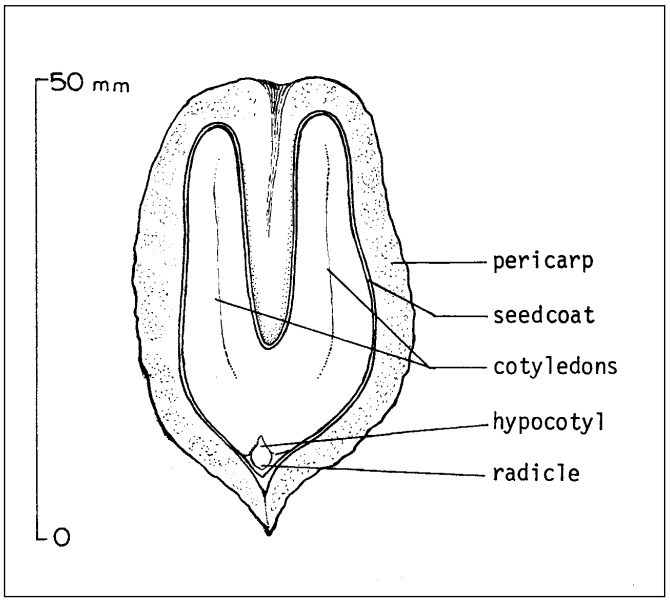
Table 2—*Juglans,* walnut: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
*J. ailantifolia**	May–June	Aug–Oct	Oct
J. californica	Mar–Apr	Fall	Fall
J. cinerea	Apr–June	Sept–Oct	After leaf-fall
J. hindsii	Apr–May	Aug–Sept	Sept–Oct
J. major	Spring	Fall	Fall
J. microcarpa	Mar–Apr	Aug–Sept	Fall
J. nigra	Apr–June	Sept–Oct	After leaf-fall
J. regia	Mar–May	Sept–Nov	Fall

Sources: Brinkman (1974), Rink (1990), Vines (1960), Williams (1990), Wyman (1947).

* Dates are for Japan and Massachusetts.

Figure 3—*Juglans cinera*, butternut: longitudinal section through a seed.



ing branches or the whole tree with mechanical shakers. Collections should start promptly after the nuts are mature to prevent losses to rodents. Maturity is generally indicated by a darkening color of the fruit husk (table 3). Healthy butternut trees will yield up to .3 hl (.9 bu) each of clean nuts, and black walnut may produce 1 hl (2.9 bu) or more of fruit. Even though black walnut nut production is under strong genetic control (Jones 1993), environmental factors are very important. Nut production on pole-sized black walnuts was doubled in one trial by application of nitrogen and phosphorus at 4.5 and 2.3 kg (9.9 and 5.1 lb), respectively, per tree (Ponder 1976). Yield was 400 to 450 nuts/tree. Three hectoliters (8.4 bu) of black walnut and Hinds walnut fruits should yield about 1 hl (2.8 bu) of sound seeds (Brinkman 1974). Yield, size, and number of fruits per weight vary considerably among species (table 4).

Extraction and storage of seeds. Nuts are easy to extract when the husks are in an early stage of softening—that is, firm on the outside but slightly soft next to the nut. Black walnut nuts collected in the eastern United States are

Table 3—*Juglans*, walnut: height, seed-bearing age, seedcrops frequency, and fruit ripeness criteria

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yrs)	Years between large seedcrops	Fruit ripeness criteria	
					Preripe color	Ripe color
J. ailantifolia	20	1860	10	1–3	—	—
J. californica	12	1889	5-8	—	Light green	Dark brown
J. cinerea	30	1633	20	2–3	Greenish bronze	Greenish brown
J. hindsii	24	1878	9	—	Light yellow-green	Dark brown to black
J. major	15	1894	—	—	—	—
J. microcarpa	6	1868	20	—	—	—
J. nigra	46	1686	12	2–3	Light green	Yellowish green
J. regia	27	Long cultivated	8	—	Light yellowish green	Black

Source: Brinkman (1974).

Table 4—*Juglans*, walnut: cleaned seed and other yield data

Species	Place collected	Fruit wt/ fruit vol		Seed wt/ fruit vol		Cleaned seeds/weight				Samples
						Range		Average		
		kg/hl	lb/bu	kg/h	lb/bu	/kg	/lb	/kg	/lb	
J. ailantifolia	Japan	—	—	—	—	130–175	60–80	155	70	2
J. californica	California	—	—	—	—	65–165	30–75	110	50	2
J. cinerea	—	—	—	—	—	33–88	15–40	66	30	13
J. hindsii	Shasta Co., California	47	36	16	12.5	64–175	29–80	100	45	3
J. major	Coconino Co., Arizona	—	—	—	—	170–225	77–102	200	90	10
J. microcarpa	—	—	—	—	—	170–235	78–107	203	92	2
J. nigra	—	62	48	—	—	25–220	11–100	88	40	20+
J. regia	California	—	—	—	—	66–110	30–50	88	40	10+

often spread on the ground in the shade to allow husks to dry and deteriorate. If husks are allowed to dry too much, however, they become very hard and removal is difficult. In the slightly soft stage, husks can be removed by hand or by running the fruits through a macerator or a corn sheller. For commercial quantities of nuts, mechanical hullers are available. After complete husk removal, unfilled nuts can be separated from filled nuts by water floatation. Seeds enclosed in their husks will germinate, but most nurseries find it easier to control seedling density in the beds with cleaned seeds. Husking is necessary if seeds are to be treated with a fungicide.

Walnut nuts are basically orthodox in storage behavior (that is, capable of surviving desiccation), but their high lipid contents put them in the sub-orthodox category (Bonner 1990). Nuts of most species can be stored with or without their husks and are commonly stored without. If their moisture contents are reduced to around 10 to 15%, nuts can be stored at below-freezing temperatures. Long-term storage of walnuts is not common, however, and nuts are commonly stored at higher temperatures and moisture contents. Nuts of Japanese and little walnuts and butternut were successfully stored for several years at relative humidities of 80 to 90% and temperatures of 1 to 4 °C (Brinkman 1974). Cleaned black walnuts with a moisture content of 20 to 40% were stored successfully at 3 °C for a year in plastic bags (Williams 1971b), and nuts with 50% moisture in a screen container were buried in an outdoor pit for 4 years without significant loss in germination capacity (Williams 1971a).

Table 5—*Juglans*, walnut: stratification period, germination test conditions and results

Species	Cold stratification period* (days)	Germination test conditions† Daily light period (hr)	Temp (°C) Day	Temp (°C) Night	Germination rate Days	Germination rate Amt (%)	Germination % Days	Germination % Avg (%)	Germination % Samples	Purity (%)
J. ailantifolia‡	0	—	—	—	42	—	—	75	3	—
J. californica	156	—	—	—	30	—	—	58	3+	—
J. cinerea	90–120	8+	30	20	50–80	54	58	65	7	96
J. hindsii	156	—	30	20	30+	—	—	41	4	—
J. major	120–190	8+	30	20	49	10	28	64	5	—
J. microcarpa	190	—	30	20	30–60	68	14	46	7	94
J. nigra	90–120	8+	30	20	15–40	60	24	50	14+	87
J. regia	30–156	—	30	20	40	—	—	82	4	High

Source: Brinkman (1974).
* Stratification temperatures ranged from 1 to 5 °C.
† Test media were soil or sand.
‡ Seeds were soaked in water for 10 days before sowing.

Table 6—*Juglans*, walnut: nursery practice

Species	Stratification* Medium	Days	Sowing season	Seedlings/area /m²	Seedlings/area /ft²	Sowing depth cm	Sowing depth in	Mulch Type	Mulch Depth cm	Mulch Depth in
J. californica	Peat	150	Spring	—	—	5	2	—	—	1
J. cinerea	Sand	90–120	Spring	—	—	2.5–5	1–2	Sawdust	2.5	1
	—	—	Fall	—	—	2.5–5	1–2	None	—	—
J. hindsii†	—	—	Fall	65–68	700–732	2.5	1	Vermiculite	2.5	1
J. major	Sand or peat	90–150	Spring	—	—	5	2	—	—	—
J. microcarpa	—	—	Fall	35–65	377–700	2.5–5	1–2	Sawdust	2.5	1
J. nigra	Sand	90–100	Spring	35–65	377–700	2.5–5	1–2	—	—	—
J. regia	Sand	30+	Spring	—	—	5	2	—	—	—

Sources: Brinkman (1974), Schultz and Thompson (1990), Williams and Hanks (1976).
* Outdoors during the winter or in a cold room at 1 to 5°C.
† Seeds were soaked in water at 88 °C for $1^{1}/_{2}$ to 2 minutes before sowing.

Pregermination treatment. Seeds of most walnut species exhibit an embryo dormancy that can be broken by stratification at temperatures of 1 to 5 °C (table 5). For Japanese walnut, however, water soaking is adequate (Brinkman 1974). In practice, walnut seeds are either sown in the fall soon after collection or stratified over winter for spring-sowing. Large amounts are sometimes stratified in moist sand covered with at least 15 cm (6 in) of soil, sand, or mulch (Rink 1988). This process can be carried out in a hole in the ground or above ground with wooden sideboards to hold sand, nuts, soil, and mulch in place. Screening is nearly always necessary to exclude rodents, and a fungicide may be applied to prevent disease during stratification. Small lots of seeds may be stratified in plastic bags, moist peat, or sand at the same temperatures for 90 to 120 days. For Illinois sources, at least 100 days of cold stratification are required to overcome dormancy (Van Sambeek and others 1990).

Germination tests. There are no official seed testing prescriptions for walnuts. Germination of stratified nuts can be tested in flats of sand, peat, or soil (table 5). An alternating temperature regime of 20 °C for 16 hours and 30 °C for 8 hours is best; light is not necessary during testing. Nuts can also be tested in laboratory germinators on thick paper wadding, but their size often makes this impractical. Properly stratified seeds usually germinate within 4 weeks, but much variation among seedlots can be expected. Examples of test results are included in table 5. Indirect estimates of viability can also be made with radiographs, although exact predictions of viability are unlikely. If radiopaque agents are employed, cracked seedcoats and damaged tissues can be detected (Vozzo 1978). Moisture determinations can be made on walnuts by breaking open the nuts and drying the pieces for 17 hours at 103 °C (Bonner 1982). If the nuts are not broken, moisture may be trapped inside during drying, and the resulting percentage calculation will underestimate the moisture content.

Nursery practice. Research has demonstrated that a good black walnut seedling should have a top length of 38 to 50 cm (15 to 20 in), a stem diameter of 8 mm ($^1/_3$ in), and 8 to 10 permanent first-order lateral roots (Schultz and Thompson 1990). Unstratified nuts may be sown in the fall soon after collection, usually with the husks removed. It has been reported that husk removal will prevent predation by rodents (Nielson 1973), but subsequent tests have not supported this claim (Phares and others 1974). A hot-water soak of 1.5 to 2 minutes preceding fall-sowing of Hinds walnut has been helpful (Stuke 1960). To minimize alternate freezing and thawing overwinter, seedbeds should be mulched with sawdust, hay, or straw. The heavier mulches must be removed when germination begins in the spring. Stratified nuts must be used for spring-sowing; in the northeastern United States, spring-sown stratified black walnuts had more than double the germination of fall-sown unstratified seeds (DeHayes and Waite 1982). Although only 100 days of stratification may be required to overcome dormancy, additional time (up to 184 days) can increase the rate of emergence (Van Sambeek and others 1990). Some nurseries broadcast the nuts on tilled beds and press them into the soil with rollers, but a more common practice is to sow the nuts by hand in drill marks at a bed density of about 160 nuts/m^2 (15/ft^2). To produce the large seedlings that are necessary for successful outplanting of black walnut, bed densities of 35 to 65 seedlings/m^2 (3 to 6/ft^2) and root pruning in July (for the midwestern United States) to a depth of 15 cm (6 in) are recommended (Schultz and Thompson 1990). Nuts should be covered with 2.5 to 5 cm (1 to 2 in) of nursery soil (table 6); screening to exclude rodents is prudent, especially for fall-sown nuts.

Nuts of Hinds walnuts often are sown directly into growing beds, and the seedlings are then thinned to leave 20 cm (8 in) between plants in the row. A special technique is used in some nurseries: (a) unhulled nuts are air-dried to reduce moisture to about 50% and kept outdoors until January; (b) the partially dried nuts then are put into "sprout beds" containing as many as 3 layers of nuts with 2.5 cm (1 in) of sand below and 2.5 cm (1 in) of vermiculite above each layer; (c) about March 15, the beds are opened up and the sprouted nuts are hand-transferred to growing beds in rows spaced 1.5 m (5 ft) apart with the nuts 20 cm (8 in) apart in the row (Brinkman 1974). Black walnut can also be grown in containers (Van Sambeek 1988a).

Black walnut is susceptible to 2 serious root rot diseases in the nursery caused by *Phytophthora citricola* Sawada and *Cylindrocladium* spp. (Williams 1990). At one time, these diseases were controlled by chemical fumigation of seedbeds, but environmental concerns have eliminated these treatments. An alternative, but less effective, method is to treat the nuts with fungicides before sowing (Brinkman 1990). Because regulations for chemical applications change frequently, persons growing walnut seedlings should check with local state and federal extension agents for the latest information.

Vegetative propagation by cuttings is possible, but difficult (Farmer 1973). Most cultivars are budded or bench-grafted on seedling understock (Dirr and Heuser 1987; Van Sambeek 1988b). There has also been considerable research activity in embryo and tissue culture of walnuts (Long and others 1995; Van Sambeek and others 1990).

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Cupressaceae—Cypress family

Juniperus L.

juniper

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Growth habit, occurrence, and use. There are about 50 species of junipers widely distributed throughout the temperate and subtropical regions of the Northern Hemisphere and south of the Equator in Africa. Most are evergreen shrubs and small trees. Thirteen species are native to the United States (Little 1979), and 11 of these are included in this book (table 1). Eastern redcedar is the most widespread juniper in the eastern United States, and Rocky Mountain juniper and Utah juniper are very common in the West. Common juniper is one of the most widespread tree species in the Northern Hemisphere, ranging from Asia to Europe and North America.

The close-grained, aromatic, and durable wood of the larger junipers was once used for furniture, interior paneling, novelties, posts, poles, fuel, and charcoal (Dealy 1990; Hemmerly 1970; Lawson 1990; Noble 1990; Wilhite 1990). The most important current uses are for firewood, furniture, paneling, and novelty products. Juniper "berries" are used for flavoring in cooking and in gin (the word "gin" is derived from the Dutch word for juniper, *jenever).* Junipers are also valuable for watershed and windbreak plantings, wildlife habitat and food, and ornamental use (Dealy 1990; Johnsen and Alexander 1974; Lawson 1990; Noble 1990; Wilhite 1990). Their utility as ornamental plants has led to the selection and propagation of many horticultural varieties (Dirr and Heuser 1987; Vines 1960). Some junipers are sources for natural oil products. Cedar-wood oil is extracted from the heartwood and foliage of Ashe juniper and eastern redcedar to produce fragrance in soaps, sprays, disinfectants, and cleaning agents. Rocky Mountain juniper oils have the potential for these uses also (Adams 1987). Because of the encroachment of junipers onto range and pasture lands, particularly in the West, considerable effort has been directed toward their control (Burkhardt and Tisdale 1976; Jameson 1966; Johnsen 1962; McPherson and Wright 1990).

Genetic variation and hybridization. Junipers exhibit considerable natural variation in their growth habit and appearance, and studies have established marked differences in color, crown form, growth rate, and disease resistance in eastern redcedar (Henderson and others 1979; Minckler and Ryker 1959; Seidel and Watt 1969; Tauer and others 1987; Van Deusen 1979), Rocky Mountain juniper (Tauer and others 1987), and western juniper (Matthews 1945). Where ranges of the junipers overlap, natural hybridization abounds. This condition probably explains the large number of reported varieties of North American junipers (Dealey 1990; Fassett 1945; Hall 1952; Hall and others 1961; Lawson 1990; Noble 1990; Ross and Duncan 1949; Vines 1960; Wilhite 1990).

Flowering and fruiting. The small, inconspicuous flowers are borne in the spring (table 2) on the ends of short branchlets or along the branchlets. The flowers are dioecious or occasionally monoecious in oneseed juniper and some sources of western juniper (Dealy 1990; Johnsen and Alexander 1974). Pollen cones are yellow, terminal, and about 3 to 4 mm long; ovulate cones are composed of pointed scales, 3 to 8 in number, that fuse to form a fleshy cone 6 to 8 mm long (figure 1) (Brown and Kirkman 1990). The fleshy cones are commonly called berries. Cones are usually greenish in color when immature and change to a bluish black or reddish brown as they mature in the autumn (table 2). Most are covered with a conspicuous glaucous bloom. Cones of alligator, Utah, and common junipers require 2 years to reach full maturity, but those of common juniper may require 3 years in some parts of its range (Johnsen and Alexander 1974; Vines 1960). Cones of the other junipers mature in the fall of the first year (table 2). The outer skins of the cones may be thin and resinous, as in Virginia redcedar and Rocky Mountain and oneseed junipers, or dry and leathery or mealy, as in alligator and Utah junipers (Johnsen and Alexander 1974).

Table 1—*Juniperus,* juniper: nomenclature and occurrences

Scientific name & synonym(s)	Common name(s)	Occurrence
***J. ashei* Buchh.** *J. sabinoides* (H.B.K.) Nees *J. mexicana* Spreng. *J. monticola* Martinez	**Ashe juniper,** mountain cedar, rock cedar, Mexican juniper	S Missouri, N Arkansas, NE & S Oklahoma, central & trans-Pecos Texas, & Mexico
***J. californica* Carr.**	**California juniper,** desert white-cedar	SW Oregon, N California to Baja California & Mexico
***J. communis* L.** *J. sibirica* Burgsd.	**common juniper,** dwarf juniper, prostrate juniper	Greenland, Newfoundland, & Labrador to NW Alaska, S in US from Washington, Montana, North Dakota, & Minnesota to California, Arizona, New Mexico, Georgia, & South Carolina; also in Europe & Asia
***J. deppeana* Steud.** *J. mexicana* Schlecht. & Cham. *J. pachyphlaea* Torr. *J. deppeana* var. *pachyphlaea* (Torr.) Martinez	**alligator juniper,** checkered-bark juniper, western juniper (lumber)	Trans-Pecos Texas to W New Mexico & central Arizona; S to N & central Mexico
***J. monosperma* (Engelm.) Sarg.** *J. occidentalis* var. *monosperma* Engelm. (Engelm.) Cory *J. mexicana* var. *monosperma*	**oneseed juniper,** cherrystone juniper, redberry juniper, west Texas juniper, *sabina*	Colorado, Utah, & Nevada S to SE Arizona, S New Mexico, central Texas, & Mexico
***J. occidentalis* Hook**	**western juniper,** Sierra juniper	W Montana, Idaho, & Washington to Oregon, S California & W Nevada
***J. osteosperma* (Torr.) Little** *J. californica* var. *utahensis* Engelm. *J. utahensis* (Engelm.) Lemmon	**Utah juniper,** bigberry juniper, western juniper (lumber), *sabina*	S Idaho & Nevada & SW Wyoming S to E & SE California, central Arizona, & W New Mexico
***J. pinchotii* Sudworth** *J. monosperma* var. *pinchotii* (Sudworth) Van Melle *J. texensis* Van Melle	**Pinchot juniper,** redberry juniper	Central to NW & trans-Pecos Texas, SW Oklahoma & SE New Mexico
***J. scopulorum* Sarg.** *J. scopulorum* var. *columnaris* Fassett	**Rocky Mountain juniper,** Rocky Mountain redcedar, redcedar, river juniper	NW to SE Alberta, E & S British Columbia, S to W North Dakota & Montana, Washington, E Oregon, Nevada, Colorado, South Dakota, Nebraska, to S Arizona, New Mexico, & trans-Pecos & NW Texas
***J. virginiana* L.** *J. viriginiana* var. *crebra* Fern. & Grisc.	**eastern redcedar,** red juniper, *savin*	SW Maine, W to N New York, S Quebec, Ontario, Michigan, Wisconsin, Minnesota to SW North Dakota, to W Kansas, Oklahoma, to central Texas & E to Georgia
***J. virginiana* var. *silicicola* (Small) J. Silboa** *J. silicicola* (Small) Bailey	**southern redcedar,** eastern redcedar	SE North & South Carolina & S & central Florida, W to S Mississippi & SE Texas

Sources: Johnsen and Alexander (1974), (1971, 1979).

There may be 1 to 4 brownish seeds per juniper cone (table 3). The seeds are rounded or angled, often with longitudinal pits (figure 2) and have thick, bony seedcoats (figure 3). Embedded within the fleshy, white- or cream-colored endosperm is a straight embryo with 2 to 6 cotyledons. Junipers begin bearing seeds when they are about 10 to 20 years old. Heavy seedcrops are irregular, but some seeds are produced almost every year. Large numbers of empty seeds are common in juniper crops, a likely result of poor pollination. Seeds disperse during the autumn, but some ripe cones of most species will persist on the trees through the winter. Seeds are naturally dispersed, usually by birds that eat the cones (Chavez-Ramirez and Slack 1994; Holthuijzen and others 1987; Livingston 1972).

Not much is known about the insects that infest seeds of junipers, or how much damage they do to seedcrops. Larvae of *Eurytoma juniperina* Marcovitch, a sawfly, have been found in seeds of Utah and western junipers and eastern redcedar. Larvae of *Periploca atrata* Hodges and another unnamed Cochylidae moth are known to feed on seeds of alligator and California junipers (Hedlin and others 1980).

Collection of cones. Juniper cones are usually collected in the fall by stripping them from the branches by hand directly into containers. Cones can also be collected by shaking or flailing the limbs to dislodge the cones onto netting or dropcloths on the ground. The larger fruits of alli-

Figure 1—*Juniperus,* juniper: strobili ("berries") of *J. ashei*, Ashe juniper (**top left**); *J. californica*, California juniper **(top center)**; *J. deppeana*, alligator juniper (**top right**); *J. occidentalis*, western juniper (**middle left**); *J. pinchotii*, Pinchot juniper (**middle center**); *J. scopulorum*, Rocky Mountain juniper (**middle right**); and *J. virginiana* var. *silicicola*, southern juniper (**bottom left**); *J. virginiana*, eastern redcedar (**bottom right**).

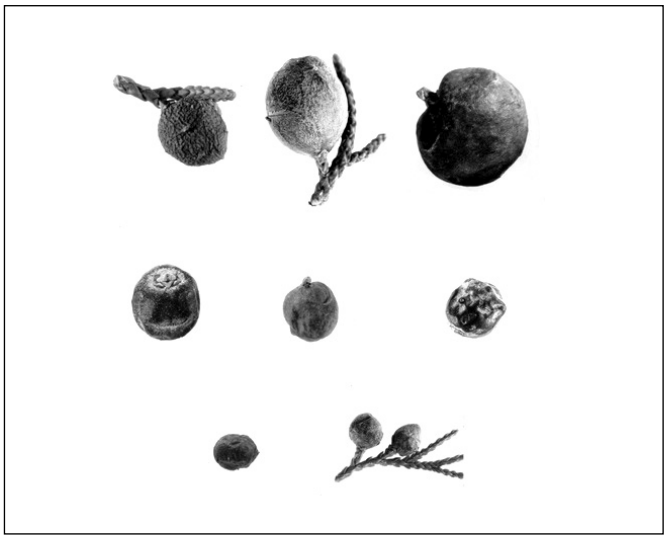
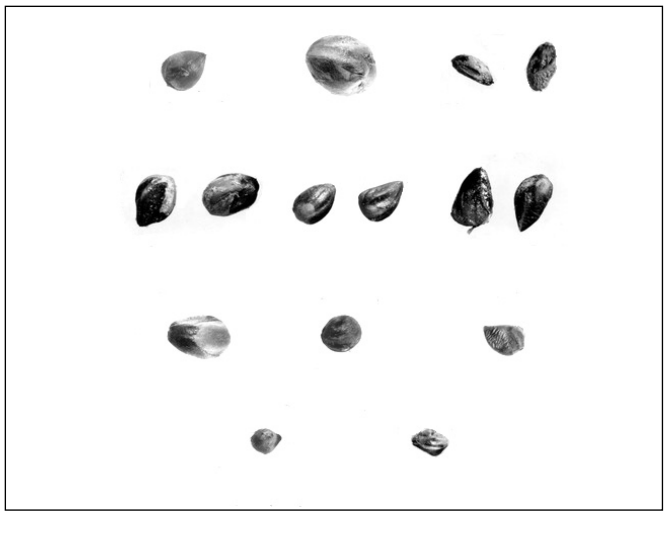


Figure 2—*Juniperus*, juniper: seeds of *J. ashei*, Ashe juniper (**top left**); *J. californica*, California juniper (**top center**); *J. communis*, common juniper (**top right**); *J. deppeana*, alligator juniper (**second row left**); *J. monosperma*, oneseed juniper (**second row middle**); *J. occidentalis*, western juniper (**second row right**); *J. osteosperma*, Utah juniper (**third row left**); *J. pinchotii*, Pinchot juniper (**third row middle**); *J. scopulorum*, Rocky Mountain juniper (**third row right**); and *J. virginiana* var. *silicicola*, southern juniper (**bottom left**); *J. virginiana*, eastern redcedar (**bottom right**).



gator and Utah junipers may be picked up from the ground after dispersal (Johnsen and Alexander 1974). Care should be taken to avoid collecting from plants with large numbers of green immature cones because they are difficult to separate from the mature ones. It is always wise to perform cutting tests on samples from each tree or group of trees to determine the percentage of filled seeds. The number of filled seeds can vary widely from tree to tree, as noted above, and collections can be adjusted to allow for this condition. Although collection can be delayed over much of the winter for some species, it is desirable to collect the fruits as soon as possible after ripening to reduce losses to wildlife. Freshly collected cones should be spread to avoid heating but should not be dried enough to make the fleshy covering tough and difficult to remove.

Table 2—*Juniperus,* juniper: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
J. ashei	—	Jan–Apr	Sept–Nov	Fall–winter
J. communis	—	Apr–May	Aug–Oct	Persists for 2 yrs (2nd–3rd yr)
J. deppeana	—	Feb–Mar	Aug–Oct	Persists for 2 seasons (2nd yr)
J. monosperma	Arizona	Mar–Apr	Aug–Sept	Oct–Nov (persists 1–2 yrs)
J. occidentalis	Oregon	Mid-Apr–mid-May	Mid-Sept	Persists for 2 yrs
J. osteosperma	Arizona	Mar–Apr	Sept (2nd year)	Persists for 2 yrs
J. pinchotii	Texas	Spring	Oct–Nov	Year-round
J. scopulorum	—	Mid–Apr–mid-June	Mid-Sept–mid-Dec	October (persists 2–3 yrs)
J. virginiana	Nebraska	Mid–Mar–mid-May	Sept–Nov	Feb–Mar (1st yr)
J. virginiana var. *silicicola*	South Carolina	Jan–Feb	Oct–Nov	—

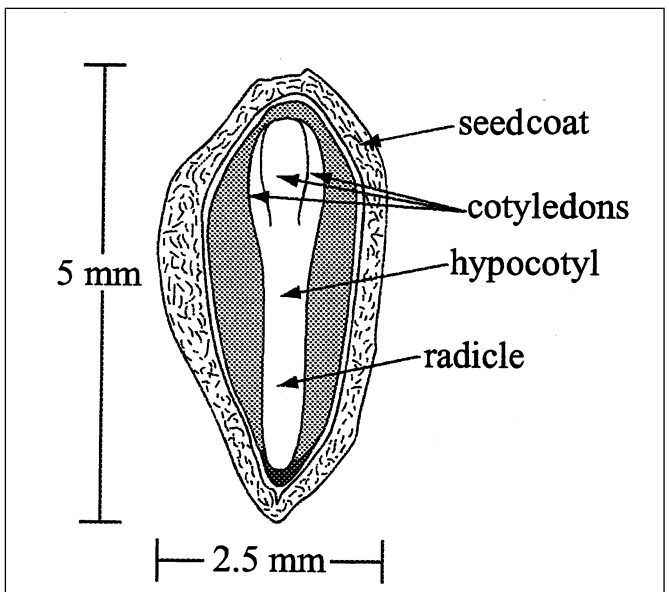
Sources: Johnsen and Alexander (1974), Rehder (1956), Vines (1960).

Table 3—*Juniperus,* juniper: height, seedcrop frequency, and fruit color

Species	Height at maturity (m)	Year first cultivated	Seeds/ cone	Years between large seedcrops	Fruit ripeness criteria	
					Preripe color	Ripe color
J. ashei	3–6	1925	1–2	—	Green	Deep blue
J. californica	1–5	—	1–2	—	Bluish w/dense bloom	Reddish brown
J. communis	1–15	1560	1–3	Irregular	Red	Bluish to black, glaucous
J. deppeana	3–20	1873	2–4	—	Green	Bluish to reddish brown, glaucous
J. monosperma	3–8	1900	1–2	2–5	Green with waxy bloom	Copper to dark blue with white waxy bloom
J. occidentalis	5–9	1840	2–3	—	Green-blue	Bluish black, glaucous
J. osteosperma	5–12	1900	1–2	2	Green glaucous	Reddish brown,
J. pinchotii	1–5	—	1	—	Green with light bloom	Copper to red to reddish brown
J. scopulorum	6–15	1936	1–2	2–5	Green with	Blue w/white waxy bloom
J. virginiana	9–30	1664	1–2	2–3	Green	Blue
J. virginiana var. *silicicola*	7	—	1–2	—	Green	Dark blue

Sources: Johnson and Alexander (1974), Sargent (1965), Vines (1960).

Figure 3—*Juniperus scopulorum*, Rocky Mountain juniper: longitudinal section through a seed.



Extraction and storage of seeds. Twigs, leaves, and other debris should be removed by winnowing, screening, or aspiration. Seeds can be easily extracted from the pulpy cones by maceration with water. Small seedlots can be cleaned with laboratory or kitchen blenders, and large lots can be cleaned in larger macerators. Full seeds should sink, and pulp and empty seeds can be floated off the top of the water (Johnsen 1959; Johnsen and Alexander 1974). For extraction of Rocky Mountain juniper and eastern redcedar seeds, a cone volume to water volume ratio of 1:2.5 is recommended. The pulp residue can then be removed from the filled seeds by adding a little liquid detergent to warm water and agitating for about 5 minutes (Van Haverbeke and Barnhart 1978). Dried fruits should be soaked in water for several hours before macerating. After the seeds have been separated from the pulp and cleaned, they can be prepared for stratification or dried for storage. Intact cones can be stored also, but this is not usually done. Seed yields and weights are listed in table 4.

Juniper seeds are orthodox in storage behavior. They should be air-dried to a moisture content of about 10% and stored at temperatures of 5 to 18 °C (Johnsen and Alexander 1974; Jones 1962; Stoeckler and Slabaugh 1965). There have been no long-term studies to compare different storage temperatures and moisture contents for juniper, but results are available from several sources. Seeds of Ashe juniper stored in a bag at about 5 °C and high humidity retained about half their original viability after 4 years, and seeds of Rocky Mountain juniper stored in sealed containers at 12 to 16 °C (both in dried cones and as cleaned seeds) showed about 30% germination after 3 $^{1}/_{2}$ years (Johnsen and Alexander 1974). The seeds of alligator, oneseed, and Utah junipers stored dry in sealed bags or jars at room temperature for 45, 21, and 9 years, respectively, yielded germination of 17, 51, and 16% (Johnsen 1959).

Pregermination treatments and germination tests. Juniper seeds germinate very slowly due to conditions of deep dormancy. Their dormancy appears to result from internal embryo dormancy, seed coat dormancy, germination inhibitors in the pulp of the cones, or a combination of all

Table 4—*Juniperus*, juniper: seed yield data

Species	Place collected	Cleaned seeds/weight: Range /kg	Range /lb	Average /kg	Average /lb	Samples
J. ashei	—	—	—	22,270	10,100	1
J. communis	—	56,120–120,170	25,450–54,500	80,480	36,500	8
J. deppeana	Arizona	19,840–34,400	9,000–15,600	28,270	12,820	5
J. monosperma	Arizona & New Mexico	33,650–44,100	15,260–20,000	40,350	18,300	10
J. occidentalis	Oregon	17,640–34,970	8,000–15,860	27,120	12,300	—
J. osteosperma	Arizona	7,940–15,660	3,600–7,100	10,910	4,950	15
J. pinchotii	Sonora & Texas	21,280–30,650	9,650–13,900	24,230	10,990	2
J. scopulorum	Arizona	39,360–92,830	17,850–42,100	59,760	27,100	36
J. virginiana	Great Plains	81,580–121,270	37,000–55,000	96,140	43,600	34

Sources: Johnsen and Alexander (1974), Stoeckler and Slabaugh (1965), Vines (1960).

three (Johnsen and Alexander 1974). There is wide variation among species in degree of dormancy. The least dormant may be eastern and southern redcedars, whereas Rocky Mountain juniper is among the most dormant (Rietveld 1989). There is also considerable variation among sources and crop years; some seedlots from alligator and oneseed junipers germinated without any stratification (Johnsen 1959; Meagher 1943; Riffle and Springfield 1968).

The most common treatment for overcoming dormancy is long periods of moist stratification at 3 to 5 °C. Periods of 30 to 180 days have been used for seeds of Ashe, alligator, and oneseed junipers and eastern redcedar (Barton 1951; Benson 1976; Johnsen and Alexander 1974; Taylor 1941). Early reports suggested freezing juniper seeds during stratification, but this method has generally been unsuccessful (Johnsen and Alexander 1974). Seeds of common, Utah, and Rocky Mountain junipers, eastern redcedar, and possibly western juniper often respond positively to warm stratification at room temperature (around 25 °C) or alternating temperatures of 20 °C (night) and 30 °C (day) for 45 to 240 days, followed by cold stratification for similar periods (Johnsen and Alexander 1974; Rietveld 1989; Van Haverbeke and Comer 1985). Young and others (1988), however, reported no response by western and Utah junipers to the 2-temperature pretreatment. The best treatment for eastern redcedar was to first soak the seeds for 96 hours in a 10,000 ppm solution of citric acid, followed by warm stratification for 6 weeks and cold stratification for 10 weeks (Van Haverbeke and Comer 1985). The use of citric acid was suggested by Cotrufo (1963), and although the nature of the stimulation is unknown, some seedlots respond with faster germination rates. Faster germination has also been reported for seeds of Pinchot and Rocky Mountain junipers and eastern redcedar that were soaked in concentrated sulfuric acid for periods of 35 to 120 minutes (Djavanshir and Fechner 1976; Johnsen and Alexander 1974), although stimulation for the latter 2 species occurred only when the carbonized layer was removed from the surface of the seeds (Djavanshir and Fechner 1976). Washing seeds of oneseed juniper in running water for 48 hours, followed by 30 minutes in 30% hydrogen peroxide, stimulated germination to 79% from 47% for untreated controls (Riffle and Springfield 1968). Another promising method reported for western and Utah junipers is 12 weeks of soaking in aerated water at 5 °C; germination percentages of around 50% were recorded for both species. If gibberellin (GA_3 at 0.289 mmol/liter) was added to the aerated solution, germination increased to 84% for western juniper and to 64% for Utah juniper (Young and others 1988).

Prescriptions for official germination tests have been established for 3 species: common juniper, eastern redcedar, and Rocky mountain juniper (ISTA 1993). Tetrazolium staining is the recommended method for these species, but alternative stratification directions are also suggested. Common juniper should be stratified for 90 days at 3 to 5 °C, whereas eastern redcedar and Rocky Mountain juniper seeds should receive 60 days at 20 °C, followed by 45 and 40 days, respectively, at 3 to 5 °C. Recommended germination temperatures are 20 °C for common juniper and 15 °C for eastern redcedar and Rocky Mountain juniper. Germination of Pinchot juniper is reported to be best at 18 °C (Smith and others 1975), but no data exist for the other junipers. There is obviously much to learn about stimulation of germination for the junipers, and more research is called for. Germination capacities for various pretreatments and test conditions are given in table 5. Germination is epigeal (figure 4).

Nursury practices. Juniper seeds are usually sown in the late summer or fall, but may be sown in the spring or early summer. All seeds should usually be stratified, no matter when they are sown, but untreated seeds can be used in some circumstances. Untreated fresh seeds may be sown in the fall within a week after collection and extraction if they are not dried (Meines 1965). Stratified seeds sown in the spring should be in the ground early enough to ensure complete germination before the air temperatures go higher than 21 °C. If stratification is successful, germination should begin 6 to 10 days after sowing and be completed in 4 to 5 weeks (Johnsen and Alexander 1974; Stoeckler and Slabaugh 1965).

Juniper seeds are usually drilled in rows 15 to 20 cm (6 to 8 in) apart and covered with about 6 mm ($^1/_4$ in) of firmed soil or sand (Stoeckler and Slabaugh 1965). The seeds are occasionally broadcast by hand onto the seedbed and covered with sand. The beds should be mulched with straw, sawdust, burlap, or plastic film to prevent winter drying, alternate freezing and thawing, and premature germination in the spring. The mulch normally must be held in place to prevent blowing (Stoeckler and Slabaugh 1965). The seedbeds should be kept moist, and burlap or plastic film mulches should be removed as soon as germination begins. Light shade should then be provided by slat-wire snow fence or plastic screening materials; young seedlings of eastern redcedar and Ashe, oneseed, and Rocky Mountain junipers should be shaded throughout the first growing season. Seedlings of alligator juniper (figure 4) should be shaded only during the germination period (Johnsen and Alexander 1974). Burlap may be used over snow-fence shade structures to conserve moisture and to protect against early spring freezing (Stoeckler and Slabaugh 1965). During the autumn,

Figure 4—*Juniperus deppeana*, alligator juniper: seedling development at 2, 17, 43, and 96 days after germination

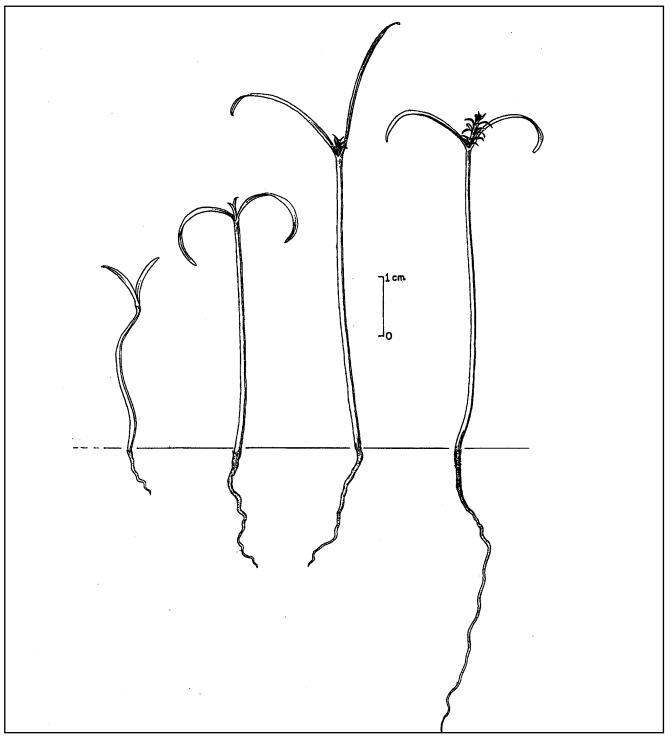


Table 5—*Juniperus,* juniper: germination test conditions and results

Species	Stratification period (days)		Germination test conditions				Germination rate		Germination percentage		Samples
	Warm*	Cold†	Daily light (hr)	Medium	Temp (°C) Day	Temp (°C) Night	Days	%	Days	%	
J. ashei	0	120	—	Sand	86	68	60	30	10	33	1
	0	120	—	Sand	50	50	60	27	29	36	1
J. communis	60–90	90+	8	Paper, sand	86	68	20–30	—	—	7–75	10+
J. deppeana	0	0	—	Paper, sand	86	68	40	—	—	16-30	2
	0	30–60	—	Sand, peat	86	68	30–40	—	—	45	1
J. monosperma	0	0	—	Sand, peat, soil	86	68	30–70	—	—	20–75	34
J. osteosperma	120	120	—	Sand, soil	86	68	70	—	—	8–49	8
J. pinchotii‡	0	0	8	Perlite	60	60	36+	—	—	63	4
	30	60	8	Perlite	60	60	—	—	—	53	4
J. scopulorum	120	120	—	Paper, sand	86	68	20–30	5–31	8–15	22	7
J. virginiana	0	30–120	—	Paper, sand	50	77	20–30	6–74	9–24	76	16
	4§	90	0	Perlite	58	58	60	84	30	87	3
	0	45	—	Kimpak	60	60	66	70	43	78	2

Sources: Cotrufo (1963), Johnsen (1959), Johnsen and Alexander (1974), Meagher (1943), Riffle and Springfield (1968).
* 30 to 20 °C alternated diurnally.
† 5 °C.
‡ Seeds soaked in sulfuric acid 45 minutes.
§ Seeds soaked in 1% citric acid for 4 days.

the seedlings may change color due to freezing weather, reduced watering, or increased light intensity resulting from removal of the half-shades. Seedlings of eastern redcedar change from green to purple, most markedly with the 1+0 seedlings. The normal green color returns the next spring.

In the West, juniper seedlings are usually transplanted in the nursery after the first or second year. Early lifting in the spring gives the best survival. Roots must be kept moist during lifting, and the seedlings can be stored as long as a week before transplanting with little damage if kept cool and moist (Afanasiev and others 1959). Spacing in the transplant bed ranges from 15 by 2.5 cm (6 by 1 in) to 20 by 5 cm (8 by 2 in) for eastern redcedar and Rocky Mountain juniper (Johnsen and Alexander 1974; Stoeckler and Slabaugh 1965). Undercutting of third-year transplants of Rocky Mountain juniper seems to stimulate strong lateral root development (Stoeckler and Slabaugh 1965).

The most serious nursery disease that affects junipers is the cedar blight, which is caused by *Phomopsis juniperovora* Hahn (Otta and others 1980; Peterson 1973; Stoeckler and Slabaugh 1965). Good sanitation practices in the nursery and chemical control measures are needed to keep this disease in check. Once established in a nursery site, it is very difficult to eradicate (Stoeckler and Slabaugh 1965). Other diseases that cause problems for junipers are cercospora blight, caused by *Cercospora sequoiae* Ellis & Everh. var. *juniperi* Ellis & Everh. (Peterson 1977; Peterson and Wysong 1968) and cedar apple rust, caused by *Gymnosporangium juniperi-virginianae* Schwein. (Stoeckler and Slabaugh 1965). Application regulations and chemical recommendations change frequently, so local extension experts should be consulted for the current chemical control measures for these diseases in the nursery.

Other nursery pests that affect junipers are nematodes, grubs, and red spiders—*Pentamerismus erythrens* Ewing. Foliage may be damaged by winter injury and drying out, even in second-year beds and transplant beds. The plants usually recover during the spring. Small juniper seedlings are also subject to frost heaving, which can be reduced by heavy mulching or overhead sprinklers (Stoeckler and Slabaugh 1965).

Many junipers can be propagated vegetatively with cuttings (Dirr and Heuser 1987). There is evidence of wide variation in rooting ability among populations of common juniper (Houle and Babeux 1994). Rooting success as high as 82% has been reported for Rocky Mountain juniper (Edson and others 1996). Treatment of the 12-cm-long (5-in-long) cuttings with 1.6 or 3.0% indole-butyric acid (IBA) accelerated rooting by several months and increased overall succes by up to 36%. Two years after transplanting to containers, 92% of the stecklings survived.

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Ericaceae—Heath family

Kalmia latifolia L.

mountain-laurel

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Synonyms. *Kalmia latifolia* var. *laevipes* Fern.

Other common names. Broad-leaved laurel, calico-bush, spoonwood, ivy, mountain ivy, big-leaved ivy, ivy-bush, laurel-leaves, and calmoun.

Growth habit and occurrence. The genus *Kalmia* L. consists of about 6 species of evergreen or deciduous shrubs native to North America and Cuba (LHBH 1976). Of these species, mountain-laurel—*Kalmia latifolia* L.—has for a number of reasons attracted the most attention. Mountain-laurel is a broad-leaved, evergreen shrub that is dense and symmetrical when young but develops an open, loose habit with age (Dirr 1990). Typically, the shrub reaches a height and spread of 1.5 to 2 m. However, heights of 4.6 to 9 m have been reported (Bridwell 1994; Dirr 1990). The species has a wide range, from coastal Maine to northwestern Florida, primarily along the Appalachian Mountain range, westward to Louisiana and northward into southern Ohio and Indiana (Fernald 1950; Jaynes 1997). This range includes USDA Hardiness Zones 4 to 9 (Dirr 1990). Mountain-laurel is often found in rocky or gravelly woods and clearings, typically on acid or sterile soils (Fernald 1950). A common associate of mountain-laurel in the mountainous regions of the southern United States is rosebay rhododendron—*Rhododendron maximum* L. Together, these 2 species form almost impenetrable thickets, sometimes known locally as "laurel slicks" or "rhododendron hells" (Olson and Barnes 1974).

Use. Mountain-laurel is an excellent ornamental shrub for shady borders and for naturalizing (Dirr 1990). As an understory shrub, it effectively prevents water runoff and soil erosion (Jaynes 1997). Clumps and thickets of mountain-laurel are a haven for wildlife, providing year-round cover and protection (Jaynes 1997). Practical considerations aside, Rehder (1986) has described mountain-laurel as one of the most beautiful American flowering shrubs. In addition to the value of the species as a landscape plant, the foliage is also used in Christmas decorations and the fine-grained and durable wood is used for making pipes and other items (Jaynes 1997). Unfortunately, the foliage of mountain-laurel is poisonous and caution should be exercised when planting in a landscape utilized by young children or grazing animals (Jaynes 1997; Mabberley 1993).

Geographic races and hybrids. Five races of mountain-laurel have been identified:

- *Kalmia latifolia* f. *angustata* Rehd.
- *Kalmia latifolia* f. *fuscata* (Rehd.) Rehd.
- *Kalmia latifolia* f. *myrtifolia* (Bosse) K. Koch.
- *Kalmia latifolia* f. *obtusata* (Rehd.) Rehd.
- *Kalmia latifolia* f. *polypetala* (Nickolsen) Beissner, Schelle, & Zabel.

There are 4 interspecific crosses that produce progeny:

- *K. polifolia* Wangenh. × *K. latifolia*—reciprocal cross did not result in seed set (Jaynes 1997)
- *K. latifolia* × *K. hirsuta* Walt.—reciprocal cross also set seed (Jaynes 1997)
- *K. angustifolia* L. × *K. latlifolia*—reciprocal cross did not result in seed set (Jaynes 1997)
- *K. polifolia* × *K. microphylla* (Hook.) A. Heller—reciprocal cross also set seed (Jaynes 1997)

There is also 1 intergeneric cross known to produce progeny:

- *K. latifolia* × *Rhododendron williamsianum* Rehd. & Wils.—putative hybrid (Jaynes 1997)

Flowering and fruiting. Mountain-laurel typically flowers between April and June, depending on local climate (Radford and others 1968). Floral color ranges from white to a deep rose with purple markings (Dirr 1990). There have been many cultivar selections across this color spectrum

(Jaynes 1997). An individual shrub commonly has hundreds of terminal inflorescences (corymbs), each with 50 to 300 flowers (Rathcke and Real 1993). Flower size also varies with different forms and cultivars of the species, but the normal diameter ranges from 2 to 2.5 cm (Dirr 1990). Flowers have an unusual pollination mechanism, with 10 anthers held in pouches along the inside of the corolla (Mabberley 1993). When pollen is ripe, a visiting insect—typically a bumble bee (*Bombus ternarius* Say)— triggers the release of the anthers (Rathcke and Real 1993). The pollen is then cast over the insect so that cross pollination can occur with the next flower of mountain-laurel visited by the insect. Typically, mountain-laurel is considered to be a non-selfing species (Fryxell 1957; Jaynes 1997). A recent study by Rathcke and Real (1993) suggested that certain populations of mountain-laurel may be able to self-fertilize in the absence of pollinators. Autogamy seems most likely to have evolved for reproductive assurance under competition for pollinator service (Rathcke and Real 1993). The fruit is a brown, 5-valved, globular dehiscent capsule about 6 mm in diameter, borne in clusters, that matures in September and October (Radford and others 1968) (figure 1).

Collection of fruits and seed extraction. Once seed capsules have turned brown and dried, seeds are mature and ready for harvest. Harvested capsules should be placed in a coin envelope, paper bag, or small vented container and allowed to dry for an additional 2 to 4 weeks at about 21 °C. Capsules will then open, and their seeds can be shaken loose (Blazich 1996; Jaynes 1997). The seeds are cleaned by gently shaking them down a creased sheet of paper (Jaynes 1997). Seeds will move down the paper faster than the chaff. This process should be repeated several times until clean seeds are separated. If the capsules are collected prematurely, they will not dehisce and must be crushed. This treatment results in large amounts of debris that can be removed effectively by sieving. Viable seeds can also be separated from chaff and empty seeds by using an air-column blower or by placing crushed capsules in water and allowing viable seeds to sink (Jaynes 1997). Seeds of mountain-laurel are extremely small, with cleaned pure seeds averaging 50,000/g (1.4 million/oz) (Jaynes 1997). Each seed is about 1 mm long and 0.3 mm wide, with a ribbed or striated surface (figures 2 and 3).

Storage. Seeds of mountain-laurel can remain viable for several years when stored at room temperature (Glenn and others 1998; Wyman 1953). However, longevity of seeds can be extended greatly (up to 15 years) if seeds are stored at 4.4 °C (Jaynes 1997). When dried to a moisture content of 5%, seeds have been stored successfully for 4 years at –18 or 4 °C with no loss in viability (Glenn and others 1998). Storage under these conditions suggests that the species is orthodox in storage behavior, and that viability can be maintained for extremely long periods of time.

Pretreatments and germination tests. After harvest, there is no inhibiting dormancy, and seeds germinate readily with no pretreatment necessary (Fordham 1960; Jaynes 1997). However, stratification (moist-prechilling) for 8 weeks or soaking seeds overnight in 200 ppm gibberellic acid may increase germination (Jaynes 1997). Seeds of mountain-laurel require light for germination (Jaynes 1971; Malek and others 1989). Malek and others (1989) conducted a 30-day germination study of seeds from a native popula-

Figure 1—*Kalmia latifolia*, mountain-laurel: cluster of capsules (**top**) and a single capsule (**bottom**).

Figure 2—*Kalmia latifolia*, mountain-laurel: seeds.

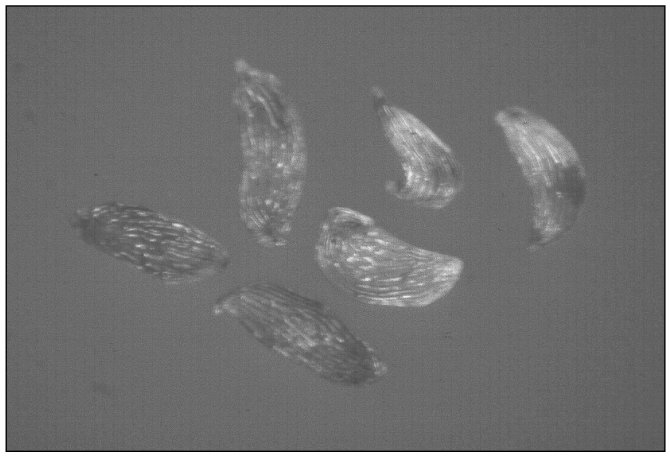
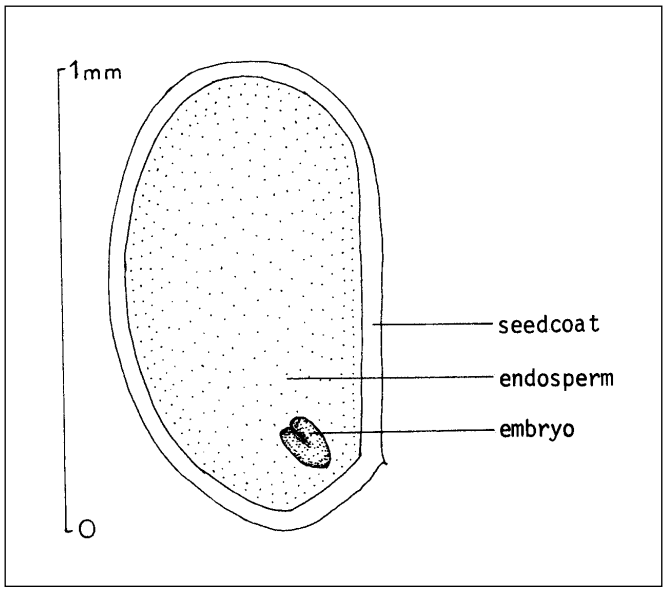


Figure 3—*Kalmia latifolia*, mountain-laurel: longitudinal section of a seed.



tion growing in Avery County, North Carolina. Seeds were germinated at 25 °C or an 8/16-hour thermoperiod of 25/15 °C with daily photoperiods of 0, $^1/_2$ hour, $^1/_2$ hour twice daily, 1 hour, or 2, 4, 8, 12, or 24 hours. The cool-white fluorescent lamps used as the light source provided a photosynthetic photon flux (400 to 700 nm) of 42 μmol/m^2/sec (3.2 klux). For both temperatures, no germination occurred during the 30-day test period for seeds not subjected to light. At 25 °C, increasing the length of the photoperiod increased germination, with germination of 82 and 90% occurring by day 27 for the 12- and 24-hour photoperiods, respectively. The alternating temperature of 25/15 °C enhanced germination when light was limiting. At this temperature, germination ≥ 87% occurred by day 24 for photoperiods ≥ 8 hours. There are no test methods prescribed for official testing of this species.

Nursery practice. Seeds should be sown directly on peat, placed under lights, and maintained at 24 °C (Dirr 1990). Other media can also be used (Jaynes 1997). Initial seedling growth is very slow (Dirr and Heuser 1987; Weinberg 1984), although Malek and others (1992) reported that seedling growth can be optimized under long-day conditions with 9/15-hour day/night temperatures of 22 to 26/22 °C. To stimulate seedling growth further, the ambient atmosphere can be supplemented with 2,000 ppm carbon dioxide (Jaynes 1997). Seedlings should be transplanted 2 to 6 months after germination into pots with a medium consisting of 70 liters (2 bu) peat, 35 liters (1 bu) perlite, 17 liters ($^1/_2$ bu) coarse sand, and 15 to 30 g (0.5 to 1 oz) hydrated lime and fertilized every 3 weeks with a 20-20-20 ($N:P_2O_5:K_2O$) water-soluble fertilizer at a rate of 1.2 g/liter (0.04 oz/1.06 qt) (Jaynes 1997).

Traditionally, mountain-laurel has been propagated vegetatively by layering, grafting, and stem cuttings. However, there has been limited success with vegetative propagation by stem cuttings and results appear to be genotype specific (Dirr and Heuser 1987). On the other hand, micropropagation (tissue culture) has proven very successful and has led to wide availability of outstanding selections and hybrids of the species (Lloyd and McCown 1980).

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Araliaceae—Ginseng family

Kalopanax septemlobus (Thunb. ex A. Murr.) Koidz.

castor-aralia

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Synonym. *K. pictus* (Nakai).

Growth habit, occurrence, and use. The genus *Kalopanax* comprises 1 species of deciduous, small to medium-sized tree that is native to China, Japan, eastern Russia, and Korea (LHBH 1976; Ohashi 1994). Castor-aralia—*K. septemlobus* (Thunb. ex A. Murr.) Koidz.—was introduced in 1865 and has been used primarily for ornamental purposes, as a shade tree yielding a tropical effect in USDA Hardiness Zones 4 to 7 (Dirr 1990; Hillier 1991; Krüssmann 1984; van Gelderen and others 1994; Wijnands 1990). It is a valuable tree in China (Zhao and others 1987) and the wood may be suitable for bentwood, carving, and some interior use (KRRT 1987). The dried bark has been used as a medicine in China for various ailments (Sano and others 1991). Analysis of the nutrient content of leaves of castor-aralia showed plentiful levels of calcium, magnesium, zinc, iron, and beta-carotene, making it a potential food source of high nutritive value (Liu and others 1998). Phytochemical investigations have allowed the isolation and characterization of saponin and phenolic compounds (Porzel and others 1992; Sano and others 1991; Shao and others 1989, 1990; Sun and others 1990) that are reported to show preventive activity against stress-induced changes in mice.

Castor-aralia is an upright, oval-rounded tree that can obtain heights of 24.4 to 27.4 m in the wild, but under cultivation practices usually 12.2 to 18.3 m (Dirr 1990). The branches are coarse, stout, and bear numerous broad-based prickles (Dirr 1990; Hillier 1991). The leaves are quite variable—but somewhat similar in shape to sweetgum, *Liquidambar styraciflua* L.—changing to yellow or red in the fall (Dirr 1990). Another variety—*K. septemlobus* var. *maximowiczii* (Van Houtte) Hand.-Mazz.—has leaves that are deeply lobed (5–7) and incised to beneath the middle of the blade (Krüssmann 1984).

Flowering and fruiting. The perfect, white flowers, which bloom in July to early August (sometimes as early as May in parts of Japan), are produced in numerous umbels, forming large terminal panicles that measure 30.5 to 61 cm across (Dirr 1990; Hillier 1991; Rudolf 1974). The fruits are globose drupes about 0.4 cm wide with a persistent style (bluish black in color) that contains 2 flat seeds (Dirr 1990; Krüssmann 1984). The fruits, which ripen in September–October, have a fleshy coat and are relished by birds (Dirr 1990; Dirr and Heuser 1987).

Collection of fruits; extraction, cleaning, and storage of seeds. The fruits are harvested by hand or shaken onto canvas as they ripen in September–October (Rudolf 1974). Fruits should be run through a macerator with water to extract the seeds (figure 1). Although more recent information was not attainable, Sins (1925, cited by Rudolf 1974) reported that about 3.6 to 4.5 kg (8 to 10 lb) of clean seeds can be obtained from 45.4 kg (100 lb) of fresh fruits. The number of cleaned seeds per weight was 220,000/kg (99,790/lb) (Satoo 1992). The seeds (figure 2) have small embryos and contain endosperm tissue (Rudolf 1974). Reports indicate that seeds can be kept satisfactorily for 1 year under ordinary storage conditions (Sins 1925, cited by Rudolf 1974). However, the use of sealed containers kept at 0 to 5 °C is suggested for longer storage periods.

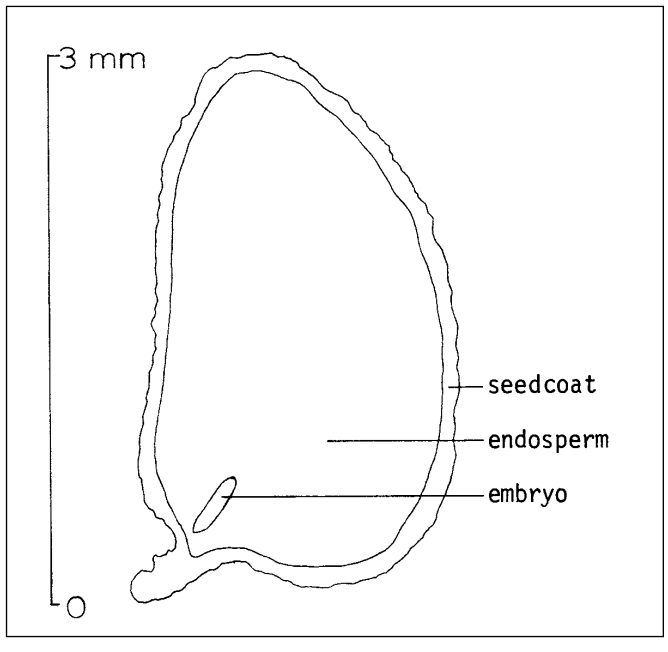
Figure 1—*Kalopanax septemlobus*, castor-aralia: cleaned seed extracted from the fleshy fruit.

Pregermination treatments. Under natural conditions, castor-aralia seeds require a 2-year germination period (Sato 1998). Dormancy of the seed is caused by neutral (coumarin) and acid (abscisic) inhibitors present in the seedcoat and endosperm, and by an impermeable seedcoat (Dirr 1990; Huang 1987a&b). Warm temperatures of 15 to 25 °C for 3 to 5 months followed by cold stratification at 0 to 5 °C for 2 to 3 months will overcome seed dormancy and give reasonable germination (Dirr and Heuser 1987; Huang 1986, 1987b; Sato 1998; Xu and Han 1988). Soaking the seeds in sulfuric acid for 30 minutes will substitute for the warm stratification period (Dirr and Heuser 1987; Rudolf 1974).

Germination tests. Tests in germinators or sand flats for 60 days is suggested (Rudolf 1974).

Nursery practice and seedling care. Fresh seeds that have been cleaned and dried can be sown in the fall but will not germinate for 2 years (Dirr and Heuser 1987; Satoo 1992). Stratified seeds should be sown in the spring (Rudolf 1974). The seeds should be sown in well-prepared beds at a rate of 1,760 to 3,300/m^2 (164 to 307/ft^2) to give 200 to 300 seedlings/m^2 (19 to 28/ft^2) (Satoo 1992). Castor-aralia can be propagated by root cuttings (Dirr and Heuser 1987; Macdonald 1986). Root cuttings, 7.6 to 10.2 cm (3 to 4 inches) in length, should be dug soon after frost and then placed upright (proximal end) in a medium kept in a cool greenhouse with bottom heat (Dirr and Heuser 1987). Stem cuttings are difficult, if not impossible, to root from mature trees (Dirr and Heuser 1987).

Figure 2—*Kalopanax septemlobus*, castor-aralia: longitudinal section through a seed.



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K

Chenopodiaceae—Goosefoot family

Kochia Roth

kochia

Stanley G. Kitchen and Stephen B. Monsen

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Growth habit, occurrence, and use. Two woody-based non-rhizomatous sub-shrub species of kochias are found in the western United States. The widely distributed native, gray molly, and its introduced and closely related counterpart (Blackwell and others 1978), forage kochia, are found in salt-desert, sagebrush, pinyon–juniper, and dry mountain brush communities (table 1). Erect to steeply ascending annual stems growing from a woody base and long-lived prostrate branches attain heights of 5 to 50 cm for gray molly (Welch and others 1987) and 10 to 100 cm for forage kochia (Baylan 1972).

Each species provides nutritious winter forage for livestock (Baylan 1972; Blauer and others 1976). Variability in preference by livestock (Shishkin 1936) and mule deer (*Odocoileus hemionis*) (Davis and Welch 1985) has been observed among ecotypes of forage kochia.

Both species have potential for use in revegetation of saline and alkaline soils on arid and semi-arid sites (Blauer and others 1976; Clarke and West 1969; Francois 1976; Romo and Haferkamp 1987) and forage kochia has been used successfully in stabilizing mine spoils (Frischknecht and Ferguson 1984). Perhaps the greatest potential use of forage kochia is in providing cover and forage on degraded western cold-deserts (McArthur and others 1974; Monsen and Turnipseed 1990; Pendleton and others 1992). Where established, it effectively competes with weeds such as halogeton (*Halogeton glomeratus* (Bieb.) C.A. Mey.) and cheatgrass (*Bromus tectorum* L.) (Blauer and others 1993; McArthur and others 1990). Natural spread of forage kochia from seeds can be rapid where perennial cover is lacking. The high water content of stems and leaves during summer months and crown sprouting capacity make this species especially desirable for desert landscapes prone to high fire frequencies (Kitchen and Monsen 1999).

Geographic races and hybrids. Blackwell and others (1978) concluded that the random variation in pubescence in gray molly did not justify dissection of this species to subspecies level. Conversely, forage kochia is a complex species represented by 3 known ploidy levels (2X, 4X, and 6X) (Pope and McArthur 1977) and extensive phenotypic variation in plant stature, stem color and diameter, leaf size and pubescence, growing season, and adaptability to soils (Baylan 1972). Numerous regional ecotypes have been grouped into as many as 4 species; however, a single species with 2 subspecies—*virescens* (Frenzl) Prat. (green-stem) and *grisea* Prat. (gray-stem and highly variable)—is the most commonly accepted (Baylan 1972).

About 40 accessions of forage kochia have been introduced to the United States, primarily for evaluation as candidates for revegetation of disturbed arid and semi-arid regions in the western United States (Kitchen and Monsen 1999). To date, a single cultivar, 'Immigrant' (2X, ssp.

Table 1—*Kochia,* kochia: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***K. americana* S. Wats.** *K. vestita* (S. Wats.) Rydb. *K. americana* var. *vestita* S. Wats.	**gray molly,** green molly	Oregon to Montana S to California, Arizona, & New Mexico
***K. prostrata* (L.) Schrad.** *K. suffruticulosa* Lessing *Salsola prostrata* L.	**forage kochia,** prostrate kochia, summer-cypress, prostrate summer-cypress	Deserts, steppes, & mtns of Central Asia, W to the Mediterranean Basin, & E to Manchuria; naturalized in W North America

Sources: Shishkin (1936), Welsh and others (1987).

virescens), has resulted from this research (Stevens and others 1995). 'Immigrant' has been planted on several thousand acres in Utah, Idaho, and surrounding states. Small plantings of other accessions (ssp. *grisea*) also exist (Blauer and others 1993; McArthur and others 1990; Monsen and Kitchen 1995; Monsen and Turnipseed 1990).

Flowering and fruiting. Kochia flowering structures are described as one to several, mostly perfect, inconspicuous, sessile flowers occurring in axils of foliose bracts (Welsh and others 1987). Stems are potentially floriferous throughout (Blackwell and others 1978). Flowering is indeterminate from May to August for gray molly and from July to September for forage kochia (Shishkin 1936). The fruit is a 1-seeded utricle that is enclosed in a thin, fragile perianth (figure 1). The perianth is horizontally winged at maturity. Perianth pubescence for forage kochia is highly variable (Baylan 1972). Seeds are oval to orbicular in shape and 1 to 2 mm in diameter. The embryo is bent into roughly the shape of a horseshoe, a common configuration for this family (figure 2).

Fruit collection and cleaning. Fruits of forage kochia ripen from September to November (Baylan 1972) whereas those of gray molly are generally ripe by mid-October. Fruits are easily dislodged when fully ripened and dry. They are hand-harvested by stripping individual stems or by beating seeds into a hand-held hopper with a badminton racket or similar device. Mechanical harvest techniques for forage kochia seeds include mowing stems just before fruits are ready to shatter, drying, and combining. Vehicle-mounted mechanical sweepers are also used to harvest fully ripened fruits from solid stands (Stevenson 1995). Although harvesting the fruits before the seeds are fully ripened can reduce losses to shattering, it also results in lower seed viability

Figure 1—*Kochia prostrata*, forage kochia: fruits in perianth.

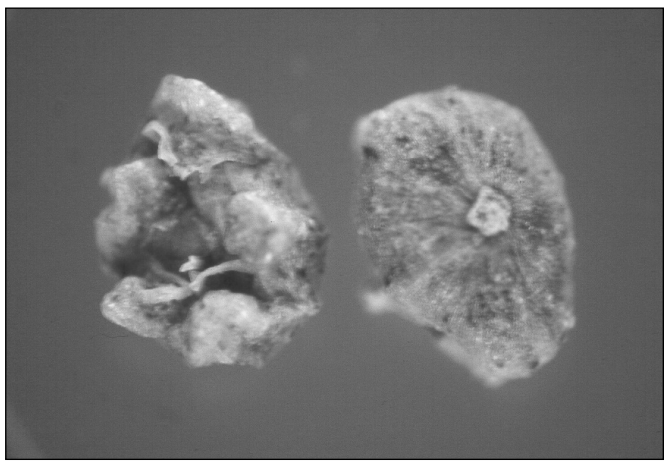
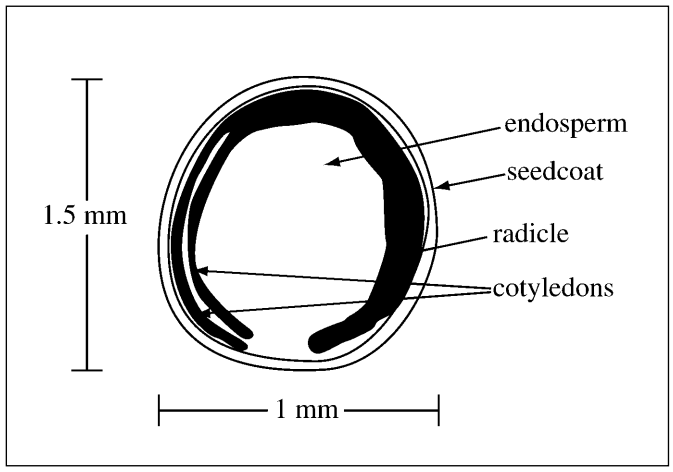


Figure 2—*Kochia prostrata*, forage kochia: longitudinal section through a seed.



percentages (Waller and others 1983).

The cleaning process removes empty fruits and fragments of fruits, leaves, and small stems using a barley debearder and multi-screened fanning mill (air-screen cleaner). Attainable purities for 'Immigrant' forage kochia depend upon harvest method and experience (Stevenson 1995). Hand-picked lots can usually be cleaned to at least 90% purity. Purities for lots harvested with mechanical harvesters are slightly lower (80 to 85%), whereas the combine method seldom produces purities greater than 70%. High-purity lots contain from 500,000 to 1,000,000 seeds/kg (225,000 to 450,000/lb) (Kitchen and Monsen 1999).

Storage. Kochia seeds are orthodox in storage behavior, but they are short-lived when storage temperatures are above 5 °C and seed moisture content is not controlled (Jorgensen and Davis 1984). Significant losses in forage kochia seed viability have been reported as early as 2 months after harvest (Baylan 1972); however, losses usually do not occur during the first 6 months of storage. Young and others (1981) reported viabilities of 18 to 34% for lots representing 13 accessions after 4 years of warehouse storage. Seed moisture contents above 7 to 8% and warm storage temperatures accelerate seed mortality. Baylan (1972) attributed this to loss of limited seed reserves through accelerated respiration rates. Storage life can be extended by drying seeds to between 4 and 8% water content and storing them in sealed containers at cool (< 5 °C) temperatures (Kitchen and Monsen 1999).

Seed germination and testing. Initial dormancy (0 to 75%) and rate of after-ripening of forage kochia seeds varies among ecotypes and years of harvest (Kitchen and Monsen 1999). After-ripening requires from 0 to 12 months at room

temperature and longer in cold storage (Baylan 1972; Kitchen and Monsen 1999). Germination of recently harvested seeds is enhanced by fluorescent light and moist chilling. Germination of after-ripened or chilled seeds occurs across a wide range of temperatures and osmotic potentials (Young and others 1981; Romo and Haferkamp 1987). Germination rate at near freezing temperatures (2 °C) for recently harvested seeds is asynchronous within accessions and highly variable among ecotypes. Mean germination time shortens as seeds after-ripen (table 2). Field studies have demonstrated that when after-ripened seeds (with a rapid, synchronized germination rate) are sown in late fall/early winter, premature germination results in poor stand establishment (Kitchen and Monsen 1999). Haferkamp and others (1990) attributed poor establishment from 1-year-old forage kochia seeds to loss of seed viability and/or vigor. Their data show that in germination tests of laboratory-stored seeds, germination rate had greatly increased for 1-year-old seed when compared to the same lots tested fresh. This suggests that the poor establishment that they observed for 1-year-old seeds may have been related, at least in part, to change in germination rate, as has been observed by Kitchen and Monsen (1999) and Stewart and others (1999). Kitchen and Monsen (1995) also observed that seeds stored for more than 2 years at refrigerated and frozen temperatures retain full viability and are able to delay germination sufficiently for successful stand establishment.

Germinating gray molly seeds tolerate higher salinity levels than do seeds of many halophytic forage plants (Clarke and West 1969). In limited germination trials conducted on a single lot of fresh gray molly seeds, the level of initial dormancy was 26% and the cold temperature germination rate was comparable to that of fresh lots of forage kochia seeds (Monsen and Kitchen 1999).

Seed viability can be difficult to determine from tetrazolium chloride staining due to interference of embryonic chlorophyll. Independent laboratory tests for the same seed lot often produce variable results. Laboratory germination tests are also sometimes inconsistent due to difficulty with seedling normality classification. Dormant healthy seeds germinate normally and rapidly after the seedcoat is pierced.

Nursery and field practice. Forage kochia transplants are easily grown as bareroot and container stock from non-dormant seeds. For best results, seeds should be sown in growth medium 4 to 6 mm ($^1/_8$ to $^1/_4$ in) deep. Germinants are susceptible to fungal root pathogens, dictating clean greenhouse culture techniques. Transplant survival from early spring planting is commonly 90% or higher using standard practices (Monsen and Kitchen 1995).

Seeding should be conducted in the fall or early winter for best establishment from direct seeding on non-irrigated untreated sites (Haferkamp and others 1990). Proper seeding rate varies from 0.5 to 4.5 kg/ha (0.5 to 4.0 lb/acre) (pure live seeds) depending on species mix, site conditions, and seeding method. Successful spring plantings have been reported using after-ripened seeds (Monsen and Turnipseed 1990). Irrigated fields can be sown during summer months. Seed placement at or near the soil surface is critical for successful establishment (Baylan 1972; Stevens and Van Epps 1984). Satisfactory stands have been achieved from broadcasting seeds on the soil surface or on snow with little or no seed-bed preparation (Kitchen and Monsen 1999).

Table 2—*Kochia prostrata,* forage kochia: mean germination times as affected by temperature of dry storage

Accession*	Mean germination times (days to 50% germination)			
	Fresh	20 °C	2 °C	–5°C
314929†	72 a	11 b	60 a	67 a
343101	51 a	12 b	46 a	55 a
356818	53 a	14 b	51 a	58 a
356826	108 a	11 c	86 b	90 b
358941	81 a	12 c	63 b	76 a
Mean	71 a	12 b	61 a	69 a

Source: Kitchen and Monsen (1999).
Note: Within an accession, means followed by the same letter are not significantly different at the P <0.05 level. Five accessions of forage kochia were germinated at 2 °C after 24 months of dry storage at 20, 2, or –5 °C; controls were freshly collected seeds.
* Accession numbers are plant introduction (PI) numbers assigned by the USDA Natural Resource Conservation Service's Plant Materials Center in Pullman, Washington.
† 'Immigrant'.

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K

Sapindaceae—Soapberry family

Koelreuteria paniculata Laxm.

panicled golden raintree

Charles H. Michler and Paul O. Rudolf

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Growth habit, occurrence, and use. Native to China, Korea, and Japan, the panicled golden raintree—also called pride-of-India, China tree, and varnish tree—is a small deciduous tree ranging from 5 to 11 m tall that has been cultivated since 1763, chiefly for ornamental purposes (Rehder 1940).

Flowering and fruiting. The irregular (or apparently polygamous) yellow flowers occur in broad, loose, terminal panicles and bloom from July to September (Krüssmann 1960; Ohwi 1965; Plouvier 1946). The fruits are bladdery, triangular, 3-celled capsules about 3 to 5 cm long (figure 1); when they ripen in September and October they change from a reddish color to brown. Within the papery walls of ripe fruit are 3 round, black seeds (figure 2) (Rehder 1940; Rudolf 1974). The seeds are naturally dispersed from fall to the next spring (Pammel and King 1930). Good seedcrops are borne almost annually (Rudolf 1974).

Collection of fruits; extraction and storage of seeds. Capsules should be collected from trees in September and October for extraction and cleaning the seeds. The yield from 46 kg (100 lb) of fruits is about 32 kg (72 lb) of cleaned seeds (Plouvier 1946). Cleaned seeds per weight ranged from 5,700 to 7,700/kg (2,600 to 3,500/lb), and averaged 6,394/kg (2,900/lb) for 3 samples. Four samples of commercial seedlots averaged 99% in purity and 95% in soundness (Rudolf 1974; Swingle 1939; Zentsch and Kaul 1968). One sample that was stored in fruit jars with loosely fastened lids and exposed to temperatures ranging from about 4 to 32 °C showed 50% germination at the end of 10 years (Toumey 1921).

Figure 1—*Koelreuteria paniculata*, panicled golden raintree: capsules (**top**) and seeds (**bottom**).

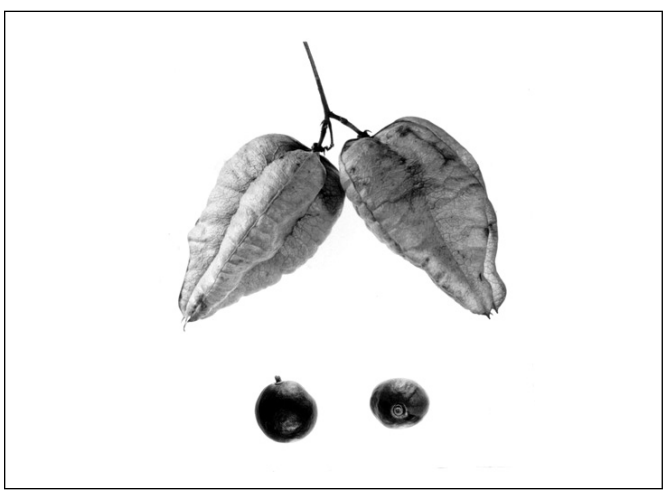
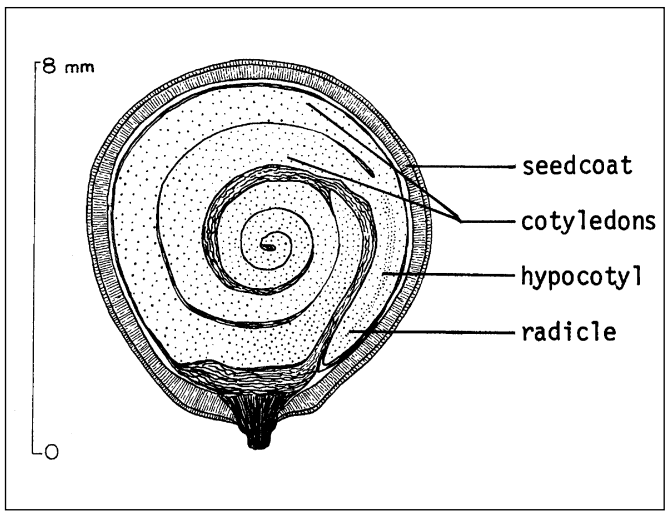


Figure 2—*Koelreuteria paniculata*, panicled golden raintree: longitudinal section through a seed.



Pregermination treatments. Dormancy in seeds appears to be caused by an impermeable seedcoat and possibly by an internal condition of the embryo. In a series of tests, soaking seeds in sulfuric acid for 1 hour plus 90 days of stratification in moist sand at 4.5 °C gave the best results (Rudolf 1974). In another series of tests, mechanically scarified seeds germinated promptly and well (Zentsch and Kaul 1968). Mechanical scarification followed by stratification for 90 days produced complete germination in 9.7 days (Garner 1979; Garner and Lewis 1980). Seed exposure to an electro-

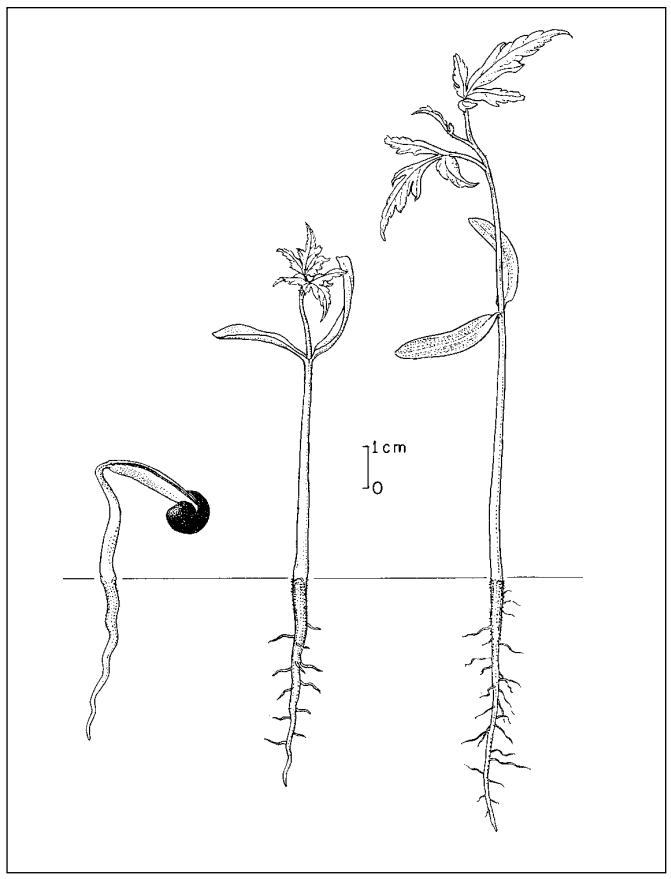
magnetic field of 100 gauss for 4.3 seconds increased germination after scarification from 56 to 97% (Maronek 1975).

Germination tests. Germination is epigeal (figure 3). Germination should be tested in sand flats or germinators for 5 to 10 days at 20 (night) to 30 °C (day), using 200 to 400 seeds that were acid treated and then stratified for each test. One test of untreated seeds gave a germination rate of only 2% in 29 days, whereas seeds of the same sample gave 52% after the acid plus stratification treatment recommended above (Rudolf 1974). In another test, 74% of untreated seeds germinated in 54 days, compared with 91% of mechanically scarified seeds in 23 days (Zentsch and Kaul 1968). Official seed testing agencies recommend tetrazolium staining for germination tests of panicled golden raintree. The suggested procedure is to soak the seeds in water for 18 hours, then remove the seedcoat before staining for 24 hours at 30 °C in a 1% solution (ISTA 1993).

Nursery practice. Untreated seeds may be sown in the fall and scarified seeds can be sown in the spring (some seedlots may require stratification after scarification) and covered with 6 to 13 mm ($^1/_4$ to $^1/_2$ in) of soil. Seedlots sown immediately after collection in fall usually give reasonably good results (Swingle 1939). A target bed density is about 300 to 315 seedlings/m^2 (30/ft^2). Tree survival is about 70% (Jack 1969). Seedlings should be lifted as 2+0 stock (Jack 1969).

This species should be planted only in sunny locations, but it is not particular as to soil type (Bailey 1939). It may also be propagated by layers, cuttings, or root cuttings (Bailey 1939).

Figure 3—*Koelreuteria paniculata*, panicled golden raintree: seedling development at 1, 3, and 5 days after germination.



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Chenopodiaceae—Goosefoot family

Krascheninnikovia lanata (Pursh) A.D.J. Meeuse & Smit

winterfat

D. Terrance Booth

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Synonyms. *Eurotia lanata* (Pursh) Moq., *Ceratoides lanata* J.T. Howell, *Diotis lanata Pursh*; see appended notes on nomenclature.

Other common names. white-sage.

Growth habit, occurrence, and use. Winterfat is a sub-shrub that in early spring appears as small bunches of new leaves closely joined to dead-looking low stems that have new shoots arising from woody bases. By late summer, the shrub's attractive foliage is 20 to 80 cm high and often crowned with dense clusters of handsome, white, fruiting bracts. The leaves can grow to 5 cm and are narrow and entire, with strongly revolute margins. Leaves and herbaceous stems have short white hairs that give the plant its characteristic gray-green color and its *Eurotia* synonym (from the Greek *euros,* meaning mold).

Winterfat habitats are characterized by drought and temperature extremes. It grows in scattered clusters or uniform stands on dry plains, foothills, and mountains from western Nebraska and Texas to California and from northern Mexico to the prairie provinces and the Yukon Territory of Canada, north to the vicinity of Lake Kluane, Alaska (Coupland 1950; Hulten 1968; Stevens and others 1977; Welsh 1974). In the Great Basin, winterfat occupies thousands of hectares in pure stands and may be found at elevations from the lower Sonoran zone to ridges over 3,048 m in elevation (Stevens and others 1977). Soils supporting winterfat are low in sodium and other soluble salts but often high in carbonates of calcium and magnesium; soil textures vary from clays to sandy and rocky loams (Nelson 1962; Stevens and others 1977).

Native stands are highly valued as forage for livestock and wildlife (Asay 1959; Jones and Barclay 1972; Nelson 1905; Plummer and others 1968), but many have been depleted or destroyed by abusive grazing or by wildfire in combination with the invasion of exotic annual grasses. Winterfat is regularly used in re-vegetating disturbed lands, has value as an ornamental, and is recommended for reseeding to restore depleted western rangelands and for providing waterfowl nesting cover on the Canadian prairies. It was first cultivated in 1895 (Springfield 1974b). Notable progress has been made in seed handling and seeding methods so that disturbed lands sown with winterfat regularly develop healthy stands.

Ecotypic variation. Winterfat displays strong ecotypic variation that appears to account for the range of habitats occupied by the species. This variation must be considered when collecting seeds for a particular environment or use (Bai and others 1997b; Plummer and others 1968; Workman and West 1969). Seed quality and seedling vigor differ by collection (Booth 1992; Moyer and Lang 1976; Springfield 1968a), with some differences appearing as adaptive compromise between seed quality and the demands of stressful environments (Booth 1990a; Booth and Haferkcamp 1995). The selection of high-vigor lines may be possible (Riedl and others 1964), but studies are needed to understand genetic and environmental interactions with seed quality and cultivar adaptability.

Flowering and fruiting. Flowers are small, gray-green, and inconspicuous and are likely cross-pollinated by wind (Riedl and others 1964). The plants are dioecious or monoecious. Flowers bloom from June to August, depending on elevation and weather. Staminate flowers have a 4-parted calyx with 4 exerted stamens. Pistillate flowers have 2 styles emerging from between 2 united bracts. At maturity the bracts have formed fluffy white diaspores (seed-containing dispersal units) that decorate the fruiting spikes and function in seed dispersal, embryo protection, and in promoting the establishment and survival of the seedling (Booth 1988, 1990b). Bract hairs are 2 to 8 mm long in spreading tufts (figure 1). Each pair of bracts enclose an indehiscent, pubescent, 1-seeded fruit (utricle) (figure 2). The seedcoat is thin and transparent and is most easily discerned on naked imbibed or germinating seeds. Diaspores disperse in the fall or winter and collect in aggregations on the soil surface (figure 3). Plants may produce seeds the first

Figure 1—*Krascheninnikovia lanata*, winterfat: fruiting spike.

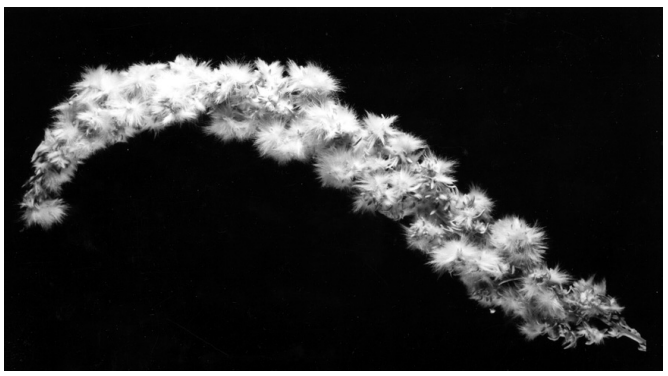
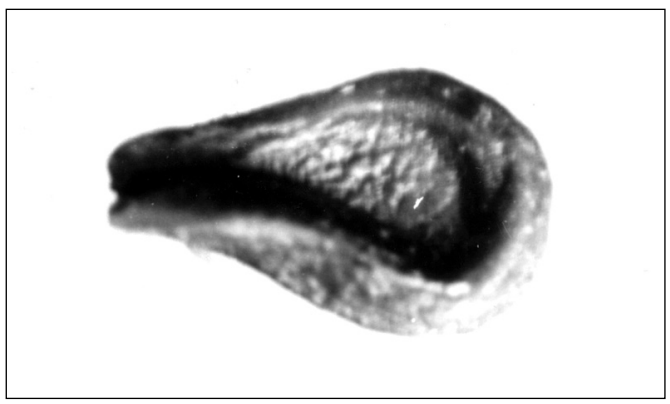


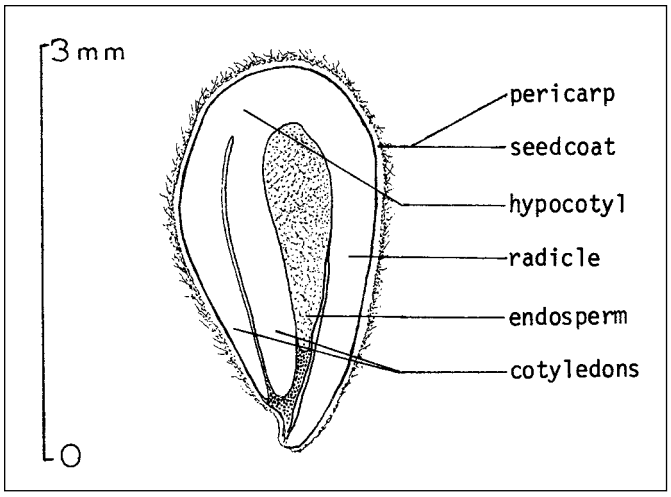
Figure 2—*Krascheninnikovia lanata*, winterfat: cleaned seed.



year and produce abundant crops annually (table 1). A 10-year-old stand has produced 78 to 90 kg/ha (70 to 80 lb/ac) of "fruit"
(diaspores) (Springfield 1974b). Good seed quality depends on the mother plant's maintaining transpiration rates during seed and diaspore development (Booth 1990a).

Seed collection and storage. Seeds are harvested by stripping the diaspores from the bushes or by cutting and drying the fruiting spikes. Harvest time is mid-September in Saskatchewan (Romo 1995) to mid-October or early November at lower latitudes (Strickler 1956; Wasser 1945; Wilson 1931). Mechanized harvest methods have been tried (Springfield 1974b), but most collectors have found it more efficient to hand-harvest. However, Majerus (2003) described harvesting winterfat seeds with a combine. Dry diaspores should be stored without threshing or other processing to prevent accelerated aging. Harvested material will contain unfilled diaspores, but there are no practical methods for separating these from the germinable diaspores (Allen and others 1987). Percentage diaspore fill may be determined by threshing small samples. This is quickly done using equipment described by Booth and Griffith (1984).

Figure 3—*Krascheninnikovia lanata*, winterfat: sectional schematic of diaspore (seed).



Winterfat seeds are orthodox in storage behavior but their viability decreases after 6 to 12 months at ambient conditions (Hilton 1941; Springfield 1968a,b; Wilson 1931). Viability is maintained longer when seeds are stored in sealed containers at 4 to 5 °C (Springfield 1968c, 1973, 1974a), but seedling vigor will continue to decrease (Booth and others 1999). To maintain seedling vigor during long-term storage (more than 6 months), winterfat diaspores should be held at –20 °C.

Germination. Diaspores germinate naturally during cold or cool weather. Seeds imbibe readily, and the rate and total weight gain vary by temperature (Bai and others 1999; Booth and McDonald 1994) and by oxygen concentration (Booth 1992). Holding imbibed diaspores at 0 to 5 °C will improve germination, germination rate, and seedling vigor of most seed lots (Booth 1992; Booth and Schuman 1983; Strickler 1956) though the vigor of fresh seeds (4 months after harvest) is unlikely to be affected by imbibition temperature (Bai and others 1998a; Booth and others 1999). Winterfat's capability to germinate at freezing temperatures is well documented (Booth 1987b; Hilton 1941; Wilson 1931; Woodmansee and Potter 1971) and is reported to allow winterfat to establish in stressful environments (Springfield 1968a; Workman and West 1967). Dettori and others (1984) measured germination of threshed seeds of 3 collections, including an Asian species, at 55 temperature combinations ranging from 0/0 to 40/40 °C. Germination occurred over a wide range of temperatures. but the optimum germination occurred most frequently at 0 to 5 °C alternating with 15 to 20°C. Allen and others (1987) noted evidence of increased mold growth with alternating temperatures and temperatures above 15 °C.

Table 1— *Kraschenninnikovia lanata,* winterfat: diaspore weights by source and harvest year

Source	Collections	Years harvested	Diaspores/weight Mean* /g	Mean* /oz	Range /g	Range /oz
Colorado	3	1982, 84, 94	147	5.2	137–203	4.8–7.1
New Mexico	3	1984	231	8.1	208–270	7.3–9.5
Nevada	1	1983	175	6.2	175	6.2
Saskatchewan	1	1994	147	5.2	147	5.2
Utah	2	1982, 84	212	7.5	167–257	5.9–9.0
Wyoming	2	1994	177	6.2	173–181	6.1–6.4
Total	12	—	—	—	—	—

Sources: Allen and others (1987), Booth (1994).
* Mean + SD = 198 + 15.8
† 'Immigrant'.

Germination is most suitably tested by imbibing diaspores at 0 to 5 °C for 4 or 5 days followed by incubation at 15 °C. A longer cold treatment, 6 to 15 days, may increase the germination rate and seedling vigor for some seedlots, especially those that are less than 3 months or more than 12 months after harvest. Seeds less than 3 months from harvest may require after-ripening (Springfield 1972). Germination is not affected by light (Hilton 1941) and is rapid at warm temperatures.

Nursery and field practice. In the past, it was considered important to thresh the seed from the diaspore to simplify seeding with mechanized equipment (Springfield 1974b). However, that practice is no longer recommended because the bracts aid in seedling establishment, and threshing damages the seeds (Booth 1984, 1989a&b, 1990b; Booth and Schuman 1983). Broadcasting diaspores results in good establishment in depressions, in litter, and in protected sites (Stevens and others 1977). Diaspores can also be sown with a cultipacker (Luke and Monsen 1984), with a hydroseeder (Pellant and Reichert 1984), as pelleted diaspores, and in seed tapes (Booth 1987a&b). Use of the cased-hole punch seeder (Booth 1995) is effective and allows diaspores to be sown through fabric mulch. Natural establishment occurs with cool temperatures and high surface moisture and with a mat of diaspores on the soil surface (figure 3) (Booth 1987b, 1989a, 1990b; Gasto 1969; Wilson 1931; Woodmansee and Potter 1971). Fall-seeding is recommended (Zabek and Romo 1998). Under-snow germination produces vigorous seedlings and contributes to seeding success. Winterfat seeds and seedlings can show freeze-tolerance (Bai and others 1997a; Booth 1987b, 1989a; Hilton 1941; Stricker 1956; Woodmansee and Potter 1971), but reduced germination or loss of seedlings can also occur (Bai and others 1997b; Booth 1989a; Hodgkinson 1975; Stevens and others 1977). Ecotype, imbibition temperature, conditioning, and stage of growth are factors influencing seed and seedling freeze-tolerance (Bai and others 1997b; Booth 1989a; Hodgkinson 1975).

Winterfat can be transplanted as container-grown or bareroot plants. Shaw and Monsen (1984) recommended beds producing bareroot seedlings contain 167 to 222 seedlings/m^2 (15 to 20/ft^2). These should be lifted as 1+0 stock in the spring before they break dormancy. Shaw and Monsen (1984) found that 93% of mechanically transplanted seedlings were alive after 5 growing seasons when these recommendations were followed.

Notes on nomenclature. The type specimen for winterfat was collected by the Lewis and Clark expedition "On the banks of the Missouri River, in open prairies" and was described as *Diotis lanata* by Pursh in 1814 (Pursh 1814). Moquin-Tendon (1840) placed the species in the genus *Eurotia* (Adanson 1763) and listed as synonyms *Diotis, Axyris* (Linnaeus 1753), *Ceratoides* (Gagnebin 1755), and *Kraschenninnikovia* (Gueldenstaedt 1772). For more than 2 centuries, botanical authors followed Adanson or Meyer's emended interpretation of Adanson's description in major botanical works and in numerous papers dealing with winterfat description, value, management, ecology, and culture (Meyer 1933, as cited by Howell 1971). In 1964, Ball reapplied the name *Kraschenninnikovia* (Tutin and others 1964). Subsequently, Howell (1971) applied *Ceratoides* to *E. lanata*, and Meeuse and Smit (1971) joined Tutin and others in using *Kraschenninnikovia*. Chu, in his Flora of China, has also choosen to use *Kraschenninnikovia* (Stutz 1995). A 1976 attempt by the Russian Grubov to conserve (retain the use of) the name *Eurotia* was rejected (Brummitt 1978).

Although the International Code of Botanical Nomenclature was changed to allow such action, *Eurotia* was unfortunately not re-submitted for conservation (Wiersema 2000). North American authors have shown a disinclination to accept the procedural name change and some have continued to publish using the name *Eurotia*.

K. lanata has 1 subspecies, *subspinosa,* in southern Arizona (Kearny and Peebles 1960; Munz and Keck 1968) and 1 released cultivar, 'Hatch' (Stevens and Monsen 1988). Losina-Losinskaja (1930) defines 5 Eurasian species and Chu defines 7 (Stutz 1995).

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Fabaceae—Pea family

Laburnum Medik.

laburnum

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Growth habit, occurrence, and use. The genus *Laburnum* includes 4 species of deciduous trees and shrubs native to central and southern Europe (Krüssmann 1984; LHBH 1976; Scheller 1974). Laburnum species have been cultivated for centuries, primarily for ornamental purposes. Laburnum arches and walks are a popular feature in many large gardens (Wasson 2001). The species is adaptable to many soil types, including limestone, but prefers well-drained soil and light shade (Dirr 1990; Krüssmann 1984; Rudolf 1974). All parts of the plant, particularly the seeds, are poisonous (Krüssmann 1984; LHBH 1976). Seeds and other parts of the plant contain the alkaloid cytisine, which can be fatal to humans and animals (Dirr 1990; Greinwald and others 1990; Leyland 1981). The 2 species and a hybrid of interest are described in table 1.

Scotch laburnum is a small tree with a short, sturdy trunk and flat to round-topped crown; it is considered to be the superior garden species (Dirr 1990). Common laburnum tends to be a low branched, bushy, wide-spreading tree (Dirr 1990; LHBH 1976). Waterer laburnum, a natural hybrid between Scotch and common laburnums, is a distinctly upright, oval to round-headed small tree or shrub (Dirr 1990). The foremost laburnum in cultivation today is Waterer laburnum 'Vossii', a superior tree with dense habit, racemes up to 60 cm in length, and a tolerance of alkaline soils (Dirr 1990; Krüssmann 1984).

Flowering and fruiting. The perfect, ornate, golden yellow flowers are 1.9 cm long and are borne on 15- to 25-cm pendulous racemes; Scotch laburnum has racemes that are 25 to 38 cm (Dirr 1990). Flowers bloom from May to June, and the flowers of Scotch laburnum and Waterer laburnum 'Vossii' are fragrant (Hillier 1991; Krüssmann 1984). The fruit is a brown legume (pod), 5.1 to 7.6 cm long, with black seeds (figures 1 and 2) (Rudolf 1974). The legume of Scotch laburnum is winged, forming a knifelike edge (Dirr 1990). The seeds are tardily dehiscent, ripening from late August to October (Rudolf 1974). Each legume contains several black seeds (only 1 or 2 for Waterer laburnum 'Vossii'), and good seedcrops are borne annually (Krüssmann 1984; Rudolf 1974).

Collection of fruits; extraction, cleaning, and storage of seeds. Legumes should be harvested from the trees beginning in September through November and spread out on flats in a shed or loft with good air circulation to dry (Macdonald 1986; Rudolf 1974). Newspaper should be placed over the legumes to prevent the seeds from being ejected away from the flats. Seeds are extracted by breaking the legumes by hand or by machine threshing (Macdonald

Table 1—*Laburnum,* laburnum: nomenclature, occurrence, growth habit, height at maturity, and date of first cultivation

Scientific name & synonym(s)	Common name(s)	Occurrence	Growth habit	Height at maturity (m)	Year first cultivated
***Laburnum alpinum* (Mill.) J. Presl.**	**Scotch laburnum,** alpine goldenchain	S Alps, N Apennines, NW Yugoslovia, S	Tree	6.1	1596
***L. anagyroides* Medik.** *L. vulgare* Bercht. & Presl.	**common laburnum,** goldenchain tree	Slovakia & Czech Republic, & Central & S Europe	Tree	6.1–9.1	1560
***L.* x *watereri* (Kirchn.) Dipp.** *L. alpinum* x *L. anagyroides*	**Waterer laburnum,** goldenchain tree	Observed (1856) wild in Tyrol & Switzerland, now in cultivation	Tree/shrub	3.7–4.6	1875

Sources: Dirr (1990), Hillier (1991), Krüssmann (1984), LHBH (1976).

Figure 1—*Laburnum anagyroide*s, common laburnum: legume (**top**) and exterior view of a seed (**bottom**).

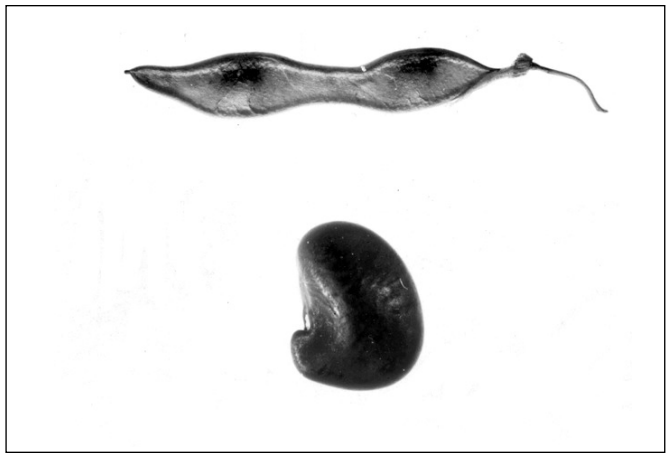
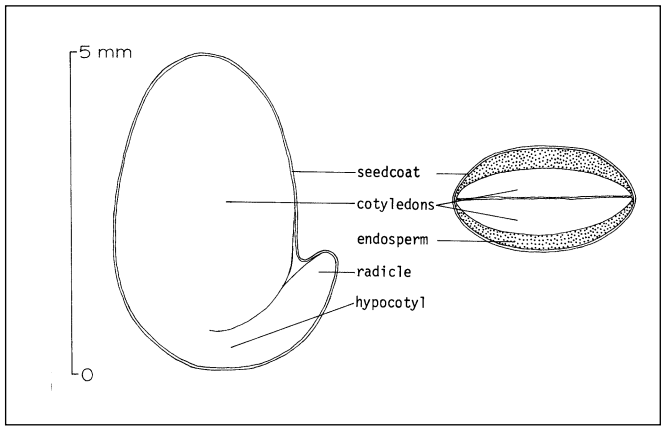


Figure 2—*Laburnum anagyroides,* common laburnum: longitudinal section through a seed.



1986). The seeds and debris are separated by sieving or by using a directed flow of air. About 45 kg (100 lb) of legumes will yield about 11 kg (25 lb) of cleaned seeds (Rudolf 1974). The following values for number of cleaned seeds per weight for laburnum species have been found: Scotch laburnum, 31,966 to 35,004/kg (14,500 to 15,878/lb); common laburnum, 35,273 to 37,478/kg (16,000 to 17,000/lb); and Waterer laburnum, 40,917/kg (18,560/lb); with 85% germination and 90 to 99% purity, depending upon cleaning techniques (Allen 1994). The dried legumes may be stored overwinter in sacks placed in a dry shed or loft. Seeds stored dry in sacks will retain good viability for 2 years (Dirr and Heuser 1987; NBV 1946, cited by Rudolf 1974).

Pregermination treatments. Laburnum seeds do not germinate readily unless the impermeable, hard seedcoat is ruptured by mechanical or sulfuric acid scarification. Mechanical scarification of common laburnum seeds resulted in 99% germination (Stilinovic and Grbic 1988). Dirr and Heuser (1987) reported that 30 to 60 minutes of sulfuric acid treatment resulted in good germination. A sulfuric acid treatment for 80 minutes and storage for at least 8 months improved germination rates for common laburnum (Laroppe and others 1996). A 2-hour sulfuric acid treatment resulted in 68% (Scotch laburnum) and 100% (Waterer laburnum) germination (Dirr and Heuser 1987). Seeds of Waterer laburnum that were collected when the seedcoat was soft (late July in Boston, Massachusetts) and left "as is"or punctured with a needle produced uniform germination in 5 days (Dirr and Heuser 1987).

Germination tests. Testing prescriptions of the International Seed Testing Association (ISTA 1993) call for mechanical scarification by piercing or by removing a piece of the testa at the cotyledon end and soaking seeds in water for 3 hours before testing them at alternating 20/30 °C for 21 days on germination paper. An alternative method is to scarify seeds by soaking them in concentrated sulfuric acid for 1 hour, washing, and germinating as above (ISTA 1993). Tests of treated seeds can also be done at a constant 20 °C for 14 days, and light is not required (Rudolf 1974). Germination rates averaged about 80% in 7 days, and percentage germination about 86% in more than 12 tests (NBV 1946; Schubert 1955, cited by Rudolf 1974).

Nursery practice and seedling care. Scarified seeds may be sown broadcast or in drills in late spring at a rate of 150 to 200/m^2 (14 to 19/ft^2) for lining-out stock and 100 to 150/m^2 (9 to 14/ft^2) for rootstocks (Macdonald 1986). The seeds are covered with 6 mm ($^1/_4$ inch) of soil. Field-planting has been done with 2+0 stock (Rudolf 1974). This species can also be propagated by layering and rooting hardwood cuttings taken during the fall and late winter; cultivars are propagated by grafting or budding onto laburnum seedling rootstocks (Dirr and Heuser 1987; Hartmann and others 1990; LHBH 1976; Macdonald 1986; Whalley and Loach 1981, 1983). Micropropagation of Waterer laburnum 'Vossii' has been reported, but plants cultured *in vitro* have slowed growth as compared to plants multiplied by grafting (Gillis and Debergh 1992).

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Lythraceae—Loosestrife family

Lagerstroemia L.

crape-myrtle

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Occurrence, growth habit, and uses. There are about 55 species in the crape-myrtle genus—*Lagerstroemia*. They are indigenous primarily to the Asian and Pacific island tropics but also occur in China, India, Korea, Japan, and Australia (Bärner 1962; LHBH 1976). Many are important timber species, producing wood of quality suitable for cabinetry and construction that is also highly resistant to decay and destructive insects (Bärner 1962; Howard 1948). Three species are cultivated in North America, all for their horticultural interest (table 1).

One species of crape-myrtle, *Lagerstroemia indica* L., and its hybrids with *L. fauriei* Koehne—both of which are called crape-myrtle—are used widely in landscape plantings in warmer parts of the continental United States, particularly the South. *Lagerstroemia indica* is indigenous to China, whereas *L. fauriei* was introduced in 1956 by Creech (1958, 1985) from seeds collected on Yakushima Island, Japan. Many cultivars have been named, including a few of strict *L. fauriei* parentage (Dirr 1998; Egolf and Andrick 1978; Raulston and Tripp 1995). Cultivars of crape-myrtles are typically cold hardy to USDA Zone 7, but some cultivars have withstood temperatures of –23 °C without injury (Egolf 1990b). There have been reports of tropical species, particularly Queen's crape-myrtle, growing in frost-free portions of the United States corresponding to USDA Zones 10 and 11 (Egolf and Andrick 1978; Everett 1981; Menninger 1962).

Crape-myrtles are deciduous trees or shrubs exhibiting considerable variability in height; they range from 0.9 to 10 m tall, with occasional specimens reaching 14 m (Dirr 1998; Egolf and Andrick 1978). They are observed commonly as upright, multi-stemmed plants, the bottom third to half devoid of leaves, generally exposing very handsome, sinuate trunks (Dirr 1998; Egolf and Andrick 1978). The crown is variably rounded to vase-shaped. Queen's crape-myrtle may reach 24 m in height in the United States and 30 m in the Asian tropics (Chudnoff 1980).

As a result of their ornamental attributes, crape-myrtles are used extensively as landscape plants. Due to their broad range of heights, they can be observed growing as specimen plants, hedges, mass plantings, or lining streets and alleys (Dirr 1998; Egolf 1981a&b, 1986a&b, 1987a&b, 1990a&b). Crape-myrtles have also been maintained successfully as herbaceous perennials by annual hard pruning to the ground, and they are treated as herbaceous plants where winter temperatures are low enough to kill aerial portions without injuring the roots (Everett 1981; Huxley 1992). Although widely adaptable, crape-myrtles grow best in full sun and in heavy loam to clay soils with a pH of 5.0 to 6.5 (Egolf 1981a&b, 1986a&b, 1987a&b, 1990a&b; Egolf and Andrick 1978). Crape-myrtles are not grown in the United States for timber use.

Table 1—*Lagerstroemia,* crape-myrtle: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***L. fauriei* Koehne**	**crape-myrtle,** crapemyrtle	Yakushima Island, Japan
***L. indica* L.** *L. elegans* Wallich ex Paxt.	**crape-myrtle,** crapemyrtle	China, Vietnam, Himalayan region, & Japan
***L. speciosa* (L.) Pers.** *L. flos-reginae* Retz.	**Queen's crape-myrtle**, pride-of-India	India, Burma, Sri Lanka, Malayan Peninsula, & Australia

Sources: Bärner (1962), Creech (1958), Huxley (1992), LHBH (1976).

Geographic races and hybrids. Various crape-myrtle species hybridize readily. Beginning in 1962, the United States National Arboretum pursued an extensive program of crape-myrtle breeding and selection, under the direction of Egolf (Egolf and Andrick 1978). Between 1981 and 1990, the National Arboretum released 20 cultivars of crape-myrtle, most of them selections of complex crosses between *L. indica* and *L. fauriei* (Egolf 1981a&b, 1986a&b, 1987a&b, 1990a&b). These cultivars combine successfully the superior flowering attributes of *L. indica* with resistance to mildew—*Erysiphe lagerstroemiae* E. West—of *L. fauriei* (Egolf 1981a&b, 1986a&b, 1987a&b, 1990a&b; Mizel and Knox 1993). Several also display the exceptional and colorful, exfoliating bark of *L. fauriei,* as well as outstanding fall foliage color (Dirr 1998; Egolf 1981a&b, 1986a&b, 1987a&b, 1990a&b).

Flowering and fruiting. Spectacular flowering is the trait that most often justifies use of crape-myrtles as landscape plants. The red, white, pink, or purple flowers, each 1.5 to 5.0 cm in diameter, are produced in 12- to 44-cm-long tapered panicles, each comprising 25 to 500 flowers. The flowers are perfect, 6-petaled, and distinctively crinkled. Stamens are numerous, as are ovules (Egolf 1990b; Egolf and Andrick 1978; LHBH 1976). The inflorescences are terminal and prominently displayed at the end of the current year's growth. Flowering occurs from June to September in the mid-Atlantic states and the Southeast, with some variability between cultivars. Many cultivars have extended flowering periods, lasting up to 3 $^1/_2$ months (Dirr 1998; Egolf and Andrick 1978). Fruits are globose, dehiscent, 6-valved capsules, 5 to 15 mm in diameter, that reach maturity in the fall and persist through the winter (figure 1). Each capsule contains 20 or more winged seeds. Seeds are 7 to 11 mm long (figures 2 and 3) (Egolf and Andrick 1978; LHBH 1976).

Collection of fruits, seed extraction, cleaning, and storage. Published information on fruit collection and seed extraction of crape-myrtles is generally lacking, but the capsules should be dried for seed extraction. Dirr and Heuser (1987) placed mature fruits in paper bags for drying, followed by shaking to remove seeds. No information is available currently regarding proper storage conditions to maintain viability, but the seeds appear to be orthodox in storage behavior, indicating that low seed moisture and temperatures would be sufficient for storage. In India, Queen's crape-myrtle seeds average 150,000 to 175,000/kg (68,000 to 79,400/lb) (Khullar and others 1991).

Figure 1—*Lagerstoemia* indica, crape-myrtle: open fruit (capsule).

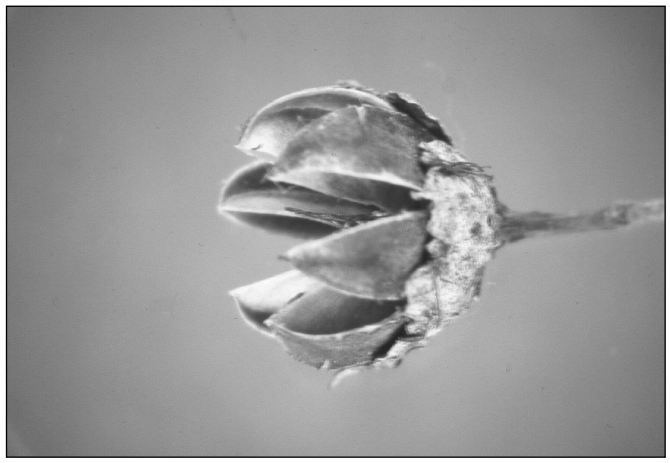


Figure 2—*Lagerstoemia* indica, crape-myrtle: seeds.

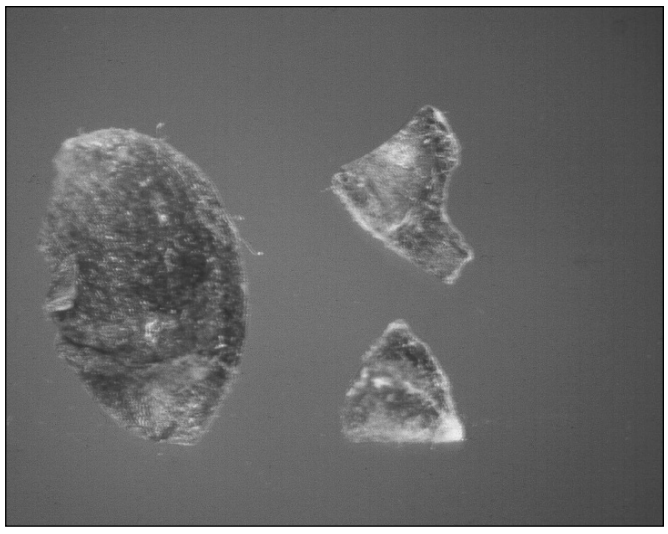
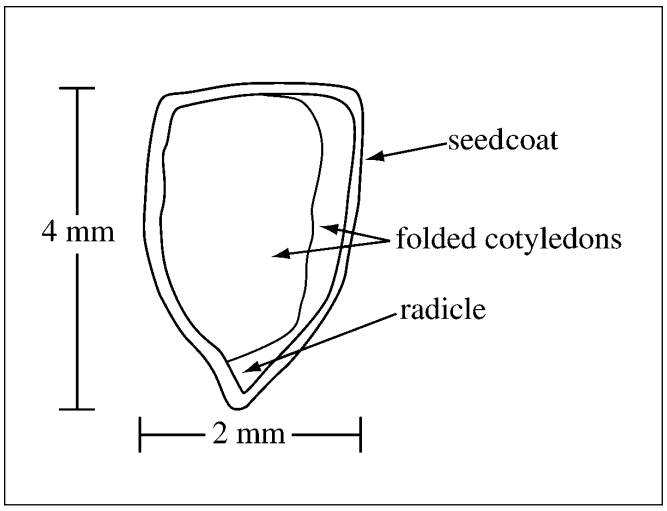


Figure 3—*Lagerstoemia indica*, crape-myrtle: longitudinal section of a seed.



Pregermination treatments and germination tests. Seeds germinate readily without pretreatment, although stratification (moist prechilling) for 1 month at 4 °C is sometimes advised to synchronize germination (Dirr and Heuser 1987; Raulston and Tripp 1995). There are no officially prescribed test procedures for this genus. However, Babele and Kandya (1986) demonstrated that tetrazolium staining is a reliable and rapid technique for determining seed viability of *L. parviflora* Roxb.

Nursery practice, and seedling care. Egolf and Andrick (1978) reported that without stratification, seeds sown at 15 °C germinated within 10 days. They recommended that seedlings be transplanted into individual pots shortly after emergence and then fertilized lightly. In a warm greenhouse, such seedlings will make rapid growth, and often bloom the first summer from a December or January sowing. Dirr (1998) reported that germination occurs in 2 to 3 weeks for seeds sown immediately following collection in January. Seedling populations of crape-myrtles, whether of hybrid origin or not, are noted for heterogeneity in height, flower color, floriferousness, and cold hardiness.

At present, commercial propagation of crape-myrtles is primarily by stem cuttings. Softwood, hardwood, or root cuttings have been used successfully (Dirr and Heuser 1987; Egolf 1990b; Egolf and Andrick 1978; Hartmann and others 2002). Micropropagation techniques have also been reported (Yamamoto and others 1994; Zhang and Davies 1986).

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Pinaceae—Pine family

Larix P. Mill.

larch

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Occurrence. The larches—*Larix* P. Mill.—of the world are usually grouped into 10 species that are widely distributed over much of the mountainous, cooler regions of the Northern Hemisphere (Hora 1981; Krüssmann 1985; Ostenfeld and Larsen 1930; Rehder 1940; Schmidt 1995). Some species dominate at the northern limits of boreal forests and others occur above subalpine forests (Gower and Richards 1990). Seven species are included (table 1)—the others, Master larch (*L. mastersiana* Rehd. & Wils.), Chinese larch (*L. potaninii* Batal.), and Himalayan larch (*L. griffithiana* (Carr.))—are rarely planted in the United States. All species (except possibly Himalayan larch) are hardy in the United States (Bailey 1939). However, the seeds should come from a site with comparable conditions, as demonstrated at the Wind River Arboretum in southwestern Washington, where 7 larch species, some with several varieties, and 1 hybrid were planted from 1913 to 1939 (Silen and Olson 1992). European larches there are doing better than Asian species in this warm, moist Washington state climate. The native western larch specimens from more continental climates with lower humidity are doing poorly. In 1992, a larch arboretum containing all species, several varieties, and 3 hybrids of larch was established at Hungry Horse, Montana, within the natural range of western larch (Shearer and others 1995).

Growth habit. *Larix* is one of the few conifer genera with deciduous needles. The trees are valued for their light green hues in the spring and shades of yellow to gold in the

Table 1—*Larix*, larch: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***L. decidua* P. Mill.** *L. europaea* DC. *L. larix* Karst	**European larch**	Mtns of central Europe up to about 2,500 m; widely planted throughout Europe & NE US (43–54°N & 7–27°E)
***L. gmelinii* (Rupr.) Rupr.** *L. dahurica* Turcz. ex Trautv. *L. cajanderi* Mayr	**Dahurian larch**	E Siberia to NE China & Sakhalin; limited planting in N Europe, Canada, & NE US (35–72°N & 89–82°E)
***L. kaempferi* (Lamb.) Carr.** *L. leptolepis* (Sieb. & Zucc.) Gord. *L. japonica* Carr.	**Japanese larch**	Japan, usually from 1,220–2,440 m; planted in N Europe, Asia, & E US (35–37°N & 138–143°E)
***L. laricina* (Du Roi) K. Koch**	**tamarack**, eastern larch, American larch, hackmatack	Newfoundland & W along tree line to Alaska; SE through NE British Columbia to Great Lakes region, E to New England; local in NW Virginia & W Maryland (41–68°N & 51–158°W)
***L. lyallii* Parl.**	**subalpine larch,** alpine larch, tamarack	High mtns of SW Alberta, SE British Columbia, N central Washington, N Idaho, & W Montana (45–52°N & 116–124°W)
***L. occidentalis* Nutt.**	**western larch,** hackmatack, Montana larch, mountain larch, tamarack, western tamarack	W Montana to E Oregon & Washington & S British Columbia (43–52°N, 117–124°W
***L. sibirica* Ledeb.** *L. russica* (Endl.) Sabine ex Trautv. *L. europaea* var. *sibirica* (Ledeb.) Loud.	**Siberian larch,** Russian larch	NE Russia & W Siberia; limited planting in N US & Canada (45–72°N & 36–112°E)

Source: Rudolf (1974).

fall. Branching is usually pyramidal with spreading branches (Hora 1981). Maximum height for the 10 species ranges widely, influenced by elevation and site conditions. Subalpine and Chinese larches often grow at or near timberline and mature trees may reach only 7 to 13 m in height (Krüssmann 1985). The tallest known subalpine larch, as reported by Arno and Habeck (1972), grows on a protected, favorable site and reached 46 m. Western larch, tallest of the world's larch species, can reach about 61 m (Schmidt and others 1976; Schmidt and Shearer 1990).

Use. Of the 3 American species, tamarack and western larch are used for reforestation. Because of its rot resistance, larch wood is especially valuable for posts, transmission poles, railroad ties, and mine props. Most larches are now recognized as important for timber production, habitat or food for wildlife, watershed protection, environmental forestry, and also for ornamental purposes (Rudolf 1974). Venetian turpentine can be obtained by tapping larches; a water-soluble trisaccharide sugar melecitose is extracted from wood chips (Dallimore and Jackson 1967; Hora 1981). Probably because of this high sugar content, black bears—*Ursus americanus cinnamomum*—often seek out vigorous young pole-size western larch in late spring and feed on the inner bark and cambium, usually on the lower 1 to 2 m of the trees (Schmidt and Gourley 1992). Often the trees are girdled and die; partially girdled trees frequently produce large cone crops following damage (Shearer and Schmidt 1987).

Genetics. Larch species vary widely in growth rates, cold hardiness, form, pest resistance, and other characteristics. This variability is often under strong genetic control and genetic gain is expected through tree improvement efforts (Eysteinsson and Greenwood 1995). Winter hardiness, change in foliage color, and cessation of height growth of Japanese larch were correlated with latitude of provenance origin, but date of bud flush was not (Toda and Mikami 1976). Further, branching habit, stem crookedness, spiral grain, and disease susceptibility varied between provenances. Genetic variation of tamarack throughout its range is comparable to other species of woody plants with extensive ranges (Cheliak and others 1988). Based on genetic differences in total height and survival of 210 clones of 5-year-old vegetatively propagated tamarack in central New Brunswick, Park and Fowler (1987) believed that clonal forestry was a good option for this species. Farmer and others (1993) also showed genetic variation in height of tamarack was related to rate and duration of shoot elongation and from differences in late-season elongation.

Conversely, low genetic variation occurs among populations of western larch for growth, phenology, and cold hardiness (Rehfeldt 1982) compared with other Rocky Mountain conifers. Rehfeldt (1983) identified an 11% variation associated with the elevation of the seed source and recommended that seedlots not be transferred more than ± 29 m or ± 2 contour bands. Based on genetic variation in allozymes of western larch seeds, Fins and Seeb (1986) cautioned transferring seeds from eastern Washington to north Idaho and recommended that seedlots for planting should include seeds from a diversity of locations within an area. Hall (1985) concluded that yields of cones and seeds from interspecific and intraspecific crosses and open-pollinated seeds of European larch were reduced in hybrid crosses compared to non-hybrid crosses. Wide variation in yield suggests that both genetic and environmental factors are important in controlling yield of seeds.

Hybrids. Larches hybridize readily (Rudolf 1974; Lewandowski and others 1994; Young and Young 1992), and geographic isolation is a major factor for lack of hybridization. Natural hybrids of western and subalpine larches occur where their ranges overlap (Carlson and Blake 1969; Carlson and others 1990). Seeds from natural hybrid trees closely resemble those of western larch (Carlson and Theroux 1993). Reciprocal cross pollinations between western and subalpine larches were successful, and germination of seeds from these crosses was higher than that of seeds from either parent (Carlson 1994).

L. kaempferi × *decidua*, known as *L.* × *eurolepis* A. Henry and commonly called Dunkeld larch, originated about 1900. It has been planted extensively in northwestern Europe and to a lesser extent in the eastern United States and Canada because it combines desirable characteristics of both parent species and grows faster than either (Eliason 1942; MacGillivray 1969). *L. kaempferi* × *sibirica,* known as *L.* × *marschlinsii* Coaz, was originated in 1901. *L. laricina* × *decidua*, known as *L. pendula* Salisb. or weeping larch, was originated before 1800 (Rehder 1940). Many other larch hybrids are known. Several larch species and hybrids were tested as potential short-rotation fiber crops for the Northeast and the Great Lakes region (Einspahr and others 1984) and in Wisconsin (Riemenschneider and Nienstaedt 1983); Dunkeld larch showed best growth in both studies. Seeds from a single provenance of Japanese larch and 6 provenances of European larch had, after 5 years, 3 times the growth potential of seeds from native red pine (*Pinus resinosa* Ait.) in another Wisconsin study (Lee and Schabel 1989).

Geographic races. Geographic races have developed in many widely distributed larch species, and these often exhibit marked differences in growth rates and other characteristics (Rudolf 1974). The European larch includes at least 5 geographic races (often considered to be subspecies or varieties) that roughly coincide with major distributional groups of the species (Debazac 1964; McComb 1955):

- Alpine, in south central Europe
- Sudeten, principally in Czechoslovakia
- Tatra, in Czechoslovakia and Poland
- Polish, principally in Silesia
- Romanian (several small outliers)

The races differ in seed size and viability, survival after planting, growth rate, phenology, form, and resistance to insects and disease (Dallimore and Jackson 1967; McComb 1955; Rudolf 1974). The races respond differently in different localities, but in the northeastern United States and Canada, the Polish and Sudeten races grow most rapidly and are recommended for planting there although they do not always have the best form (Hunt 1932; MacGillivray 1969). Sindelar reported (1987) that in Czechoslovakia, seedlings of Dunkeld larch and *L. decidua* × *gmelinii* grew better on sites with high levels of pollution than did European larch seedlings. Sindelar (1982) recommended that seed orchards of European larch contain many clones in order to prevent excessive propagation of a few fertile clones. A Scots race mentioned in older references probably developed in Scotland from plants of Sudeten origin (Rudolf 1974). European seed sources perform similarly in northeastern United States as in Great Britain, Germany, and Italy (Genys 1960).

Some varieties of Dahurian larch that are confined to definite areas appear to be geographic races (Debazac 1964). These include the following varieties:

- *japonica* (Maxim. ex Regel) Pilg.
- *principis-rupprechti* (Mayr) Pilg.
- *olgensis* (A. Henry) Ostenf. & Syrach., known as Olga Bay larch (Rehder 1940)

In China, *L. principis-rupprechti* and Olga Bay and Chinese larches are recognized as distinct species rather than geographic races of Dahurian larch (Chinese Academy of Sciences 1978). Tests in Finland showed marked differences in survival, growth rate, cold hardiness, and susceptibility to insect attack between trees from Korean and Sakhalin seed sources (Kalela 1937). A limited trial in North Dakota was unsuccessful (Cunningham 1972). Trees of Olga Bay larch seem suitable for planting in north central United States and adjacent Canada.

Because of the extensive natural range of tamarack, geographic races probably exist. Studies by Cheliak and others (1988); Farmer and others (1993), and Park and Fowler (1987) reported differences in growth, such as total height based on latitude and late-season elongation. Two-year-old seedlings of tamarack grown in Minnesota from seeds from several origins showed significant differences in total height and a tendency for bud set to occur earliest in seedlings from northern sources (Pauley 1965).

Japanese larch is native to a 363-km^2 area in the mountains of central Honshu, where it grows in scattered stands at elevations of 900 to 2,800 m (Asakawa and others 1981). Despite this small native range, test plantings of Japanese larch in several parts of the United States and eastern Canada, Japan, China, Great Britain, and Germany have shown significant differences among seed sources in tree height, survival, terminal bud set on leader, number of branchlets, insect resistance, winter and spring cold damage, and susceptibility to sulfur fumes (Hattemer 1968; Heimburger 1970; Lester 1965; MacGillivray 1969; Wright 1965). Progeny of seeds from diverse sources respond differently to particular environments, so that no general recommendations can be made as to the best races for specific localities. However, seeds from sources in the northern part and the higher elevations of Honshu have produced progeny with earlier hardening off and less early frost damage than have seeds collected from farther south and at lower elevations (Hattemer 1968; Heimburger 1970; Lester 1965; Wright 1965).

Siberian larch stock grown from seeds from the Altai region seem to be less cold hardy than stock grown from seeds from other parts of the range (Tkachenko and others 1939). Limited trials in North Dakota suggest that this species could be used as the tallest member of a multiple-row shelterbelt (Cunningham 1972).

Flowering. Male and female flowers of the larches are borne separately on the same tree. Cones are usually scattered throughout the non-shaded crown with seed cones more frequent higher in the crown and pollen cones more frequent lower in the crown (Eis and Craigdallie 1983), but there usually is considerable overlap. They occur randomly with the leaves on the sides of twigs or branches and usually open a few days before needle elongation. The male flowers are solitary, yellow, globose-to-oblong bodies that bear wingless pollen. The female flowers are small, usually short-stalked, erect, red or greenish cones that ripen the first year.

The seed cones and pollen cones usually are differentiated in terminal positions on short-shoot axes that completed at least 1 cycle of annual growth (Krüssman 1985; Owens and Molder 1979a). However, the seed and pollen cone buds of tamarack (Powell and others 1984) and Japanese larch (Powell and Hancox 1990) can differentiate laterally on long shoots the year they elongate. Furthermore, as tamarack plantations go from 5, 6, to 7 years of age, the number of trees bearing seed and pollen cones and the number of cones per tree increased each year (Tosh and Powell 1991). Top-grafting buds of 2-, 5-, 9-, 45-, and 59-year-old Japanese larch on 17-year-old trees shortened the time to produce female and male strobili by about 5 years over untreated controls (Hamaya and others 1989). Loffler (1976) found that yield of European larch seeds in seed orchards usually increased with graft age and in comparison to the natural forest, the cones provided more and larger seeds of better quality. Ten years after planting in a common garden, western larch cone production was twice as great for trees grafted with mature scions as for seedlings and five times greater than for rooted cuttings (Fins and Reedy 1992). The number of seed and pollen cones increased on 30- to 32-year-old western larch as average spacing expanded from 2 m to 3 m and wider (Shearer and Schmidt 1987). The average number of cones produced per tree during a good cone crop increased 27 times as the diameter classes increased from 10 to 15 cm to 30 to 36 cm, a reflection of the greater crown volume (Shearer 1986). Xu (1992) found similar relationships for Dahurian larch in China.

There was no relationship of the number of cone scales of Olga Bay larch or their color, shape, size, or structure to site characteristics, developmental stage of trees, or other biological factors (Suo 1982). Developing larch cones range in color from red to green with a range of intermediate shades. Raevskikh (1979) reported that red- and green-coned forms of Dahurian larch produced better quality seeds than did rosy-coned forms. Western larch cones are red, green, and brown in color, but no differences were detected in seed quality by color (Shearer 1977). Ripe cones become brownish and have woody scales, each of which bears 2 seeds at the base (Dallimore and Jackson 1967; Rehder 1940). The seed has a crustaceous, light-brown outer coat; a membranaceous, pale chestnut-brown, lustrous inner coat; a light-colored female gametophyte; and a well-developed embryo (figures 1 and 2) (Dallimore and Jackson 1967; Rehder 1940). Occasionally, atypical cones are found on larches. Tosh and Powell (1986) identified and studied proliferated and bisporangiate cones on tamarack planted 5 or 6 years earlier.

Figure 1—*Larix occidentalis*, western larch: seed with wing.

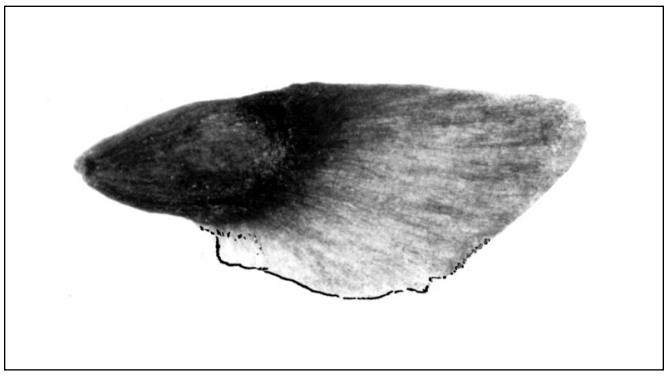
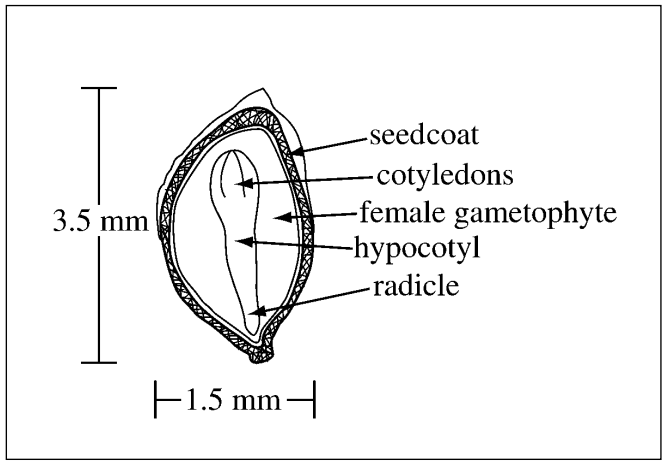
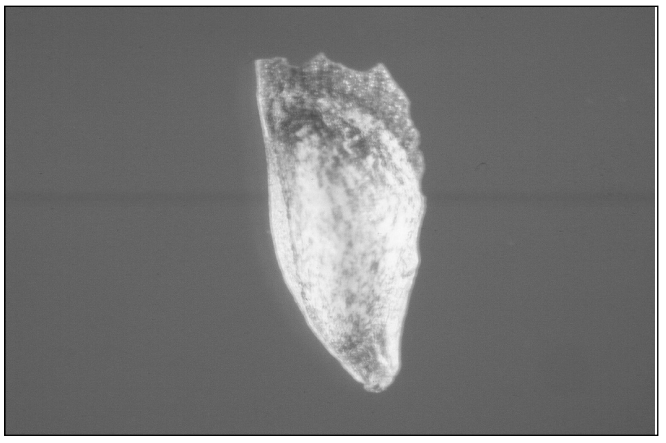


Figure 2—*Larix*, larch: longitudinal section through a seed of *L. laricina*, tamarack (**top**) and a de-winged seed of *L. occidentalis*, western larch (**bottom**).





A 10-year phenological record of western larch in the Northern Rocky Mountains showed a wide range in time of bud-burst, pollination, and cone opening (Schmidt and Lotan 1980). A 21-year phenological study of subalpine larch showed that spring temperature, not photoperiod, was a chief factor that determined bud-burst date (Worrall 1993). Morphological studies increased our understanding of characteristics of cones and seeds of tamarack (O'Reilly and

Farmer 1991) and for subalpine and western larches and their natural hybrids (Carlson and Theroux 1993). Seedcoats of subalpine larch are thicker than those of western larch and may be a partial barrier to germination (Carlson 1994).

Larch seeds are winged, nearly triangular in shape, and chiefly wind dispersed. Empty cones may remain on the trees for an indefinite period. Seeds of western larch carry long distances (Shearer 1959), but seeds of tamarack in Alaska fall close to the point of origin (Brown and others 1988).

An embryological study of European, Japanese, and Siberian larches showed that the embryos attained full size by early- or mid-August and that the seeds were fully developed by the end of August. The development was most rapid in Siberian larch (Hakansson 1960). Larches often have a high proportion of hollow seeds, as reported by Shearer (1990) and Trenin and Chernobrovkina (1984). The time of pollination is critical to development of viable and high-quality western larch seeds (Owens and others 1994). The high proportion of non-viable seeds was attributed to (1) underdeveloped ovules at pollination; (2) ovules that either were not pollinated or were not fertilized; (3) factors that prevented pollen germination, pollen tube growth, or fertilization; (4) problems associated with self-pollination; and (5) inhibited ovule development. Shin and Karnosky (1995) identified abortion of female strobili and embryo degeneration as major factors reducing seed yields of tamarack and European, Japanese, and Siberian larches in the upper peninsula of Michigan, although the previously mentioned 5 factors also caused seed loss. Factors contributing to empty seeds in European larch included lack of pollination, disturbances during megasporogenesis, failure of pollen to reach and germinate on the nucellus, and embryo degeneration (Kosinski 1986, 1989).

Throughout much of the range of western larch, frost often limits the number of developing cones that mature (Shearer 1990). Lewandowski and Kosinski (1989) described spring frost damage to 14 grafted Polish clones in a seed orchard of European larch. In late May 1968, frost completely killed the cone crop of Olga Bay larch growing above 1,000 m in northeastern China (Suo 1982). Frost may also limit cone production of subalpine larch most years (Arno 1990). Loffler (1976) found that late spring frost killed a high proportion of European larch cones. An inexpensive electrical resistance device that prevents frost damage has been used to protect pollinated female strobili of European and Dunkeld larches after controlled crossings (Ferrand 1988).

Indoor (potted) orchards are used to produce western larch seeds and to control the environmental conditions that often limit cone production in natural or planted stands (Remington 1995). Ross and others (1985) suggested many other advantages. Flowering of tamarack was promoted on potted, indoor, and field-grown grafts by foliar sprays of giberellin ($GA_{4/7}$) and root pruning (Eysteinsson and Greenwood 1990). Seed cone flowering decreased per centimeter of branch length as ortet age increased from 1 to 74 years (Eysteinsson and Greenwood 1993). Ross (1991) determined that response to combinations of stem girdles and $GA_{4/7}$ injections on 17-year-old western larch varied greatly in flowering response. Only the effects of girdling (not $GA_{4/7}$) were effective in promoting strobilus production in grafts on 10-year-old Japanese larch (Katsuta and others 1981).

Damage. During poor cone crop years with some larch species, many of the seeds are destroyed by weevils (Rudolf 1974). Several insects limit western larch cone and seed production. The major cone feeding insects are the larch cone maggot (*Strobilomyia laricis* Michelsen), western spruce budworm (*Choristoneura occidentalis* Freeman), a woolly adelgid (*Adelges viridis* Ratzeburg), and cone scale midges (*Resseliella* sp.) (Dewey and Jenkins 1982; Jenkins and Shearer 1989; Miller and Ruth 1989; Shearer 1984, 1990). Turgeon (1989) determined that larvae of the larch cone maggot infested more tamarack cones in the upper and mid-crowns than cones in the lower crowns. Larvae of the larch cone maggot also feed on cones of Siberian, European, Dahurian, and Japanese larches and tamarack in southern and central Finland (Pulkkinen 1989). During infestations of the western spruce budworm, the insect larvae decrease cone production of western larch by severing cone-bearing twigs and also by damaging developing cones and seeds on the trees (Fellin and Schmidt 1967; Fellin and Shearer 1968). Similarly, the eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) greatly decreases cone and seed production of tamarack (Hall 1981). The eastern spruce budworm and cone fly (*Lasiomma viarium* Huckett) larvae caused most damage to seeds of tamarack in 1982 and 1983 in New Brunswick and Maine, whereas other insects caused lesser damage (Amirault 1989; Amirault and Brown 1986). A recent review of insects that may influence larch cones and seeds in Canadian seed orchards listed 19 species in 4 families: 1 insect species for subalpine larch, 17 species within 4 families for tamarck, and 4 species within 3 families for western larch (de Groot and others 1994). In British Columbia, neither tamarack nor western larch have major insect pests (Eremko and others 1989).

Atmospheric fluorides can reduce the size of seeds, percentage germination, numbers of seeds per cone, and numbers of cones per tree. Reproductive failure and mortality of tamarack in Newfoundland have resulted in their replacement by more tolerant species (Sidhu and Staniforth 1986).

Micropropagation and genetic engineering. Micropropagation techniques can supplement reliance on larch seeds for a broad range of tree improvement and regeneration needs. Karnosky (1992) suggests biotechnology can help produce genetically superior larch by (1) mass propagation, (2) disease screening, and (3) transfer of genetic information through genetic engineering techniques. Organogenesis from young and mature larch callus tissues is reported (Bonga 1984; Chapula 1989). Lelu and others (1993) developed somatic embryogenesis techniques for several species and hybrids of larch. Full-sib immature zygotic embryos were produced from induction of embryonal masses for European and Dunkeld larches and *Larix* × *leptoeuropaea* (Lelu and others 1994a). Thompson and von Aderkas (1992) successfully regenerated western larch from immature embryos. Protoplasts of Dunkeld larch can be effectively isolated from embryonal mass and cultured to produce somatic plantlets (Charest and Klimaszewska 1994). Further, Lelu and others (1994b) showed that the number of mature somatic embryos of *Larix* × *leptoeuropaea* produced per gram (fresh weight) of embryonal mass was influenced by embryogenic line, sucrose concentration, and abscisic acid concentration. No universal maturation medium was recommended because of the interactive effects of these 3 factors. High plantlet survival was achieved in the greenhouse through either of 2 acclimatization methods (Lelu and others (1994c). In gymnosperms, gene transfer was first accomplished in European larch; transfer was mediated by *Agrobacterium rhizogenes* and subsequent regeneration of the transgenic plants (Huang and others 1991). Shin and others (1994a&b) reported that transgenic European larch plants were produced that use *Agrobacterium*-mediated single gene transfer to promote insect (*Bt* toxin gene) and herbicide (*aroA* gene) resistance.

Collection of cones. Larch cones should be collected as soon as they ripen; different species ripen at various times from August to December (table 2). Larch cones are picked from trees in forests, seed production areas, seed orchards, and potted tree collections or they can be gathered from felled trees, slash, or squirrel caches. In Tyrol, European larch seeds were picked from the snow by hand; they can also be gathered in late winter from canvas spread on the ground before the trees were shaken to release the seeds (Rudolf 1974). In most species, ripe cones are brown. Tests show that seedcoats are hard and that female gametophytes are firm. Often seeds mature earlier than expected and the period for cone collection for tamarack (Smith 1981) and western larch (Shearer 1977) can be expanded. Cones of Siberian larch should be harvested when needles start to turn yellow to assure high-quality seeds (Lobanov 1985). Data on height, seed-bearing age, seed crop frequency, and ripeness criteria are listed in tables 3 and 4.

Exraction of seeds. Freshly collected cones should be spread out in thin layers to dry in the sun or in well-ventilated cone sheds. The cones can be opened by solar heat, by heating in a cone kiln or room, or by tearing them apart mechanically (Rudolf 1974; Tkachenko and others 1939). Recommended kiln schedules are 8 hours at 49 °C for tamarack and 7 to 9 hours at 43 °C for western larch (Rudolf 1974).

After opening, cones should be run through a shaker to remove the seeds. Sometimes equipment must be modified to extract larch seeds (Saralidze and Saralidze 1976). Seeds can then be de-winged by a de-winging machine, by treading in a grain sack, or by hand-rubbing. The integument, which attaches the wing to the seed, is difficult to remove in normal processing without damage (Edwards 1987). Finally,

Table 2—*Larix,* larch: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
L. decidua	Europe, E US & Canada	Mar–May	Sept–Dec	Sept–spring
L. gmelinii	Russia	—	Sept–Nov	Feb–Mar
	NE China	May–June	Sept	—
	Japan	Late Apr–early June	Early–late Sept	—
L. kaempferi	Japan, Europe	Apr–May	Sept	Winter
	Japan	Late Apr–mid-May	Mid–late Oct	—
L. lyallii	Rangewide	May–June	Aug–Sept	Sept
L. occidentalis	W Montana & N Idaho	Apr–June	Aug–Sept	Sept–Oct
L. sibirica	Russia	Apr–May	Sept–Nov	Sept–Mar

Sources: Arno and Habeck (1972), Asakawa and others (1981), Chinese Academy of Sciences (1978), Kaigorodov (1907), Ohmasa (1956), Rudolf (1974), Shearer (1990), Tkachenko and others (1939).

Table 3—*Larix,* larch: height, seed-bearing age, and seedcrop frequency

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yrs)	Years between large seedcrops
L. decidua	9–40	1629	10	3–10
L. gmelinii	20–30	1827	14–15	2–4
L. kaempferi	30–40	1861	15	3
	—	—	12–16	4–8
L. laricina	9–20	1737	40	3–6
L. lyallii	9–25	1904	30	2–10
L. occidentalis	30–55	1881	25	2–10
L. sibirica	??–40	1806	12	3–5

Sources: Arno and Habeck (1972), Asakawa and others (1981), ODLF (1962, 1966), Schmidt and Shearer (1990), Tulstrup (1952).

Table 4—*Larix,* larch: color and size of mature cones

Species	Preripe color	Ripe color	Length (mm)
L. decidua	Green, rosy, brown	Light brown	19–38
L. gmelinii	—	—	19–25
	—	Yellow brown–deep brown	17–27
	—	Light purple–deep purple	16–24
	—	Light red–red with shine	17–24
	—	Dark red with shine	26
L. kaempferi		Brown	19–32
L. laricina	—	Brown	13–19
L. lyallii	Green–purple	Green–dark purple	38–51
L. occidentalis	Green-brown-purple	Green-brown-purple	25–38
L. sibirica	—	Brownish	25–38

Sources: Raevskikh (1979), Rehder (1940), Rudolf (1974), Shearer (1977), Suo (1982)

seeds should be cleaned with a blower or fanning mill. A mechanical macerator is routinely used for processing tamarack cones and for de-winging larch seeds (Wang 1995). Seed yields for 5 species are listed in table 5 and the number of cleaned seeds for 7 species is shown in table 6. Simak (1973) reported that, although European larch seeds can be upgraded by flotation in 80% to absolute alcohol for 5 to 15 minutes with a loss of less than 5% germinability, he recommended using water as an optimal liquid for flotation. In addition, Simak (1966) also reported that a seed sample of Himalayan larch had 28% filled seeds and weighed 4.68g /1,000 seeds (214,000 seeds/kg). Cooling cones and seeds of western larch so that the resin forms globules and becomes less sticky facilitates extraction and cleaning (Zensen 1980).

Purity of larch seedlots has ranged from 84 to 94%, but filled seed values have consistently been low at 50 to 70% (Rudolf 1974). The low percentage of filled seed may be attributed to the development of many unfertilized seeds and to woody or resin deposits in them. The woody tissue or resin hinders their removal in the cleaning process (Edwards 1987; Rudolf 1974). In lots of tamarack seeds from Ontario, 50% were sound; most of the unsound seeds had incompletely developed embryos and endosperm (Farmer and Reinholt 1986). Hall and Brown (1977) found similar conditions among seeds of European and Japanese larches and their hybrids. Seeds of western larch also have a high proportion of embryo failures (Owens and Molder 1979b). Use of X-radiography was recommended to evaluate the quality of tamarack seeds because flotation in 95% ethanol killed 52% of germinable seeds (Eavy and Houseweart 1987). A purity of 80% and a viability (germinative capacity) of 20% were recommended in 1966 as minimum standards for western larch (WFTSC 1966). Current standards for tree seeds to be certified under OECD Certification in Ontario require a minimum of 95% purity for tree seeds, resulting in an average germinability of 75 to 80% at 15 years for tamarack (Wang 1995).

Storage of seeds. Because larch seeds can be stored for long periods at seed moisture contents of 5 to 10% in sub-freezing temperatures, Bonner (1990) classifies them as "true orthodox" seeds. Gordon (1992) found that larch seeds can be stored at 6 to 8% moisture content at 1 to 3 °C for 25 years with little or no loss of germination quality. European

larch seeds keep well for a year or two if stored in the cones (Rudolf 1974). Tamarack seeds store very well at 2 °C for 10 years (Wang 1982). Details on seed storage for 6 species are shown in table 7. There was no significant difference in viability of European larch seeds stored at 0 °C or in liquid nitrogen (–196 °C) for 1 to 6 days (Ahuja 1986). European larch seeds (Sudeten source) collected in 1956 and stored at 9% moisture content showed little decrease in germination, if any at all, over a 12-year period (Hill 1976).

Pregermination treatments. Seeds of most larch species germinate without pretreatment, but stratification in moist medium usually hastens the germination process. Subalpine larch has a thick seedcoat and seeds rarely germinate after 30 days of stratification on moist blotting paper, but Carlson (1994) and Shearer and Carlson (1993) obtained good germination by stratifying seeds for 30 days in a slightly acid, sphagnum-based soil. Germination of subalpine larch also improved after seeds were soaked in 1% hydrogen peroxide for periods of 6 to 24 hours (Shearer 1961). Other pre-germination treatments used for western larch seeds include soaking them in water for 18 days at 1 °C or in USP 3% hydrogen peroxide (H_2O_2) for 12 to 24

Table 5—*Larix,* larch: seed yield data

Species	Place collected	Cone wt/cone vol		Seed yield/cone vol	
		kg/hl	lb/bu	kg/hl	lb/bu
L. decidua	NE US Ontario, &	31	24	1.16	0.90
	Europe	—	—	.96	0.75
		24–35	19–27	0.96–2.57	0.75–2.00
L. gmelinii	Japan	26.3	20	—	—
L. kaempferi	Japan & Europe	35.5–37	28–29	—	—
		24–35	19–27	0.96–1.28	0.75–1.00
L. laricina	Great Lake states	32	25	0.96	0.75
	Ontario	—	—	0.71	0.55
L. occidentalis	Idaho & Montana	32	25	64	0.50
L. sibirica	Russia	—	—	*	—

Sources: Asakawa and others (1981), Eliason (1942), Eremko and others (1989), NBV (1946), Ohmasa (1956), ODLF (1966), Rudolf (1974), Tulstrup (1952).
* Here, 1.81 kg of seeds were extracted from 45.36 kg of cones (Gorshenin 1941).

Table 6—*Larix,* larch: numbers of cleaned seeds

Species	Place collected	Cleaned seeds (x1,000)/weight				Samples
		Range		Avg		
		/kg	/lb	/kg	/lb	
L. decidua	Alps*	93–214	42– 97	154	70	141+
	Tatra Mtns (Slovakia)	161–269	73–122	198	90	20
	Sudeten Mtns†	205–265	93–120	229	104	4
	—	150–229	68–104	187	85	12
	Romania	152–225	69–102	179	81	4
	Europe & NW US	93–269	42–122	159	72	190+
L. gmelinii	—	176–465	80–211	265	120	21
	Sakhalin	359–425	163–193	390	177	5
	Korea	203–331	92–150	236	107	12
	Japan	241–551	109–191	—	—	—
L. kaempferi	NE US	170–302	77–137	249	113	14
	Japan	150–503	68–228	265	120	68+
	Europe	126–335	57–152	254	115	17+
	Japan	117–333	53–151	190	86	—
L. laricina	—	463–926	210–420	701	318	16
	Ontario	494–723	224–328	556	252	10+
L. lyallii	NW US	231–359	105–163	313	142	4
L. occidentalis	NW US	216–434	98–197	302	137	131+
L. sibirica	Europe	68–163	31– 89	97	44	71+

Sources: Asakawa and others (1981), Eliason (1942), Heit and Eliason (1940), NBV (1946), Ohmasa (1956), ODLF (1966), Rudolf (1974), Shearer (1961, 1977), Simak (1967).
* Alpine race.
† Sudeten race.

Table 7—*Larix*, larch: storage conditions for seeds in sealed containers

Species	Seed moisture content (%)	Temp (°C)	Viable period (yr)
L. decidua	9	9–10	12
	7.5	2–4	14
L. gmelinii	6.2	2–4	15
L. laricina	7	2	10
	5.5–9.8	2–4	17–18
L. kaempferi	12.1	2–4	23
L. lyallii	4–8	-18	—
L. occidentalis	6–9	-18	—
	6	4	16*
L. sibirica	6–8	1–3	25
	6	2–4	13

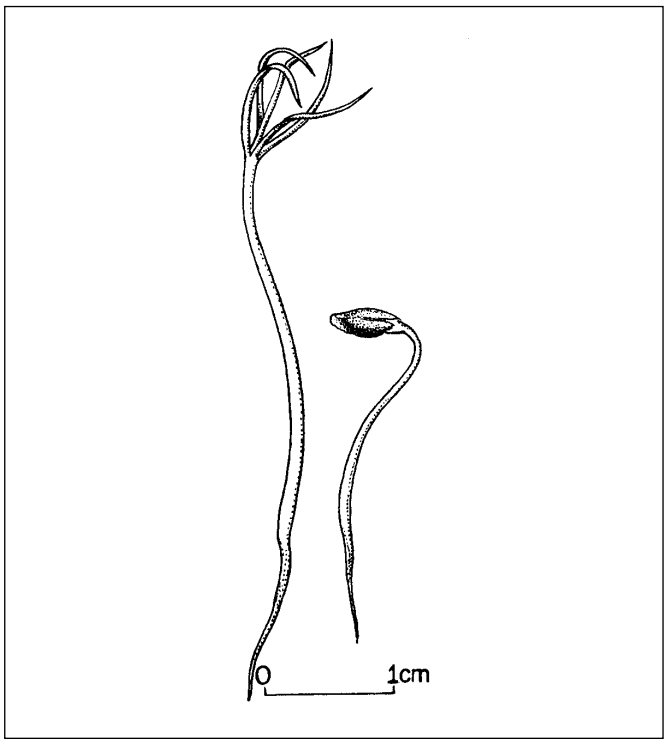
Sources: Heit (1967), Kiaer (1950), Rudolf (1974), Schubert (1954), Wang (1982), Wang and others (1993).
*Viability of 5% retained after 16 years of storage.

hours (Schmidt 1962; Shearer and Halvorson 1967). Unstratified seeds of tamatrack from Ontario provenances germinated completely in light at a range in incubation temperatures but only stratified seeds could be germinated in the dark at lower temperatures (Farmer and Reinholt 1986). Brown (1982) reported similar results for tamarack seeds from Alaska. Wang (1995) reported pregermination results for 4 species of larch:

- Daurian larch seeds did not require cold stratification or prechilling for maximum germination, but seeds stratified for 3 weeks germinated more uniformly with or without light. Non-stratified seeds germinate best with a 16-hour photoperiod than in darkness or with an 8-hour photoperiod.
- Japanese larch seeds that were stratified for 3 weeks showed significantly more germination than those that were not stratified.
- European larch seeds did not require stratification for maximum germination.
- Tamarack seeds did not require stratification for maximum germination but their germination rate was much improved.

One or two cycles of cold stratification followed by dehydration improved percentage and speed of germination of a variety of Dahurian larch (*L. gmelinii* var. *principis-rupprechtii* Mayr) (Chang and others 1991). Kuznetsova (1978) found that germination of Dahurian larch seeds was enhanced by storing moist seeds in cloth bags on frozen soil under snow.

Figure 3—*Larix laracina*, tamarack: seedling development at 1 **(right)** and 8 (**left**) days after germination.



Germination. Germination of larch seeds is epigeal (figure 3) and may be tested in germinators or sand flats. Both the Association of Official Seed Analysts (AOSA 1993) and the International Seed Testing Association (ISTA 1993) recommend the same germination test procedures: germination on top of moist blotters or other paper products for 21 days at temperatures alternating diurnally from 20 °C during a 16-hour dark period to 30 °C during an 8-hour light period. For western larch, duplicate tests of untreated seeds and seeds that are stratified for 21 days at 3 to 5 °C are recommended. An attainable standard for purity and viability for western larch seeds is 90 and 60%, respectively (Stein and others 1986). Further, they recommend that test seeds be germinated either on the top of blotters or in petri dishes at 20 to 30 °C for 3 weeks in light. Li and others (1994) showed that light may reduce germination of stratified seeds and had no effect on unstratified seeds of western larch. Sorensen (1990) recommended short stratification periods for germination in a warm greenhouse but longer ones will improve uniformity of emergence. Methods used and average results for 6 larch species are summarized in table 8. Less-used techniques to increase germination of Siberian larch include (a) presoaking seeds and subjecting them to laser radiation (Dobrin and others 1983) and (b) subjecting seeds to UHF electromagnetic field exposure (Golyadkin and others 1972).

Table 8—*Larix,* larch: germination test conditions and results

Species	Cold stratification (days)	Germination test conditions*				Germination rate		Germination	
			Temp (°C)			Amount		Avg	
		Medium	Day	Night	Days	(%)	Days	(%)	Samples
L. decidua	0	Moist paper	30	20†	30	—	—	36	368
	0	Moist paper or blotters	30	20	21	—	—	—	—
L. gmelinii	0	Moist paper, sand	30	20	30	47	18	52	23
L. kaempferi	0–30	Moist paper	30‡	26§	30	25	20	43	179
	21	Moist paper or blotters	30	20	16	—	—	—	—
L. laricina	60	Sand	30	20	50	33	29	47	16
	0	Moist paper	30	20	21	—	—	—	—
L. lyallii	0//	Moist paper	18	18	39	3	21	14	1
L. occidentalis	30	Soil	—	—	100	—	—	15	1
	0–42	Moist paper	30	20	30	—	—	57	104
	21	—	30	20	21	—	—	—	—
L. sibirica	0	Moist paper or blotters	30	20	21	—	—	—	—

Sources: AOSA (1993), Carlson and Blake (1969), Heit and Eliason (1940), ISTA (1993), Rudolf (1974), Shearer (1961), Simancik (1968).
* Daily light period was 8 to 16 hours.
† Constant temperatures at 26 °C and at 20 °C also were used.
‡ Cold stratification generally recommended for at least 21 days.
§ Constant temperatures at 24 °C and at 20 °C also were used.
// Seeds were soaked in USP 3% H_2O_2 for 24 hours in lieu of stratification.

Table 9—*Larix,* larch nursery practice

Species	Sowing season	Seedlings		Sowing depth		Mulch			Tree percent	Outplanting age (yrs)
							Depth			
		/m²	/ft²	mm	in	Type	mm	in		
L. decidua	Fall or spring	431–538	40–50	3–6	0.13–.25	Straw, litter, or burlap*	—	—	10	2+0, 1+1, 2+1, or 1+2
L. laricina	Fall	269	25	6	0.25	None	—	—	35	2+0
L. leptolepis	Spring†	753–861	70–80	3–6	0.13–.25	None	—	—	10–20	1+1 or 2+1
L. occidentalis	Spring†	323–592	30–35	3–6	0.13–.25	Sawdust	10	.38	40	1+0
L. sibirica	Spring†	323–431	30–40	3–6	0.13–.25	—	—	—	30	2+0 & 1+1

Source: Rudolf (1974).
* Only fall-sown beds should be mulched.
† Only seeds that have been stratified in moist sand or vermiculite at 0 to 9.5 °C for 14 to 42 days.

Nursery practice. Larch seeds should be sown unstratified in the fall or stratified in the spring and covered with 3 mm (0.13 in) of sand or nursery soil. Fall-sown beds should be covered with burlap or mulched with straw or litter over the first winter; the mulch can be removed before germination commences in the spring (Rudolf 1974). Hrabi (1989) determined that soaking European larch seeds in water for 24 hours followed by drying, also for 24 hours, permitted mechanized sowing and resulted in high germination. Some details as to nursery practice for 5 species are listed in table 9. Larches have few enemies in the nursery, although a species of the fungus *Verticillium* sometimes damages western larch plantations in the seedbed (Rudolf 1974).

The weight of Japanese larch seeds had some effect on initial size of seedlings, but most variation was attributed to differences in the rate of germination (Logan and Pollard 1981).

Larches grow in almost any kind of soil, including clay and limestone, but they develop best when grown in the open on somewhat moist, but well-drained soils. Proper selection of planting sites and seed sources reduce the risks associated with growing non-native larch (Robbins 1985). Tamarack and introduced larches growing on appropriate sites produce high fiber yields on rotations that are economically attractive (Carter and Selin 1987). The larch casebearer (*Coleophora laricella* (Hübner)) and the western spruce budworm (*Choristoneura occidentalis* Freeman) may cause serious damage to western larch plantations in the West (Fellin and Schmidt 1967) and the larch sawfly (*Pristiphora erichsonii* (Hartig)) may damage all species of larch in many areas.

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Zygophyllaceae—Caltrop family

Larrea tridentata (Sessé & Moc. ex DC.) Coville

creosotebush

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Synonyms. *Larrea tridentata* (DC.) Cov.

Other common names. greasewood, *gobernadora, hediondilla*.

Growth habit and occurrence. Creosotebush—*Larrea tridentata* (Sessé & Moc. ex DC.) Coville—is an evergreen shrub native to the arid subtropical regions of the southwestern United States, Mexico, Argentina, and Chile (Benson and Darrow 1945). Whether the North American species *L. tridentata* is distinct from the South American species *L. divaricata* Cav. has been unclear (Benson and Darrow 1945), but most recent authors recognize *L. tridentata* as a separate species. It is the dominant shrub in all 3 warm deserts of the United States: the Mojave, Sonoran, and Chihuahuan Deserts (Barbour and others 1980). Although creosotebush can grow on a variety of substrates, it is most abundant on calcareous soils (Musick 1978). Stands vary in density and stature, depending on the aridity of the site (Woodell and others 1969). Under very low rainfall, shrubs are smaller and more widely spaced than those in stands under more mesic conditions. Morphological and physiological adaptations of the genus *Larrea* to growth under xeric conditions are well studied (Barbour and others 1974, 1977). Despite dominance of the species in xeric sites, the emergence and growth of seedlings is favored by mesic conditions. Moisture, neutral pH, low salinity, and moderate temperatures are conducive to successful germination and seedling establishment (Barbour and others 1977).

Use. Creosotebush is not browsed by livestock. Although an edible livestock feed has been made from creosotebush and a valuable antitoxidant has been extracted from the shrub (Duisberg 1952), no economically feasible program for gathering and using large amounts of creosotebush has been developed. Creosotebush, like other common plants with peculiar odor or taste, has been used in traditional medicine to cure various ills (Benson and Darrow 1945). In arid and semiarid parts of the Southwest, creosotebush is used for landscaping and reclamation of disturbed lands (Day and Ludeke 1980; Graves and others 1978; Williams and others 1974).

Flowering and fruiting. Creosotebush has perfect flowers. It blooms most profusely in the spring but may flower from time to time throughout the year (Kearney and Peebles 1951; Valentine and Gerard 1968). The fruit is a densely white, villous, 5-celled capsule (Kearney and Peebles 1951). When fruits are cast, they separate into individual carpels, each normally containing 1 seed (figures 1 and 2) (Martin 1969). Carpel fill under natural conditions averages 35% (range 12 to 62%) (Valentine and Gerard 1968). Plants may fruit sparingly at 4 to 6 years of age and reach full fruiting maturity at 8 to 13 years (Martin 1974). Annual production ranges from 39 to 278 fruits/100 g (11 to 79/oz) of branch or from 119 to 1,714 fruits/plant (Valentine and Gerard 1968).

Collection, extraction, and storage. Ripe fruits may be collected from the shrub in the late spring or early summer. Fumigation or dusting fruits with insecticide is advisable to prevent insect damage. Clean seeds, extracted from the carpels, are small—there are about 374,800/kg (170,000/lb)—and are not usually available on the market (Knipe and Herbel 1966; Martin 1969). Viability of seeds in carpels declined little after 2 to 4 years in dry storage at room temperatures, and some 7- to 8-year-old lots germinated well (Barbour and others 1977; Valentine and Gerard 1968). This information strongly suggests that the seeds are orthodox in storage behavior and should store well for many years at low temperatures and moisture contents.

Figure 1—*Larrea tridentata*, creosotebush: single carpel.

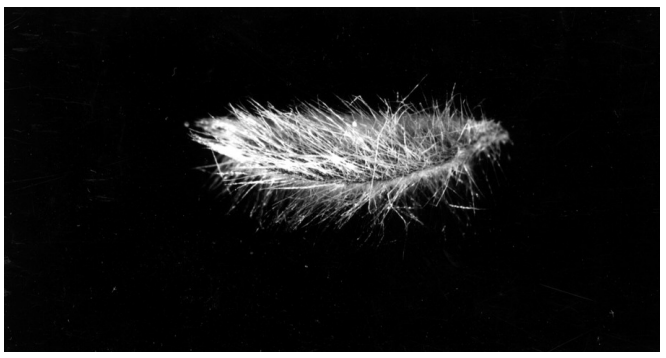
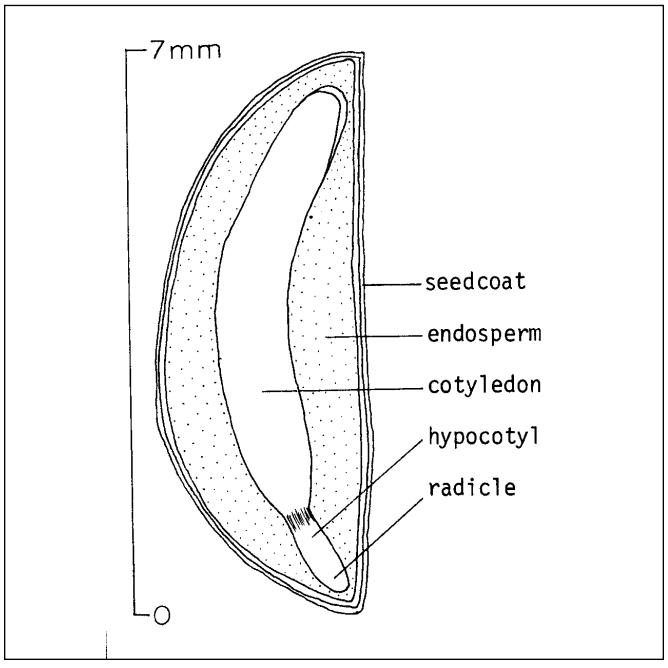


Figure 2—*Larrea tridentata*, creosotebush: longitudinal section through a carpel.



Pregermination treatments. Creosotebush seeds in carpels exhibit some seedcoat dormancy (McGee and Marshall 1993). Germination can be increased by removal of the carpel (Tipton 1984) and, to a lesser extent, by leaching of the intact carpel (Barbour 1968; Tipton 1984). Partial destruction of the carpel by mechanical abrasion is known to increase germination. Seeds in carpels so treated have a high average percentage germination (93%) over a range of 10 to 60 °C. Yet, exposing seeds to warm temperatures (over 37 °C) has been found to reduce germination, and continuous exposure to cold temperatures prior to sowing is desirable (Barbour 1968). Storage in partially sealed plastic bags with activated carbon for 30 days at 2 °C is recommended for high percentage germination (Graves and others 1975).

Germination. There are no official testing prescriptions for creosotebush. In one series of tests, germination of unscarified seeds (computed on filled carpel basis) in carpels at 17 °C ranged from 55 to 90% (average 74%) (Valentine and Gerard 1968). Carpels were dusted with fungicide and placed on moist blotter paper in petri dishes in humidified germinators (Valentine and Gerard 1968). Fungicide treatments may delay and reduce germination, however (Tipton 1985). Conditions conducive to germination include darkness (Barbour 1968; Tipton 1985), high moisture with wetting and drying cycles (Barbour 1968; McGee and Marshall 1993), temperatures near 23 °C, low salinity, and near-zero osmotic pressure (Barbour 1968).

Seedling care. Seedling survival is very low in natural populations (Ackerman 1979), and large-scale seedling establishment is thought to be rare (Barbour 1968). Heavy rains in late summer increase seedling germination and survival (Ackerman 1979; Boyd and Brum 1983). Under laboratory conditions, maximum root growth occurred at 29 °C in a medium that was slightly acidic, non-saline, and near-zero in osmotic pressure (Barbour 1968). Seedlings grown in acidic media are highly susceptible to phosphorus toxicity (Musick 1978).

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Ericaceae—Heath family

Ledum L.

Labrador-tea

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Other common names. trapper's-tea, trapper's tea.

Growth habit, occurrence and use. The genus *Ledum*—Labrador-tea—comprises 3 evergreen shrubs with a wide distribution (table 1). Plants range from 0.3 to 0.8 m tall and are much-branched. The leaves are leathery, lance-shaped, and hairy on the lower surface and have a characteristic spicy fragrance. Labrador-tea produces seeds vigorously; in its natural environment it can reproduce either from seeds (McGraw and Shaver 1982) or vegetatively (Sumner 1964). The below-ground system develops as result of layering by the above-ground shoots, and as much as 5 times more biomass has been documented below-ground than above, with clones covering 5 to 10 m^2 (Calmes and Zasada 1982). Marsh Labrador-tea is an alternate host for spruce needle rust—*Chrysomyxa ledicola* Legerh. (Ziller 1974). Sumner (1964) gives a detailed description of Labrador-tea morphology in interior Alaska. Leaves of marsh Labrador-tea can be boiled to make an aromatic tea; excessive doses can cause drowsiness or intestinal disturbance. Labrador-tea produces a sesquiterpene, germacrone, that makes it highly unpalatable to snowshoe hares (Reichardt and others 1990). Western Labrador-tea contains toxic alkaloids known to be poisonous to livestock (MacKinnon and others 1992).

Flowering and fruiting. Flower buds are initiated in the summer months at the tips of new shoots. They overwinter and flower the following spring, in late May and early June (Reader 1982). Flowers are white, with protruding stamens; they occur in numerous umbel-like clusters. Fruits occur as drooping clusters of dry capsules (figure 1). A large number of seeds are produced per flower. Sumner (1964) found a range of 34 to 181 seeds per fruit in her study of marsh Labrador-tea in interior Alaska. Extensive flowering is common. Seeds are small (bog Labrador-tea, 1.8 to 3.0 mm by 0.2 to 0.3 mm; marsh Labrador-tea, 1.4 to 2.0 mm by 0.2 to 0.3 mm) (Karlin and Bliss 1983). Seedcoats are golden and translucent, with a loose, elongated testa that aids wind dispersal (Densmore 1997). Calmes and Zasada (1982) found that only 45% of bog Labrador-tea seeds were filled.

Extraction, cleaning, and storage of seeds. Seed capsules open as they dry, readily releasing seeds. Empty capsules can be separated from seed with a fine-mesh sieve. Most seed viability is lost within 1 year of collection. When seeds were stored for 22 months at 4 °C, germination dropped from 58 to 16% (Karlin and Bliss 1983).

Pre-germination treatments. Labrador-tea does not require cold stratification for germination, but most data suggest that stratification improves germination. In a study of marsh Labrador-tea, seeds exhibited shallow dormancy (Calmes and Zasada 1982); 30 days of cold stratification

Table 1—*Ledum,* Labrador-tea: nomenclature and occurrence

Scientific name & synonym	Common name	Occurrence
***L. glandulosum* Nutt.**	**western Labrador-tea**	N Europe
***L. palustre* L. ssp. *decumbens* (Ait.) Hulten** *L. palustris* ssp. groenlandicum (Oeder) Hulten	**marsh Labrador-tea**	SE & interior Alaska; Canada E to Newfoundland, S to New Jersey, Ohio, Minnesota, & Washington
***L. groenlandicum* Oeder.** *L. decumbens* (Ait.) Lodd ex Steud.	**bog Labrador-tea**	Alaska & E through Canada to Greenland; S to Labrador & Hudson Bay; also N Europe & Asia

Sources: Juntila (1972), Viereck and Little (1972).

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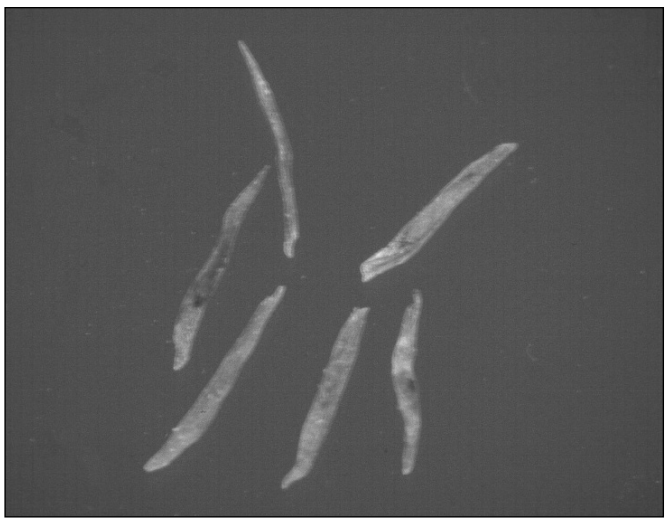
Figure 1—*Ledum groenlandiicum*, bog Labrador-tea: individual dry capsules.



increased the rate and percentage of germination. Densmore (1997) achieved 100% germination of marsh Labrador-tea at 20 °C and with 20 hour day-length following cold stratification. In another study, marsh Labrador-tea germinated best without any stratification (Karlin and Bliss 1983).

Germination tests. Seeds can be sprinkled on the surface of a moist substrate and covered with clear plastic film. Light is required for germination (Calmes and Zasada 1982; Karlin and Bliss 1983); germination is enhanced with longer day-lengths (Densmore 1997). In addition to light, optimal germination conditions include a continually moist, somewhat acidic substrate (pH 5.5) and mean daily temperatures ≥ 17 °C (Karlin and Bliss 1983). Treating seeds with gibberellic acid greatly increased germination under a variety of environmental conditions (Junttila 1972).

Nursery practice. Marsh Labrador-tea has been successfully propagated from seeds for horticultural purposes. The seeds should be sown thinly in boxes of pure, finely sifted peat moss, and then covered with a fine dusting of peat moss (Sheat 1948). Cuttings taken from mature plants in mid-December rooted well (Dirr and Heuser 1987), but below-ground stem cuttings produced few new shoots (Calmes and Zasada 1982). Half-mature side shoots can be pulled off and rooted in a mixture of peat moss, loam, and sand (Sheat 1948).

Seedling care. Labrador-tea seedlings are fragile and slow-growing. After 4 months of growth in a greenhouse, seedlings of bog Labrador-tea were only a few millimeters tall (Sumner 1964). Though seeds can germinate in water-saturated substrates, seedling survival and establishment are enhanced with better drainage.

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Fabaceae—Pea family

Lespedeza Michx.

lespedeza

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Growth habit, occurrence, and use. The genus *Lespedeza* includes about 140 species of shrubs, sub-shrubs, and herbs (Hensen 1957). Most species are native to the temperate regions of eastern Asia and only about 11 species are considered native to North America (Clewell 1966). All native species are herbaceous; however, several species of shrub lespedeza have been introduced into the United States (table 1). The non-native shrub lespedezas tend to have herbaceous stems with woody bases. All species listed in table 1 are planted for conservation and management purposes (Kelsey and Dayton 1942; Strausbaugh and Core 1964). Both shrub and Thunberg lespedezas are commonly referenced in the floristic literature (Gleason and Cronquist 1991). Leafy lespedeza, a less frequently referenced species, is noted by some to occur in the central-eastern United States (Clewell 1966; Isely 1990; Kartesz 1994). Although the name *L. japonica* has been used since the 1930s, many of the *L. japonica* materials have been re-identified as *L. thunbergii* (Vogel 1974). Classification of these shrubs is difficult and confused because of variation resulting from interspecific hybridization (Clewell 1966). Shrub lespedeza is the most common and widely planted shrub in the genus in the United States (Davison 1954; Vogel 1974).

Lespedeza shrubs are adapted primarily to the southeastern two-thirds of the United States, except for southern Florida (Clewell 1966; Davison 1954). They are planted mainly for wildlife food and cover (Owsley and Surrency 1989) and for erosion control (Gabrielson and others 1982; USDA SCS 1980). Soil enrichment by nitrogen-fixing symbionts is also a potential benefit (Allen and Allen 1981). The seeds are preferred quail food (Crider 1952; Davison 1954; Vogel 1974). Some plantings have been made for ornamental purposes (Clewell 1966; Crider 1952). Grown to maturity, plants of shrub lespedeza may reach a height of 3 m but more commonly 1.2 to 2.4 m (Crider 1952; Davison 1954; Vogel 1974). In management for seed production, stems of some shrub lespedezas must be cut back to the ground (Davison 1954; Vogel 1974).

Superior strains. Superior strains of shrub lespedeza have been selected and developed mostly at the plant material centers of the USDA Natural Resources Conservation Service (formerly the Soil Conservation Service) in the East and Southeast (Vogel 1974). Strains 100 and 101 of shrub lespedeza were developed for their greater production of seed and persistence of fruits on the plants after ripening (Davison 1954). *L. bicolor* 'Natob' matures seeds much earlier and is more winter-hardy than any other strain of shrub lespedeza grown in the United States. Thus, it can be grown farther north than other shrub lespedezas (Clewell 1966). A selection of Thunberg lespedeza called VA-70 (USDA SCS

Table 1—*Lespedeza,* lespedeza: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***L. bicolor* Turcz.**	**shrub lespedeza,** bicolor lespedeza	Origin: E Asia; Arkansas to Virginia, S to N Florida & Texas
***L. cyrtobotrya* Miq.**	**leafy lespedeza,** shrub lespedeza	Origin: temperate E Asia; central E US
***L. thunbergii* (DC.) Nakai** *L. sieboldii* Miq. *L. racemosa* Dipp. *L. formosa* Koehne *L. japonica* Bailey *Desmodium penduliflorum* Oudem.	**Thunberg lespedeza**	Origin: E Asia; similar range as shrub lespedeza but not as far N; best adapted to N Florida, S Alabama, & S Mississippi

Sources: Clewell (1966), Isely (1990), Kartesz (1994), Vogel (1974).

1980) ripens seeds a month earlier than most strains of shrub lespedeza, thus adapting it to the mountains and more northerly areas of the South (Vogel 1974).

Seeds of these strains have been marketed, but production has been so erratic that seed supplies can be scarce or nonexistent. Some problem exists in maintaining seed supplies of pure strains, apparently because of cross-pollination.

Flowering and fruiting. The flowers are loosely arranged on elongate racemes and are mostly rose-purple, with gradation to white in some variants (Ohwi 1965; Rehder 1940; Strausbaugh and Core 1964). The chasmogamic flowers may be self- or cross-pollinated (Clewell 1966; Crider 1952; Ohwi 1965). Honey bees (*Apis mellifera* L.), bumble bees, and other insects are necessary for pollination (Crider 1952; Graetz 1951).

Time of flowering and fruiting varies among species and strains, but it is also controlled by the latitude where the plants are grown. Flowering occurs mostly in July and August but will begin in June in Mississippi and as late as September in Maryland. The brown fruits are 1-seeded indehiscent legumes (pods) that mature mostly in late September and October (Vogel 1974) (figure 1). The legumes fall to the ground when ripe, and most of them are down by early winter (Crider 1952).

A light seedcrop may occur the first year from 1-year-old transplants, and good seedcrops can be expected each succeeding year (Crider 1952). Seeds of shrub lespedeza are pale brown to olive and copiously flecked with purple. Seeds of Thunberg lespedeza are solid dark purple (Musil 1963) (figure 1). Seeds of lespedeza have little or no endosperm (figure 2).

Collection of fruits; extraction and storage of seeds. Shrub lespedeza seeds are most commonly harvested with a combine as soon as the fruits are ripe and moderately dry. The combined material, which includes stems, intact legumes, and hulled seed, is air-dried and then cleaned to separate seed and legumes from the stems and inert matter. Seeds that remain in their legumes can be hulled by running them again through a combine or through a huller-scarifier and then should be cleaned (Vogel 1974).

Seed yields may exceed 560 kg/ha (500 lb/ac) (Byrd and others 1963), but more commonly yields range from 336 to 447 kg/ha (300 to 400 lb/ac) (Crider 1952; Vogel 1974). Weight of cleaned seeds per volume was 67 kg/bu (60 lb/bu) (Vogel 1974). The number of cleaned seeds is about 187,000/kg (85,000/lb) for common shrub lespedeza (Crider 1952; Strausbaugh and Core 1964; Vogel 1974); 140,000/kg (64,000/lb) for 'Natob' bicolor (Crider 1952; Vogel 1974); and 154,000 to 159,000/kg (70,000 to 72,000/lb) for Thunberg lespedeza (Strausbaugh and Core 1964; Vogel 1974).

Seeds are stored at 10 °C and 40% relative humidity. They may be stored either hulled or unhulled, but seeds stored in the hull remain viable longer than hulled seeds. Length of viability varies with harvest years and storage treatment, but seeds have been viable after 20 years of storage (Vogel 1974).

Figure 1—*Lespedeza, lespedeza:* legumes (**above**) of *L. bicolor*, shrub lespedeza (**left**) and *L. thunbergii*, Thunberg lespedeza (**right**); and seeds (**below**) of *L. bicolor*, shrub lespedeza (**left**) and *L. thunbergii*, Thunberg lespedeza (**right**).

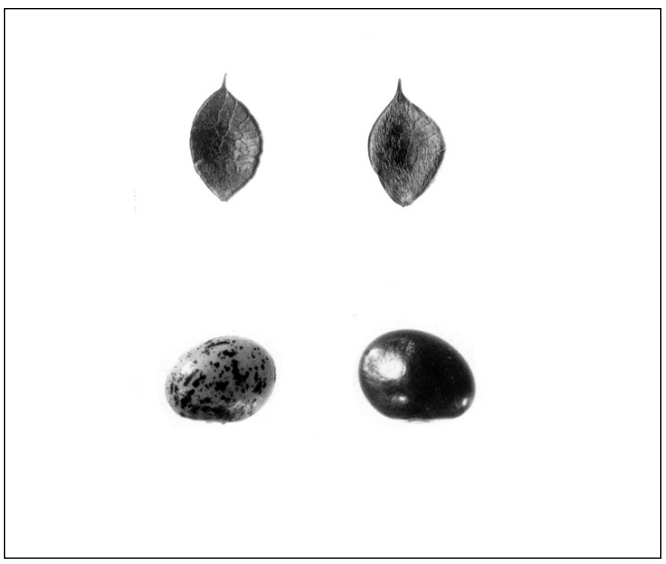
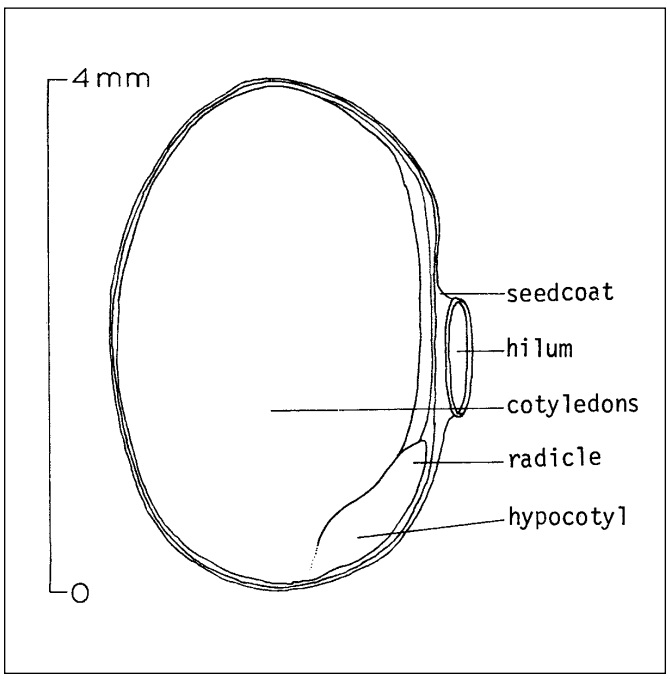


Figure 2—*Lespedeza thunbergii*, Thunberg lespedeza: longitudinal section through a seed.



Pregermination treatments. A high percentage of shrub lespedeza seeds have hard seedcoats and should be scarified before planting. Mechanical scarification is the preferred method. A huller-scarifier is one machine used for this purpose (Vogel 1974). About 50% of the seeds cleaned in a hammermill will be scarified. Fifty percent scarification allows a good stand to become established the first year but holds some seeds dormant for germination the second year. This could help assure stand establishment in case of failure or poor establishment the first year (Vogel 1974). Seeds can also be scarified by immersion in concentrated sulfuric acid for 30 minutes, followed by washing and drying (Crider 1952). The acid treatment causes less damage to older brittle seeds than does mechanical treatment (Vogel 1974).

Germination tests. Germination tests can be made by placing seeds between blotters in a petri dish, in a rolled towel (either horizontally or vertically), or in sand or soil and holding them at temperatures of 20 °C for 16 hours and 35 °C for 8 hours for each day. Light is not required, but it has been used with no effect on germination. First counts of germinated seeds are made at 7 days and last counts at 21 days. Percentage germination is similar for all 3 species; the average is about 76%. Seed purity is 95% or higher (Vogel 1974).

Nursery practices. Seeds should be broadcast in large quantities—11 to 16 kg/ha (10 to 14 lb/ac)—on a firm seedbed lacking weeds (USDA SCS 1980). Inoculation with a specific *Rhizobium* strain is recommended at the time of planting (USDA SCS 1980). When growing seedlings for transplanting, rows should be spaced 0.9 to 1.2 m (3 to 4 ft) apart and planted with 39 to 66 seeds/m (12 to 20 seeds/ft) of row. Seeds inoculated with group 4 (cowpea) inoculant are sown in shallow furrows and covered 6 to 13 mm ($^1/_4$ to $^1/_2$ in) deep. Mid-spring is the ideal time for seeding. The time interval for seeding starts in the spring at the last expected frost date and continues thereafter for about 6 weeks. Seeds are treated with tetramethethylthiuram disulfide (thiram) for fungus control. About 95% of the 1-year-old seedlings are usable. For producing wildlife food, direct seeding in the field is more popular than transplanting seedlings (Crider 1952; Vogel 1974). Optimal growth occurs in well-drained, non-acidic soils (USDA SCS 1980).

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Fabaceae—Pea family

Leucaena leucocephala (Lam.) de Wit.

leucaena

C. D. Whitesell and John A. Parrotta

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Other common names. leadtree, *zarcilla*, *popinac*, *koa haole, tantau*.

Synonyms. *Leucaena glauca* (L.) Benth., *L. blancii* Goyena, *L. glabrata* Rose, *L. greggii* Watson, *L. latisiliqua* (L.) W.T. Gillis, *L. salvadorensis* Standl.

Growth habit, occurrence, and use. The genus *Leucaena* includes about 50 species of trees and shrubs that are native to Central America and southeast Asia. Leaves, legumes (pods), and young seeds of at least 4 *Leucaena* species have been used by humans for food since the time of the Mayans (Brewbaker and others 1970). Leucaena—*Leucaena leucocephala* (Lam.) de Wit.—the most widespread member of the genus, originated in Mexico and Central America (Brewbaker and others 1972) but is now considered pantropical. It is found throughout the West Indies from the Bahamas and Cuba to Trinidad and Tobago and has become naturalized in southern Texas and southern Florida; it also has been planted in California (Little and Wadsworth 1964). The species was introduced to Puerto Rico and the Pacific Islands during the Spanish colonial era and to Hawaii about 1864. It invades cleared areas and forms dense thickets, either as a shrub or small tree up to 10 m in height (Takahashi and Ripperton 1949). This species is evergreen when moisture is not a limiting factor. Strains of leucaena can be categorized as one of two types: the "common" (or "Hawaiian") and the "giant" (or "Salvadorian") (Brewbaker and others 1972). The common type, representing the strains most commonly naturalized outside of the species' native range, is a drought-tolerant, branchy, abundantly flowering, and aggressive shrub or small tree. The Salvadorian type is an erect tree that attains heights up to 20 m (Brewbaker and others 1972; NAS 1984). In many parts of the world, the species is considered a weed.

Leucaena is used for a variety of purposes, including timber, fuelwood, forage, and organic fertilizer. It is planted as a shade tree for coffee, cacao, and other cash crops; for soil fertility improvement; erosion control; and site preparation in reforestation (Neal 1965; NAS 1984; Parrotta 1992; Whitesell 1974). The light reddish heartwood is easily worked but is of low to medium durability. It is used for light construction, boxes, and particleboard. The wood is considered a promising source of short-fiber pulp for paper production. The protein-rich leaves and legumes are widely used as fodder for cattle, water buffalo, and goats. The protein content of dry forage ranges from 14.0 to 16.2% (Oaks and Skov 1967). Depending on variety, the protein consists of 19 to 47% mimosine (Brewbaker and others 1972), an amino acid that can cause weight loss and ill health in monogastric animals such as pigs, horses, rabbits, and poultry when leucaena fodder comprises more than 5 to 10% (by weight) of the diet. Ruminants (cows, buffalo, and goats) in most parts of the world (except for Australia, Papua New Guinea, and parts of Africa and the Pacific) have stomach microorganisms that render mimosine harmless.

Flowering and fruiting. Flowering phenology varies widely among varieties and with location. The common type varieties flower year-round, often beginning as early as 4 to 6 months after seed germination. The giant varieties flower seasonally, usually twice a year. The spherical, whitish flower heads are 2.0 to 2.5 cm in diameter and are borne on stalks 2 to 3 cm long at the ends or sides of twigs (Parrotta 1992). The fruits, generally produced in abundance from the first year onward, are flat, thin legumes that are dark brown when ripe; they measure 10 to 15 cm long and 1.5 to 2.0 cm wide. A legume contains 15 to 20 seeds (Parrotta 1992). The seeds are small (8 mm long), flat, teardrop-shaped, shiny, and dark brown with a thin but fairly durable seedcoat (figures 1 and 2). The seeds are usually released from dehiscent legumes while still on the tree, although unopened or partially opened legumes may be carried some distance by wind. The legumes are commonly eaten by and pass through the digestive tracts of livestock, which appear to be important dispersal agents in pastures.

Figure 1—*Leucaena leucocephala*, leucaena: seed.

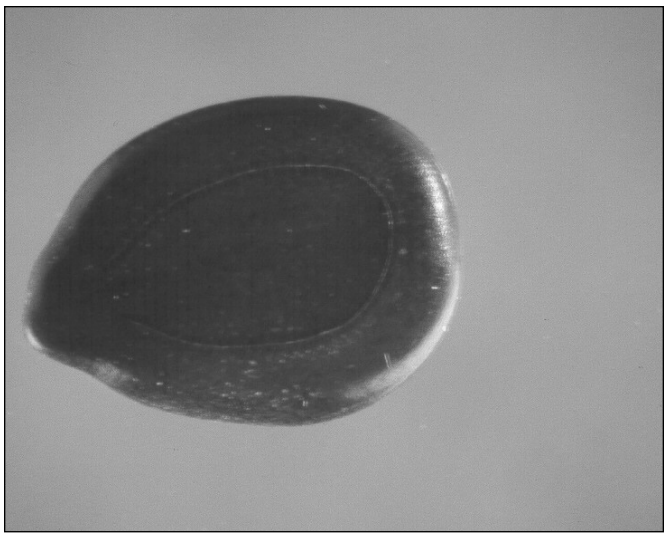
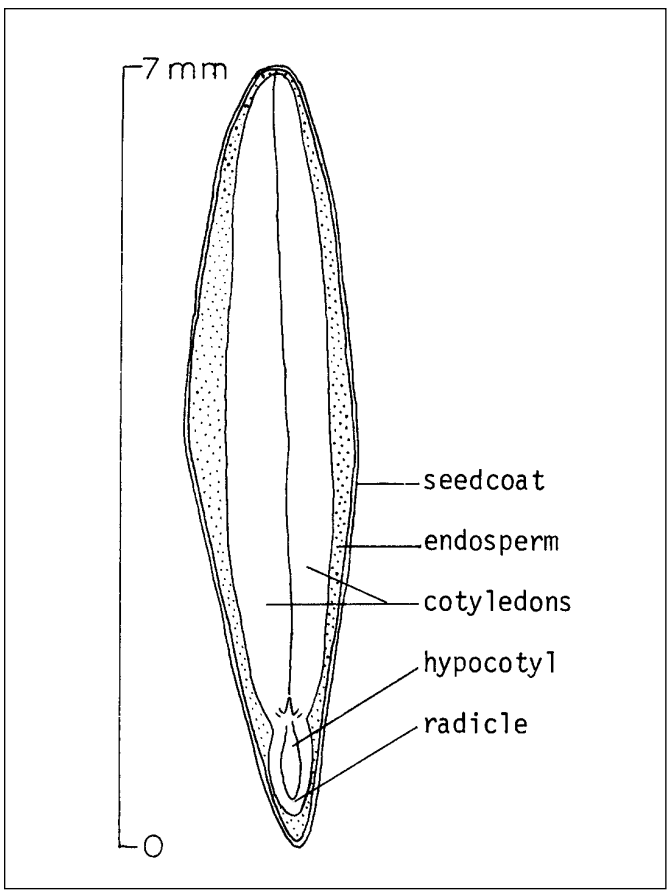


Figure 2—*Leucaena leucocephala*, leucaena: longitudinal section through a seed.



Collection, extraction, and storage. Legumes may be collected from branches when ripe, before dehiscence; they should be sun-dried and then threshed to release seeds. Threshing is commonly done by beating the dried legumes in cloth bags. There are about 17,000 to 24,000 clean seeds/kg (11,000/lb) (Parrotta 1992). Unscarified seeds will remain viable for more than 1 year when stored under dry conditions at ambient temperatures and up to 5 years stored at 2 to 6 °C. Dried, scarified seeds will remain viable for 6 to 12 months (van den Beldt and others 1985; Daguma and others 1988; Parrotta 1992).

In Hawaii the larvae of a recently introduced beetle—*Araecerus levipennis* Jordan—can destroy the seed. At times, virtually all of the legumes in certain stands are infested (Sherman and Tamashiro 1956). Seeds should be fumigated as soon as possible after collection to kill the larvae. Because of the uncertain status of methyl bromide at this time, local extension authorities should be consulted about an appropriate fumigant to use.

Pregermination treatments. Although seeds may be sown without scarification, mechanical scarification (abrasion with sandpaper or clipping the seedcoat) or either of the following 2 treatments are used to ensure more rapid and uniform germination (Parrotta 1992): (a) immersion in hot water (80 °C) for 3 to 4 minutes followed by soaking in water at room tmperature for up to 12 hours or (b) soaking in concentrated sulfuric acid for 15 to 30 minutes. Scarification may be followed by inoculation with nitrogen-fixing *Rhizobium* bacteria (mixed with finely ground peat) after coating the seeds with a gum arabic or concentrated sugar solution. Pre-sowing inoculation of seeds facilitates good field establishment in soil devoid of effective rhizobia strains.

Germination tests. Germination rates are commonly 50 to 98% for fresh seeds (Daguma and others 1988; NAS 1984). Scarified seeds germinate 6 to 10 days after sowing; unscarified seeds germinate 6 to 60 days after sowing (Parrotta 1992). Germination in leucaena is epigeal.

Nursery practice. Leucaena seeds germinate on or near the soil surface and should not be planted deeper than 2 cm ($^3/_4$ in). Nursery media should be well-drained, have good nutrient and water-holding capacity, and have a pH between 5.5 and 7.5 (van der Beldt and Brewbaker 1985). Light shade is recommended during the first few weeks of seeding development, and full sun thereafter (Parrotta 1992). Taproot development is rapid in young seedlings. Seedlings generally reach plantable size (height of 20 cm or 8 in) in 2 to 3 months. Plantations may be established by direct seeding (Francis 1993) or by planting container seedlings, bareroot seedlings, stem cuttings (2 to 5 cm in diameter).

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Ericaceae—Heath family

Leucothoe fontanesiana (Steud.) Sleum.

drooping leucothoe

Frank A. Blazich and Mark C. Starrett

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Synonyms. *Andromeda fontanesiana* Steud.; *Leucothoe catesbaei* (Walter) A. Gray, *Leucothoe editorum* Fern. & Schub.

Other common names. highland doghobble, doghobble, switch ivy, fetterbush.

Growth habit, occurrence, and uses. Drooping leucothoe—*Leucothoe fontanesiana* (Steud.) Sleum.)—as its common name implies, has a graceful, arched habit (Bridwell 1994). The plant is a broad-leaved, evergreen shrub, 1 m tall, with a spread of 1.2 to 1.8 m (Halfacre and Shawcroft 1975). Drooping leucothoe spreads by underground stems and can produce impenetrable thickets (Halfacre and Shawcroft 1975). These dense thickets have often hindered hunting from horseback, ensnaring both dogs and horses, hence the common names "doghobble" and "fetterbush." This species occurs naturally in moist wooded areas along the Appalachian Mountains of the United States, from Virginia to Georgia and Tennessee (Ingram 1961). In its native habitat, drooping leucothoe occurs as an undergrowth accompaniment to taller shrubs such as rhododendron (*Rhododendron* L. spp.) or mountain-laurel (*Kalmia latifolia* L.) (Melvin 1981). Drooping leucothoe is a robust, hardy shrub that can be cultivated in USDA Hardiness Zones 5 to 8. However, a cool, shady, well-drained site must be selected for the southern landscape (Dirr 1990).

The species is best suited for landscape use in lightly shaded sites with moist soil that is high in organic matter (Ingram 1961). Typically, the plant is utilized as an understory shrub to complement other understory plants that have a leggy habit (Dirr 1990). Drooping leucothoe can best be used as a cover on shady banks and is especially effective in mass plantings (Dirr 1990). An additional quality that increases the value of this plant in the landscape is its rich, lustrous, dark green foliage, which becomes reddish bronze in autumn and eventually turns bronze-purple in winter, thus providing seasonal interest (Halfacre and Shawcroft 1975; Odenwald and Turner 1987). No geographic races or hybrids have been described currently in the literature.

Flowering and fruiting. White, waxy, urn-shaped flowers are borne on small, pendant, axillary racemes in May and scent the air with a pungent fragrance (Dirr 1990; Odenwald and Turner 1987). Although individual flowers are small (0.6 cm long), they are clustered along 5.0- to 7.5-cm-long racemes and provide a striking contrast to the dark green foliage (Dirr 1990).

Collection of fruits, seed extraction, cleaning, and storage. Capsules and seeds ripen in mid- to late autumn and can be collected at that time (Wyman 1953). Capsules are removed from the plant and lightly beaten, then rubbed to open them completely (Dirr and Heuser 1987); then, seeds are shaken from the capsules. Viability can be poor if seeds are not graded rigorously. Seeds are quite small (figures 1 and 2). When dried to a moisture content of 3% and cleaned, pure seeds averaged 22,900/g (650,000/oz) (Blazich and others 1991). Seeds will remain viable if stored dry at room temperature and used within 2 years (Wyman 1953).

Figure 1—*Leucothoe fontanesiana*, drooping leucothoe: seeds.

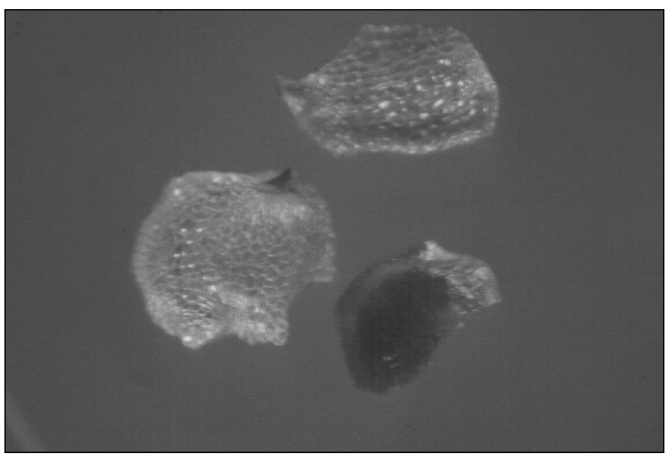
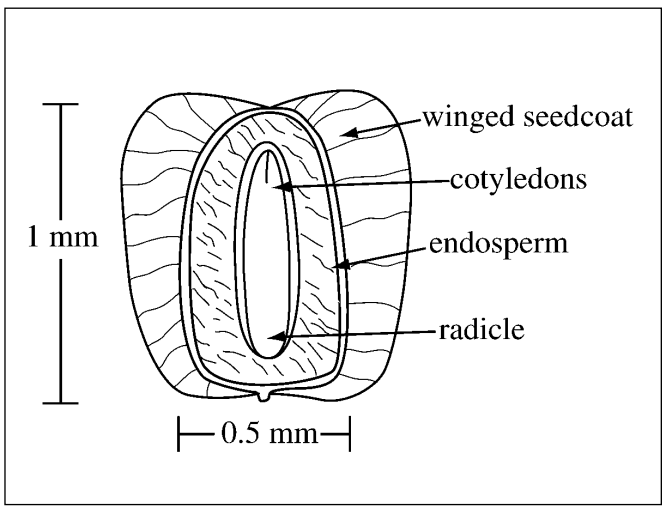


Figure 2—*Leucothoe fontanesiana*, drooping leucothoe: longitudinal section of a seed.



Glenn and others (1998) reported that seeds will remain viable for several years if stored in a sealed container at –18 or 4 °C. This suggests that the seeds are orthodox in storage behavior.

Germination tests. There are no prescribed methods for official tests of this species, but the seeds germinate readily without pretreatment (Dirr and Heuser 1987; Fordham 1960). Seeds of drooping leucothoe require light for germination (Blazich and others 1991). Blazich and others (1991) conducted a 30-day germination study utilizing seeds from a native population of plants growing in Henderson County, North Carolina. Seeds were germinated at 25 °C or an 8/16 hour thermoperiod of 25/15 °C with daily photoperiods of 0, $^1/_2$, $^1/_2$ twice daily, 1, 2, 4, 8, 12, or 24 hours. The cool-white fluorescent lamps utilized as the light source provided a photosynthetic photon flux (400 to 700 nm) of 35 μmol/m^2/sec (2.8 klux). For both temperatures, no germination occurred during the 30-day test period for seeds not subjected to light. At 25 °C, increasing photoperiod increased percentage germination values of 60 and 68% occurring by day 24 for the 12- and 24-hour photoperiods, respectively. The alternating temperature of 25/15°C enhanced germination when light was limiting. At this temperature, germination ≥ 85% was reached by day 27 for photoperiods ≥ 2 hours. Germination is epigeal.

Nursery practice. Typically, the germination medium is kept at 24 °C via bottom heat (Bir 1987). Seeds are sown on the surface of a steam-pasteurized medium, such as pinebark sifted through a 6-mm-mesh (0.25-inch-mesh) screen. They are irrigated slightly and the surface of the germinating medium is thereafter never allowed to dry completely (Bir 1987). One recommended practice is to fertilize seedlings at the first true leaf stage with a half-strength solution of a 15-45-5 ($N:P_2O_5:K_2O$) fertilizer (Bir 1987). After 2 weeks, the seedlings are then fertilized with a full-strength solution applied weekly until they are transplanted into liner flats or pots (Bir 1987). Drooping leucothoe can also be propagated vegetatively by rooting stem cuttings (Dirr and Heuser 1987). The species roots readily from cuttings taken during the months of June through December without a need for exogenous auxin application (Dirr and Heuser 1987).

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Oleaceae—Olive family

Ligustrum L.

privet

Daniel A. Mikowski and William I. Stein

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Growth habit, occurrence, and uses. The genus *Ligustrum*—the privets—includes about 50 species native in eastern Asia and Malaysia to Australia, with 1 species occurring in Europe and North Africa (Bean 1978; Rehder 1940). Privets have been widely distributed and cultivated outside of their indigenous distributions, and many varieties and cultivars are recognized (Bailey 1947; Bean 1978; Ohwi 1965; Rehder 1940). At least 4 species have naturalized in the United States, several over broad geographic regions (table 1). European, or common, privet is widely naturalized in eastern North America. California privet has been planted from coast to coast in the southern United States and has naturalized extensively in the Southeast.

The privets are deciduous or evergreen shrubs or small trees ranging from 2 to 12 m in height (table 2). Maximum heights reported in the United States are 7.8, 24.9, and 12.8 m, respectively, for California, Chinese, and Japanese privets (AFA 1996). Growth form ranges from compact dense shrubs to small trees with slender spreading branches. Privets grow readily in many kinds of soil (Bailey 1947; Bean 1978; Meikle 1958) and in moisture regimes ranging from very dry to stream-side and floodplain (Lee and others 1991; Seymour 1982). They establish on roadsides, sand dunes, open and closed woodlands, tree borders, and other disturbed areas (Bailey 1947; Radford and others 1968; Seymour 1982; Wilson and Wood 1959).

Table 1—*Ligustrum,* privet: nomenclature and occurrence

Scientific name	Common name(s)	Occurrence
***L.ovalifolium* Hassk.**	**California privet**	Planted across S US from Virginia to California; extensively naturalized from Virginia to Florida
***L. japonicum* Thunb.**	**Japanese privet**	Planted in SE US from North Carolina to Alabama, to Louisiana & Texas; naturalized locally
***L. lucidum* Ait. f.**	**glossy privet**	Scattered from Pennsylvania S to Texas
***L. sinense* Lour.**	**Chinese privet,** *trueno de seto*	Planted in SE US from Virginia to Georgia, Oklahoma, & Texas; widely naturalized
***L. vulgare* L.**	**European privet,** common privet	Widely naturalized in E North America

Sources: Little (1979), Rehder (1940), Wilson and Wood (1959), Vines (1983).

Table 2—*Ligustrum,* privet: height, leaf habit, color, and size of mature fruit

Species	Height at maturity (m)	Leaf habit	Fruit color	Fruit size (mm)
L. ovalifolium	5	Deciduous or half-evergreen	Purple-black, black	5–8
L. japonicum	2–12	Evergreen	Purple-black, blue	6–10
L. lucidum	3–10	Evergreen	Purple-black, blue-black	8–10
L. sinense	4–10	Deciduous or half-evergreen	Purple-black, blue-black	4–7
L. vulgare	5	Deciduous or half-evergreen	Lustrous black	6–8

Sources: Bean (1978), McMinn and Maino (1937), Ohwi (1965), Radford and others (1968), Rehder (1940), Vines (1983).

The privets are valued for landscape shrubbery because of their handsome white flowers and dark green foliage; ready establishment; and resistance to insects, dust, and air pollution (Bailey 1947; Howe and Woltz 1981). California privet grows well even in the spray of salt water (Bailey 1947). Japanese privet is an excellent evergreen shrub for shaping into hedges, screens, or topiary (distinctive shapes such as globes or animals) (Vines 1983). Glossy privet is an evergreen tree suited for growing in narrow areas, making it a fine choice for a street or lawn tree. Several privets have been used as garden hedges, but their innumerable, fibrous roots are invasive and may impoverish adjacent flower beds (Meikle 1958).

Privets are also useful as wildlife habitat, windbreaks, and erosion-control plantings. Although the lengthy availability of fruits and seeds indicates that they are not generally relished by wildlife, some consumption by birds has been observed (Martin and others 1951; Van Dersal 1938; Vines 1983).

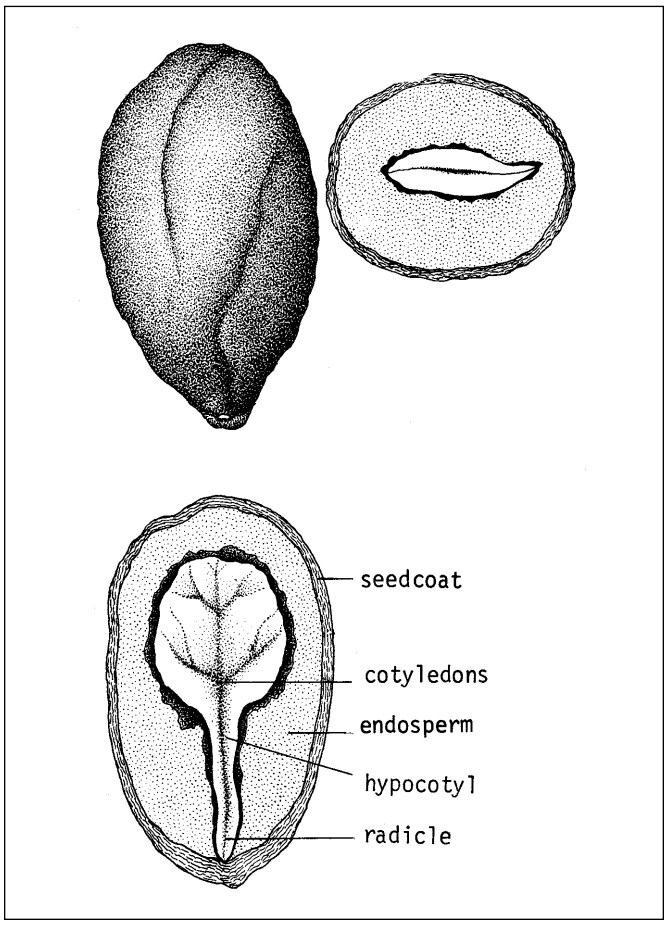
Flowering and fruiting. The terminal panicles bearing privet flowers range from 3 to 20 cm long and are usually somewhat narrower in width than length (Bean 1978). The flowers are small, perfect, always a shade of white, and usually fragrant. However, the fragrance of some privet flowers may be considered "objectionable at close quarters" (Bean 1978). Summer is the main flowering period, but timing and duration varies by species (table 3). There is evidence that Japanese privet seedlings require winter chilling to stimulate blooming (Morita and others 1979).

The fruits are 1- to 4-seeded berrylike drupes with membranaceous to stony endocarps about 4 to 10 mm long (figures 1 and 2; table 2). Fruits ripen from September to November (table 3) and those of some species often remain on the panicles into winter (Rehder 1940). Ripened fruits generally range in color from dark blue to black. The fruits in some varieties of European privet, however, are not black: f. *chlorocarpum* (Loud.) Schelle has green fruits; f. *leucocarpum* (Sweet) Schelle, white fruits; and f. *xanthocarpum* (G. Don) Schelle, yellow fruits (Bean 1978).

According to incidental observations, privet species produce seedcrops almost annually, but systematic records of crop size and occurrence are not available (Dirr and Heuser 1987).

Collection, extraction, and storage. Ripe privet fruits may be stripped from panicles by hand in the fall or early winter. If the fruits are already dry, they can be stored uncleaned, but prompt cleaning is generally better. Seeds can be separated from fresh or remoistened pulp by running the fruits with ample water through a macerator. For some privet species, particular care must be taken during cleaning to ensure that their soft-coated seeds are not damaged (figure 1).

Figure 1—*Ligustrum sinense*, Chinese privet: oblong seed (**upper left**); longitudinal section (**lower left**) and cross section (**right**).



Privet seeds are relatively small and vary in size and weight by species (table 4). In one sampling, seeds of European privet constituted 54% of fruit biomass on a dry-weight basis (Lee and others 1991).

Storage of cleaned European privet seeds in ordinary dry conditions was recommended long ago (Chadwick 1935), but little has been reported on the success of this practice. It seems likely that their longevity could be prolonged by closed storage at cool temperatures or even at –18 °C, which has proven satisfactory for many tree species that tolerate low moisture content.

Pregermination treatments and germination tests. Fresh privet seeds that have been cleaned will germinate in 60 days without stratification (Heit 1968; Dirr and Heuser 1987). Stored seeds, however, require 30 to 60 days of cold stratification at 0 to 5 °C to induce prompt germination (Chadwick 1935; Dirr and Heuser 1987; Heit 1968; Shumilina 1967). Fifteen days of warm stratification at 18 to 20 °C or alternating warm and cold stratification were suc-

Figure 2—*Ligustrum lucidum,* glossy privet: seeds.

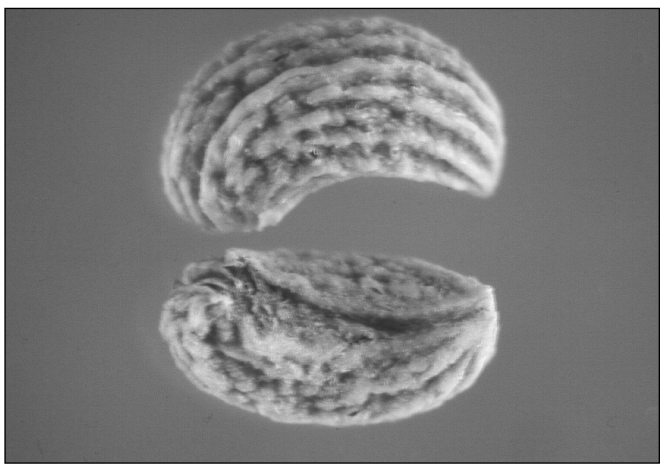


Table 3—*Ligustrum,* privet: phenology of flowering and fruiting

Species	Flowering	Fruit ripening
L. ovalifolium	June–July	Sept–Nov
L. japonicum	June–Sept	Sept–Nov
L. lucidum	July–Sept	Sept–Oct*
L. sinense	Mar–July	Sept–Nov*
L. vulgare	June–July	Sept–Oct*

Sources: Radford and others (1968), Rehder (1940), Vines (1983).
* Fruits persist into winter.

cessful treatments on some seedlots in Russia (Shumilina 1967). Some germination may occur in lengthy stratification.

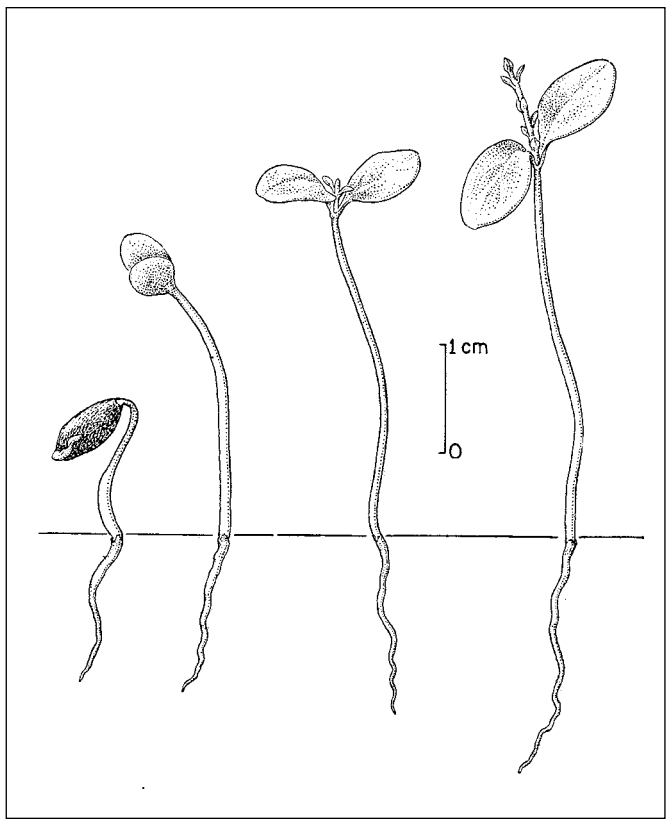
Best germination results have been obtained by running tests for 60 days at 10 °C for 16 hours/day and 30 °C for 8 hours (Heit 1968). In Australian tests, optimum constant germination temperature for fresh seeds of glossy privet was 15 °C and for Chinese privet, 20 to 25 °C (Burrows and Kohen 1983). Germination of European privet seeds ranged from 88 to 92% in tests conducted in New York (Heit 1968). Germination is epigeal (figure 3), and light is not needed for germination.

Viability of seeds can also be determined by a tetrazolium (TZ) staining test as recommended by the International Seed Testing Association (ISTA 1996). Privet seeds should be soaked in water for 18 hours at 20 °C, then cut transversely at the distal end and longitudinally with a scalpel or razor blade to expose the embryo, followed by immersion in a 1% TZ solution for 20 to 24 hours at 30 °C. Those seeds with the embryo and all nutritive tissue stained red are considered viable.

Nursery practice. Fall-sowing is advisable for best seedling production, maximum growth the first year, and less early seedling losses (Heit 1968). Fresh, cleaned privet seeds germinate readily when sown in the fall. In spring sowings, seeds from storage may require 1 or 2 months of stratification to ensure uniform germination with minimum hold-over (Bailey 1947; Dirr and Heuser 1987). One- or two-year seedlings are used for outplanting.

Vegetative propagation is the preferred method for producing privet species or varieties and ensuring continuation of the same characteristics in successive generations. All species are easy to root from vegetative stem cuttings and many growers root them in outside beds (Bailey 1947; Dirr and Heuser 1987; Keever and others 1989; Regulski 1984). Non-dormant cuttings should be rooted under a mist system to prevent them from drying out during summer months. Dormant cuttings can be set in rows outdoors during the fall, winter, or early spring. Shoot and root initiation and growth of dormant and non-dormant privet cuttings can be accelerated, even doubled, by appropriate applications of growth regulators, bleach, and wetting agents (Dirr and Heuser 1987; Yang and Read 1991, 1992; Rauscherova and Tesfa 1993). Pre-emergence herbicides did not affect stock plants of glossy privet or the rooting of cuttings taken from them (Cantanzaro and others 1993).

Figure 3—*Ligustrum vulgare*, European privet: seedling development 1, 5, 50, and 132 days after germination.



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Lauraceae—Laurel family

Lindera Thunb.

spicebush

Victor Vankus, Kenneth A. Brinkman, and H. M. Phipps

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Growth habit, occurrence, and uses. The genus *Lindera*—spicebush—comprises 80 species of deciduous or evergreen trees or shrubs (Huxley and others 1992). The 3 deciduous species (table 1) native to the United States are generally found in moist woodlands, usually as understory plants. Common spicebush is a deciduous shrub to 4.6 m tall; it has been cultivated since 1683 and is valuable for wildlife food and environmental plantings. The fruits are eaten by grouse (*Bonasa umbellus*), quail (*Colinus virginianus*), pheasants (*Phasianus colchicus*), and other birds (Grimm 1957). The dried fruit has been used as a substitute for allspice and the leaves, bark, and fruit for their medicinal properties as a treatment for coughs and colds (Bremness 1994; USDA Forest Service 1948). Both common and Japanese spicebushes (table 1) are grown and sold by the horticultural industry for their spring flowers and aromatic and colorful fall foliage (Huxley and others 1992). Common spicebush is commonly used as a root stock for cuttings of Japanese spicebush (Boyle 1997). Pondberry and bog spicebush are both much less abundant than common spicebush and have much smaller ranges (table 1). Pondberry was listed as an endangered species by the USDI Fish and Wildlife Service in 1986.

Flowering and fruiting. The yellow to yellow-green flowers of spicebush are dioecious or polygamous and appear from March to May before the leaves (Fernald 1950). The fruits, which begin developing in May, are red drupaceus berries ripening in August or September (Rehder 1940). Each fruit contains a single seed that is light violet-brown with flecks of darker brown (figures 1 and 2). The affects of sun and shade habitats on flower production, sex ratio, and resulting population dynamics of common spicebush have been studied by Niesenbaum (1992) and Cipollini and others (1994).

Collection of fruit; extraction and storage of seeds. Spicebush fruits should be collected at maturity from August to October (Van Dersal 1935). Seedcrops can vary from year to year. Seed collectors must pay careful attention to fruit maturity to ensure that seeds are collected at the optimal time and to limit loss of seeds to birds. Fruits collected before maturity had seeds with low or no viability (Boyle 1997). The fresh fruits should be de-pulped in water, the pulp floated off, and the seeds thoroughly air-dried (Brinkman and Phipps 1974). Seeds should not be stored or planted still within the berry. There are about 10,000 seeds/kg (4,550/lb). Forty-five kilograms (99.2 lb) of fruits

Table 1—*Lindera,* spicebush: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***L. benzoin* (L.) Blume** *Benzoin aestivale* (L.) Nees	**common spicebush**, northern spicebush, Benjamin bush, feverbush, wild allspice	Maine to Ontario & Kansas; S to Florida & Texas
***L. melissifolia* (Walt.) Blume** *Benzoin melissifolium* (Walt.) Nees *Laurus melissifolia* Walt.	**pondberry,** southern spicebush, Jove's fruit	North Carolina to Missouri; S to Georgia & W to Louisiana
***L. obtusiloba* Blume** *Benzoin obtusilobum* (Blume) O. Kuntze *L. cercidifolia* Hemsley *L. obtusiloba f. velutina* T.B. Lee	**Japanese spicebush**	Japan, Korea, & China
***L. subcoriacea* B.E. Wofford**	**bog spicebush**	North Carolina S to Florida & W to Louisiana; also New Jersey

Source: Brinkman and Phipps (1974).

Figure 1—*Lindera benzoin*, common spicebush: seed.

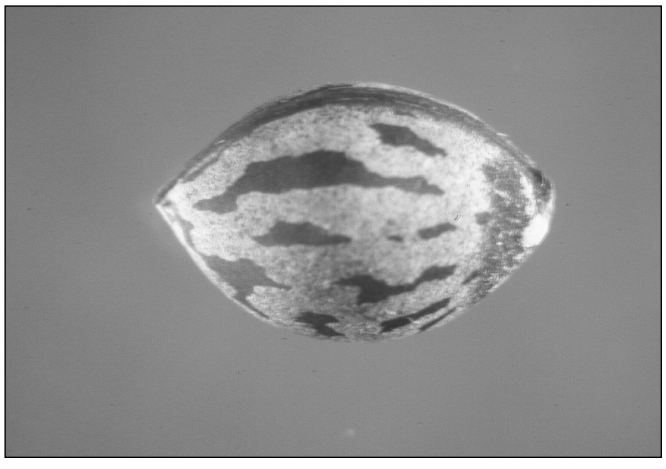
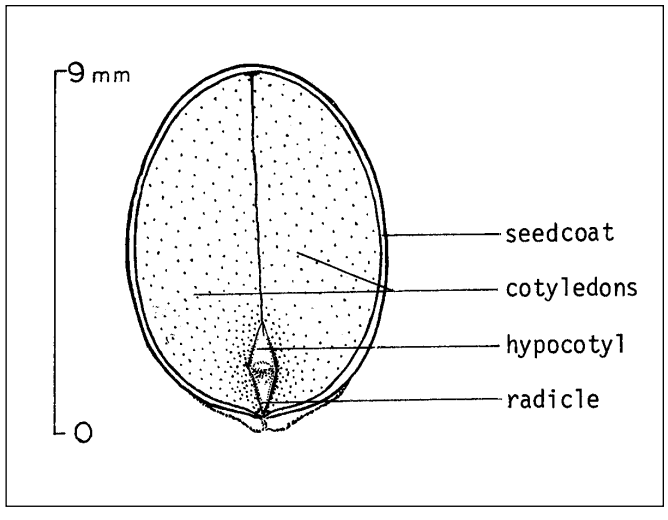


Figure 2—*Lindera benzoin*, common spicebush: longitudinal section through a seed.



of common spicebush yields about 7 to 11 kg (15 to 25 lb) of seeds (Brinkman and Phipps 1974). Common spicebush seeds usually lose their viability soon after maturity, but storage at 1 to 5 °C will prolong viability for 1 to 2 years (Boyle 1997; Murphy 1997).

Pregermination treatment. Common spicebush has a dormant embryo that responds to warm incubation for 30 days at 25 °C followed by 90 days of moist stratification at 1 to 5 °C (Schroeder 1935). Good results were also obtained with 120 days of moist stratification in peat or sand at 5 °C (Barton and Crocker 1948; Brinkman and Phipps 1974). In another test, Olney (1960) reported best results after stratifying seeds for 105 days in sand at 5 °C. Dirr and Heuser (1987) believe that seeds of Japanese spicebush should be stratified cold for 3 months, and they also reported 85 to 90% germination with 3 months of cold stratification for common spicebush. Seeds of pondberry sent to the USDA Forest Service's National Tree Seed Laboratory in 1993 (in accordance with a permit issued by the USDI Fish and Wildlife Service for the purpose of germination and propagation) were germinated using 3 different stratification schemes. Each scheme (table 2) produced good results. Some seeds germinated during the 28-day warm cycle of the warm-cold stratification scheme. This would suggest that the dormancy present in common spicebush may not be present to the same degree in pondberry.

Germination tests. Tests may be made in moist peat or sand at a constant temperature of 25 °C, or at alternating temperatures of 30 °C in the day and 20 °C at night. Germination rate may be 70 to 100% in 14 to 28 days for treated seeds, and total germination should range from 85 to 100% (Brinkman and Phipps 1974). Tetrazolium staining and excised embryo tests will also provide accurate testing information. Excised embryos can develop into seedlings if they are not damaged during excision.

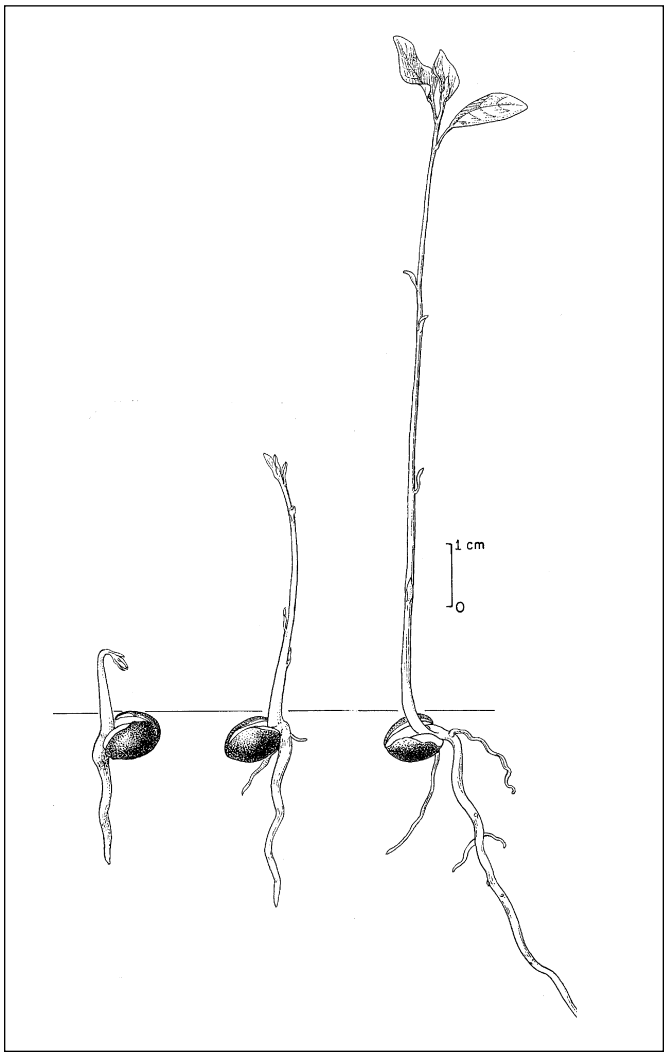
Nursery practice. Common spicebush seeds should be sown in the fall and mulched over winter. The mulch should be removed in April or May before germination begins. Stratified seeds may be sown in the spring. From 70 to 80% of the sound seeds can be expected to produce seedlings (figure 3). Spicebush grows well in sandy soils of pH 4.5 to 6.0 (Brinkman and Phipps 1974; Laurie and Chadwick 1931).

Table 2—*Lindera*, spicebush: stratification treatments and germination

Species	Stratification (days)		Percentage germination
	Warm	Cold*	
L. benzoin	30†	90	—
	—	105	—
	—	120	—
	—	90	85–90
L. melissifolia	28‡	91	100
	—	56	84
	—	119	88
L. obtusiloba	—	90	—

Sources: Barton and Crocker (1948), Brinkman and Phipps (1974), Dirr and Heuser (1987), Olney (1960), Schroeder (1935).
* 1 to 5 °C. † 25 °C. ‡ 20 to 30 °C.

Figure 3—*Lindera benzoin*, common spicebush: seedling development at 2, 3, and 10 days after germination.



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L

Hamamelidaceae—Witch-hazel family

Liquidambar styraciflua L.

sweetgum

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Other common names. redgum, American sweetgum, sapgum, bilsted.

Growth habit, occurrence, and use. Sweetgum—*Liquidambar styraciflua* L.—is found on a variety of sites from Connecticut and southeastern Missouri, south to central Florida and southeastern Texas. It also occurs in scattered locations from Mexico south to Nicaragua (Kormanik 1990) and is considered by some to be a very promising species for the American tropics (McCarter and Hughes 1984). This large deciduous tree reaches heights of over 45 m and diameters of 1.2 m at maturity (Brown and Kirkman 1990). Sweetgum has some value for pulp, lumber, and veneer. The seeds are eaten by many species of birds (Van Dersal 1938), and the tree is planted as an ornamental. It was first cultivated in 1681 (Bonner 1974).

Sweetgum exhibits quite a bit of variation over its wide natural range (McCarter and Hughes 1984; McMillan and Winstead 1976; Wells and others 1991; Williams and McMillan 1971). Minor differences in germination and seedling growth and morphology have been reported, but there is no strong evidence for distinct geographic races in the species.

Flowering and fruiting. The small, greenish, monoecious flowers bloom in March to May. The pistillate flowers are borne in axillary, globose heads that form the 22- to 35-mm-diameter multiple heads of small 2-celled capsules (figure 1). The lustrous green color of the fruiting head fades to yellowish green or yellow as maturity is reached in September to November (Bonner 1974; Vines 1960). At the point of color change, moisture content of the fruit head should have dropped below 70% (Bonner 1972). The beaklike capsules open at this time, and the small, winged seeds (figures 2 and 3), 1 or 2 per capsule, are dispersed. Empty fruiting heads often remain on the trees over winter. Fair seedcrops occur every year and bumper crops about every 3 years. The flowers are susceptible to late spring freezes that can greatly reduce seedcrops. Crop reductions of up to 44% have also been reported from damage by seed bugs—*Leptoglossus oppositus* (Say)—in North Carolina (Ebel and Summerville 1983). Some trees have been known to flower and bear fruit 4 and 5 years after planting (Mohn and Randall 1970), but good crops are not common until the tress reach 20 to 30 years of age (Bonner 1974).

Figure 1—*Liquidambar styraciflua*, sweetgum: fruiting head.

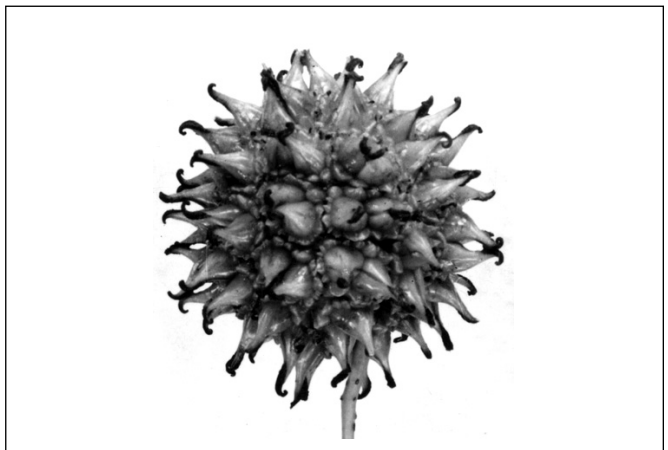
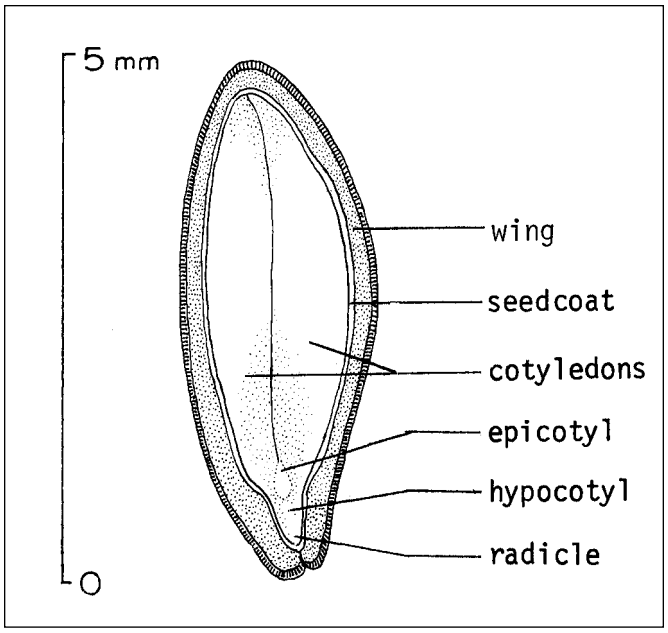


Figure 2—*Liquidambar styraciflua*, sweetgum: seed.

Collection and extraction. Mature fruit heads must be picked from standing trees or logging slash before seed dispersal. The best indicator of maturity is the fading of

Figure 3—*Liquidambar styraciflua*, sweetgum: longitudinal section through a seed.



their green color. Fruit heads should be dried to completely open the capsules so that the seeds can be extracted by shaking or tumbling. Drying may be done indoors on well-ventilated screen racks or outdoors on plastic or canvas sheets in the sun (Bonner 1987). Indoor drying takes approximately 7 to 10 days, whereas outdoor drying in typical fall weather in the South should require only 3 to 5 days. The fruit heads should be stirred daily, and those dried outdoors should be covered at night and during rain (Bonner 1987). Canvas sheets are preferred over plastic, as plastic tears easily and also tends to promote condensation of moisture (Robbins 1984).

Fruit heads picked prematurely may be ripened in moist storage at 5 °C for about a month (Bonner 1970). The fruit heads should then be spread to dry until they open and release the seeds. This operation may take longer than drying fruits that were picked when mature, and the seed yields may be less.

Leaves, twigs, and the sawdust-like aborted seeds can be removed most easily with hand screens and laboratory blowers or with air-screen cleaners, depending on the size of the lot (Bonner 1974). Round-hole screens are best for this job, but variations in seed size due to geographic origin or weather during maturation may require a variety of hole sizes (Bonner 1987). Two passes through an air-screen cleaner should produce seedlot purities of 98%. Seedlots may then be upgraded by removing empty seeds with laboratory blowers or by flotation in water (Bonner 1987). From mostly southern collections, the following yield data were obtained (Bonner 1974):

- Weight per volume of air-dried fruiting heads (1 sample) was 11 kg/hl (or 8.5 lb/bu).
- Weight of cleaned seeds per volume of fruiting heads (3 samples) was 1.0 kg/hl (0.8 lb/bu).
- Number of seeds per fruiting head (144 samples) was 56.
- Range in number of seeds per weight (40 samples) was 143,300 to 217,000/kg (65,000 to 98,400/lb), with an average of 180,000/kg (82,000/lb).

In Mississippi, there were significantly more seeds per fruiting head on trees in the Mississippi River flood plain than on trees from other parts of the state (Kearney and Bonner 1968).

Storage. Sweetgum fits in the storage category of orthodox seeds, that is, its seeds can be stored for a number of years at low temperatures and moisture contents (Bonner 1994). Seed moisture should be maintained in the 5 to 10% range. For storage periods of 5 years or less, temperatures should be kept at 0 to 5 °C; for longer storage, subfreezing temperatures (–18 °C) should be used (Bonner 1987). The ultimate storage potential of the species is not known, but seeds stored at –18 °C for 14 years at the USDA Forest Services's Forestry Sciences Laboratory, in Mississippi State, Mississippi, lost no viability.

Pregermination treatments. Sweetgum seeds exhibit what can be described as only a shallow dormancy (Nikolaeva 1967). Studies of geographic variation in sweetgum have shown that stratification requirement increases from south to north (Wilcox 1968; Winstead 1971), but even the southernmost sources will respond to stratification with increased germination rates (Bonner and Farmer 1966; Rink and others 1979). Moist stratification at 3 to 5 °C for 2 to 4 weeks should produce timely germination both in the laboratory and in nurserybeds (Bonner 1987). Satisfactory treatment has also been achieved by soaking the seeds for 14 to 20 days in water at 3 to 5 °C (Bonner 1974). Older seeds from storage may not require as much stratification, especially if they have been stored above freezing. Stratification of lots stored longer than 7 years under such conditions should be cut in half (1 to 2 weeks) (Bonner 1987).

Germination tests. Satisfactory tests may be obtained with either constant or alternating temperature regimes, but alternating temperatures of 20 °C at night for 16 hours, and 30 °C in the day for 8 hours are recommended for official

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Table 1—*Liquidambar styraciflua,* sweetgum: germination test conditions and results

Stratification* (days)	Daily light (hrs)	Germination test conditions: Medium	Temp (°C): Day	Temp (°C): Night	Germination test conditions: Days	Germination rate: %	Germination rate: Days	Germination: Avg (%)	Germination: Samples
0	8	Blotter paper	30	20	28	76	21	85	14
30	8	Kimpak	30	20	25	86	14	95	23
15–45	0	Blotter paper	30	30	30	—	—	85	13

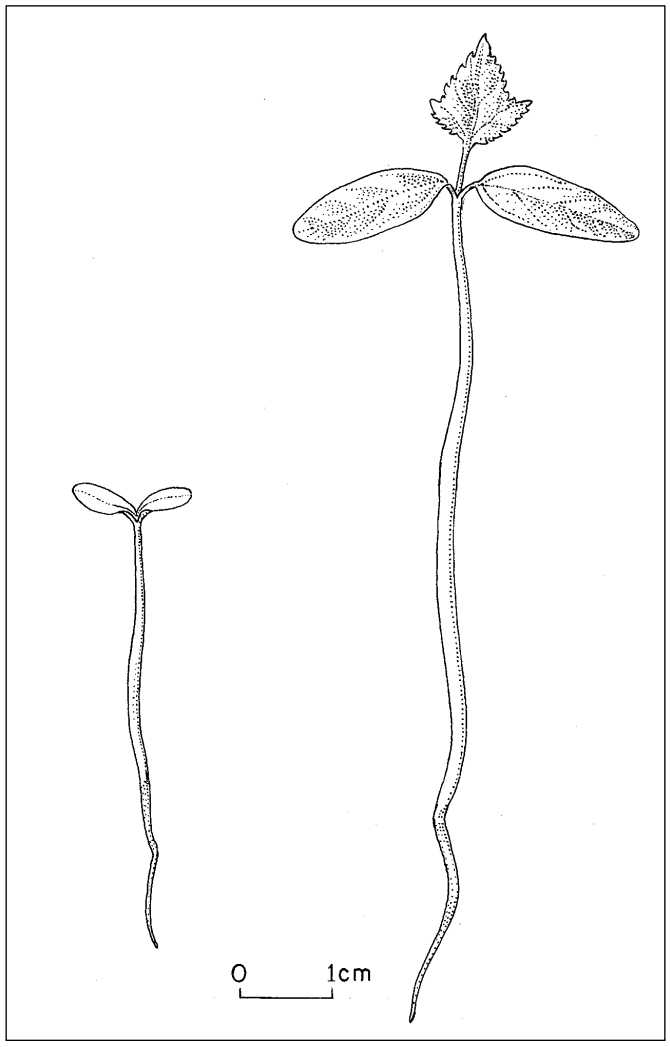
Sources: AOSA (1993), Bonner (1974).
* Stratification at 3 °C.

testing (table 1) (AOSA 1993). Light is not absolutely necessary for germination of stratified seeds (Bonner 1967), but it is normally used in all testing. Tetrazolium staining (Bonner and Gammage 1967), radiography (Belcher and Vozzo 1979), and the excised embryo method (Bonner and Gammage 1967; Flemion 1948) also provide reliable tests of viability. Germination is epigeal (figure 4). For moisture testing, duplicate samples of 4 to 6 g each should be dried for 17 ± 1 hour at 103 ± 2 °C (ISTA 1993), or electric meters can be used for rapid measurements (Bonner 1981).

Nursery practice. Stratified seeds should be broadcast or drilled in the spring to achieve an initial seedling density of 100 to 160/m^2 (9 to 15/ft^2) (Barham 1980). Aluminum powder may be mixed with wet stratified seeds at a rate of 15 ml/45 kg of seeds (4 tablespoons/100 lb) to achieve easy flow in seeders (Bonner 1974). The seeds should be sown on the surface and lightly into the soil with a roller. A 6- to 12-mm ($^1/_4$- to $^1/_2$-in) mulch of sawdust, sand, or chopped pine straw should be applied (Bonner 1974; Coleman 1965; Vande Linde 1964), although some nurseries have reported better results with wood fiber mulches at rates of 1,400 to 2,900 kg/ha (1,250 to 2,600 lb/ac) (Barham 1980).

Ornamental cultivars of sweetgum are usually propagated vegetatively. Cuttings taken in early June will root, and budding is common also (Dirr and Heuser 1987).

Figure 4—*Liquidambar styraciflua*, sweetgum: seedling development at 2 and 30 days after germination.



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Magnoliaceae—Magnolia family

Liriodendron tulipifera L.

tuliptree

Franklin T. Bonner

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Other common names. yellow-poplar, poplar, tulip-poplar, white poplar, whitewood.

Growth habit, occurrence, and uses. Tuliptree—*Liriodendron tulipifera* L.—occurs naturally throughout the eastern United States from Vermont and southern Michigan south to Louisiana and north-central Florida (Little 1979). It grows under a variety of climatic conditions from sea level to 1,370 m elevation in the Appalachian Mountains and to 300 m in the northern part of its range. This large deciduous tree is among the tallest in the eastern United States and reaches considerable age: tuliptrees planted by George Washington still grow at Mount Vernon (Griswold 1999). It can attain heights of 61 m and diameters of 2.4 to 3.7 m at maturity (Beck 1990). The wood is very valuable for lumber and veneer. It is a good honey tree and is planted extensively as an ornamental. Tuliptree has been cultivated since 1663 (Bonner and Russell 1974).

Flowering and fruiting. The large, perfect, greenish-yellow flowers of tuliptree open from April to June (Little and Delisle 1962). The fruit is an elongated cone composed of closely overlapped carpels that are dry, woody, and winged (figure 1). Each carpel (samara) contains 1 or 2 seeds (figure 2). The cones turn from green to yellow to light brown as they ripen; they mature from early August in the northern part of the range (Guard 1943) to late October in the South (Bonner and Russell 1974). As the mature cones dry on the trees, they break apart and the samaras are scattered by the wind. Peak dissemination occurs in October and November, but a few samaras fall as late as the following March (Carvell and Korstian 1955; Whipple 1968). In South Carolina, seedfall is usually at least 90% complete by early December (Goebel and McGregor 1973).

Good seedcrops occur almost every year; failures, as well as bumper crops, occur infrequently. In North Carolina, 1 large tree produced 29,000 sound seeds, and seedfall of 1.5 million seeds/ha is not uncommon (Beck 1990). In a South Carolina study, 1 of 5 seedcrops was heavy (Goebel

Figure 1—*Liriodendron tulipifera*, tuliptree: cone (**left**) and single samara (**right**).

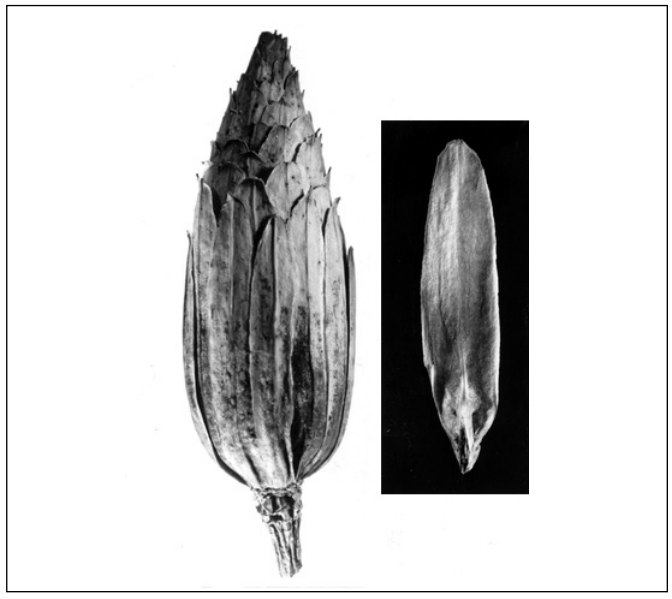
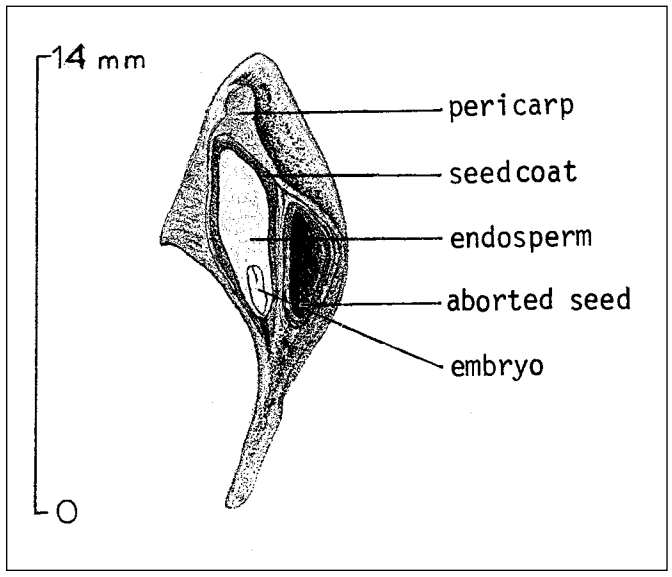


Figure 2—*Liriodendron tulipifera,* tuliptree: longitudinal section through an embryo of a samara.



and McGregor 1973). Although trees as young as 9 years old have been reported to bear fruit, the normal commercial seed-bearing age of tuliptree is 15 to 20 years (Bonner and Russell 1974).

Tuliptree is pollinated by insects, and the number of filled samaras per cone is very low in natural stands (Boyce and Kaeiser 1961). There is considerable variation among trees, but a general average seems to be about 10% (Bonner and Russell 1974; Carvell and Korstian 1955; Heit 1942; Limstrom 1959; Sluder 1964; Swingle 1939; Whipple 1968). At the extreme northern part of the species' range in southern Ontario, the filled samara proportion was 8 to 10% in isolated trees and 20% in old-growth, high-density stands (Kavanagh and Carleton 1990). Filled samara proportions in central Mississippi have ranged from 3.5% in isolated trees to 35% in older stands of mixed hardwoods with numerous large tuliptrees. Controlled pollinations in seed orchards have produced filled seed yields as high as 75% (Houston and Joehlin 1989). Some seed orchard managers have placed hives of honey bees (*Apis mellifera* L.) in their orchards to increase seed production; results have been varied.

Collection of fruits. Mature cones may be picked by hand from standing trees or from logging slash. In the southern United States, cone maturity is first indicated by the color changes in cones from green to yellow, which usually occurs in late October. At this point, cone moisture content is still high (over 60% of fresh weight), and cones must be handled carefully to avoid overheating. Maturity is assured when cones turn dark brown in color, but dry weather can quickly cause cones in this condition to break apart and scatter the samaras (Bonner 1976b). Cones may be collected from logging slash felled as much as 4 weeks before natural maturity, but they must be dried slowly to allow maturation of the seeds. One way to do this is to wait 2 to 3 weeks after felling to pick the cones (Bonner 1976b). Cones and seeds may also be shaken onto canvas or plastic sheets from standing trees in early winter. A mechanical shaker was used successfully to dislodge cones from trees in West Virginia; from 9 to 95% of cones were collected from individual trees without apparent damage (Cech and Keys 1987). Cones from the upper two-thirds of the crown yield more full seeds than cones from the lower one-third (Guard and Wean 1941), probably because of inefficient pollination in the lower branches.

Cones should be spread out to dry immediately after collection. Drying sufficient to separate the samaras usually requires 7 to 20 days, depending on temperature, humidity, and cone moisture content (Bonner and Russell 1974). Cones may be dried more quickly by using the forced air systems of pine cone tray driers, but no heat should be applied.

Extraction, cleaning, and storage of seeds. Thoroughly dried cones can be broken apart by hand by shucking, flailing, or treading, or by running them through a hammer mill or macerator (Bonner and Russell 1974; Steavenson 1940). Tuliptree seeds can be de-winged in macerators or in oat de-bearders. After wing fragments and fruit axes are removed with air-screen cleaners, many of the empty (unfertilized) seeds can be removed with gravity tables or aspirators (Bonner and Switzer 1971). By this process, filled seed percentages of 6 to 10% can be upgraded to 60 or 65%. There are 80 to 100 samaras/cone (Bonner and Russell 1974). Yield data from various locations (table 1) suggest that samaras from southern trees are larger than those from northern trees.

Tuliptree seeds are orthodox in storage behavior; they may be stored at low seed moisture contents (6 to 10%) and low temperatures (2 to 5 °C). No long-term storage data are available, but storage for several years under these conditions without loss of viability is common (Bonner and Russell 1974). Excellent results have also been reported for 3 to 4 years of moist storage in outdoor soil pits (Paton 1945; Williams and Mony 1962) or in drums of moist sand held in cold storage at 2 °C (Bonner and Russell 1974).

Pregermination treatments. Seeds to be sown in the spring and seeds taken from dry storage need pretreatment to overcome dormancy. The traditional method of moist storage in well-drained pits or mounds of mixed soil, sand, and peat, can successfully overwinter seeds for as long as 3 years (Bonner and Russell 1974; Williams and Mony 1962). Cold, moist stratification in plastic bags, both with or without peat moss or other media, in refrigerators for 60 to 90 days is widely used (Bonner and Russell 1974). Recommended temperatures for cold stratification are a constant 2 to 5 °C (Adams 1968; Bonner and Russell 1974), but alternating weekly temperatures of 0 and 10 °C (Chadwick 1936) or 2 and 12 °C (Boyce and Hosner 1963) have also been successful. Percentage and rate of germination of some sources of tuliptree have been significantly increased by soaking seeds in solutions of the potassium salt of gibberellic acid (GA_3) (100 and 1,000 mg/liter), but no practical application of this method has been reported (Bonner 1976a).

Germination tests. Germination tests should be carried out at the common alternating temperature regime of 20 °C in the dark for 16 hours and 30 °C in light for 8 hours. Seeds should be given cold, moist stratification for 60 to 90 days before testing on the top of moist blotters for a

Table 1—*Liriodendron tulipifera,* tuliptree: seed yield data

Place collected	Cone wt/ cone vol kg/hl	Cone wt/ cone vol lb/bu	Seed wt/ cone vol kg/hl	Seed wt/ cone vol lb/bu	Cleaned seeds/weight Range /kg	Range /lb	Average /kg	Average /lb	Samples
Mississippi									
Warren Co.	39	30	8	6	9,455–17,200	4,288–7,804	12,680	5,750	3
Oktibbeha Co.	32	25	—	—	—	—	—	—	—
North Carolina*	—	—	—	—	32,430–75,080	14,710–34,050	41,200	18,700	9
E Tennessee	—	—	9	7	—	—	—	—	—
New York	—	—	—	—	15,170–30,980	6,880–14,050	23,440	10,630	9
	—	—	9–24	7–19	22,050–52,920	10,000–24,000	30,870	14,000	—

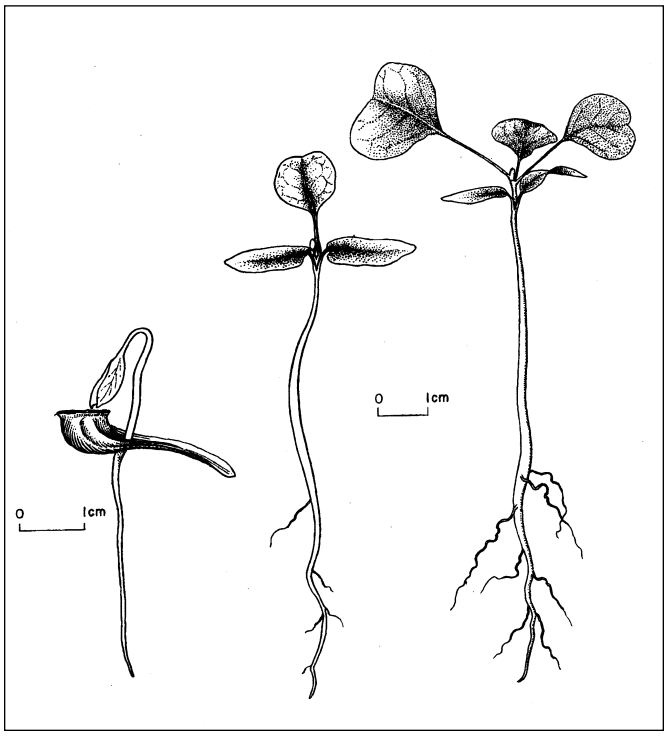
Sources: Bonner and Russell (1974), Heit (1942).

* Seed moisture content was 10% when the counts were made.

period of 28 days (AOSA 1993). If empty seeds have not been removed from test samples, germination percentages will be quite low because of the naturally low proportion of filled seeds common in this species. Germination of the filled seeds should be good, however; percentages of 80 to 90% are common (Bonner and Russell 1974). Seeds ungerminated at the end of a test should be cut to determine if any embryos are present. Viability can also be estimated by tetrazolium staining (ISTA 1993) and by radiography (Belcher and Vozzo 1979; Kaeiser and Boyce 1962; Taft 1962). Germination is epigeal (figure 3).

Nursery practice. Untreated seeds may be sown in the fall, but stratified seeds must be used for spring sowing. Seeds may be broadcast at rates of 25 to 75 kg/m^2 (1 to 3 lb/ft^2) of bed space or sown in rows 20 to 30 cm (8 to 12 in) apart at a rate of 80 to 100 seeds/m (24 to 30/ft) (Bonner and Russell 1974). Bed densities of 110 seedlings/m^2 (10/ft^2) are recommended (Williams and Hanks 1976). To assure proper bed density, the proportion of filled seeds must be known before sowing. The seeds should be covered with 6 mm ($^1/_4$ in) of soil or 12 to 25 mm ($^1/_2$ to 1 in) of sawdust and beds should be shaded for 1 to 2 months from the start of germination (Bonner and Russell 1974). Fumigation with MC-33 (67% methyl bromide plus 33% chloropicrin) was recommended for control of cylindrocladium root rot—*Cylindrocladium scoparium* Morg. (Affeltranger 1969). Because of the uncertain status of methyl bromide at this time, local extension authorities should be consulted about an appropriate fumigant to use.

Figure 3—*Liriodendron tulipifera*, tuliptree: seedling development at 1, 18, and 48 days after germination.



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L

Fagaceae—Beech family

Lithocarpus densiflorus (Hook. & Arn.) Rehd.

tanoak

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Occurrence and growth habit. This evergreen hardwood species, the sole representative of its genus in North America, is considered a link between the chestnuts (*Castanea*) and the oaks (*Quercus*) (McMinn 1939). Tanoak (also known as tanbark-oak)—*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.—has flowers that resemble those of the chestnuts, but acorns that resemble those of the oaks. Tanoak is found from just north of the Umpqua River in southwestern Oregon southward throughout the coastal ranges to the eastern end of the Santa Ynez Mountains in western Ventura County, California. Its range then extends eastward to near Grants Pass, Oregon, and the lower slopes of Mt. Shasta, and then intermittently southward along the western slopes of the Sierra Nevada to Mariposa County, California (Griffin and Critchfield 1972).

A striking characteristic of the tanoak species is that, throughout its range, the tree form is found where moisture is present—from the soil, from fog, or from high relative humidity (McDonald and Tappeiner 1987). Another characteristic of the species is that shade is a requirement, but the amount varies by reproductive mode. Seedlings from acorns need shade to become established and grow. Sprouts from root crowns, which are often found in burned or otherwise severely disturbed areas, grow best in full sunlight, but only until the crowns close. From then on, and whether from acorns or sprouts, only toplight is needed. Indeed, full sunlight is then deleterious.

Because partial shade is necessary, tanoak is often found in dense stands, usually in mixture with several conifer and hardwood species. Pacific madrone (*Arbutus menziesii* Pursh) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) are its most common associates. The species is particularly abundant in a belt surrounding the redwood forest in northern coastal California and in Yuba and Butte Counties in the Sierra Nevada (Sudworth 1908). But even though abundant, it is reported to "never" form pure stands (Jepson and others 1911). However, extensive pure stands of tanoak, 40 to 50 years old, have developed in northwestern California after logging and fire (Thornburgh 1994). Tanoak often forms part of the overstory, but almost always in a codominant position. It is rarely found in a dominant position, except possibly when part of a ragged overstory with Douglas-fir. Because tanoak cannot withstand sudden exposure to full sunlight, leaving scattered mature tanoak trees after heavy logging is a sure way to cause blighted tops and decreased acorn production (McDonald and Tappeiner 1987). Tanoak also is abundant in the understory in intermediate and suppressed crown positions.

As a codominant forest tree, tanoak has a crown that is shaped much like the tapering cone of its principal conifer associate, Douglas-fir. It has a long, straight bole, often clear of branches for 9 to 24 m (Roy 1974); narrow crown; and slender upright branches. Leaning, forking, and crooked trees are uncommon. In stature, tanoak is best described as medium in height, with most trees growing to a range of 13 to 47 m.

Tanoak also has a recognized shrubby form—*L. densiflorus* var. *echinoides* (R. Br.) Abrams—and possibly another, unrecognized one. The recognized form is reported in northern California in Shasta, Siskiyou, and Trinity Counties and on the lower slopes of Mt. Shasta. In these areas, it is restricted to rocky exposed ridges intermixed with tanoak trees that reach heights of 17 m in protected spots (Griffin and Critchfield 1972). They also describe the shrubby form at the end of the species' southern range in the Sierra Nevada. Roy (1974) states that the northern California variety has a typical shrub form, low stature, and "small, thin" leaves. The unrecognized form is found in the northern Sierra Nevada in a narrow elevational band just above that occupied by the tree form (McDonald and Litton 1987; McDonald and others 1989). Here large clumps, often flattened by heavy snow, are found with stems straggling downslope for 5 m or more (Tappeiner and others 1990). In addition, the thick, dark-green leaves of these plants are as

large or larger than those of the tree form. Sudworth (1908) was doubtful about classifying this shrubby form as a variety. He stated that it was "...not to be worth of separation because it is connected with the larger tree forms by numerous intermediate ones."

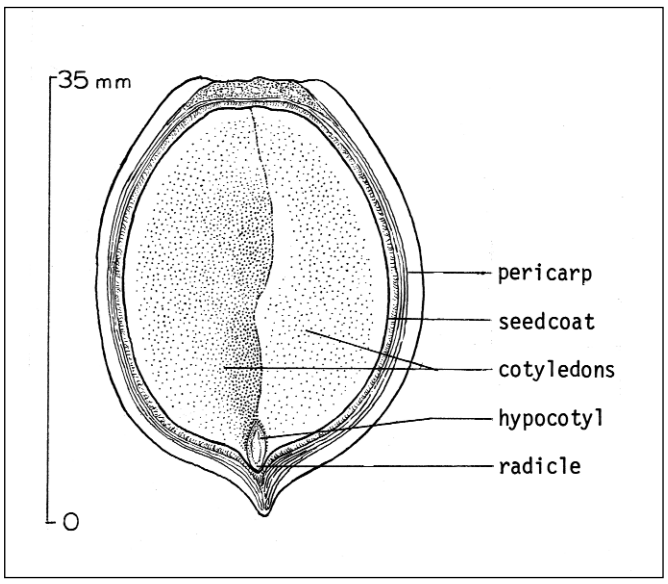
Use. The hard, strong, fine-grained wood has a long but intermittent record of use in California and Oregon (Huber and McDonald 1992). It has been used for flooring, railcar decking, paneling, veneer, plywood, gunstocks, pallets, crossties, baseball bats, pulpwood, and fuelwood (EDA 1968). In the past, tannin was extracted from the bark for tanning heavy leathers (Jepson and others 1911), hence its common names.

Flowering and fruiting. Tanoak produces flowers in the spring and irregularly during autumn. Most flowers arise from the axils of new leaves, occasionally from buds at the base of year-old leaves (Peattie 1953). April, May, and June are the months of heaviest flowering. Pistillate (female) flowers form at the base of the catkins, below the spike of the staminate (male) flowers (Hickman 1993). The pistillate flowers are 5 to 10 cm long and form crowded clusters in such profusion as to conceal the foliage. Initially, their color is white, eventually turning to yellow.

The fruit is a fairly large, heavy acorn (figures 1 and 2), maturing at the end of the second season, and numbering about 242/kg (110/lb) (Mirov and Kraebel 1937). Acorns are borne singly or in clusters of 2 to 4. They ripen in September to November, with peak fall occurring when the relative humidity is low, often when a dry north wind is blowing (McDonald 1978). Generally, the first and last acorns to fall are unsound. The minimum seed-bearing age (from root-crown sprouts) is 5 years, with abundant production occurring after age 30 to 40. On a good site in northern California, annual records showed that, during a 24-year

Figure 1—*Lithocarpus densiflorus*, tanoak: acorns.

Figure 2—*Lithocarpus densiflorus*, tanoak: longitudinal section through an acorn.



period (1958–1981), tanoak produced 4 medium to heavy and 9 very light to light seedcrops (McDonald 1992). The number of acorns per mature tree is reported to range between 3,900 and 110,000 (Tappeiner and others 1990). Soundness of just-fallen acorns varies from 49 to 79%.

Collection, extraction, and storage. Although it fairly "rains acorns" in the fall of a bumper seed year, few remain by spring. Consumption by a host of birds, rodents, and other animals typically is heavy. In a study in several clearcuttings in southwest Oregon (Tappeiner and others 1986) and in studies in northwestern California (Thornburgh 1994), consumption after 3 annual sowings was over 99%. Many acorns are killed by insolation and freezing but, even though they are embryo-dead, they are still prime food for birds, rodents, and other animals. Acorns should be gathered during or shortly after the time of maximum seed fall, preferably from shady, covered locations. Those that fall in an exposed environment overheat and become embryo-dead in a few days, possibly even in a few hours. Freezing temperatures also kill embryos of exposed acorns (McDonald 1978).

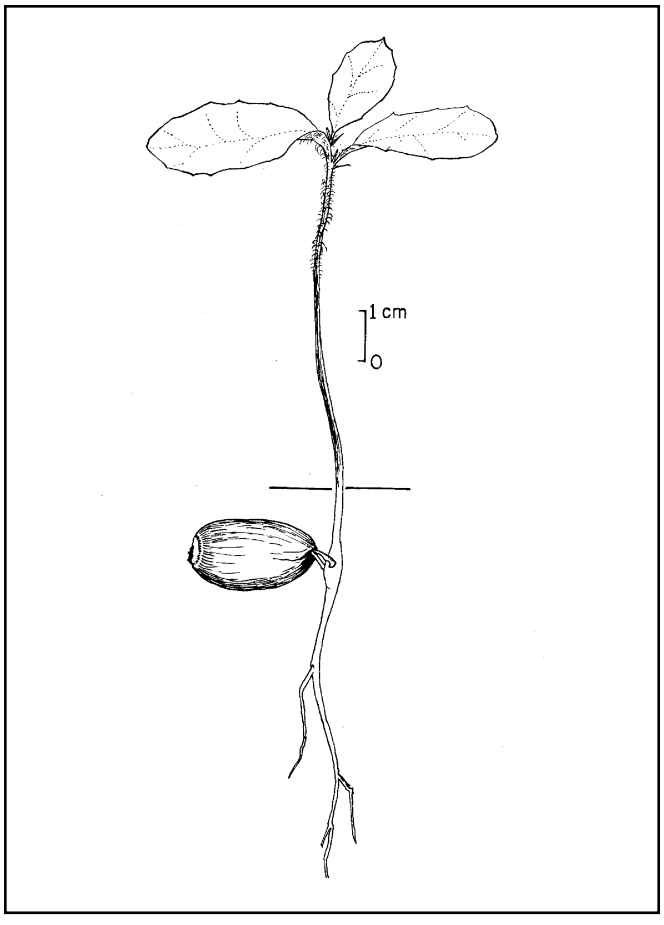
Tanoak acorns generally are stored without the cups. Storage for any length of time can be risky. Death or germination often occur. Acorns can be stored in sacks in cool shaded places or in plastic bags containing a small amount of moist material at temperatures just above freezing. The most effective and efficient technique is to place sound acorns in wire containers buried near the planting site and covered with soil and dead leaves. Here, they stratify in tune with the local environment and produce tiny radicles in the

spring. Seeding germinated acorns almost guarantees a high initial seed-to-seedling ratio.

Pregermination treatments. Stratification in moist peat moss at temperatures just above freezing is all that is needed to give high germination values (97% and 6 days). Germination is hypogeal (figure 3).

Germination. Acorn position is a major influence on germination and subsequent seedling survival and development. Reversing polarity (placing acorns so that the pointed end is up) enhances the speed and completeness of germination, as well as seedling development. In a test in a conventional plantation (clearcutting) with 840 acorns placed point-up and 772 point-down, germination was 53% for point-up acorns and 21% for point-down acorns. Germination rate was 12 versus 41 days, respectively (McDonald 1978). Early germination, however, subjected the just-emerged (7-day-old) seedlings to late spring frost and many were frozen. It is of interest that 75% of these seedlings eventually sprouted from the root crown, but with multiple stems. Perhaps shade from the outer stems provides the inner stems with a more favorable environment and is at least part of the reason for this phenomenon.

Figure 3—*Lithocarpus densiflorus*, tanoak: seedling development 2 months after germination



Nursery practice. Tanoak seedlings are difficult to grow in the nursery. The emergent seedling produces a fast-growing taproot that quickly exceeds the depth of conventional containers and should not be clipped.

Seedling care. Extensive trials on a good site in northern California involved seeding sound acorns and outplanting container seedlings. In spite of the utmost care in site preparation—yearly removal of competing plants, loosened soil at each seed spot, careful seeding, use of acorns known to be viable when seeded, rodent protection, fertilization, and irrigation—seedling survival and growth were poor. Survival of 4- and 6-year-old seedlings was about 34% and mean height was 30 cm (12 in). Many plants had multiple stems from repeated dieback and sprouting (McDonald 1978). Most eventually died. The fate of container-grown seedlings that were given extensive care and artificial shading was little better. Survival after 2 growing seasons was 46%; height growth after outplanting was essentially nil (McDonald 1978). Most seedlings eventually died. The clipped taproot did not renew and the seedling's poorly developed root system did not extend beyond the already loosened soil. When that dried out, the seedlings died.

Survival and growth of natural tanoak seedlings is best described as fair and slow, respectively. We cannot grow tanoak seedlings in conventional sunlit plantations. An environment of moderate shade and plentiful organic material seems necessary for survival and establishment of both artificial and natural seedlings. How to achieve consistent and reliable seedling growth remains a mystery.

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Caprifoliaceae—Honeysuckle family

Lonicera L.

honeysuckle

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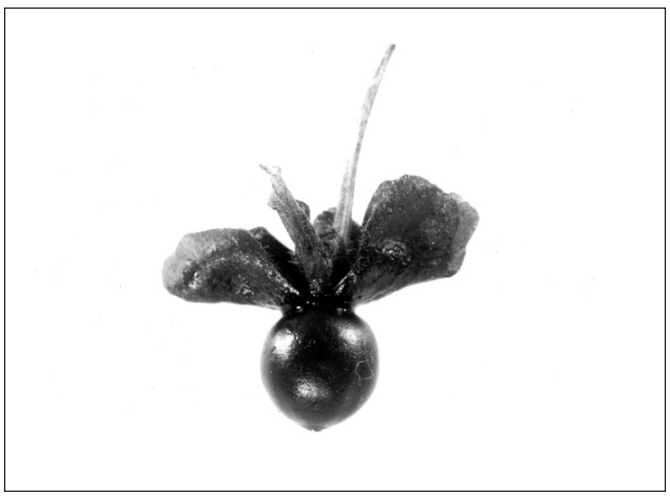
Occurrence, growth habit, and uses. Honeysuckles include about 180 species of deciduous or evergreen, bushy, scandent, twining, or creeping shrubs, found throughout the Northern Hemisphere, south to Mexico and North Africa, Java, and the Philippines (Huxley 1992). Many species are cultivated for their attractive, often-fragrant flowers and for their ornamental fruits. Some species furnish food and cover for wildlife, whereas others are valuable for erosion control and shelterbelt planting (Brinkman 1974; Huxley 1992). They are valued also for their extreme cold hardiness (Herman and Davidson 1997). Many species introduced in the United States have escaped cultivation and have become naturalized within this century (table 1). Japanese, Amur, and Tatarian honeysuckles are now considered invasive weeds (Luken and Thieret 1997)

Scientific and common names. The nomenclature of honeysuckles has been the object of many revisions over time. Many species were once classified as varieties, and vice versa, making synonyms common. The names currently accepted for species native to, naturalized, or in cultivation in the United States are listed in table 1.

Geographic races and hybrids. Erstad (1991) demonstrated extensive genetic variation between black twinberry plants from various northwestern American provenances. Thirty North American honeysuckles have been assigned varietal status (Kartesz 1994). Among the 74 cultivated honeysuckles reported by the Liberty Hyde Bailey Hortorium (1976), 10 species are of hybrid origin.

Flowering and fruiting. The small, perfect flowers vary from white or yellow to pink, purple, or scarlet. They are borne in axillary pairs or sessile, 6-flowered whorls in terminal spikes or panicles. Time of flowering varies not only among species but also by geographic locality within species (table 2). The attractive fruits are berries, white, red, orange, blue, or black at maturity (table 2). They occur often in coalescent pairs that ripen in the spring, summer, or early fall (figure 1). Depending on the species, each berry contains a few to many small seeds that measure about 4 mm in diameter (figures 2 and 3) (Brinkman 1974; Huxley 1992).

Figure 1—*Lonicera involucrata*, black twinberry: fruit (berry).



Bountiful seedcrops of Amur and Tatarian honeysuckles are borne nearly every year. No data are available concerning the age that plants must be to produce a good seedcrop. Seeds are dispersed primarily by birds and other animals. Fruits of Amur, Morrow, and Tatarian honeysuckles persist well into the winter (Brinkman 1974).

Collection of fruits. Fruits should be hand-picked or stripped from the branches as soon as possible after ripening to reduce consumption by birds (Brinkman 1974). Belcher and Hamer (1982) advocate flailing pruned branches of Amur honeysuckle inside a large drum as a time-saving method. Although pruned plants do not bloom the following season, greater quantities of fruits are produced from these plants the second year after pruning.

Fruit color is generally used as an indicator of maturity. Cram (1982) reported, however, that the germination rate of seeds of Tatarian honeysuckle collected several weeks prior to the "color-ripe" stage was not significantly different from that of seeds extracted from ripe fruits. It is generally recommended that fruits be collected from isolated plants or

Table 1—*Lonicera,* honeysuckle: scientific and common names, native occurrence and North American occurrence of introduced species and height at maturity

Scientific name & synonym(s)	Common names(s)	Native occurrence	N Am occurrence of introduced species	Height (m)
***L. albiflora* Torr. & Gray** *L. albiflora* Torr. & Gray var. *dumosa* (Gray) Rehder *L. dumosa* Gray	**western white honeysuckle**	Arizona E to Oklahoma & Texas	—	Scandent to 4 m
***L. arizonica* Rehd.**	**Arizona honeysuckle**	Arizona & New Mexico	—	5.5 m
***L. x bella* Zabel**	**Belle honeysuckle,** whitebell honeysuckle	Wyoming N to Saskatchewan, E to South Carolina & New Brunswick	—	2.5 to 3 m
***L. caerulea* L.**	**bearberry honeysuckle,** sweetberry honeysuckle	Europe to NE Asia	California N to British Columbia, E to Pennsylvania & Newfoundland	2 m
***L. canadensis* Batr. ex Marsh.** *Xylosteon ciliatum* Pursh	**fly honeysuckle**	Tennessee N to Iowa, E to Georgia & Nova Scotia	—	1.5 m
***L. caprifolium* L.**	**Italian woodbine,** Italian honeysuckle	Europe to W Asia	New Jersey to Massachusetts & Nova Scotia	Scandent to 6 m
***L. chrysantha* Turcz. ex Ledeb.**	**coralline honeysuckle,** honeysuckle	NE Asia to Japan	No occurrence except in cultivation	4 m
***L. ciliosa* (Pursh) Poir. ex DC.**	**orange honeysuckle**	California N to British Columbia, E to Utah & Montana	—	5.5 m
***L. conjugialis* Kellogg**	**purple flower honeysuckle**	California N to Washington, E to Nebraska & Idaho	—	1.5 m
***L. dioica* L.**	**limber honeysuckle,** mountain honeysuckle	Arizona N to British Columbia, E to Georgia, Quebec, & Missouri	—	1.5 m
***L. etrusca* Santi**	**Etruscan honeysuckle**	Mediterranean region	California to British Columbia	Scandent to 4 m
***L. flava* Sims** *L. flava* Sims var. *flavescens* Gleason *L. flavida* Cockerell ex Rehder	**yellow honeysuckle**	Oklahoma N to Illinois, E to South Carolina & Ohio	—	2.5 m
***L. fragrantissima* Lindl. & Paxton** *Xylosteon fragrantissimum* (Lindl. & Paxton) Small	**winter honeysuckle,** sweet-breath-of-spring	China	Utah; Louisiana N to Ohio E to South Carolina & North Carolina	2 m
***L. hirsuta* Eat.** *L. hirsuta* Eat. var. *interior* Gleason *L. hirsuta* Eat. var. *schindleri* B. Bovin	**hairy honeysuckle**	Nebraska N to Saskatchewan, E to Pennsylvania & Quebec	—	3.5 m
***L. hispidula* (Lindl.) Dougl. ex Torr. & Gray**	**California honeysuckle**	California to British Columbia	—	—
***L. interrupta* Benth.**	**chaparral honeysuckle**	California to Oregon & Arizona	—	—
***L. involucrata* Banks ex Spreng.**	**black twinberry,** bearberry honeysuckle, inkberry, skunkberry, twinberry honeysuckle	California N to Alaska, E to New Mexico & New Brunswick	—	2 m

Table 1—*Lonicera,* honeysuckle: scientific and common names, native occurrence and North American occurrence of introduced species and height at maturity (continued)

Scientific name & synonym(s)	Common names(s)	Native occurrence	N Am occurrence of introduced species	Height (m)
***L. involucrata var. ledebourii* (Eschsch.) Zabel** *L. ledebourii* Eschsch.	—	Coastal California	—	2 m
***L. japonica* Thunb.** *L. japonica Thunb. var. chinensis* (P.W. Wats.) Baker *Nintooa japonica* (Thunb.) Sweet	**Japanese honeysuckle,** gold-and-silver-flower	E Asia	California N to Oregon, E to Texas & N to Nebraska, E to Florida & Maine	Scandent to 10 m
***L. korolkowii* Stapf**	**blueleaf honeysuckle**	Central Asia, Afghanistan, & Pakistan	No occurrence except in cultivation	3 m
***L. maackii* (Rupr.) Herder**	**Amur honeysuckle**	Japan, Korea, Manchuria, N China, Amur, Ussuri	Texas to South Carolina & Ontario	5 m
***L. morrowii* Gray**	**Morrow honeysuckle**	Japan	New Mexico N to Saskatchewan, E to Virginia & New Brunswick	3 m
***L. oblongifolia* (Goldie) Hook.**	**swamp fly honeysuckle**	Michigan N to Manitoba, E to Nova Scotia	—	1.5 m
***L. periclymenum* L.**	**woodbine honeysuckle,** European honeysuckle	Europe, N Africa, & W Asia	British Columbia to Ontario, Maine, Nova Scotia, & Newfoundland	4 m
***L. reticulata* Raf.** *L. prolifera* (Kirchn.) Booth ex Rehder *L. prolifera* (Kirchn.) Booth ex Rehder var. glabra Gleason *L. sullivantii* Gray	**grape honeysuckle**	SE China	Arkansas N to Nebraska, E to Tennessee, Ontario, & Nova Scotia	—
***L. ruprechtiana* Regel** *L.* x *muscaviensis* Rehder	**Manchurian honeysuckle**	NE Asia, Manchuria, & China	Illinois, Indiana, Michigan, & New York	6 m
***L. sempervirens* L.**	**trumpet honeysuckle,** coral honeysuckle	Texas N to Connecticut, E to Florida	—	4 m
***L. standishii* Jacques**	**Standish honeysuckle**	China	Illinois, Kentucky, Maryland, New York, & Pennsylvania	3.5 m
***L. subspicata* Hook. & Arn.**	**southern honeysuckle**	Central & S California	—	2.5 m
***L. tatarica* L.**	**Tatarian honeysuckle**	S Russia to Altai Mtns & Turkestan	California N to Alberta, E to Virginia & Nova Scotia	4 m
***L. utahensis* S. Wats.**	**Utah honeysuckle**	California N to British Columbia, E to New Mexico & Alberta	—	1.5 m
***L. villosa* (Michx.) J.A. Schultes**	**mountain fly honeysuckle**	Alberta E to Pennsylvania & New Brunswick	—	1 m
***L. xylosteum* L.**	**European fly honeysuckle,** dwarf honeysuckle	Europe, Siberia, & China	Missouri N to Ontario, E to Virginia & Quebec	3 m

Sources: BONAP (1996), Brickell and Zuk (1997), Brinkman (1974), Cullina (2002), Dirr (1990), Dwelley (1980), FNPS (2002), Huxley (1992), Kartesz (1994), LHBH (1976).

Table 2—*Lonicera,* honeysuckle: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Color of ripe fruit
L. albiflora	—	Spring	—	Orange
L. arizonica	Arizona	June–July	—	Red
L. x bella	—	Early summer	—	Red
L. caerulea	—	Spring	—	Dark blue
L. canadensis	—	Apr–July	July–Aug	Red, orange-red
L. caprifolium	—	—	—	Orange-red
L. chrysantha	NE US	May–June	July–Sept	Coral red, dark red
	Japan	June	July–Aug	—
L. ciliosa	—	—	—	Red
L. conjugialis	—	Early summer	—	Red
L. dioica	—	May–July	July–Sept	Red
L. etrusca	—	Summer	—	Red
L. flava	—	Late spring	—	Red
L. fragrantissima	—	Winter–early spring	—	Red
L. hirsuta	—	May–Aug	Sept–Oct	Yellow, red
L. hispidula	—	Summer	—	Red
L. interrupta	—	Early summer	—	Red
L. involucrata	E US	June	Aug	Purple-black, glossy
	N Rocky Mtns	June–July	July–Aug	—
	W US	Apr–Aug	—	—
L. involucrata var. *ledebourii*	California	Mar–July	—	Black
L. japonica	—	Summer	—	Black
L. korolkowii	—	Late spring	—	Bright red
L. maackii	NE US	June	Sept–Nov	Dark red, black
	Japan	May	Aug–Sept	—
L. morrowii	NE US	May–June	June–Aug	Yellow, red, dark red
	Japan	May	Aug–Sept	—
L. oblongifolia	—	May–June	July–Aug	Orange-yellow to red to deep red
L. periclymenum	—	Summer	—	Red
L. reticulata	—	—	—	Black
L. ruprechtiana	—	Late spring	—	Red
L. sempervirens	—	Summer	—	Red
L. standishii	—	Early spring	—	Red
L. subspicata	—	—	—	Yellow or red
L. tatarica	—	May–June	July–Aug	Yellow, orange, red
L. utahensis	W US	April–June	June–Sept	Red
L. villosa	—	June	July–Aug	Blue-black
L. xylosteum	—	Late spring	—	Dark red

Sources: Bailey (1949), Brickell and Zuk (1997), Brinkman (1974), Dwelley (1980), FNPS (2002), , Hériteau (1990), Huxley (1992), Krüssmann (1985), Las Pilitas Nursery (2002), LHBH (1976), Maisenhelder (1958).

groups of plants, as honeysuckles are believed to hybridize freely (Brinkman 1974).

Seed extraction and storage. Unless seeds can be extracted immediately, fresh fruits should be spread out in thin layers to prevent heating. Extraction is accomplished by macerating the fruits in water and allowing the empty seeds and pulp to float and the viable seeds to sink. Munson (1986) has described the use of modified kitchen and shop implements to facilitate extraction. After a short drying period, seeds are ready for sowing or storage. Data regarding seed yields are presented in table 3. Honeysuckle seeds are apparently orthodox in storage behavior. Storage of air-dried seeds at room temperature results in loss of viability over several years. One study showed that germination of swamp fly honeysuckle decreased 20% after 1 year (Brinkman 1974). In another experiment, seeds of Tatarian honeysuckle stored at 15 to 29 °C showed a more or less continuous decrease in viability with length of storage, with negligible germination after 6 years. In contrast, storage of dried seeds in sealed containers at 1 to 3 °C for 15 years resulted in little loss of viability (Brinkman 1974).

Pregermination treatments. Seeds exhibit considerable variation in dormancy. Some species have both seedcoat and embryo dormancy, whereas others have only embryo dormancy or lack dormancy entirely. This variability also occurs among different seedlots of the same species (Hartmann and others 2002; Romanyuk 1989). Swingle (1939) reported that 75 to 90 days of cold stratification

Figure 2—*Lonicera*, honeysuckle: seeds of *L. dioica*, limber honeysuckle (**top**); *L. maackii*, Amur honeysuckle (**second**); *L. involucrata*, black twinberry (**third**); and *L. tatarica*, Tatarian honeysuckle (**bottom**).

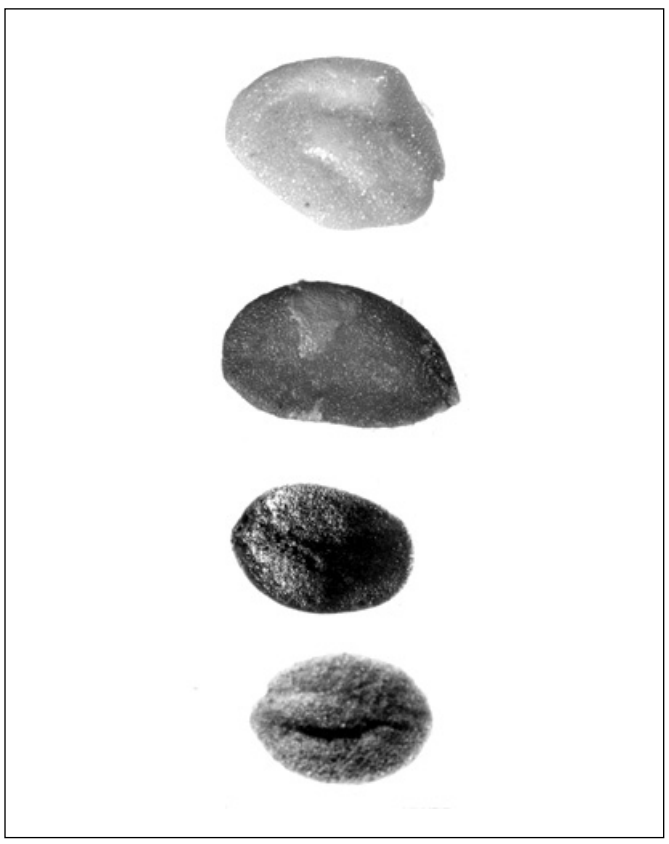
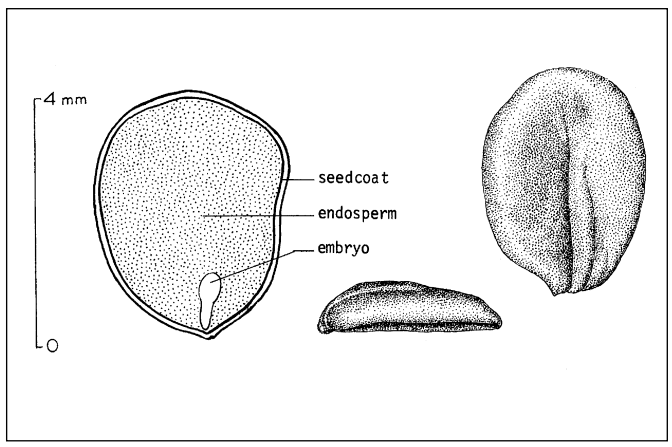


Figure 3—*Lonicera tatarica*, Tatarian honeysuckle: seed in longitudinal section (**left**) and exterior views of seed (**center and right**).



(moist prechilling) were needed for Amur honeysuckle, whereas Luken and Goessling (1995) found that seeds of the same species collected in northern Kentucky showed no dormancy and had a rapid drop in viability after dispersal.

Cold stratification in moist sand or peat for 60 to 90 days at 4 °C is generally recommended to overcome embryo dormancy. Seedcoat dormancy has been reported repeatedly in hairy and swamp fly honeysuckles but has never been confirmed experimentally. When seedcoat dormancy is known or suspected, Brinkman (1974) recommends that cold stratification be preceded by warm moist stratification for 60 days at 20 to 30 °C (table 4). He indicated that without such treatments, germination may be prolonged over a period of 6 months or longer.

Germination tests. Germination is epigeal (figure 4), and germination tests can be conducted in flats or in a germinator. Light is not necessary, at least for Tatarian honeysuckle. For most species, alternating temperatures of 30 and 20 °C yield satisfactory results (table 5). Brinkman (1974) reported conflicting results in 2 studies conducted to determine the optimal germination temperature of Tatarian honeysuckle. One study reported that 20 °C or less was required for complete germination, whereas the other reported that 18 to 20 °C was the minimum needed, with the most rapid germination occurring at 25 to 27 °C. Swingle (1939) reported that tests by the USDA Soil Conservation Service (which is now called the Natural Resources Conservation Service) showed no correlation between seed viability, as estimated by cutting tests, and germination rates as measured by germination tests. There are no official testing protocols for honeysuckle species.

Nursery practice and seedling care. Seeds of species of honeysuckle that only exhibit embryo dormancy can be

Table 3—*Lonicera,* honeysuckle: cleaned seeds per weight

Species	Range		Average	
	/kg	/lb	/kg	/lb
L. involucrata	500,000–1,050,000	227,000–477,000	720,000	326,500
L. maackii	260,000–430,000	116,000–194,000	330,000	148,000
L. morrowii	250,000–440,000	114,000–191,000	335,000	152,000
L. oblongifolia	520,000–530,000	234,000–239,000	520,000	236,000
L. tatarica	260,000–440,000	116,000–198,000	310,000	142,000

Source: Brinkman (1974).

Table 4—*Lonicera*, honeysuckle: stratification treatments

Species	Warm period		Cold period	
	Temp (°C)	Days	Temp (°C)	Days
L. hirsuta	20–30	60	5	60
L. maackii	—	—	0–10	60–90
L. oblongifolia	20–30	60	5	90
L. tatarica	—	—	5	30–60

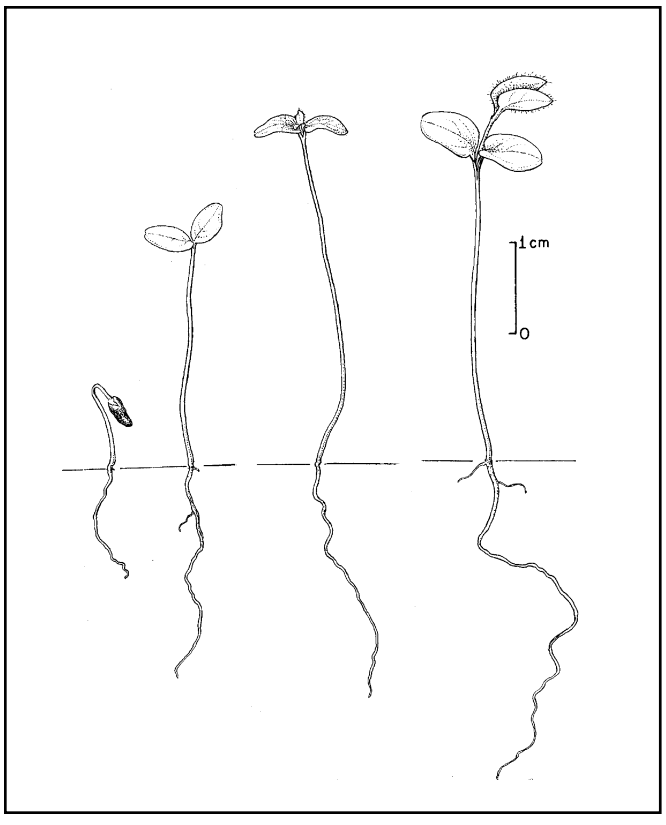
Source: Brinkman (1974).

Table 5—*Lonicera,* honeysuckle: germination test conditions and results

Species	Germination conditions				Germination rate		Total germination (%)
	Medium	Temp (°C) Day	Temp (°C) Night	Days	Amount (%)	Days	
L. canadensis	Sand	30	20	90	—	—	100
L. chrysantha	—	—	—	—	—	—	78–91
L. dioica	Sand	30	20	80–100	—	—	95
L. hirsuta	Sand	30	20	100	—	—	43
L. involucrata	—	—	—	—	—	—	83
L. oblongifolia	Sand	30	20	60	33	25	37
L. tatarica	Sand	30	20	60–90	58	33	85

Source: Brinkman (1974).

Figure 4—*Lonicera tatarica,* Tatarian honeysuckle: seedling development at 1, 3, 13, and 31 days after germination.



sown either broadcast or by drills in the fall, or cold-stratified and sown in early spring. Seeds of species believed to have an impermeable seedcoat as well, however, should be sown as soon as possible after collection to ensure germination the next spring. Nondormant seeds may be sown in the spring without pretreatment. Seeds should be covered with 3 to 6 mm ($^1/_8$ to $^1/_4$ in) of nursery soil. Mulching with 5.0 to 7.5 cm (2 to 3 in) of straw prevents excessive drying of the soil and seeds. Germination of Tatarian honeysuckle usually is complete in 40 to 60 days after spring-sowing. This time can be shortened by soaking seeds in water for 2 to 3 days before sowing. About 15% of sown seeds of Tatarian honeysuckle result in usable seedlings. One- or 2-year-old seedlings of this species and Amur honeysuckle are suitable for field planting (Brinkman 1974).

Vegetative propagation of honeysuckles by stem cuttings is also possible. Most species can be propagated readily by softwood, semi-hardwood, or hardwood cuttings (Dirr and Heuser 1987; Hartmann and others 2002).

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Myrtaceae—Myrtle family

Lophostemon confertus (R. Br.) P.G. Wilson & Waterhouse

brushbox

Edwin Q. P. Petteys and Franklin T. Bonner

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Synonyms. *Lophostemon australe* Schott., *Tristania conferta* R. Br., *T. subverticillata* Wendl.

Other common names. Brisbane-box, scrub-box, vinegar-tree.

Growth habit, occurrence, and uses. Brushbox is a straight-boled evergreen tree that obtains heights of 35 to 45 m (18 m in Hawaii) (Carlson and Bryan 1959; Francis 1951; Maiden 1904). It is native to the eastern coastal region of Australia and has become naturalized throughout India and Africa as well as in California, Florida, and Hawaii (Bailey 1906; Little and Skolmen 1989; Streets 1962). It has been planted for timber and for ornamental purposes in Hawaii (Little and Skolmen 1989). The wood grown in Hawaii is moderately resistant to decay and termites, whereas wood grown in Australia is considered to be very resistant to both. In Hawaii, the wood is used for pallets, flooring, and pulp chips, whereas in other regions it is used extensively for construction, shipbuilding, bridges, railway crossties, and pallets (Little and Skolmen 1989). This species is a hardy ornamental and shade tree with handsome foliage (Streets 1962)

Flowering and fruiting. The white brushbox flowers appear in clusters of 3 to 7 on short branches at leaf bases and the backs of leaves. Individual flowers are about 2.5 cm wide. The fruits are bell-shaped capsules 1 to 1.5 cm in diameter and light green to brown in color (Little and Skolmen 1989; Neal 1965). Individual seeds are flat, elongated (figure 1), light brown in color, and less than 4 mm long (figure 2). Seeds are produced moderately well at 15 to 20 years of age (Carlson and Bryan 1959). In Hawaii, trees can be found in all stages of the reproductive cycle at any time during the year, depending on the aspect and elevation at which they are growing (Petteys 1974).

Collection, extraction, and storage. In Hawaii, the capsules are picked by hand when they turn from green to greenish brown in color. They should be spread out on trays or tables to complete the drying process. Once the capsules are dry, simple agitation will separate the seeds from the capsules. There are almost 5 million seeds/kg (2.2 million/lb), but as few as 2 or 3% of these may be viable (Petteys 1974). The seeds are orthodox in storage behavior,

Figure 1—*Lophostemon confertus*, brushbox: seed.

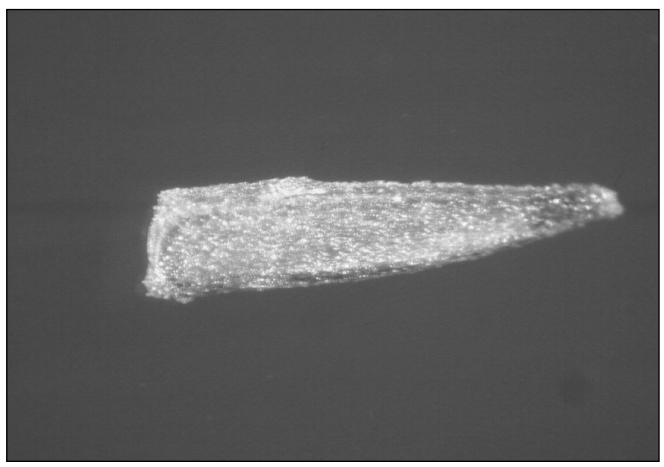
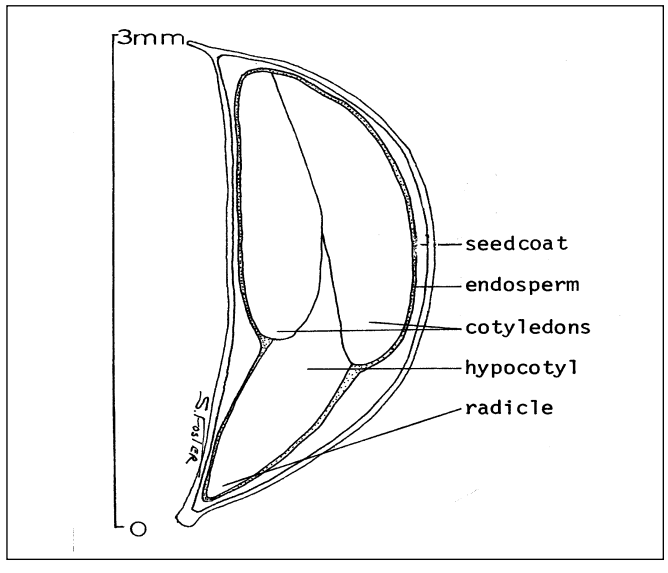


Figure 2—*Lophostemon confertus*, brushbox: longitudinal section through *a* seed.



as they have stored well in sealed polyethylene bags at low moisture contents and temperatures of –18 to –23 °C (Petteys 1974).

Germination. Brushbox is not dormant and no pregermination treatments are necessary for timely germination. Germination of full seeds for one group of samples averaged about 70% (Petteys 1974).

Nursery and field practice. Brushbox seeds are mixed with fine soil and the mixture is applied to beds with a fertilizer spreader. Germination usually begins in 10 to 14 days. Mulching and shading are not necessary. Seeds are usually sown from November to March and seedlings are outplanted the following winter as 1+0 stock. Bed densities of 215 to 320 seedlings/m^2 (20 to 30/ft^2) are recommended. Seedlings must be treated and planted with care to minimize the high mortality common to this species (Petteys 1974).

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Fabaceae—Pea family

Lupinus L.

lupine

Don E. Riemenschneider, Tim D. Davis, Wayne A. Mackay, and Raymond D. Ratliff

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Growth habit, occurrence, and use. The genus *Lupinus* is a large genus of herbs and shrubs that are distributed worldwide (Christofolini 1989). Only 10 to 14 Old World species, all herbaceous, are recognized (Williams and others 1983). New World lupines are more diverse, with 147 species found in North America (USDA SCS 1982), 200 in Mexico, 30 to 40 in Central America, and about 500 in South America (Christofolini 1989). Four shrub species are considered here (table 1). Three species are commonly planted in California. Pauma lupine can reach a maximum height of about 2.5 m (Hickman 1993). As far as can be determined, Pauma lupine was first cultivated in 1928 and has since proved to be valuable as an ornamental plant and for watershed protection and erosion control. Though some plants may live for 10 years, Pauma lupine is generally short-lived (Everett 1957). Whiteface lupine, a more northerly shrub species in California, often reaches a maximum height of 3 m. Since it was first cultivated in 1927, it has been planted for wildlife purposes, watershed protection, and more recently for environmental forestry. Four varieties of whiteface lupine are recognized: *Lupinus albifrons* var. *collinus* Greene; var. *douglassii* (J.G. Agardh) C.P. Sm.; var. *flumineus* C.P. Sm.; and var. *eminens* (Greene) C.P. Sm. (Hickman 1993; USDA SCS 1982). Bush lupine, a large, fast-growing but short-lived shrub found in the northern coastal scrub of California, has been planted for dune stabilization in northern California (Davidson and Barbour 1977; Gadgil 1971a,b&c). Inyo bush lupine is not positively distinct from whiteface lupine, and they are often grouped together.

Flowering and fruiting. Flowers are bisexual, irregular, blue, purple, and yellow in racemes. Pauma lupine will bear viable seeds at 1 year of age (Everett 1957). It flowers from April to May (Munz and Keck 1959) and its seeds ripen from May to August (Ratliffe 1974). Whiteface lupine flowers from March to June (Hickman 1993) and its seeds mature from early June to late July.

Collection, extraction, and storage. The legumes (pods) of both Pauma and whiteface lupines pop open when ripe and disperse 2 to 12 seeds (figures 1 and 2). Hence, it is necessary to collect the legumes while the seeds are somewhat green (Ratliffe 1974). Immature legumes can be gently air-dried until they open. The coarse material can be removed by screening. The number of clean Pauma lupine seeds per weight in 2 samples was 39,700 to 52,900/kg (18,000 to 24,000/lb) (Mirov and Kraebel 1937). Information on seed weight is lacking for whiteface lupine; however, for the closely related Inyo bush lupine, the num-

Table 1—*Lupinus,* lupine: nomenclature and occurrence

Scientific name	Common name(s)	Occurrence
***L. albifrons* Benth ex. Lindl.**	**whiteface lupine,** silver lupine	Coastal range & Sierra Nevada
***L. arboreus* Sims**	**bush lupine**	N California coast
***L. excubitus* M.E. Jones**	**Inyo bush lupine**	California & Nevada
***L longifolius* (S. Wats) Abrams**	**Pauma lupine,** longleaf bush lupine	S California

Sources: Davidson and Barbour (1977), Everett (1957), Gadgil (1971a,b&c), Hickman (1993), USDA SCS (1982).

Figure 1—*Lupinus*, lupine: seeds of *L. albifrons*, whiteface lupine (**left**) and *L. longifolius*, Pauma lupine (**right**).

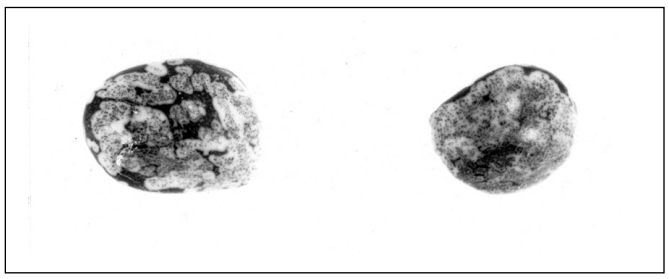
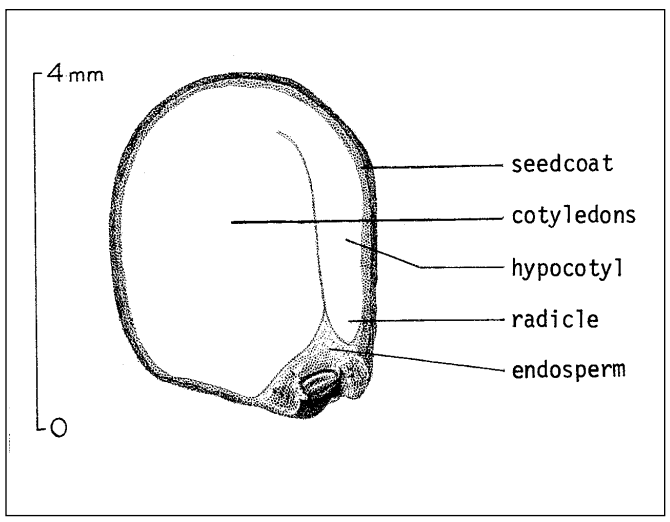


Figure 2—*Lupinus longifolius*, Pauma lupine: longitudinal section through a seed



ber of clean seeds per weight was reported to be 59,500/kg (27,000/lb) (Mirov and Kraebel 1937). In 1 sample, purity was 91% and soundness was 76% (Ratliffe 1974).

When adequately dried, mature seeds of lupine can be stored for extended periods. Seeds stored for 30 years at room temperature were found to be viable, and variations in the color of these seeds had no effect on viability (Everett 1957).

Germination. Stored seeds of the lupines have hard seedcoats that require pretreatment to induce prompt germination. Seeds of the west Australian blue lupine (*L. angustifolius* L.) became impermeable to water when their moisture content was reduced to 10 to 12% (Quinlivan 1962). Each of 3 treatments—mechanical scarification, a hot water soak, and cold stratification for 72 days at 2 °C—induced prompt germination (Ratliffe 1974). In addition, the hard seeds of this lupine became permeable to water when exposed to simulated surface soil temperature fluctuating between 16 and 60 °C (Quinlivan 1962). Ongoing research on sundial lupine (*Lupinus perennis* L.) suggests that seeds from both the northeastern and southwestern United States germinate poorly (10%) without scarification, but that treatment with concentrated sulfuric acid for 30 to 60 minutes (depending on source of seed) improves germination to near 90%. Preliminary comparisons with bush lupine further suggest that seeds from the 2 species respond similarly to acid treatment.

Germination percentage has been variable for both untreated fresh seeds and pretreated stored seeds (table 2), which may reflect species or population-dependent scarification requirements. Current nursery practices for breaking hardseededness in lupines include nicking, sandpaper scarification, and hot water soaking (Kaplow 1996; Wilson 1996).

Nursery and field practices. Container production of shrubby lupines is somewhat difficult. Young seedlings are susceptible to slug and snail damage. Soil temperatures must be kept low; pot-heating in summer greenhouses may cause major mortality. Root systems are delicate and transplant survival is often low (Kaplow 1996). Wilson (1996) recommeded planting seeds directly into large containers and using a well-aerated soil mix. Shrubby lupines may be direct-seeded after scarification to break hardseededness. They do best in poor, rocky, or sandy soils where competition from perennial grasses is minimal.

Table 2—*Lupinus,* lupine: pregermination treatments and germination test results

Species	Storage (yrs)	Wet chilling (days)	Test duration (days)	Germination percentage	Tests
L. albiftons	2	72	—	90	1
L. excubitus	0	0	6	92	1
L. longifolims	0	0	10+	92	1
L. arboreus	0	0	95	4–45	3

Sources: Davidson and Barbour (1977), Mirov and Kraebel (1937), Ratliff (1974).

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Solanaceae—Potato family

Lycium L.

wolfberry

Paul O. Rudolph and Richard T. Busing

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Other common names. matrimony vine, desert-thorn, boxthorn, squawthorn.

Growth habit, occurrence, and use. The wolfberries—*Lycium* L.—include about 100 species of shrubs native to the temperate and subtropical regions of both hemispheres (Rehder 1940). Deciduous or evergreen as well as thorn-bearing and unarmed forms occur in the genus. Species of wolfberry native to the United States tend to be desert shrubs (Benson and Darrow 1954; Wallace and others 1980; Webb and others 1987). Wolfberries are used as ornamental shrubs because of their showy berries, but they also provide wildlife habitat and watershed protection. At least 1 species is grown for shelter hedges. The 2 introduced species—Chinese wolfberry and matrimony vine—have been grown horticulturally for the longest most extensively in this genus. It is likely that geographic races have developed within widely distributed wolfberry species. Some botanical varieties may be geographical races. Hitchcock (1932) mentions apparent racial development in Anderson wolfberry. Natural hybrids occur where species ranges overlap, as is the case with Anderson wolfberry and Torrey wolfberry (*L. torreyi* Gray) and Rich wolfberry (Hitchcock 1932). Information on 5 species (table 1) is included here.

Flowering and fruiting. The perfect flowers, grading by species from white to lavender, usually bloom in the summer (table 2). They are followed by bright red (rarely yellow or black) berries (table 3), each with few to many seeds (figures 1 and 2). Good seedcrops are borne almost every year by matrimony vine (NBV 1946) and probably by other wolfberry species. Arizona desertthorn produces seed abundantly (Van Dersal 1938).

Collection of fruits; extraction and storage of seeds. Ripe berries may be picked from the bushes in the fall. The berries are soft and may be pulped by forcing them through a screen and floating out the pulp (Rudolf 1974). For extraction on a larger scale, berries may be fermented, mashed in water, and then run through a hammermill equipped with screens of suitable sizes (Glazebrook 1941). After extraction, the seeds should be dried and stored in sealed containers at 5 °C (NBV 1946; Rudolf 1974), or stratified in moist sand (Glazebrook 1941; NBV 1946). Stratified seeds of matrimony vine will maintain good viability for 6 months (NBV 1946), but there is no information on long-term storage of dry seeds. They appear to be orthodox, however, so storage should not be a problem. Seed data are listed in table 4.

Germination. Dormancy in wolfberry seeds is variable. Seed samples of Anderson wolfberry and Arizona desert-thorn germinated well without pretreatment. They had germination of 68 and 94% (Swingle 1939). Germination of matrimony vine seeds, however, was hastened and improved by stratification in moist sand for 60 to 120 days at 5 °C. After cold stratification, the average germination capacity for 19 samples was 74% (Glazebrook 1941; NBV 1946; Rudolf 1974). These tests were run in sand flats for 30 to 40 days at diurnally alternating temperatures of 30 to 20 °C. Germination after 18 days was 54%. Seeds of Rich wolfberry probably would benefit from similar pretreatment,

Figure 1—*Lycium barbarum*, matrimony vine: cleaned seed.

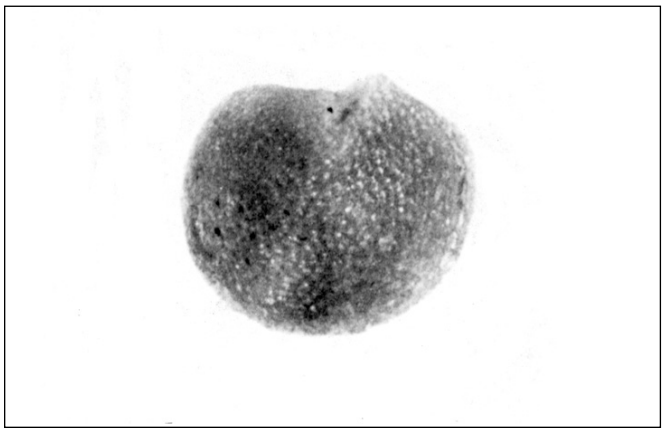


Table 1—*Lycium*, wolfberry: nomenclature and occurrence

Scientific name & synonym(s)*	Common name(s)	Occurrence
***L. andersonii* Gray**	**Anderson wolfberry,** Anderson desert thorn, & water jacket, squawberry	New Mexico to California, N to Colorado, Nevada, & Utah, & in Mexico (Sinaloa Sonora) on gravelly washes, & sandy or alkali flats up to 1,524 m
***L. barbarum* L.** *L. halimifolium* P. Mill.	**matrimony vine,** boxthorn, European desert thorn	China to SE Europe; commonly cultivated in much of the US, West Indies, & Mexico
***L. chinense* P. Mill.**	**Chinese wolfberry**, Chinese matrimony-vine, Chinese desertthorn	In thickets along riverbanks in Japan, Korea, Manchuria, China, Ryukyu Islands, & Formosa
***L. exsertum* Gray** *L. fremontii* var. *bigelovii* Gray	**Arizona desert thorn**	Arizona & New Mexico & NW Mexico up to 1,219 m
***L. richii* Gray** *L. palmeri* Gray *L. pringlei* Gray	**Rich wolfberry,** Baja desert thorn	S California & Sonora, Sinaloa, & Baja California in Mexico

* See Chiang (1983) for nomenclatural history.

Table 2—*Lycium*, wolfberry: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
L. andersonii	W US	Apr–June	—
	SW US	Jan–May	—
	California	Nov–Apr	—
	Arizona	Feb–Apr	Aug–Sept
L. barbarum	Holland, NE US	June–Sept	Aug–Oct
L. chinense	NE US	June–Sept	Aug–Oct
	Japan	Aug–Nov	—
L. exsertum	Arizona	Jan–Feb*	—
L. richii	California	May–Sept	June–Oct

Sources: Bailey (1939), Kearney and Peebles (1942), McMinn (1951), Mirov and Kraebel (1939), NBV (1946), Ohwi (1965), Rehder (1940), Van Dersal (1938), Vines (1960), Wyman (1947).

* Most abundant then, but flowers throughout the year (Kearney and Peebles 1942).

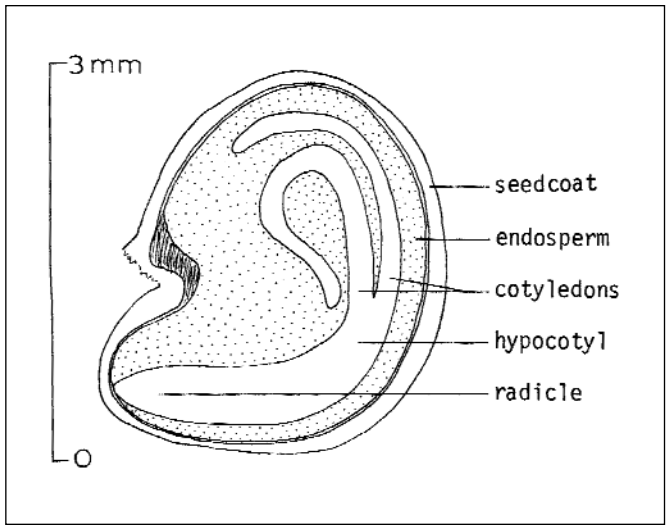
Table 3—*Lycium*, wolfberry: height, length of cultivation, flower color, and fruit characteristics

Species	Height at maturity (m)	Year first cultivated	Flower color	Ripe fruit color	Seeds/fruit
L. andersonii	0.3–3	Before 1935	Light purple, lavender,	Red or white	Very many
L. barbarum	1–6	Long cultivated	Dull, lilac-purple sometimes yellow	Scarlet to orange-red	3–20
L. chinense	1–2*	Before 1709	Purple	Scarlet to orange-red	—
L. exsertum	1–4	Before 1935	Whitish to purple	Orange or red	20–30
L. richii	1–4	Before 1935	Lilac	Bright red	30–50

Sources: Bailey (1939), Benson and Darrow (1954), Hitchcock (1932), Kearney and Peebles (1942), McMinn (1951), Rehder (1940), Standley (1924), Vines (1960).

* Up to 4 m long as a prostrate rambler.

Figure 2—*Lycium barbarum*, matrimony vine: longitudinal section through a seed.



because germination was only 11% without pretreatment (Mirov and Kraebel 1939).

Nursery practice. One recommendation is to sow the seeds in the fall as soon as the fruits ripen (Laurie and Chadwick 1934). Another suggestion is to sow stratified seed in the spring and cover them lightly by sifting-on about 6 mm ($^1/_4$ in) of soil (NBV 1946). Tree percent has been from 10 to 15 for Chinese wolfberry and matrimony vine (Swingle 1939). Two-year-old seedlings may be outplanted.

Table 4—*Lycium*, wolfberry: seed data

Species	Seed soundness (%)	Cleaned seeds/weight				Samples
		Range		Average		
		/kg	/lb	/kg	/lb	
L. chinense	99	—	—	377,000	171,000	1
*L. barbarum**	98	555,600–586,400	252,000–266,000	573,000	260,000	3
L. richii	—	—	—	3,022,600	1,371,000	1

Sources: Glazebrook (1941), Mirov and Kraebel (1939), Swingle (1939).
* Seed purity was 92% in one sample (Rudolf 1974).

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Moraceae—Mulberry family

Maclura pomifera (Raf.) Schneid.

Osage-orange

Franklin T. Bonner

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Synonym. *Toxylon pomiferum* Raf. ex Sarg.

Other common names. *bois-d'arc*, bodark, bowwood, hedge, horse-apple.

Growth habit, occurrence, and uses. Osage-orange—*Maclura pomifera* (Raf.) Schneid.—is native to the bottomlands of southern Arkansas, southeastern Oklahoma, and eastern Texas. It is most abundant in the Red River Valley of Oklahoma but was widely planted in all 48 conterminous states and southeastern Canada as "living fences" on the treeless prairies during the mid-1800s and has now naturalized in many of these locations (Burton 1990; Little 1979; Sargent 1965). Osage-orange is a small deciduous tree chiefly valued for posts and windbreak plantings. Fruits have some value as wildlife food. A typical height at maturity is 9 m, but some individuals have grown to 21 m.

Flowering and fruiting. The small, green, dioecious flowers open from April to June; they are wind-pollinated. The large, globose, yellow-green, aggregate fruit, or syncarp, is composed of many 1-seeded drupelets (figure 1). The fruits ripen in September and October and soon fall to the ground (Bonner and Ferguson 1974). Fruits reach diameters of 7.6 to 15 cm and often weigh more than 1 kg (Burton 1990). Trees bear fruits by age 10, and good crops occur annually (Bonner and Ferguson 1974). Female trees often produce abundant fruit when there are no nearby pollen sources, but these fruits do not contain seeds (Burton 1990).

Collection, extraction, and storage. Fruits should be picked up soon after they fall from the trees but can be collectioned throughout autumn and winter. Seeds (figure 2) may be extracted by macerating the fruits in water and floating off or screening out the pulp. Extraction and cleaning are easier if the fruits are allowed to ferment for several months before maceration. Fruits left in a pile outdoors until late March or early April become very soft and mushy and easy to macerate (Myatt and others 1991). Seeds extracted in this manner have a pronounced purple streak and pleasant fragrance, and they germinate promptly (Bonner and Ferguson 1974.

After extraction, the seeds should be air-dried and cleaned by screening to remove small pieces of fruit tissue. Common air-screen cleaners serve this purpose very well (Myatt and others 1991). Yield data from 22 scattered samples (Bonner and Ferguson 1974) are as follows:

No. of fruits/volume	227/hl	80/bu
No. of seeds/volume of fruit	70,000/hl	24,650/bu
Seed weight/volume	2.9kg/hl	2.25lb/bu
Cleaned seeds weight		
Average	30,900/kg	14,000/lb
Range	15,400–35,300/kg	7,000–16,000/lb

Purity of 96% and soundness of 95% have been attained (Bonner and Ferguson 1974). Long-term storage data are lacking for Osage-orange, but good viability has been reported for clean air-dried seeds stored for 3 years in sealed containers at 5 °C (Engstrom and Stoeckler 1941).

Pregermination treatment and germination tests. Osage-orange seeds typically exhibit a slight dormancy that may be overcome by moist stratification for 30 days at 5 °C or by soaking in water for 48 hours (Engstrom and Stoeckler 1941). Fresh seeds extracted from rotted fruits are not usually dormant and need no pretreatment (Bonner and Ferguson 1974), but stratification or water soaking should probably be used on stored seeds or seeds dried to low moisture contents (10% or below). Tests have been made in flats of sand or soil with pretreated seeds for 40 days at 20 °C nights and 86

Figure 1—*Maclura pomifera*, Osage-orange: aggregate fruit composed of 1–seeded druplets, $^1/_2$ x.

Figure 2—*Maclura pomifera*, Osage-orange: exercised embryo and nutlet (seed) 6 x.

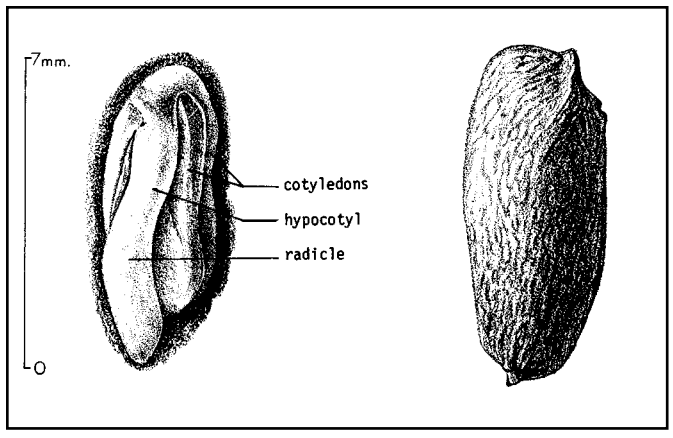
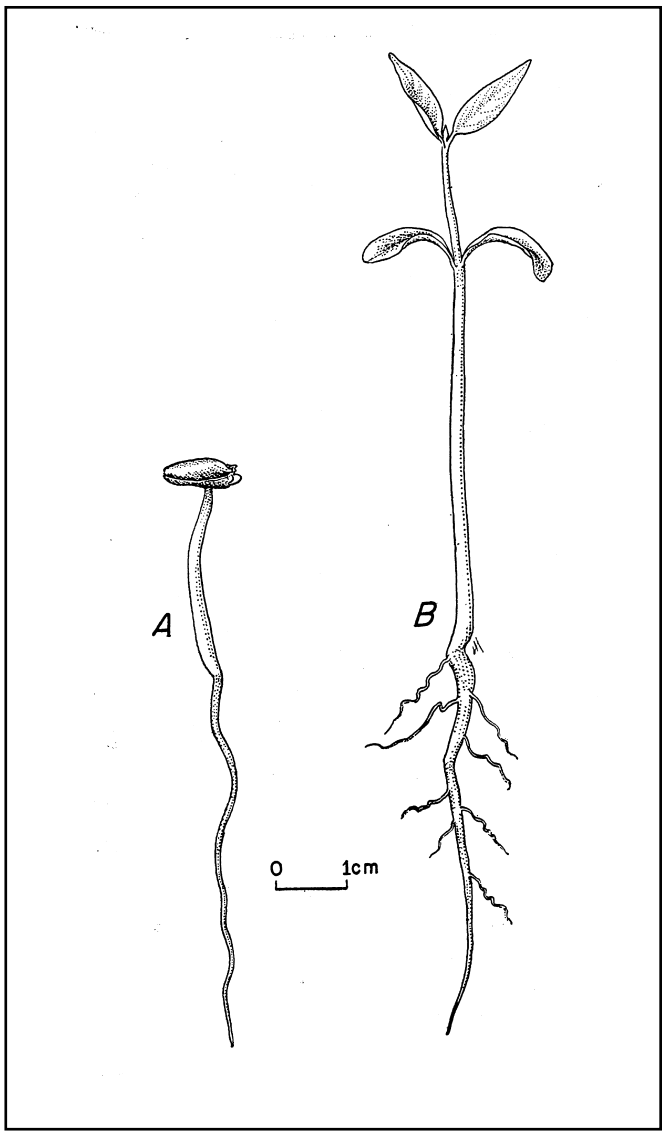


Figure 3—*Maclura pomifera*, Osage-orange: seedling development after 1 and 8 days of germination.



°C days. Average germination for 13 samples under these conditions was 58%. Germination rate was fair: 20 to 79% in 14 to 34 days (Bonner and Ferguson 1974). Germination may also be tested in incubators on paper media. Germination is epigeal (figure 3).

Nursery practice. Untreated seeds may be sown in the fall, but a pregermination treatment should normally be used before spring-sowing. If seeds are freshly extracted from fruits that have been rotting overwinter, however, they have had a "natural" stratification and can be sown without further treatment. Seeds may be drilled in rows 20 to 30 cm (8 to 12 in) apart or sown in bands 7.5 to 10 cm (3 to 4 in) wide if single-row procedures are used. Seeds should be covered with 6 to 13 mm (1/4 to 1/2 in) of firmed soil. Fall-sown beds should be mulched, but not spring-sown beds (Bonner and Ferguson 1974). Recommended bed densities are 100 to 160 seedlings/m^2 (10 to 15/ft^2) (Williams and Hanks 1976).

Osage-orange can also be propagated by softwood cuttings taken in June or by hardwood cuttings taken in January. Cuttings should be treated with indole butyric acid (IBA) at 5,000 or 10,000 ppm and placed in sand under mist (Dirr and Heuser 1987).

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Magnoliaceae—Magnolia family

Magnolia L.

magnolia

Jill R. Barbour

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The genus *Magnolia* comprises about 80 species of trees naturally distributed throughout eastern North America and southeastern Asia (Callaway 1994). It is the largest genus in the family Magnoliaceae. There are 10 species and varieties native to the United States (Callaway 1994) and 2 others native to Puerto Rico (table 1) (Figlar 1982, 1984a). Cucumber magnolia is the only species native to Canada. There are no indigenous magnolias in Europe (Johnson 1973). Sweetbay was the first native American magnolia to be cultivated in Europe in 1688 (Hora 1981).

Based on records of early fossil pollen and leaves, the magnolias are considered the most ancient of all flowering plants (FNAEC 1993). These plants are the base from which all other angiosperms have evolved (FNAEC 1993). Fossil records suggest that magnolias once occurred throughout western North America, western Asia, and Europe. Their range became restricted when the continents in the southern hemisphere separated and cold water moved northward, changing the humid tropical paleo-environment to a drier, colder climate (FNAEC 1993). In the past 20,000 years, the warm temperature taxa have not been disrupted and are in dynamic equilibrium (FNAEC 1993)

Magnolia species are widely planted as ornamentals (Dirr 1990). The leaves and flowers of magnolias are highly prized for decoration, and the fruits make excellent food for wildlife (Callaway 1994). Less than 2% of hardwood timber in the southeastern United States is from magnolias and is usually lumped together with that of tuliptree—*Liriodendron tulipifera* L. (Burns and Honkala 1990).

Table 1—*Magnolia,* magnolia: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***M. acuminata* (L.) L.** *Tulipastrum acuminatum* (L.) Small	**cucumber magnolia,** cucumbertree, yellow cucumber magnolia	S Ontario & New York to Illinois, to E Oklahoma & Georgia
***M. ashei* Weatherby**	**Ashe magnolia**	Banks of Apalachicola River in Florida Panhandle & SE Alabama
***M. fraseri* Walt.** *M. auriculata* Lam.	**Fraser magnolia,** mountain magnolia	Mtns of Maryland, West Virginia, & Virginia, S to N Georgia, Alabama, & South Carolina
***M. grandiflora* L.** *M. foetida* (L.) Sarg.	**southern magnolia,** evergreen magnolia, bull bay	Coastal plain from SE North Carolina to central Florida, & to E Texas
***M. macrophylla* Michx.**	**bigleaf magnolia,** greatleaf(ed) magnolia, large-leaf cucumbertree	Ohio & Kentucky S to Georgia, W to Arkansas & Kentucky
***M. portoricensis* Bello**	**Puerto Rico magnolia**	W Puerto Rico
***M. pyramidata* Bartr.**	**pyramid magnolia,** ear-leaf(ed) magnolia, ear-leaf umbrellatree	Banks of the Ochlochnee*, Apalachicola, & Escambia Rivers of the Florida Panhandle, SE Alabama, W to Texas
***M. splendens* Urban**	**shining magnolia**	E Puerto Rico
***M. tripetala* (L.) L.**	**umbrella magnolia**	Streams or swamps from Pennsylvania to Georgia, W to Arkansas & Mississippi
***M. virginiana* L.** *M. australis* Ashe *M. glauca* L.	**sweetbay,** swamp-laurel, sweetbay magnolia, southern sweetbay, evergreen sweetbay	Coastal swamps from Massachusetts to Florida, W to E Texas

Sources: Callaway (1994), Figlar (1984a, b), Fordham (1960), LHBH (1978), Sargent (1965), Wasson (2001)..

* Sometimes spelled Ochlokonee.

Floral biology. The large, perfect flowers of the magnolias are borne singly at the ends of the branches in the spring and summer. The flowers appear after the leaves between April and June, except for cucumber magnolia, which flowers before leaf bud-break. In section Rhytidospermum, the flowers have 6 to 9 tepals (sepals and petals), in section Magnolia, 8 to 12 tepals and in section Tulipastrum, 9 to 12 tepals (table 2) (Fernald 1970). The flowers have a pleasant fragrance, except those of umbrella magnolia, which have an unpleasant odor (Burns and Honkala 1990).

Magnolia flowers are highly specialized for cantharophily—pollination by beetles, which predate the other pollinators, that is, bees, wasps, butterflies, and moths (Peigler 1988). Beetle-pollinated flowers are characterized by their large size, white or pink color, lack of nectar, and abundance of pollen (Peigler 1988). The flowering is protanderous to prevent the flower from being pollinated with its own pollen. Magnolia flowers close at night. The beetles (members of the Mordellidae and Nitidulidae families) chew through the tepals with their strong mandibles to feed on the flower parts (Peigler 1988). While feeding, the beetles get covered with pollen. When the flower opens, the stigmas are no longer receptive, and the stamens have dehisced and detached from the gynandrophore (central axis of flower). The beetles, covered with pollen, leave the flower to feed on another flower, thus effecting cross-pollination (Thien 1974). The self-incompatible species—such as Fraser and pyramid magnolias, sweetbay, and cucumber magnolia—cannot receive pollen from other flowers on the same tree (McDaniel 1963). Nonviable seeds may have been collected from trees that are self-incompatible. It is best to select other trees for future collections.

Seed biology. The fruits develop from the gynandrophore into a follicetum (figure 1) (Callaway 1994). The individual fruits are referred to as follicles and usually contain 1 to 2 seeds. The follicetum contains between 2 and 60 seeds/fruit (Burns and Honkala 1990). Seeds are released from the follicle when ripe and are suspended on a funiculus (Kozlowski 1972). The bright red color of the sarcotesta is adapted to an endozoochorous mode of dispersal (Kozlowski 1972). At maturity, the seeds are 6 to 18 mm long (figure 3). The seeds of cucumber magnolia are 0.7 to 1.5 cm long, 0.3 to 0.6 cm thick, and 0.5 to 1 cm wide (Afanasiev 1937).

The primitive, angiospermous seeds of the magnolias are characterized by having a very small embryo with copious endosperm (figure 3) (Bouman 1977). The underdeveloped embryo is about 1 mm long and 0.4 mm in diameter and is located at the micropyle end of the seed (Afanasiev 1937; Evans 1933). The endosperm is 51% oil with no starch present. The embryo will not start to grow until it undergoes a cold, moist treatment followed by a warm treatment.

Figure 1—*Magnolia*, magnolia: "cones" (multiple follicles) of *M. acuminata*, cucumber magnolia (**top left**); *M. virginiana*, sweetbay (**bottom left**); *M. fraseri*, Fraser magnolia (**middle**); *M. grandiflora*, southern magnolia (**right**).

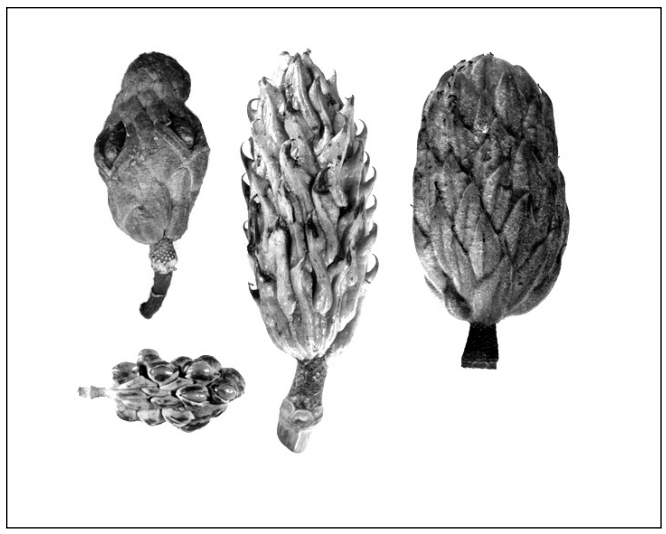


Table 2—*Magnolia,* magnolia: characteristics

Species	Ploidy	Flower color	Leaves, underside color, & hair	Tepals
M. acuminata	2N=76	Yellow-green, yellow	Deciduous, green, & tomentose	9–12
M. ashei	2N=38	White	Deciduous, silver, & pubescent	9
M. fraseri	2N=38	Creamy white	Deciduous, pale green, & glabrous	6–9
M. grandiflora	2N=114	Creamy white	Evergreen, rusty brown, & tomentose	9–15
M. macrophylla	2N=38	White	Deciduous, silver, & pubescent	9
M. portoricensis	2N=114	Creamy white	Evergreen, rusty brown, & glabrous	9–12
M. pyramidata	2N=38	Creamy white	Deciduous, pale green, & glabrous	6–9
M. splendens	2N=114	Creamy white	Evergreen, rusty brown, & pubescent	9–12
M. tripetala	2N=38	White	Deciduous, gray-green, & pubescent	6–9
M. virginiana	2N=38	Creamy white	Deciduous or evergreen, silver, & glabrous	8–12

Sources: Callaway (1994), Johnson (1973), LHBH (1978), McDaniel (1968).

Magnolias have the most primitive seedcoat of the angiosperms. The seedcoat consists of 3 layers (Earle 1962)—the fleshy, outer, red sarcotesta; the parenchymatic middle layer (made up of 57% oil and reducing sugars); and the stony sclerotesta.

Seed crops from magnolia species vary according to environmental conditions. The viability of southern magnolia seedlots averages 50% (Burns and Honkala 1990). Cucumber magnolia reaches seed-bearing age at 30 years (Burns and Honkala, 1990). Seed size ranges from 10,000 to 16,000 seeds/kg (4,550 to 7,530 seeds/lb) (table 3).

Figure 2—*Magnolia*, magnolia: seeds of *M. acuminata*, cucumber magnolia (**top left**); *M. fraseri*, Fraser magnolia (**top right**); *M. grandiflora*, southern magnolia (**bottom left**); *M. virginiana*, sweetbay (**bottom right**).

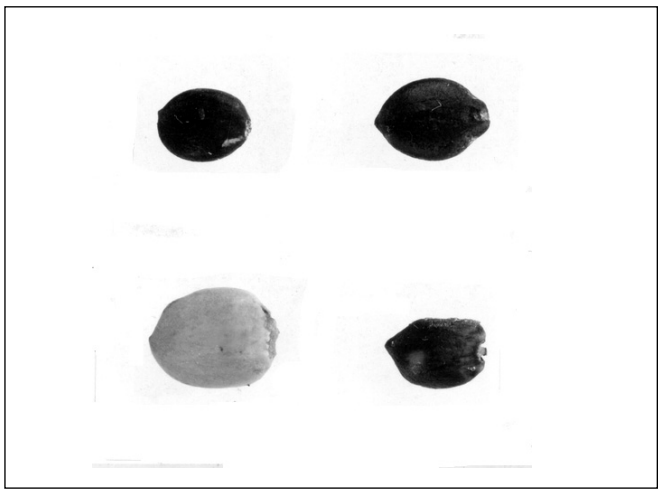
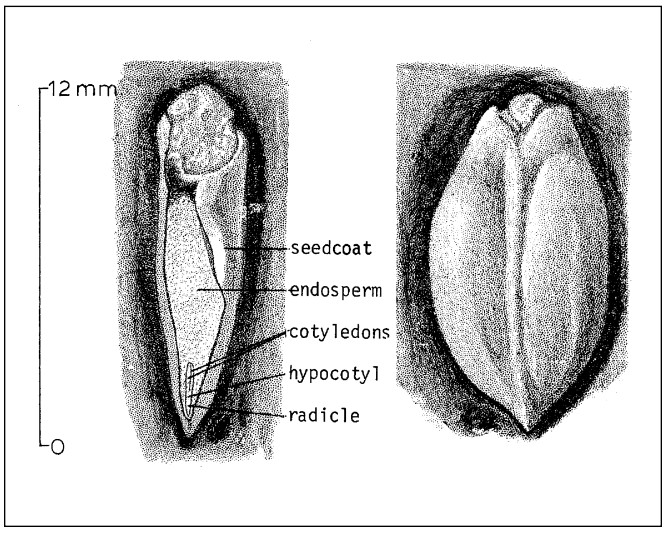


Figure 3—*Magnolia grandiflora*, southern magnolia: longitudinal section through a seed (**left**) and seed with sarcotesta removed (**right**).



Collection of fruits; extraction and storage of seeds. The fruits are usually picked from standing trees or from trees recently felled in logging. The seeds mature in August or September. It is recommended that the fruits be collected before the follicles open to eliminate competition with seed predators (Murphy 1996). The unopened fruit aggregates can be laid on screens to dry (Galle 1953).

The red sarcotesta can be removed by mechanical maceration or by rubbing the seeds over a screen. The oily residue left on seeds can be removed by rinsing them in soapy water, then in clean water (Callaway 1994). The seeds must be kept moist while in storage to retain their viability (Browse 1986; Hanchey and Kimbrough 1954). Saturated sphagnum moss can be added to a plastic bag to keep the seeds moist until sowing (Callaway 1994). Dead and damaged seeds can be removed by floating the seeds in water before storage or planting (Hanchey and Kimbrough 1954). Seeds that float—"floaters"—usually are not viable. Storage of seeds at 0 °C is recommended to reduce the level of infection by fungi (Afanasiev 1937).

Pregermination treatments. Del Tredici (1981) and Evans (1933) found that magnolia seeds exhibit double dormancy. Embryos will not develop until seeds are exposed to warm, moist temperatures after cold, moist temperatures. It takes a minimum of 2 months of cold, moist stratification at 0 to 10 °C to yield the greatest germination (Evans 1933). Stratification medium can be any absorbent material such as sphagnum moss, moss and sand, or vermiculite. During the after-ripening period, the oil and proteins are converted to reducing sugars and the water content of a seed increases from 49 to 61% (Evans 1933). Within 14 days of sowing, the embryo is 50% as long as the seed (Del Tredici 1981).

Other pretreatments such as freezing and sulfuric acid (H_2SO_4) soaks have proved injurious to magnolia seeds (Afanasiev 1937; Hanchey and Kimbrough 1954). Hot water soaks also were not beneficial to seed germination (Hanchey and Kimbrough 1954). Increasing oxygen to the seed had no effect on germination, but eliminating oxygen did inhibit germination (Afanasiev 1937).

Germination tests. Germination is epigeal (figure 4) and occurs rapidly following proper stratification and placement in a standard germination medium (table 4) (Galle 1953). Official tests (AOSA 2001) recommend 45 days of prechilling followed by alternating temperatures of 20/30 °C for 42 days on top of moist blotters. Evans (1933) found that the seeds of southern magnolia germinate most rapidly at 29 °C and give the greatest total germination at 15 to 35 °C. Hanchey and Kimbrough (1954) found that 88% of the seeds of southern magnolia germinated after 2 months of storage in vermiculite at 15 °C. Seeds of sweetbay germinated 93% in 33 days after 58 days of prechilling (Del Tredici

Table 3—*Magnolia,* magnolia: seed data

Species	Cleaned seeds/weight				Samples
	Range		Average		
	/kg	/lb	/kg	/lb	
M. acuminata	6,400–14,500	2,900–6,600	12,020	5,450	15
M. fraseri	5,470–12,460	2,480–5,650	10,030	4,550	12
M. grandiflora	12,800–15,000	5,800–6,800	14,220	6,450	8
M. macrophylla	—	—	9,550	4,330	1
M. portoricensis	—	—	7,410	3,360	1
M. tripetala	—	—	16,540	7,500	1
M. virginiana	—	—	16,600	7,530	5

Sources: Bonner (2002), Dirr and Heuser (1987), Francis and Rodriguez (1993), Heit (1968), Olson and others (1974).

Table 4—*Magnolia,* magnolia: germination test conditions and results for stratified seeds

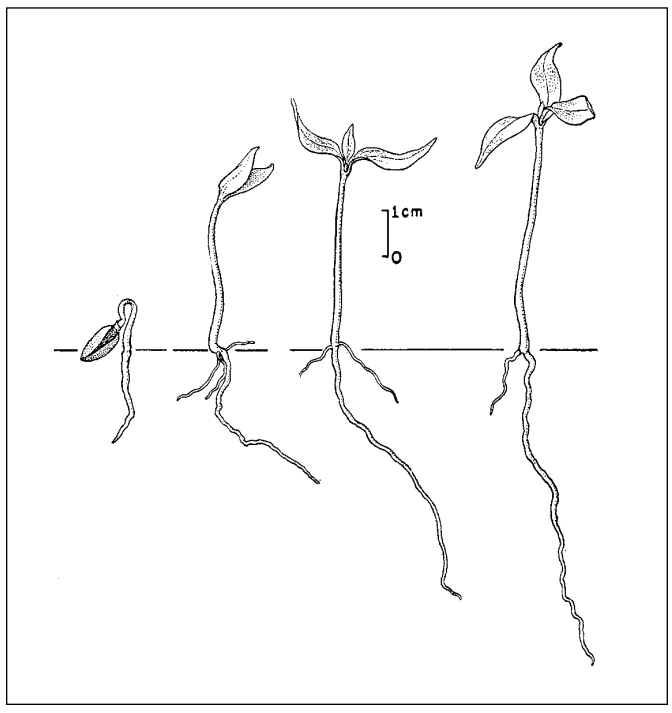
Species	Medium	Germination test conditions			Germinative capacity	
		Temp (°C)				
		Day	Night	Days	Avg (%)	Samples
M. acuminata	Sand–perlite	26–30	15–20	35–60	8–86	4
M. fraseri	Sand–perlite	30	20	40–100	8–21	6
M. grandiflora	Sand–vermiculite	30	20	30–50	43–90	9
M. macrophylla	—	22	22	35	71	35
M. portoricensis	Potting mix	24	30	44	64	—
M. virginiana	Sand–peat	18	18	33	93	1
	Kimpac	30	20	47–61	32–50	4

Sources: Afanasiev (1937), Del Tredici (1981), Francis and Rodriguez (1993), Hanchey and Kimbrough (1954), Jones, (1969), Olson and others (1974), Seitner (1981), Toumey (1942).

1981). For seeds of cucumber magnolia, germination started earliest and progressed most rapidly at a constant temperature of 30 °C, but the highest germination was reached when the temperatures alternated between 15 °C in the dark for 6 hours and 18 hours of light at 26 °C (Afanasiev 1937). At 20 °C, seeds of cucumber magnolia germinated later and more slowly than at the higher temperatures; temperatures above 35 °C resulted in the death and decay of the seeds.

There are 3 viability tests performed on magnolia seeds that correlate with germination. The endosperm of cucumber magnolia will produce green pigment in 2 to 3 days when placed on moist blotting paper at 24 to 30 °C (Afanasiev 1937). The proportion of seeds producing the green pigment is the proportion of viable seeds. Heit (1955) preferred the excised-embryo test for magnolia seeds and recommended soaking them in water up to 4 days to soften their seedcoats. The third viability test is staining with tetrazolium chloride (TZ). Seeds are soaked overnight, then each seed is cut latitudinally to expose the embryo and placed in TZ solution for 18 to 24 hours at 37 °C (NTSL 1997). Embryos that stain red are considered viable.

Figure 4—*Magnolia*, magnolia: seedling development at 1, 5, 13, and 31 days after germination.



Nursery practice. Sowing seeds in a nursery bed is the preferred method of propagating magnolias when a large quantity of seedlings are required for reforestation. The seeds can be planted in October or November in nurserybeds and allowed to naturally stratify over the winter months. The seeds can be sown with or without their sarcotestas if the seeds have not been stored (Papetti 1996). When seed quantities are limited, hand-sowing is the preferred method. Magnolia seeds have been sown with a mechanical seeder at 3 drills/bed and 210 seeds/m (64/ft) (Murphy 1996). A fertilizer distributor has also been used to sow magnolia seeds (Buchanan 1996). It drops a seed every 5 cm (2 in), with 2 passes being made over the nurserybed. When planting in the spring, it is considered common practice to sow cleaned, prechilled seeds.

If rodents or birds are a problem, the seeds need to covered with a ground cloth to prevent predation (Bosch 1996). Coating seeds with Benlate or captan will deter seed fungi (Papetti 1996). For fall-sowing, the seeds should first be covered with 6 to 12 mm ($^1/_4$ to $^1/_2$ in) of mulch, then with the same amount of pine bark or pine straw (Buchanan 1996). For spring-sowing, the seeds need only be covered with the pine mulch.

In more-northern climates, magnolias are grown for 2 years to reach a height of 30 to 60 cm (12 to 18 in) (Murphy 1996). In southern nurseries, a 30-cm (12-in) seedling can be grown in 1 year. Heit (1939) found that shading the newly sprouted plants through the hot summer was beneficial to the survival and development of cucumber magnolia seedlings. Larvae of the black vine weevil—*Otorhynchus sulcatus* F.—are a widespread pest of magnolias. Lamb and Kelly(1985) reported that larvae feed on the roots and kill the plants by eating the bark just below ground and recommend using diazinon as a protectant. Root pruning with a reciprocating blade makes lifting the large, fleshy root system easier (Buchanan 1996). Hand-lifting is the preferred method of lifting magnolias out of the nursery bed, because of the small quantities grown.

Fertilization is needed to stimulate the height growth of magnolias. In Florida nurseries, a blended fertilizer with no additional phosphorus is applied monthly (Buchanan 1996). In a Virginia nursery, a slow-release fertilizer applied just once lasts for 9 months until the lifting season (Papetti 1996).

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M

Berberidaceae—Barberry family

Mahonia Nutt.

Oregon-grape

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Growth habit, occurrence, and use. *Mahonia*—the Oregon-grape—is a genus of about 100 evergreen shrubs native to Asia, Europe, North Africa, and the Americas (Ahrendt 1961). Some authorities (Hitchcock and others 1964) place these species in the genus *Berberis,* and that nomenclature was accepted in the 1974 edition of this book (Rudolf 1974). However, most authorities (LBHB 1976; USDA NRCS 1999) now separate the genera by placing the evergreen species with compound leaves in *Mahonia*. The distinction is far from clear, however: "barberry" is a common name for some *Mahonia* species (table 1) and intergeneric hybrids have been reported (Ahrendt 1961).

Several Oregon-grape species are valued as ornamentals because of their foliage, flowers, or fruits (Bailey 1939; Dirr and Heuser 1987; Rehder 1940; Schlosser and others 1992). Like the closely related barberries, Oregon-grapes also are of value for wildlife food (Decker and others 1991), cover, and erosion-control planting. The names, heights, habits, and ripe fruit colors of some common species are listed in table 1. Six species that have potential value for conservation planting are listed in table 2. Like the barberries, some Oregon-grapes are alternate hosts for the black stem rust of grains—*Puccinia graminis* Pers: Pers). Some species, for example, hollyleaf barberry, Cascade Oregon-grape, and Oregon-grape, are resistant (Rehder 1940).

Like the seeds of the genus *Berberis,* seeds of some members of the genus *Mahonia* contain chemical substances of potential commercial value. The seeds of the Beale

Table 1—*Mahonia,* Oregon-grape: nomenclature, height, and color of ripe fruit

Scientific name & synonym	Common name(s)	Height at maturity (m)	Color of ripe fruit
***M. aquifolium* (Pursh) Nutt.** *B. cerberis aquifolium* Pursh	**hollyleaf barberry,** Oregon grapeholly	0.6–3.0	Blue-black, bloomy
***M. bealei* (Fortune) Carr.** *B. bealei* Fortune	**Beale Oregon–grape,** leatherleaf mahonia	1.8–3.0	Light blue, bloomy
***M. fortunei* (Lindl.) Fedde** *B. fortunei* Lindl.	**Chinese mahonia**	1.5–1.8	Purple-black
***M. fremontii* (Torr.) Fedde** *B. fremontii* Torr.	**Fremont mahonia**	0.9–4.6	Bluish black
***M. haematocarpa* (Woot.) Fedde** *B. haematocarpa* Woot.	**red barberry**	0.9–3.7	Blood red
***M. japonica* (Thunb.) DC.**	**Japanese mahonia**	1.8–3.0	Blue
***M. nervosa* (Pursh) Nutt.** *B. nervosa* Pursh	**Cascades Oregon–grape,** Cascades barberry	0.3–1.8	Deep blue, bloomy
***M. nevinii* (Gray) Fedde** *B. nevinii* Gray	**Nevin barberry**	0.9–1.8	Yellowish red to deep red
***M. pinnata* (Lag.) Fedde** *B. pinnata* (Lag.)	**cluster mahonia**	2.4–3.0	Pruinose blue
***M. repens* (Lindl.) G. Don** *B. repens* Lindl.	**Oregon–grape,** creeping barberry	0.3–2.4	Purple, bloomy

Sources: Ahrendt (1961), Dirr (1990), Dirr and Heuser (1987), Hitchcock and others (1964), McMinn (1951), Rehder (1940), Rudolf (1974), USDA NRCS (1999), Vines (1960).

Table 2—*Mahonia*, Oregon-grape: occurrence of species used for conservation planting.

Species	Occurrence
M. aquifolium	British Columbia to Alberta, S to W Montana, W Idaho, through Washington & Oregon to California
M. fremonti	Extreme W Texas, New Mexico, Arizona, California, Colorado, Utah, & Nevada at 1,220 to 2,130 m, & in Baja California & Sonora, Mexico
M. haematocarpa	Dry, sunny sites up to 1,340 m in W Texas, Colorado, New Mexico, Arizona, & adjacent Mexico
M. nervosa	British Columbia S to central California, mainly W of Cascades in Oregon & Washington, E to N Idaho
M. nevinii	California
M. repens	Montana to British Columbia, S to New Mexico & California, including W South Dakota

Source: Rudolf (1974).

Oregon-grape contain alkaloids that are used in folk medicine in Asia (Zhao and others 1991), and seeds of hollyleaf barberry contain tertiary alkaloids of note (Kostalova and others 1986).

Flowering and fruiting. Perfect yellow flowers are borne in the spring in racemes, panicles, umbels, fascicles, or individually, depending on the species (Ahrendt 1961). Stamens are contact-sensitive, and they respond to a tactile stimulus by snapping toward the stigma (Millet 1976, 1977). The fruit (figure 1) is a berry with one to several seeds (figures 2 and 3). A single sample of 100 fruits indicated that most Cascade Oregon-grape berries have about 3 seeds (Minore 1994). Good fruit crops are borne almost annually; the fruits ripen in the summer and autumn (table 3). Seed dispersal by both birds and mammals is widespread (Rudolf 1974; Vines 1960).

Collection of fruit; extraction and storage of seeds. Ripe fruits may be picked by hand (with gloves) or flailed onto cloths or receptacles spread beneath the bushes. The fruits may be run through a macerator or blender with water and the pulp then screened out or floated off. The seeds should then be dried superficially and either sown immediately or stored in sealed containers at temperatures slightly above freezing (Heit 1967; NBV 1946; Rudolf 1974). Seed purity and soundness can be in the 90% range (Rafn and Son nd; Rudolf 1974). Seeds of Fremont mahonia and Oregon-grape did not loose viability for 5 years when stored in unsealed containers in an unheated shed in a temperate climate (Plummer and others 1968). Fruit yields, seed yields, and numbers of seeds per weight are listed in table 4.

Figure 1—*Mahonia nervosa*, Cascade Oregon-grape: a spike of berries.

Pregermination treatments. Seeds of Fremont mahonia and red barberry usually germinate without pretreatment (Dirr and Heuser 1987; Rudolf 1974; Swingle 1939). The seeds of Fremont mahonia have some intermediate embryo dormancy, however, and germination is improved by 6 to 10 weeks of cold stratification at day/night thermoperiods of 5/1 °C (Baskin and others 1993). Beale Oregon-grape and Japanese mahonia should germinate well with only 1 to 2 months of cold stratification (Dirr and Heuser 1987). Seeds of other species also have embryo dormancy that requires cold stratification to overcome (table 5), but simple cold stratification is not always successful. Seeds of cascade Oregon-grape did not germinate after 90 days of cold stratification (Rudolf 1974); up to 5 months of treatment may be required for this species (Dirr and Heuser 1987). Immature or improperly developed embryos are probably present in some species, as maximum germination of hollyleaf barberry was obtained with 4 months of warm stratification followed by 4 months of cold stratification (Dirr and Heuser 1987). A third stratification period (cold + warm + cold) is best for seeds of Oregon-grape (McLean 1967). Under natural conditions, Oregon-grape seeds germinate in the spring after seeds are dispersed (Kern 1921).

Germination tests. Germination of seeds from 4 species of Oregon-grape has been tested in sand-filled flats, in petri dishes, on paper or blotters, or in standard germinators. Day temperatures of 16 to 30 °C, night temperatures of 13 to 21 °C, and germination periods of 20 to 95 days have been used (table 5). Actual germination tests are not prescribed for species of Oregon-grape by the International Seed Testing Association, but germination estimates with tetrazolium chloride (TZ) staining procedures are recommended (ISTA 1993). Seeds should be pre-moistened for 18 hours at 20 °C, cut open by removing a third of the seed at

Figure 2—*Mahonia*, Oregon-grape: seeds of *M. aquifolium*, hollyleaf barberry (**top left**); *M. nervosa*, Cascades mahonia (**top right**); *M. nevins*, Nevin barberry (**bottom left**); and *M. repens*, Oregon-grape (**bottom right**).

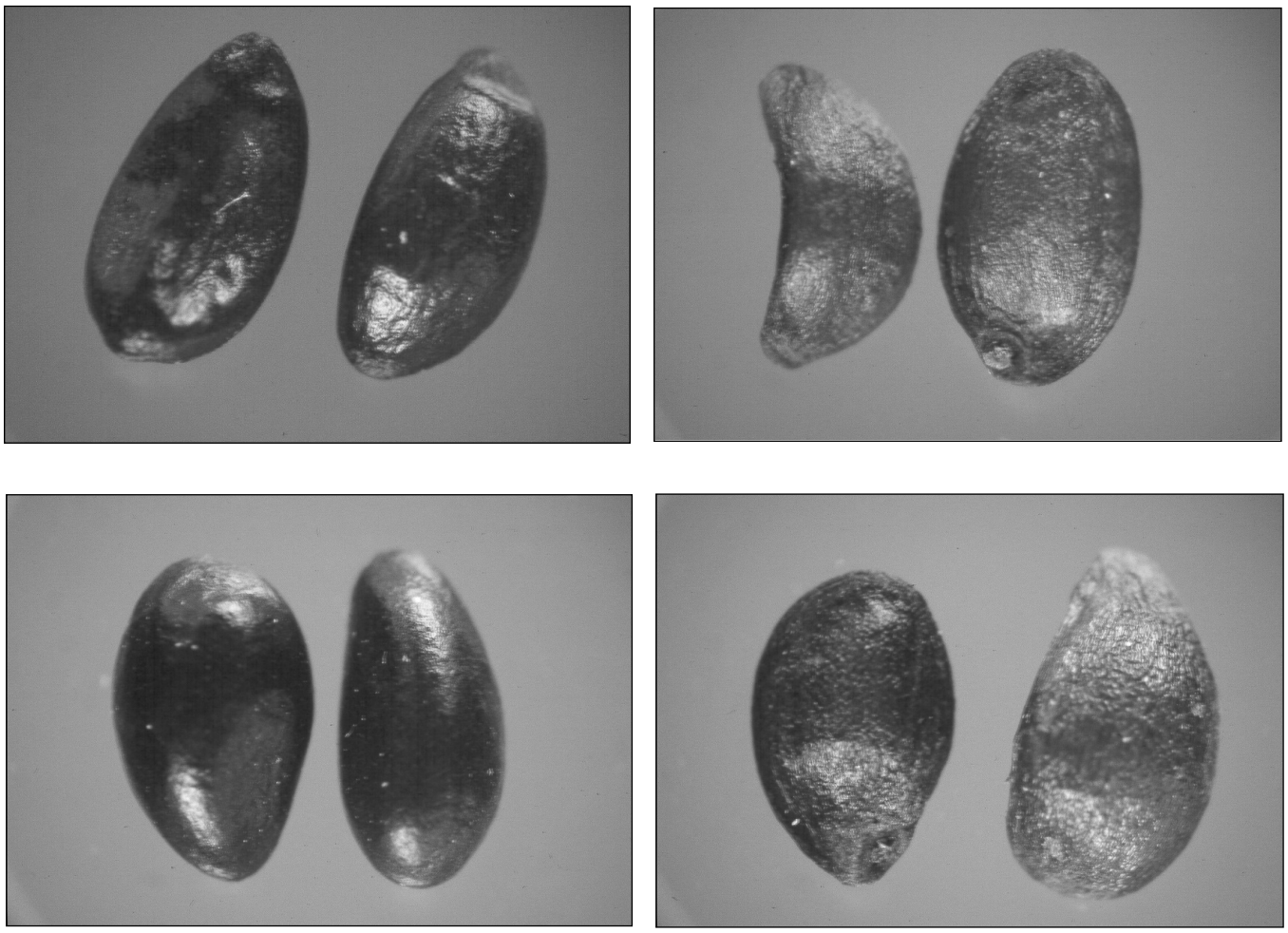


Table 3—*Mahonia*, Oregon-grape: phenology of flowering and fruiting

Species	Location (& altitude)	Flowering	Fruit ripening
M. aquifolium	Mineral Co., Montana (975 m)	Late Apr–early May	Late July–early Aug
	Jackson Co., Oregon (685 m)	Mar–May	Sept–Oct
M. fremontii	Texas, NE US	May–June	Aug–Sept
	Utah & California	May–June	July –Aug
M. haematocarpa	Texas & SW US	Spring	June–Aug
M. nervosa	Clackamas Co., Oregon (90 m)	Early Apr	Mid–Aug
	Jackson Co., Oregon (990 m)	Mid-May	Late Aug
	—	Apr–June	July–Aug
M. nevinii	California	Mar–May	June
M. repens	Black Hills, South Dakota (1,830 m)	May –June	June–July
	—	Apr– May	Aug–Sept

Sources: Bailey (1939), Loiseau (1945), McMinn (1951), Mirov and Kraebel (1939), NBV (1946), Ohwi (1965), Plummer and others (1965), Radford and others (1964), Rudolf (1974), Van Dersal (1938), Vines (1960), Wappes (1982), Wyman (1947).

Table 4—*Mahonia,* Oregon-grape: seed yield data

Species	Place collected	Fruit weight/vol		Seed weight/fruit vol		Cleaned seeds x1,000 /weight				Samples
						Range		Average		
		kg/hl	lb/bu	kg/hl	lb/bu	/kg	/lb	/kg	/lb	
M. aquifolium	Jackson Co., Oregon	44	34	4	3	—	—	73	33	1
	Pacific Northwest	—	—	—	—	84–95	38–43	90	41	2
M. fremontii	Utah	—	—	—	—	—	—	93	42	1+
M. haematocarpa	—	—	—	—	—	—	—	227	103	1
M. nervosa	Clackamas Co., Oregon	39	43*	—	—	—	—	51	23	1
	Pacific Northwest	—	—	—	—	—	—	66	30	2
M. nevinii	California	—	—	—	—	—	—	126	57	1
M. repens	Basin, Montana; & Utah	—	—	—	—	119–157	54–71	136	62	2

Source: Rudolf (1974).

* Data are for berries without stems; data for other species are for berries with stems.

Table 5—*Mahonia*, Oregon-grape: stratification periods, germination test conditions, and percentage germination

Species	Cold stratification* (days)	Daily light (hrs)	Germination test conditions				Germination rate		Percent germination		Purity	Soundness
				Temp (°C)			Amount					
			Medium	Day	Night	Days	(%)	Days	Avg (%)	Samples	(%)	(%)
M. aquifolium	90	8	Sand or perlite	30	20	30	22	12	25	1	95	99
M. fremontii	0	—	—	—	—	—	—	—	85	2+	90	90+
M. nevinii	90	—	Soil	—	—	95	—	—	77	1	—	—
M. repens	196‡	—	Wet paper	21	21	10	62†	150	74	*1*	*90*	—

Sources: Heit (1968a&b), McLean (1967), Mirov and Kraebel (1939), Morinaga (1926), Plummer and others (1968), Rafn and Son (nd), Rudolph (1974), Swingle (1939), Vines (1960).

* Cold stratification temperatures ranged from –1 to 5 °C.

† Maximum germination was obtained with 4 months of warm stratification at 20 °C, followed by 4 months of cold stratification at 2 to 4 °C (Dirr and Heuser 1987).

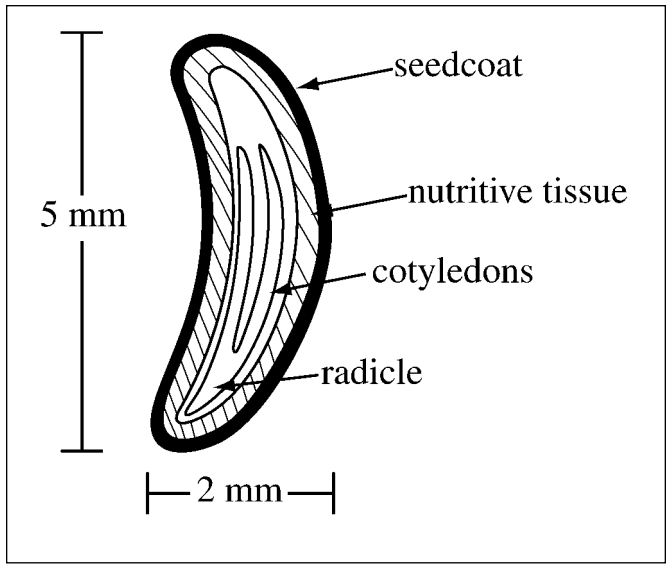
‡ Successive stratification periods were 30 days at 1 °C, 60 days at 21 °C, and 196 days at 1 °C. During the final cold period, 62% of the seeds germinated. An additional 12% germinated after the temperature was again raised to 21 °C for a total of 74%.

the distal end, and incubating in 1% TZ for 18 hrs at 30 °C. All tissues should stain in viable seeds. For the closely related Japanese and common barberries, the Association of Official Seed Analysts (AOSA 1993) recommends germination of excised embryos in covered petri dishes at temperatures of 18 to 22 °C for 10 to 14 days. This method may also be satisfactory for species of Oregon-grape.

Nursery practice. Whole berries or (preferably) cleaned seeds may be sown in the fall, or stratified seeds may be sown in the spring. Injury from molds is more likely if whole berries are used (Chadwick 1936). Fall-sown beds should be mulched until germination begins (NBV 1946). The seeds should be covered with 0.3 to 1.3 cm ($^1/_8$ to $^1/_2$ in) of soil plus 0.6 cm ($^1/_4$ in) of sand (Rudolf 1974). Germination is epigeal (Terabayashi 1987).

Oregon-grapes can be propagated from rooted stem cuttings. Many species root best when hardwood cuttings are collected in the autumn or winter (Dirr and Heuser 1987). They should be treated with indole-butyric acid (IBA) rooting hormone in talc or in solution.

Figure 3—*Mahonia repens*, Oregon-grape: longitudinal section through a seed.



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M

Rosaceae—Rose family

Malus Mill.

apple

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Growth habit, occurrence, and use. The apple genus—*Malus* Mill.—includes about 25 species of deciduous trees or shrubs native to the temperate regions of North America, Europe, and Asia. Taxonomic classification of the native North American apples is the subject of active debate (Green 1996; Yanny 1996). Rehder (1940) recognized 9 native species—*M. angustifolia, M. bracteata, M. coronaria, M. fusca, M. glabrata, M. glaucescens, M. ioensis, M. lancifolia, and M. platycarpa*. Fiala (1994) suggests that, based on chromosome number, there are 3 distinct native species—M. coronaria, M. fusca, and M. ioensis. Other taxonomic structures having intermediate numbers of species have proponents (Green 1996). The nomenclature and occurrence of commonly recognized species are presented in table 1.

Native apples and planted cultivars occur throughout much of North America. In general, apple performs best in full sunlight in deep, well-drained soils. Growth and vigor are best in rich sandy loams, but apple will grow well in heavier clay soils as long as they are well-drained (Fiala 1994). Ideal soil pH ranges from 5.5 to 6.5, but soils with pH in the range of 5.0 to 7.5 will support apple species (Fiala 1994).

The Oregon crab apple, the only native apple in western North America, occurs along the Pacific Coast from northern California to Alaska, occupying mesic to wet habitats at less than 800 m elevation (Hickman 1993). In California and Oregon, it occurs in open forests of the coast ranges and the foothills of the Cascade Range (Hickman 1993). In British Columbia and southern Alaska, its range includes coastal climatic regions as well as zones of gradual transition to continental climate (Pojar 1996; Vierdeck and Little 1972). Oregon crab apple occurs as an early seral species occupying gaps within old-growth forests, as a component of estuarian and riparian complexes in major river valleys, and in upland Sitka spruce–red cedar swamps having locally perched water tables. In tidal marshes, it can form thickets as the dominant canopy species in association with grasses and forbs. It also occurs in the coastal fringe forest as scattered, slow-growing individuals on rocky shorelines and inland passages where it is protected from wind and salt spray. Oregon crab apple is somewhat tolerant of brackish water and short-term inundation.

In the upper mid-West of the United States, prairie and Great Lakes crab apples occur in open areas, on well-drained soils, near forest margins, in abandoned pastures, in oak savannahs, and at prairie margins (Kromm 1996; Little 1980; Yanny 1996). Common associates include shrubs of hawthorn (*Crataegus* spp.) and bur (*Quercus macrocarpa*) and black (*Q. velutina)* oaks. In southeastern Wisconsin, the native crab apples occur with greater frequency on clay and loam soils than on sandy soils. However, in contrast to Oregon crab apple, neither prairie or Great Lakes crab apples occur in wet areas (Kromm 1996).

In the southeastern United States, southern crab apple occurs at low altitudes on moist soils of valley bottoms and lower slopes. It is found in abandoned fields, along fence rows, and at forest margins, often forming dense thickets (Little 1980).

Native apples have served as a supply of food for both wildlife and humans. Indigenous peoples in both the eastern and western regions of North America have consumed crab apples (Pojar 1996; Vierdeck and Little 1972; Yarnell 1964). The occurrence of crab apples may be locally abundant in areas traditionally inhabited by indigenous peoples, but it is not known whether the trees were cultivated or grew from discarded fruit remains (Pojar 1996).

Consumption of fruit by birds and mammals is common. Known consumers include grouse (*Bonasa umbellus*), pheasant (*Phasianus colchicus*), rabbits (*Sylvilagus* spp.), squirrels *(Sciurus* spp.*)*, opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), skunks (*Conepattus* spp.) and foxes (*Vulpes vulpes*) (Little 1980). The abundance of crab apples along fencelines and riparian areas is thought to reflect dispersal by wildlife. However, the large fruit size and retention of the stem upon falling make transport by

Table 1— *Malus*, apple: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***Malus angustifolia* (Ait.) Michx.**	**southern crab apple,** narrow-leaf crab apple	SE US from Virginia to Florida & W to Mississippi
***Malus baccata* (L.) Borkh.** *Pyrus baccata* L.	**Siberian crab apple**	Asia; planted extensively in US
***M. coronaria* (L.) Mill.** *P. bracteata* Baily; *P. coronaria* L. *M. bracteata* (Baily) Rehd.	**American crab apple,** wild sweet crab apple, garland-tree	E US; New York to Alabama, W to E Indiana
***M. coronaria* var. *dasycalyx* Rehd.** *P. coronaria* var. *dasycalyx* (Rehd.) Fern. *P. coronaria* var. *lancifolia* (Rehd.) Fern. *P. lancifolia* (Rehd.) Baily *M. coronaria* var. *lancifolia* (Rehd.) C.F. Reed *M. lancifolia* Rehd.	**Great Lakes crab apple**	S Ontario to Ohio & Indiana
***M. floribunda* Sieb. ex Van Houtte** *M. pulcherrima* (Sieb.) Makino	**Japanese flowering crab apple**	Japan; planted extensively in E US
***M. fusca* (Raf.) Schneid.** *P. rivularis* Dougl. ex Hook. *P. fusca* Raf. *M. diversifolia* (Bong.) M. Roemer	**Oregon crab apple**, Pacific crab apple, western crab apple, wild crab apple	Pacific Coast region from N California to S Alaska
***M. glabrata* Rehd.**	**Biltmore crab apple**	SE US; North Carolina to Alabama
***M. glaucescens* Rehd.** *P. glaucescens* (Rehd.) Baily	**Dunbar crab apple**	E US; New York to North Carolina & W into Alabama
***M. ioensis* (Wood) Britt.** *P. ioensis* (Wood) Baily	**prairie crab apple**, Iowa crab apple, midwest crab apple	Minnesota & Wisconsin to Nebraska & Kansas & to Texas & Louisiana
***M. pumila* P. Mill.** *P. pumila* (P. Mill.) Borkh. *M. communis* Poir *M. domestica* (Borkh.) Borkh.	**common apple,** apple, paradise apple	Europe & W Asia; cultivated horticulturally and agriculturally in US
***M. x robusta* (Carr.)** Rehd. *M. baccata x (M. prunifolia* (Willd.) Borkh.	**red Siberian crab apple**	Asia
***M. sargentii* Rehd.**	**Sargent apple**	Japan
***M. sylvestris* P. Mill.** *P. malus* L. *M. malus* (L.) Britt.	**European crab apple,** apple	Europe & W Asia

Sources: Crossley (1974), Fiala (1994), Little (1980).

most species of frugivorous birds unlikely (Snow and Snow 1988). Observations suggest that deer may be the principal dispersal agent of crab apples in Europe (Snow and Snow 1988) and in southern Wisconsin (Kromm 1996).

Members of the apple genus have traditionally been some of our most important fruit bearers and ornamentals (table 1). Siberian crab apple has been used in shelterbelts. Larger stems of southern crab apple have been used to make tool handles. More recently, propagation of native crab apples has become increasingly important for habitat restoration (Callahan 1996) and apple cultivars have been considered for use in revegetation of minespoil (Brown and others 1983). Seedling propagation of native prairie crab apple as an ornamental is increasing in the mid-West as a means of avoiding the poorly adapted plants that can arise as sprouts from non-native rootstock following shoot girdling or browsing (Yanny 1996). Many cultivated varieties have been developed from the common or cultivated apple and from the Siberian crab apple, but these varieties are usually propagated vegetatively. Common apple and European crabapple are most often used as the rootstock for cultivars of crab apple (Fiala 1994).

Flowering and fruiting. The pink to white perfect flowers appear in the spring with or before the leaves. Flowering time varies among species from March to June (table 2). The fruit is a fleshy pome in which 3 to 5 carpels, usually 5, are embedded. Each carpel contains 2 seeds or 1 by abortion (figure 1) (Sargent 1965). Seeds have a thin lining of endosperm (figure 2), except in the cultivated, or common, apple, which has almost no endosperm (Martin 1946). Depending upon species, fruits ripen as early as August or as late as November (table 2). The fruits drop to the ground soon after ripening. Color of ripe fruit varies among the species (table 2).

Good crops of fruits and seeds generally occur every 2 to 4 years (Crossley 1974); however, good seed production

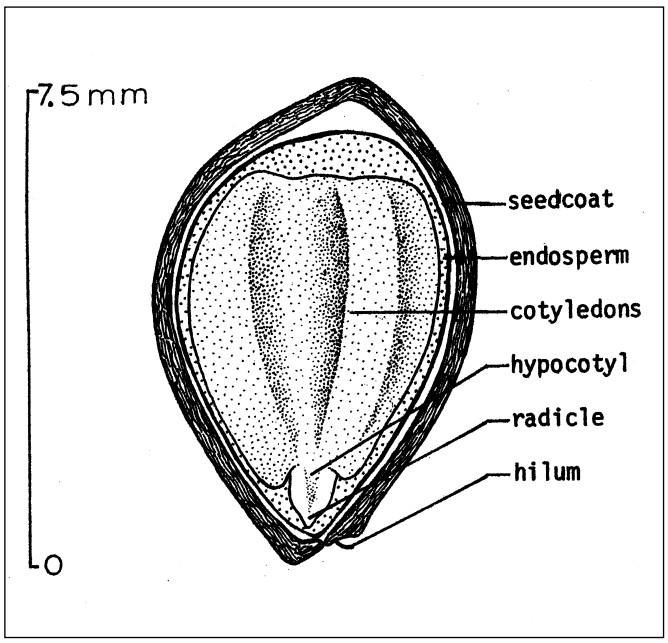
Table 2—*Malus,* apple: phenology of flowering and fruiting, color of ripe fruit, and height of mature trees

Species	Flowering	Fruit ripening	Color of ripe fruit	Height of mature trees (m)	Year first cultivated
M. baccata	May	Aug–Oct	Red or yellow	12.2	1784
M. coronaria	Mar–May	Sept–Nov	Yellow-green	9.2	1724
M. floribunda	May	—	Red or yellow	3.6–10.0	1862
M. fusca	—	Oct–Nov	Green-yellow to yellow & red	8–12.2	1836
M. ioensis	May–June	Sept–Oct	Greenish waxy	—	1885
M. pumila	May	Aug–Oct	Yellow to red	15.4	Ancient times
M. x robusta	Apr–May	—	Red or yellow-green	—	1815
M. sargentii	—	—	Red	1.8–2.5	—

Sources: Callahan (1996), Crossley (1974), Fiala (1994), Krüssmann (1960), Nielsen (1988), Rehder (1940), Sudworth (1908), Van Dersal (1938).

Figure 1—*Malus pumila*, common apple: seeds.

Figure 2—*Malus coronaria*, American crab apple: longitudinal section through a seed.



has been observed annually for select stands of prairie crab apple in Wisconsin (Kromm 1996) and for many crab apple cultivars (Fiala 1994). Seed production may be negatively affected by late-spring frosts. The severity of frost effect on seed production depends on the stage of fruit development at the time of frost. Late-flowering cultivars of apple are less susceptible to fruit damage by late frosts than early and medium flowering cultivars (Nybom 1992). Cultivars of apple exposed to freezing temperatures during the pink to early-bloom stages of fruit development demonstrated seed abortion and fruit pedicle damage, but they continued to produce a smaller, but economically significant fruitcrop (Simons and Doll 1976). A similar phenomenon has been observed in a wild stand of prairie crab apple, where a normal crop of crab apples were produced, yet the fruits bore no seeds (Kromm 1996).

Biennial bearing is a problem for commercial apple production (Williams 1989). Alternate-year fruit production arises from competitive effects of vegetative production, fruit development, and flowering. Trees bearing fruit with a large complement of seeds tend to initiate fewer flowers. Chemical methods, including the post-bloom application of thinning agents or growth regulators, have been used in manipulating fruit set and fruit quality (shape, firmness, russeting, and seed set) in commercial cultivars of apple (Greene 1989; Looney and others 1992; Williams 1989).

Collection of fruits; extraction and storage of seed. Ripe apples may be collected either by picking the fruits

from the tree or by gathering fallen fruits from the ground (Crossley 1974). In contrast to domesticated varieties of apples, crab apples may persist in good condition on the ground for 2 to 3 weeks. Fruits from wild trees need to be collected soon after they ripen, for wildlife may rapidly forage and deplete crops in the wild. Large amounts of seeds from domesticated apple cultivars may be extracted from cores obtained at food-processing plants (Richardson 1966). Seeds from cider mills, however, are often damaged (Crossley 1974) and may have a very low germinative capacity.

Accepted methods for seed extraction from the ripe fruits are cumbersome procedures involving combinations of after-ripening, mashing, and separation of pulp and seeds. After-ripening is the partial fermentation of the fruit. This can be done in a large container where the fruits are maintained at 10 to 18 °C for 2 to 4 weeks to soften (Callahan 1996; Nielson 1988). The softened fruits are then covered with water and mashed. The seeds may be sieved or left to settle out while the pulp is floated over the top with running water (Richardson 1966). Care should be taken to avoid high temperatures or excessive fermentation, as this may injure or kill the seeds (Heit 1967). Seeds may also be extracted by putting the fruits through a mechanical macerator (blender) with water, floating off the pulp, and then screening out the seeds (Nielson 1988). Mechanical macerators or presses must be used with caution, as the seedcoats of apple species are thin and easily damaged, resulting in loss of germinative capacity. Extraction may be enhanced by carefully slitting the endodermis of the fruit before mashing (Yanny 1996). Wisconsin native populations of prairie and Great Lakes apples yield 1 to 2 and 3 to 4 viable seeds per fruit, respectively (Kromm 1996). The numbers of seeds per weight of fruit for various species are listed in table 3.

Seeds extracted in the above fashion can be sown immediately. If there is a need for overwintering, the seeds can be air-dried at room temperature for 3 months and then placed in refrigerator in a 50:50 sand and peat mixture for an additional 3 months. As with seeds of commercial varieties of apple, seeds from native crab apples may germinate in cold storage, resulting in difficult sowing.

Apple seeds are orthodox in storage behavior; long-term storage of seeds can be accomplished by drying the seedlot to lower moisture contents. Seeds dried to a moisture content less than 11% have been stored in a sealed container at 2 to 10 °C for over 2 years without loss of germinative capacity or seedling vigor (Solovjeva and Kocjubinskaja 1955). Decline in seed viability as a function of storage temperature and seed moisture content has been modeled for cultivars of cultivated apple (Dickie and Bowyer 1985). They determined that seedlots dried to 14.5% moisture content (fresh-weight basis) and stored at 6 °C lose half their viability in 323 days. With further drying to 5%, the estimated storage life increases to 37 years at –5 °C storage temperature or 100 years at –18 °C storage temperature (Dickie 1986).

Germination. Apple seeds display dormancy which has been overcome by cold stratification (table 4). Stratification is achieved by placing the seeds in a moist medium and storing at a temperature of 2 to 5 °C. A minimum of about 30 days under stratification conditions is required to remove embryonic dormancy (Zhang and Lespinasse 1991). After stratification, apple seeds exposed to diurnally alternating day/night temperatures of 30/20 °C, germinated in 30 to 60 days (table 4). Germination is epigeal (figure 3).

The application of growth-regulating chemicals, including gibberellin A_3 (GA_3), ethephon (E), and benzylaminopurine (BAP), has been used to obtain germination from non-stratified seeds (AOSA 1965; Litvinenko 1959; Sinska 1989; Zhang and Lespinasse 1991). Chemical treatments often involve soaking excised embryos in growth regulator solutions for periods of 1 to 24 hours. Variations in the concentration of growth substance and duration of soaking have

Table 3—*Malus*, apple: seed yield data

Species	Seeds/fruit wt /100 kg	Seeds/fruit wt /100 lb	Cleaned seeds/fruit weight Range /kg	Range /lb	Average /kg	Average /lb	Samples
M. bacatta	1.2	2.5	10,850–42,000	22,000–85,000	30,000	66,000	5
M. coronaria	0.5	1	—	—	6,350	14,000	1
M. fusca	1.2	2.4	—	—	24,500	54,000	1
M. floribunda	—	—	—	—	26,800	59,000	—
M. ioensis	—	—	—	—	13,600	30,000	1
M. pumila	0.4	0.75	3,460–13,300	7,000–27,000	9,100	20,000	5+
M. x robusta	—	—	—	—	7,700	17,000	—

Sources: Crossley (1974), Swingle (1939).

significant impacts on both the percentage embryo germination and the quality of the resulting plants. Germination of nearly 100% of non-stratified embryos has been obtained with GA_3 applied at concentrations of 12.5 to 50.0 mg/liter for periods of 1 to 24 hours and with BAP applied at 12.5 to 100 mg/liter for periods of 6 to 24 hours. Such treatments have resulted in 50 to 60% germination in less than 10 days and nearly 100% germination in 30 days (Zhang and Lespinasse 1991). Some plants produced from treated embryos demonstrate reduced growth, abnormally thick stems, or poorly developed roots. The percentage of abnormal plants produced tends to increase with increasing growth regulator concentration or increasing period of soaking. Successful application of growth regulator treatments as a substitute for stratification requires careful attention to protocol and is beyond the needs of most propagators as germination percentages of 90% or greater are commonly achieved using the relatively simple cold stratification process.

Nursery practice. Seedlings for use in landscape restoration or as apple rootstocks are often grown from seeds in nurseries (Richardson 1966; Callahan 1996). Untreated seeds have been sown in late fall (Bakke and others 1926; Callahan 1996; Kromm 1996; Yanny 1996) and stratified seeds have been sown in the spring (Crossley 1974; Yanny 1996). In a Washington nursery, seeds are stratified by first soaking them in water for 5 to 7 days, then placing sacks of seeds between layers of ice in a sawdust pit for 6 to 8 weeks. Seeds are subsequently dried only enough to flow freely through a mechanical planter (Crossley 1974). Seeds are sown in rows 20 cm (8 in) wide and 106 cm (42 in) apart (Davis 1940), 1.25 to 2.5 cm ($^1/_2$ to 1 in) deep on loose friable soil. A thin sawdust mulch aids seedling emergence on soils that form a crust after watering. Seedlings may be sprayed weekly with a fungicide to control powdery mildew. By the end of the growing season most of the seedling stems should be pencil-thick and about 38 cm (15 in) high (Richardson 1966). A height of 23 cm (9 in) is regarded as minimum size for grafting (Davis 1940). Most commercial varieties are propagated by budding or grafting onto seedling rootstocks (Crossley 1974; Fiala 1994; Richardson 1966; Solovjeva and Kocjubinskaja 1955).

In Wisconsin, crab apples for landscape use have been produced from seeds sown in the fall at a density of 270/m^2 (5/ft^2) and covered with 2.5 cm (1 in) of sand. Apple seeds are among the first to germinate in the spring, often while

Figure 3—*Malus coronaria*, American crab apple: seedling development at 1, 3, 9, and 16 days after germination.

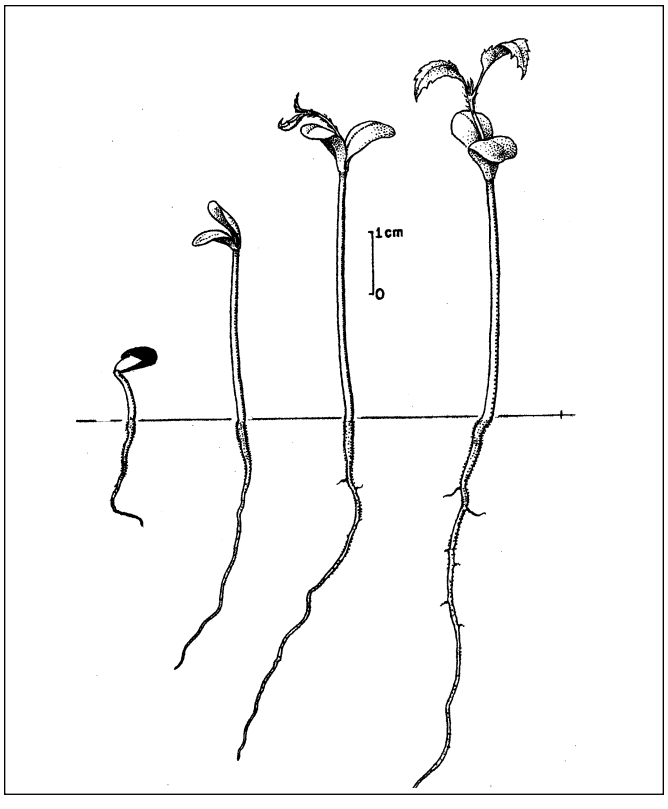


Table 4—*Malus*, apple: effects of cold stratification and germination test conditions on germination results

Species	Cold stratification (days)	Germination conditions: Temp (°C) Day	Germination conditions: Temp (°C) Night	Germination conditions: Days	Germinative energy %	Germinative energy days	Germinative capacity (%)	Samples
M. bacatta	30	30	20	30	48	8	54	2
M. coronaria	120	10	10	30	93	19	96	1
M. fusca	90	—	—	—	—	—	—	—
M. floribunda	60–120	—	—	—	—	—	—	—
M. ioensis†	60	30	20	10	48	4	58	1
M. pumila	60	30	20	60	—	—	65	1+
M. x robusta	60–120	—	—	—	—	—	—	—

Sources: Crossley (1974), Heit (1967), Kallio (1962).

* In a moist medium at temperatures of 2 to 5 °C.

† In another test, fresh seeds from slightly green fruit were sown in a nurserybed without pretreatment and germinated 100%.

soil temperatures are less than 4.5 °C, and the seedlings are generally hardy with respect to spring frost. Seedlings may be grown for 2 years without undercutting, reaching a size of 30 to 60 cm (1 to 2 ft) in height and a caliper of 1.25 cm ($^1/_2$ in) (Kromm 1996).

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M

Meliaceae—Mahogany family

Melia azedarach L.

chinaberry

Franklin T. Bonner

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Other common names. chinatree, bead tree, Indian lilac, pride-of-India, umbrella chinaberry, umbrella-tree, *paráiso*.

Growth habit, occurrence, and use. Chinaberry—*Melia azedarach* L.—is a short-lived deciduous tree, native to southern Asia and Australia, that has been cultivated and naturalized in tropical, subtropical, and warm temperate regions throughout the world. It has naturalized locally in the southeastern United States from Virginia and Oklahoma south to Florida and Texas. It can also be found in California, Hawaii, Puerto Rico, and Virgin Islands (Little 1979). The tree reaches a maximum height of 15 m in the United States, where it is planted as an ornamental, yet has some value for timber and wildlife food. In India the wood is used for furniture, agricultural implements, and the manufacture of writing and printing paper (Guha and Negi 1965). Extracts of the leaves and fruits have insecticidal properties (Al-Sharook and others 1991; Atwal and Pajni 1964), and the fruits are valuable livestock and game food. Birds and animals are common seed dispersal agents (Vines 1960).

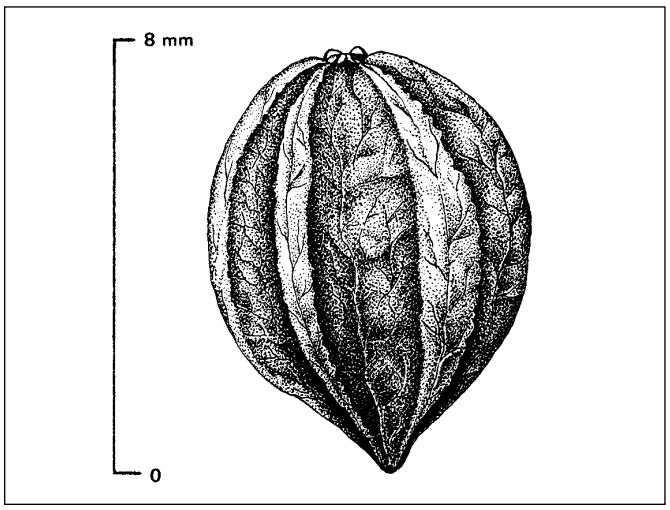
Flowering and fruiting. The flowering habit is either perfect or polygamo-dioecious (Nair 1959). The pretty, lilac-colored perfect flowers are borne in axillary panicles 10 to 15 cm long in March to May. The fruit is a subglobose, fleshy, round, drupe, 13 to 19 mm in diameter, that ripens in September and October and persists on the tree well into winter (Vines 1960). It turns yellow and wrinkled as it ripens (figure 1). Inside the fleshy mesocarp is a single, fluted, light brown or yellowish stone that contains 3 to 5 pointed, smooth, black seeds (figures 2 and 3). Abundant seed crops are borne almost annually.

Collection, extraction, and storage of seeds. Fruits can be collected by hand after the leaves have fallen in late autumn or early winter. Some seeds will germinate when the fruit coats are still green, but it is best to wait until they turn yellow for collection (Moncur and Gunn 1990). The pulp should be removed from the fruits before storage or planting. This can easily be done in mechanical macerators with water, with the pulp floated off or screened out (Amata-Archachai and Wasuwanich 1986). There are about 1,400 fruits/kg (640/lb) (7 samples). Chinaberry is an oily seed of the tropics and subtropics, yet several tests suggest that they are orthodox in storage behavior (Bonner and Grano 1974; Moncur and Gunn 1990). Under refrigerated, dry conditions fruits may be stored for at least a year without loss of viability. Additional research on storage of this species is needed.

Figure 1—*Melia azedarach* L., chinaberry: fruit and stone (**lower left**).

Germination tests. Pregermination treatments are not necessary (Bonner and Grano 1974), but germination is usually improved if the fruit pulp is removed (Moncur and Gunn 1990). In nature, the epigeous germination usually occurs during the spring following dispersal. One fruit may produce up to 4 seedlings. Suggested germination test conditions are 21 °C (night) to 30 °C (day) for 60 days with 200 seeds/test in sand flats. Fresh stones from southeastern Arkansas had a germinative capacity of 81% at 90 days in sand flats in a greenhouse; germination rate was 54% at 30 days (Bonner and Grano 1974). Seeds from tropical sources

Figure 2—*Melia azedarach* L., chinaberry: stone (**left**) and seeds (**right**).



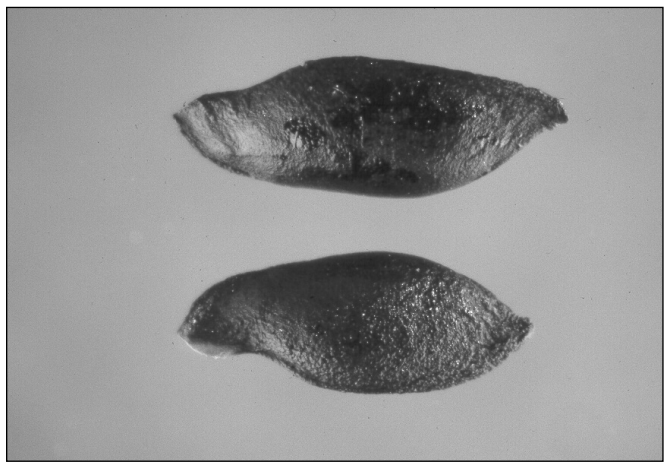
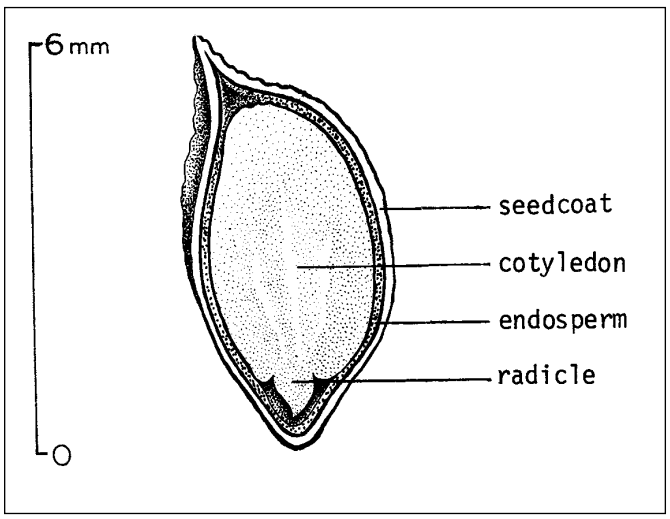


Figure 3—*Melia azedarach* L., chinaberry: longitudinal section through a seed.



seem to require higher temperatures for germination. Moncur and Gunn (1990) reported very little germination below a regime of 30 to 35 °C for Australian collections

Nursery practice. Stones are usually sown intact immediately after collection in the fall or in the following spring. They should be sown 5 to 7 cm (2 to 3 in) apart in drills and covered with about 2.5 cm (1 in) of soil. Germination takes place about 3 weeks after a spring sowing. As planting stock, 1-year-old seedlings are preferred. Older stock should be top-and-root pruned. Chinaberry may also be propagated from cuttings and root suckers and by direct seeding (Bonner and Grano 1974; Dirr and Heuser 1987).

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M

Menispermaceae—Moonseed family

Menispermum canadense L.

common moonseed

Kenneth A. Brinkman and H. M. Phipps*

Drs. Brinkman and Phipps retired from the USDA Forest Service's North Central Research Station

Growth habit, occurrence, and use. Common moonseed—*Menispermum canadense* L.—is a climbing woody vine growing to a height of 3.6 m (Rehder 1940) that is capable of spreading from underground stems (Wyman 1949). It is native from Quebec and western New England to southeastern Manitoba, south to Georgia, Alabama, and Oklahoma (Fernald 1950). The plants are seldom eaten by livestock (Van Dersal 1938), but the fruits are of value to wildlife, although reportedly poisonous to humans (Kingsbury 1964). This species has been cultivated since 1646 for its attractive foliage and fruit (Rehder 1940).

Flowering and fruiting. The dioecious flowers appear from May to July and the bluish-black drupes ripen from September to November (Grimm 1966; Redher 1940). The seeds are flattened stones in the form of a crescent or ring (figures 1 and 2).

Collection of fruits and seed extraction. Fruits may be collected from September to November (Rehder 1940). Seeds may be extracted by washing the macerated fruits in water. One sample showed 16,758 seeds/kg (7,600/lb) (Brinkman and Phipps 1974).

Germination. Stratification of one seedlot at 5 °C for 60 days resulted in 65% germination in 11 days and 98% in 26 days. An unstratified seedlot showed germination of 83% in 28 days and 92% in 60 days (Brinkman and Phipps 1974). Germination was tested in sand under light at alternating temperatures of 30 (day) and 20 °C (night).

Nursery practice. Common moonseed is propagated readily by seeds stratified and sown in the spring or planted as soon as ripe (Bailey 1935). Vegetative propagation also is possible from cuttings.

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*Note: Review of the literature by Jill R. Barbour, germination specialist at the USDA Forest Service's National Seed Laboratory, Dry Branch, Georgia, found no new information.

Figure 1—*Menispermum canadense* L., common moonseed: fruit (**top**) and seeds (**bottom**).

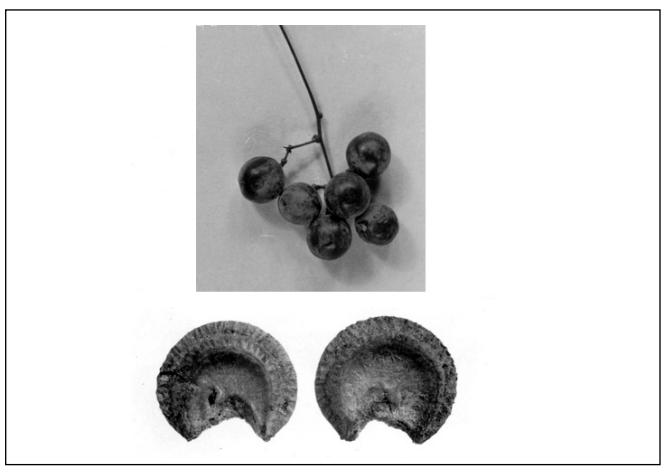
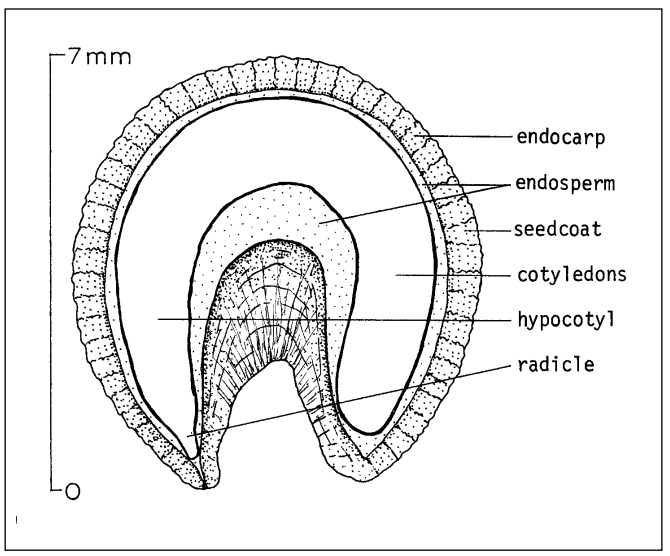


Figure 2—*Menispermum canadense* L., common moonseed: longitudinal section through a seed.



Oleaceae—Olive family

Menodora scabra Gray

rough menodora

Stanley L. Krugman and John C. Zasada

Dr. Krugman retired from the World Bank and the USDA Forest Service's Research and Development National Office, Washington, DC; Dr. Zasada retired from the USDA Forest Service's North Central Research Station

Growth habit, occurrence, and use. Rough menodora—*Menodora scabra* Gray—is a low herbaceous to woody shrub 0.2 to 0.8 m in height. It is native to dry rocky areas and desert grasslands from 462 to 2,155 m in southern California, Arizona, New Mexico, western Texas, Colorado, and Utah (Munz and Keck 1965; Vines 1960). It provides browse for livestock and game animals (Krugman 1974). Due to the type of habitat in which it is usually found, it should grow on strip-mined land (Sabo and others 1979). The genus *Menodora* is represented by 14 species in North America (Turner 1991). Rough menodora is recommended for use as a rock garden plant.

Flowering and fruiting; seed collection and storage. The yellow, often showy flowers of rough menodora appear from May through August (Krugman 1974; Vines 1960). The fruit, a bispherical thin-walled capsule with 2 seeds in each cell, ripens in September to November. Seeds are dispersed during October and November (Krugman 1974; Munz and Keck 1965; Vines 1960). Seeds should be collected from September to November (Krugman 1974). The mature seeds are about 4 to 5 mm in length and 3 mm wide, flat greenish to brownish with a yellowish narrow wing (figures 1 and 2) (Munz and Keck 1965; Vines 1960).

Good seedcrops of rough menodora usually occur annually (Krugman 1974). The number of cleaned seeds per weight in 2 samples was 224,000 and 246,000/kg (102,000 and 112,000/lb). Vines (1960) reported that purity of seedlots was 41% and soundness 98%. Storage in a dry place at room temperature has been satisfactory.

Germination. Sabo and others (1979) reported that germination occurred at alternating and constant temperatures between 14 to 40 °C. The best germination (about 80%) was under alternating temperature regimes of 24 °C for 8 hours and 17 °C for 16 hours and 17 °C for 8 hours and 24 °C for 16 hours. The mean day of germination varied from to about 6 to 10 days under these temperature regimes. Light was not required for germination. Percentage and rate of germination of showy menodora—*M. longiflora* Gray—a

Figure 1—*Menodora scabra*, rough menodora: seed.

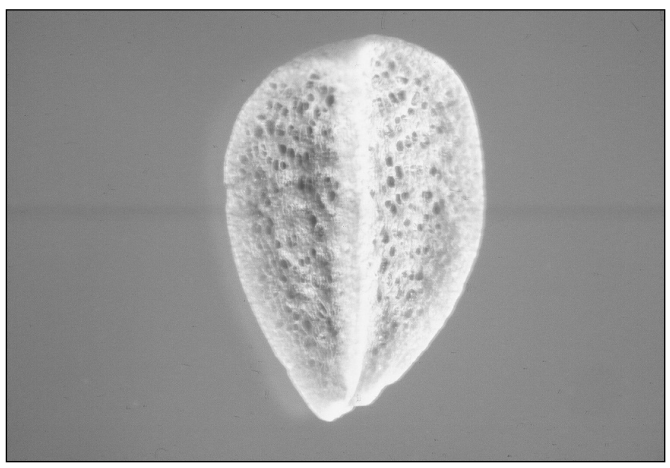
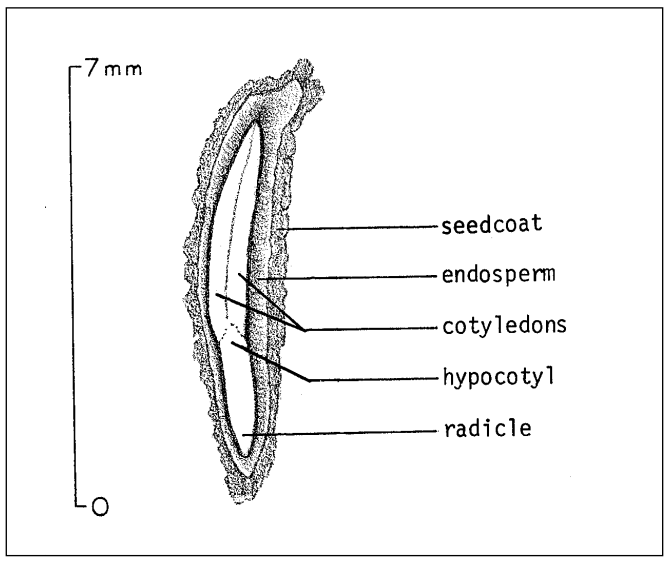


Figure 2—*Menodora scabra*, rough menodora: longitudinal section through a seed.



related sub-shrub, was improved by acid scarification. However, at a temperature regime of 30/20 °C, 60% of unscarified seeds germinated. Germination rate of scarified seeds increased with increasing temperature up to 30/20 ·°C but declined at warmer temperatures. Seeds of showy menodora germinated in the dark, but both germination rate and germination percentage were greater in a light regime with 12 hours light (Fulbright and Flenniken 1986).

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Taxodiaceae—Redwood family

Metasequoia glyptostroboides Hu & W.C. Cheng

dawn-redwood

John P. Sloan and LeRoy C. Johnson

Mr. Sloan is at the USDA Forest Service's Lucky Peak Nursery, Boise, Idaho; Mr. Johnson retired from the USDA Forest Service's Pacific Southwest Forest and Range Experiment Station

Growth habit, occurrence, and use. Dawn-redwood—*Metasequoia glyptostroboides* Hu & W.C. Cheng—is the only known living example of its genus (Hu and Cheng 1948). It is often called a "living fossil" because until 1946 it was known only from the fossil record (Hu 1948; Merrill 1945; Shao 1982). The natural range is quite restricted: a few trees are found near the village of Mo-tao-chi in eastern Szechuan Province and the bulk of the native groves are found in Shui-hsa-pa Valley (south of Mo-tao-chi) in the northwestern corner of Hupeh Province, People's Republic of China (Chu and Cooper 1950; Shao 1982). It has been introduced to many other parts of China, as well as the United States and Europe, for a total of 50 other countries (Shao 1982).

Since its introduction into the United States in 1948, this deciduous conifer has mostly been planted as an ornamental, especially at museums and in arboreta. The wood is soft, weak, and brittle, so it has little value as a source of lumber (Wyman 1968), although it is used for building timbers in China (Shao 1982). Pulping characteristics are similar to, and its fibers are stronger than, southern pines (Wyman 1968). In the United States, Wyman (1968) reported height growth was as much as 18 m in 20 years. In China, Shao (1982) described 4-year-old dawn-redwood trees averaging 7 m tall and 11 cm dbh. In its natural range, dawn-redwood grows in the submontane zone at elevations between 100 and 1500 m. The species is hardy in Massachusetts, where the winter temperatures may drop to -34 °C, and thrives in Placerville, California, where summer temperatures often exceed 35 °C and there is usually no summer rainfall (Johnson 1974).

Geographic races. Although great phenotypic diversity exists between planted trees, no geographic races are known to exist. Several cultivars have been described (Broekhuizen and Zwart 1967; DeVos 1963). Of the 6 trees growing at the USDA Forest Service's Institute of Forest Genetics at Placerville, California, half are of the normal single-stemmed conifer shape and the others are bush-shaped with no single branch showing dominance. Johnson (1974) speculates that some of the seeds may have come from self-pollinated trees. According to Shao (1982), dawn-redwood shows a strong apical dominance and produces a straight stem.

Flowering and fruiting. Dawn-redwood is monoecious. Trees that produce female cones begin to do so several years before trees of the same age produce male cones (Em 1972; Li 1957; Wyman 1968). Female trees do not begin to produce seeds until they are 25 to 30 years old and bear heavily until they are 40 to 60 years old, when production diminishes (Shao 1982).

Male cone buds form in leaf axis or on branch tips and become visible in the fall just prior to leaf drop. At this time, they are about 2.5 mm long. Female cones are borne singly, opposite along branches (rarely terminal). Male and female buds begin to grow in late January and are readily seen by early- or mid-February. Pollination takes place in March before the tree puts on needles (Hwa 1945, 1948). This early emergence of the cones makes them susceptible to late winter frosts, which can destroy the cone crop.

Male cone buds are 4 to 6 mm long when closed and 6 to 10 mm long when expanded and shedding pollen. Each staminate strobilus has 20 to 30 distichously arranged microsporophylls with 3 microsporangia per sporophyll. Pollen grains are wingless and covered with a sticky substance that causes them to clump together in masses (Johnson 1968). Female cones have 16 to 26 distichously arranged scales, with 5 to 8 seeds per scale. Mature cones are pendulous (with a 10- to 30-mm peduncle), subquadrangular, and shortly cylindrical; they ripen the same year they are pollinated. Cones ripen in early December and shed their seeds in late December and early January.

Collection, extraction, and storage. Mature cones are light brown, but color is not a good indication of ripeness. Cones should be collected late in the year just before they begin to open. Cones picked when they first turn from green to light brown do not open and the scales must be pried apart. But cones picked when the scales naturally begin to separate will readily open with 1 to 2 weeks of dry-

ing at room temperature. Tumbling is necessary because some seeds are firmly welded to the scales. Because seed wings are minute, de-winging is unnecessary (Johnson 1974).

Seedcoats of dawn-redwood are thin and fragile. Seeds with wings attached are light brown, 5 to 6 mm long, 2 to 4 mm wide, obovate (rarely orbicular-oblong), and notched at the apex (figure 1) (Johnson 1974; Nakai and Furuno 1974). Wings are adnate and appear as tegumentary extensions of the seed (Sterling 1949). Average weight per seed is 8 mg (0.0003 oz) (Nakai and Furuno 1974). Nakai and Furuno (1974) found an average of 70 to 90 seeds per cone, with a range of 50 to 110. One kilogram of cones contains 430,00 to 560,000 seeds (1 lb contains 195,000 to 254,000 seeds) (Shao 1982). Dawn-redwood often produces a high proportion of hollow seeds (CDF 1977). Presumably, seeds can be stored in the same manner as those of other genera in Taxodiaceae such as redwood (*Sequoia*) and arborvitae (*Thuja*). Storage of dry seeds in airtight containers at 1 to 4 °C has been satisfactory for these genera (Johnson 1974).

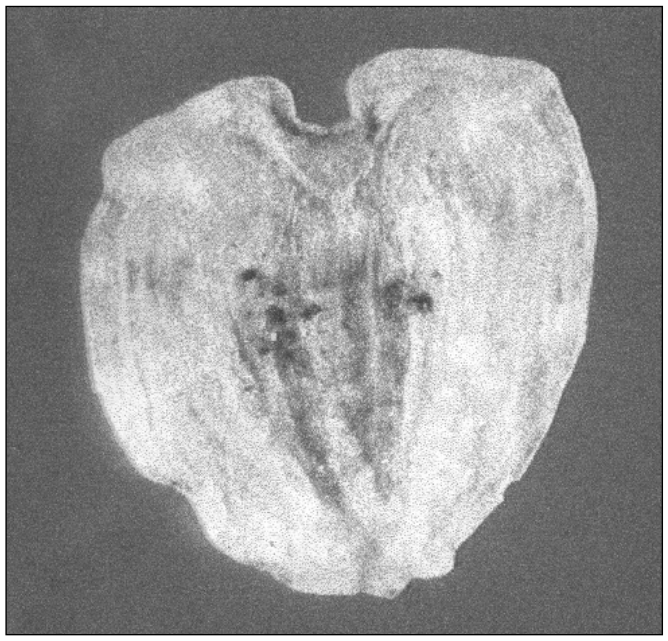
Mechanical separation of seeds is not recommended. Hollow (figure 1) and filled seeds can be identified with x-radiography, but a simpler and more efficient method is to use a light table. The seeds should be scattered 1-layer thick on a light table and then back-lit with the room lights off. The hollow seeds can be picked out with tweezers. However, this method is feasible only on a small scale. If large quantities of seeds become available, all seeds should be stored and then sown, making allowances for seed-fill when the seeding rate is calculating (Johnson 1974).

Germination and nursery practice. Seeds of dawn-redwood do not require chilling (Johnson 1968; Shao 1982; Smith 1950). Germination takes 4 to 8 days (Nakai and Furuno 1974) and is epigeal. After germination, the seedcoat sheds in 3 to 5 days, exposing the cotyledons (Johnson 1974). There are no official testing prescriptions for this species.

Seeds sown directly on soil and mulched with fine sand or Sponge Rok® begin germinating within 5 days (Johnson 1968). During the first 5 weeks of growth, the tender succulent seedlings are particularly susceptible to damping-off (Johnson 1974; Shao 1982). Losses can be minimized by sowing on heat-sterilized or fumigated soil. Young seedlings thrive in high humidity like that found in a greenhouse equipped with automatic overhead sprinklers. In hot climates the young seedlings should be shaded during the first growing season (Johnson 1974).

Because seeds of dawn-redwood are scarce, the species is often propagated from cuttings. Although cuttings are very easy to root (Johnson 1968; Mirov and Blankensop 1955; Shao 1982), growing stock can be produced faster from seeds than from cuttings (Johnson 1974). Cuttings root best when they are taken in early summer through late fall. Rooting is promoted by treatment with 50 ppm of α-naphthalene acetic acid (NAA). Rooting capability of cuttings decreases with increasing age of the mother plant (Shao 1982).

Figure 1—*Metasequoia glyptostroboides*, dawn-redwood: filled seed.



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M

Rubiaceae—Madder family

Mitchella repens L.

partridgeberry

Kenneth A. Brinkman, G. G. Erdmann, and Jill R. Barbour

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Growth habit, occurrence, and use. Partridgeberry—*Mitchella repens* L., also called two-eyed berry or running-fox—is an evergreen vine or herb with fruit valuable as food for birds, raccoons (*Procyon lotor*), and red foxes (*Vulpes vulpes*) (Van Dersal 1938). The natural range is from Texas to Florida, north to southwest Newfoundland, and west to Ontario and Minnesota (Fernald 1950). This attractive plant was introduced into cultivation in 1761 and is often used in rock gardens (Rehder 1940).

Flowering and fruiting. The distylous flowers appear from June to August and can be separated into 2 genetic compatibility groups (Rehder 1940). Plants with short-styled flowers ("thrums") have exserted stamens 15 mm above the ovary and stigmas 10 mm above the ovary; whereas plants with long-styled flowers ("pins") have stamens 11 mm above the ovary and exserted stigmas 16 mm above the ovary (Ganders 1975). The only pollinations that are compatible are those between anthers and stigmas of the same height, that is, between pin and thrum and thrum and pin. The genetic control is by a single gene (S), with thrums the heterozygotes (Ss) and pins the recessive homozygotes (ss) (Allard 1960). Thrums contribute more than three-quarters of all genes transmitted through ovules, and pins more than three-quarters of all genes transmitted through pollen (Hicks and others 1985). Pins and thrums contribute almost equally to gene flow via pollen and ovules.

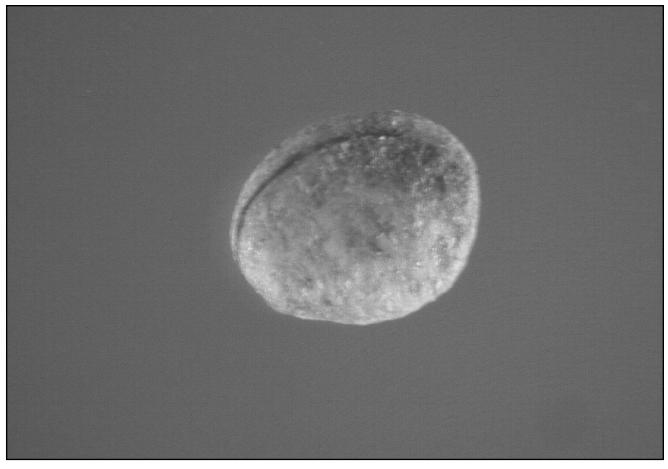
The flowers occur in pairs on a short peduncle with the base of the calyces fused. Each flower has 1 style and 4 stamens (Fernald 1950). Fruit-set occurs when both flowers of a pair have been pollinated. Bumble bees (*Bombus* spp.) are the principal pollinators of partridgeberry. They fly around a patch of partridgeberry for a mean of 2.3 ± 2.3 minutes, visiting 34 ± 43 inflorescences per minute (Hicks and others 1985).

Fruits are scarlet drupaceous berries 7 to 10 mm wide that ripen in July but usually persist overwinter (Petrides 1958). The maximum number of seeds that a single full berry may contain is 8 (Hicks and others 1985). The level of natural fruit-set is near 100% for both pins and thrums. In a flowering study in North Carolina, the overall fruit-set level for pins and thrums was 100%, whereas in New York, the fruit-set was 96.1% for pins and 86.5% for thrums (Hicks and others 1985). A Massachusetts study revealed fruit-set values of 96.8% for pins and 96.3% for thrums (Keegan and others 1979).

Collection of fruits; extraction and storage of seeds. Partridgeberry fruits may be picked in late fall. Fruits should be macerated in water and screened to remove the seeds (figures 1 and 2). About 45 kg (100 lb) of fruit yield about 5.4 kg (12 lb) of cleaned seeds (Swingle 1939). Two samples averaged 427,770 seeds/kg (194,000/lb); 98% of the seeds were sound after cleaning (Brinkman and Erdmann 1974; Swingle 1939). Seeds are orthodox in storage behavior and can be stored for some time in sealed containers at low temperature.

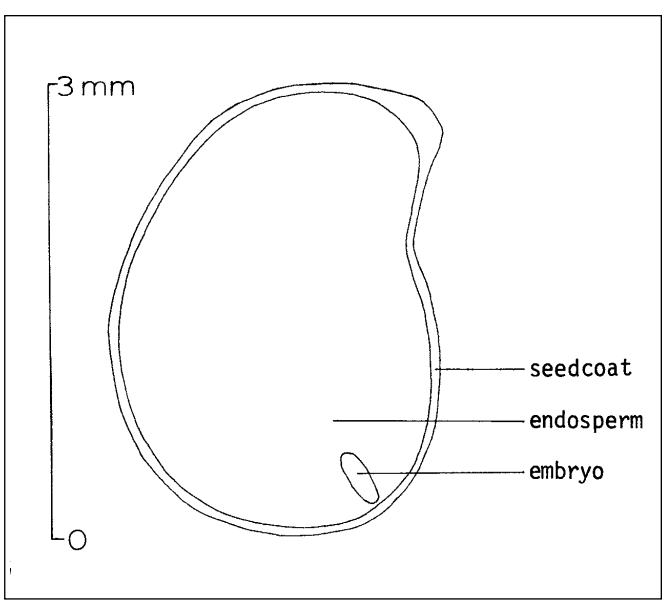
Germination tests. Partridgeberry seeds have internal dormancy, but this can be overcome by 150 to 180 days of stratification at 5 °C (Barton and Crocker 1945). No data are available on results of germination tests.

Figure 1—*Mitchella repens*, partridgeberry: seed.



Nursery practice. Seeds of many other species exhibiting embryo dormancy germinate satisfactorily when sown in the fall, so partridgeberry probably can be handled in the same way. Mulching overwinter should reduce drastic temperature changes and maintain adequate moisture.

Figure 2—*Mitchella repens*, partridgeberry: longitudinal section through a seed.



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M

Moraceae—Mulberry family

Morus L.

mulberry

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Growth habit, occurrence, and use. The mulberry genus—*Morus*—comprises about 12 species of deciduous trees and shrubs native to temperate and subtropical regions of Asia, Europe, and North America (Rehder 1956). Seeds of 2 native species and 2 naturalized species are described here (table 1). White (sometimes called "Russian") mulberry was introduced to the United States by Mennonites from Russia in 1875. The United States Prairie States Forestry Project planted an average of over 1 million trees of this species annually from 1937 through 1942 for windbreaks in the Great Plains from Nebraska to northern Texas (Read and Barnes 1974). The high drought resistance of white mulberry makes it well suited for shelterbelt planting (Read and Barnes 1974).

There are 2 mulberries indigenous to North America. Littleleaf mulberry occurs in Arizona, New Mexico, Oklahoma, Texas, and Mexico and has not been cultivated (table 1). Red mulberry has a wide range that covers most of the eastern United States, Great Lakes region, and the southern Great Plains. Though once common, red mulberry is decreasing over its range, possibly because of an unidentified bacterial disease (Moore and Thomas 1977). Its place is being taken by the introduced and naturalized white mulberry (Core 1974).

White mulberry is highly prized in Asia for its leaves, which are eaten by the silkworm—*Bombyx mori* L. The 7 or more forms and varieties of white mulberry differ in their relative drought resistance and in chromosome number and may be climatic races. Both white and red mulberry are diploids (2n=2x=28), but black mulberry has a high polyploidy level (2n=22x=308) (Ottman 1987).

Mulberries are valuable as food for birds and animals. Up to 18 bird species have been recorded eating the fruit in northeastern Kansas, with catbirds (*Dumetella carolinensis*) and robins (*Turdus migratorius*) consuming the most fruit (Stapanian 1982). Opossums (*Didelphis virginiana*), raccoons (*Procyon lotor*), fox squirrels (*Sciurus niger*), and eastern gray squirrels (*S. carolinensis*) eat the fruit in appreciable amounts, and cottontail rabbits (*Sylvilagus floridanus*) feed on the bark in winter (Core 1974).

All the mulberry species have white sap that contains latex (Hora 1981). The heartwood is durable, making it

Table 1—*Morus*, mulberry: nomenclature and occurrence

Scientific name & synonyms	Common name(s)	Occurrence
***M. alba* L.** *M. alba* var. *tatarica* (L.) Ser.	**white mulberry,** Russian mulberry, silkworm mulberry	China; naturalized in Europe & North America
***M. microphylla* Buckl.**	**littleleaf mulberry,** Texas mulberry, mountain mulberry	Arizona, New Mexico, Oklahoma, Texas, & Mexico
***M. nigra* L.**	**black mulberry,** Persian mulberry	Iran; widely cultivated in Europe
***M. rubra* L.**	**red mulberry**	Vermont & Massachusetts to New York, extreme S Ontario, Michigan, & Wisconsin, SE Minnesota, SE Nebraska, central Kansas, W Oklahoma, central Texas, E to S Florida

Sources: Core (1974), Read and Barnes (1974), Wasson (2001).

usable for fenceposts. Other specialty products include farm implements, cooperage, furniture, interior finish, and caskets (Burns and Honkala 1990).

Flowering and fruiting. Mulberry plants are normally dioecious, but they can also be monoecious on different branches of the same plant. The pendulous pistillate (female) and staminate (male) catkins are arranged on spikes and appear in April and May (Rehder 1956). The pistillate catkins in white mulberry are 0.5 to 2 cm long and staminate catkins are 2.5 to 4 cm long (FNAEC 1997; Radford and others 1968). The pistillate catkins in red mulberry are 1 to 3 cm long and the staminate catkins are 3 to 5 cm long (Radford and others 1968).

The green, female flowers have 4 sepals, 1 pistil that is 2-parted at the top, and a 2-locular ovary positioned above the floral organs. The ovary is about 2 mm long (Radford 1968). The style in white mulberry is red-brown and 0.5 to 1 mm long; the styles in red and littleleaf mulberries are whitish and about 1.5 mm long (FNAEC 1997). All mulberries have hairy stigmas. On the average, 44% of the pistillate inflorescences are parthenocarpic, with seedless fruits being somewhat smaller than seeded fruits (Griggs and Iwakiri 1973). Some varieties—such as Illinois everbearing mulberry, a cross between red and white mulberries—do not produce seeds (Reich 1992).

The male flowers are green tinged with red and have 4 sepals and 4 stamens; the filiform filaments vary from 2.7 mm in white mulberry to 3 to 3.5 mm in red mulberry (FNAEC 1997). The anthers open longitudinally (Fernald 1970). The sepals are pubescent and vary from 1.5 mm long in white mulberry to 2 to 2.5 mm in red mulberry (FNAEC 1997).

According to Griggs and Iwakiri (1973), the mulberry ovary is similar to that of other fleshy drupaceous fruits both morphologically and in growth pattern; therefore, the seed should be classified as a drupelet rather than an achene or nutlet. In the development of the mulberry fruit, the calyx adheres to the ovary and becomes an accessory part of the drupelet.

The multiple fruit is composed of many small, closely appressed drupelets (figure 1). Cultivated fruits are about 2 cm long, but fruits from native-grown trees are usually less than 1 cm long and have a cylindrical shape (Hora 1981). White mulberry fruits measure 1.5 to 2.5 x 1 cm, littleleaf mulberry fruits, 1 to 1.5 cm long, and red mulberry fruits, 1.5 to 6 x 1 cm (FNAEC 1997).

Red mulberry bears on the average 50 multiple fruits per branch and yields about 8.6 fruits/g or 8,600 fruits/kg (3,900 fruits/lb) (Burns and Honkala 1990; Griggs and Iwakiri 1973; Halls 1973). Mature trees can produce about 3.7 hl (10 bu) of fruit (Reich 1992). Open-grown trees produce up to about 7 times the amount of fruits per plant than do trees growing in the understory (Halls 1973).

Figure 1—*Morus*, mulberry: fruit and leaves of *M. alba*, white mulberry (**left**) and *M. rubra*, red mulberry (**right**).

Each fruit contains a dozen or more small drupelets (figures 2 and 3) that have thin, membranous coats and endocarps (stones) (Griggs and Iwakiri 1973). White mulberry yields about 10.7 to 32.0 drupelets per fruit, whereas red mulberry yields 10.7 to 30.0 drupelets per fruit (Stapanian 1982). Red mulberry seeds ("stones") are 2.8 mm long and 1.8 mm wide, white mulberry seeds are 2 to 3 mm long, and littleleaf mulberry seeds are about 2 mm long (FNAEC 1997). Red and littleleaf mulberry seeds are yellowish, whereas white mulberry seeds are light brown. Seed yield is up to 22 g/tree for open-grown plants and up to 3 g/tree for understory plants (Halls 1973). Seed embryos are curved, with cotyledon tips nearly touching the radicle (figure 3).

Fruits ripen and drop from the trees during the months of June to August (table 2), though they are often dispersed by birds and animals. Fruiting season can be extended by applying plenty of water during the summer months (Reich 1992). Varieties differ in size and color of ripe fruit (figure 1 and table 3) and vary in taste from insipid to sweet. The fruits stain everything they touch, so that planting mulberries along patios, sidewalks, driveways, and parking lots is NOT recommended (Reich 1992). Large fruit crops appear nearly every year on white mulberry in the Great Plains (Read and Barnes 1974) (table 3). Seed bearing begins at about 5 years of age for white mulberry, 2 years for open-grown red mulberry, and 4 years for red mulberry in the understory (table 3) (Halls 1973). In forest stands, optimum

Figure 2—*Morus alba*, white mulberry: longitudinal section through a seed.

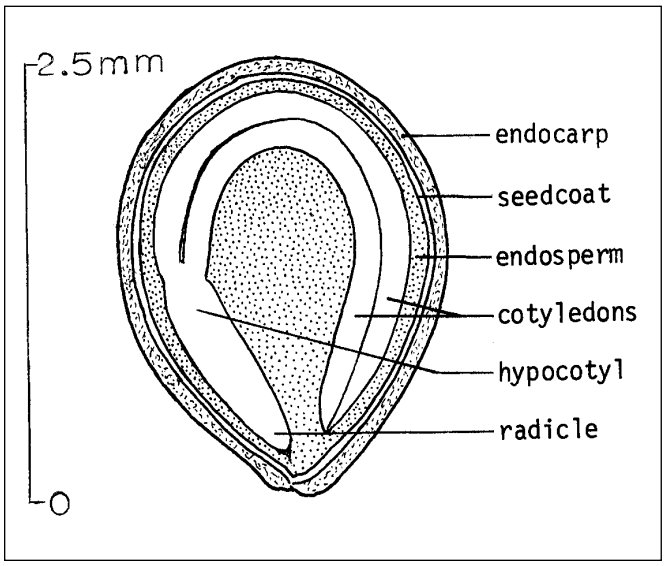
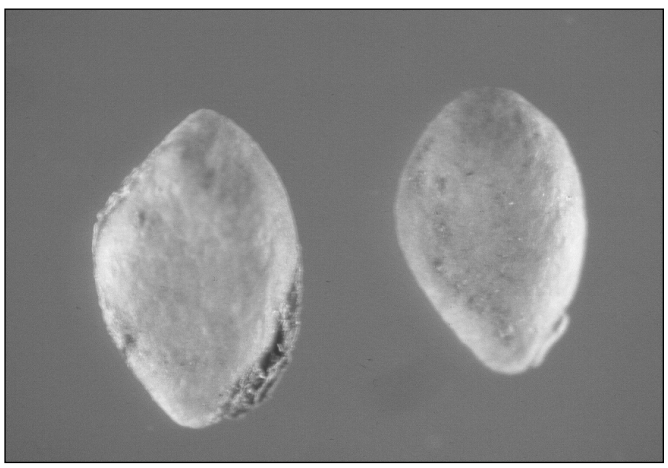


Figure 3—*Morus rubra*, red mulberry: cleaned seeds.



seed-bearing age is 30 to 85 years; the maximum being 125 years (Lamson 1990).

Collection of fruits. Before the fruits are collected, fruits from every tree should be sampled and checked, because mulberry fruits can develop without seeds. Ripe mulberry fruits may be collected by stripping, shaking, flailing, or waiting for them to fall from the tree onto a ground cloth. Fruits should be collected as soon as most are ripe to avoid loss to birds and animals. Seedlots of red mulberry fruits collected 4 to 5 days after falling yielded 89% germination, whereas seeds from fruits collected 1 to 2 weeks after falling reduced germination to 73% (Huffman 1996). Soaking red mulberry seeds in water for 48 and 72 hours reduced germination to 56 and 33%, respectively, making it advisable to not soak seeds for more than 24 hours (Huffman 1996). Seedlots from white mulberry fruits collected in early July that were cleaned and sown immediately showed 75% germination (Dirr and Heuser 1987). Fresh fruits, placed in tubs, can be stored in a cooler at 3 to 5 °C for up to 2 weeks without harming the seeds. Forty-five kilograms (100 lb) of fresh fruit of either species yields from 0.9 to 1.4 kg (2 to 3 lb) of clean seeds (Read and Barnes 1974) (table 4).

Extraction and storage of seeds. Fresh fruits are usually soaked in water and run through a macerator, where pulp and empty seeds are skimmed or floated off. If the fruits are not sufficiently ripe, soaking them in water for 24 hours will aid in the maceration. Fermentation at moderate indoor temperatures for 1 to 2 days before maceration facilitates extraction and improves viability of white mulberry seeds (Taylor 1941). A more efficient method is to spread the fruits on a clean floor, allow them to soften at room temperature for 4 to 5 days and then run them through a seed macerator with the water adjusted so that only the pulp goes through (the plate should be adjusted to 4 mm) (Engstrom

Table 2—*Morus*, mulberrry: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
M. alba	E US	May	July–Aug
	Nebraska	May	June–Aug
	Oklahoma	Apr	Late May–June
M. microphylla	SW US	Apr–May	June–Aug
M. rubra	E US	Apr–May	June–Aug

Sources: Engstrom (1969), FNAEC (1997), Little and Delisle (1962), Read and Barnes (1974), Rehder (1956).

Table 3—*Morus,* mulberry: height, seed-bearing age, seedcrop frequency, and fruit ripeness criteria

	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yr)	Years between large crops	Fruit ripeness criteria	
					Preripe color	Ripe color
M. alba	3–14	1700s	5	—	White	White, pinkish, or purplish
M. microphylla	7.5	—	—	—	Dark green	Red, purple, or black
M. nigra	10	1548	—	Yearly	Greenish red	Purple to black
M. rubra	12	1629	10	2–3	—	Dark red, dark purple to black

Sources: Little and Delisle (1962), Read and Barnes (1974), Rehder (1956), Sargent (1940), Small (1933).

1969). The now-clean seeds remain. Small samples may be cleaned by rubbing the fruits gently through a 2.4-mm (#6) round-hole screen and floating off the pulp (Read and Barnes 1974). A 1% lye solution can be used to remove any sticky pulp left on the seeds after maceration.

Cleaned seeds should be spread to air-dry in the shade, then cleaned by fanning before storage or use. Lightweight trash and seeds can be removed with a gravity table (Myatt and others 1991). Subfreezing temperatures of –23 to –18 °C are recommended for storage of dry mulberry seeds (Engstrom 1969). Numbers of seeds per weight are listed in table 4.

Pregermination treatments. Germination of untreated seeds in the laboratory may vary greatly because part of each collection may consist of seeds with dormant embryos and impermeable seedcoats (Read and Barnes 1974). Engstrom (1969) found that some seeds that had no pretreatment—but were extracted from fruits that were fermented before the seeds were extracted—did germinate completely under light at low night and high day temperatures. Fresh seeds sown in the fall are usually not pretreated (Lamson 1990). For spring-sowing, stratification in moist sand at 0.6 to 5 °C for 30 to 120 days has improved germination (Afanasiev 1942; Core 1974; Lamson 1990; Read and Barnes 1974; Taylor 1941).

Germination tests. The International Seed Testing Association (ISTA 1999) recommends testing mulberry seeds on top of moist blotters for 28 days at diurnally alternating temperatures of 30 °C (day) for 8 hours and 20 °C (night) for 16 hours. No pretreatment is stipulated in the rules. Germination is epigeal. Red mulberry requires light to germinate under laboratory conditions (Dirr and Heuser 1987). Germination values of red mulberry seedlots obtained from official laboratory tests vary greatly. The germination after 30 days of cold moist stratification was 88% with 95% full seeds; germination after 60 days of cold moist stratification was 1 to 66% and after 90 days it was 3 to 68% (USDA FS 2002).

Tests on pretreated seeds run on wet absorbent paper, wet sand, and mixtures of sand and peat at the same temperature regime for 15 to 45 days with a daily light period of 8 to 16 hours resulted in germination ranging from 20 to 92% (Heit 1968; Read and Barnes 1974; Taylor 1941). In a laboratory study of seeds planted in sand, red mulberry seeds exhibited very high seedling emergence at 25 °C under moderate moisture conditions (4 to 20%) but did not germinate at 5 or 10 °C (Burton and Bazzaz 1991). Seedling emergence was calculated as 75% of the final emerging seedlings divided by the number of days required to achieve 75% emergence (Burton and Bazzaz 1991).

Nursery practice. In fall or spring, properly pretreated mulberry seeds mixed with sand may be broadcast or sown in drills. Rows can be drilled 20 to 30 cm (8 to 12 in) apart, with 164 seeds/m (50/ft) of row, and barely covered with soil. In Oklahoma, white mulberry is sown with 65 to 82 viable seeds/m (20 to 25/ft) in a 7.5- to 10-cm (3- to 4-in) band to produce 33 usable seedlings/m (10/ft) (Engstrom 1969). One Nebraska nursery uses a seedling density of 197 to 262/m of drill (60 to 80/ft) (Korves 1969). Freshly harvested and processed white mulberry seeds have been successfully hand-sown in July at 312 seeds/m^2 (29 seeds/ft^2), lightly raked, rolled, and then covered with straw mulch: germination occurred 2 weeks later (Peaslee 2002).

Beds should be mulched with straw, leaves, or burlap and kept moist until germination begins. Beds should be half-shaded for a few weeks after germination, which usually begins 1 to 2 weeks after spring-sowing (Dirr and Heuser 1987). Twelve to 50% of the seeds of white mulberry should produce usable seedlings. One-year-old seedling stock is used for field planting; seedlings should be dug about 25 cm (10 in) deep with a very sharp blade—main roots are rather stout and tough (Engstrom 1969).

Bacterial canker can be serious threat to white mulberry seedlings in the southern Great Plains; however, treatment of soil with formaldehyde solution before seeding has provided

Table 4—*Morus*, mulberry: seed yield data

Species	Seeds (x1,000)/weight				Samples
	Range		Average		
	/kg	/lb	/kg	/lb	
M. alba	286–770	130–350	517	235	18+
M. rubra	440–1,100	200–500	792	360	4

Sources: Engstrom and Stoeckler (1941), Read and Barnes (1974), Swingle (1939).

adequate control. Mulberry seedbeds should not be located near older mulberry trees (Davis and others 1942). Damping-off may occasionally be a problem, but losses are usually minimal, probably due to nursery cultural methods presently used (Wright 1944). Fungal leaf-spot caused by *Cercospora* spp. and *Mycosphaerella mori* (Fuckel.) E.A. Wolf, as well as bacterial leaf-spot caused by *Pseudomonas mori* (Boy. & Lamb.) Stev. may cause damage.

Mulberries are easy to root from summer softwoods; June and July are optimum months (Dirr and Heuser 1987). When mid-July cuttings were treated with 8,000 ppm IBA in talc and stuck into sand, 100% rooted in 3 weeks (Dirr and Heuser 1987).

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Myricaceae—Bayberry family

Myrica L. *and Morella* Lour.

bayberry

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Synonyms and common names. Considerable disagreement exists regarding taxonomy of the Myricaceae, particularly the number and classification of genera within the family. Inclusion of the genera *Myrica* and *Comptonia* L'Hér. ex Aiton in the Myricaceae appears to be universal (Bornstein 1997; Kartesz 1994; Radford and others 1968; Small 1933; Weakley 2000; Wilbur 1994). However, species within the genus *Myrica* and its division into 2 separate genera are still being debated (Bornstein 1997; Weakley 2000; Wilbur 1994). If the Myricaceae are divided into 3 genera, sweet gale *(M. gale* L.*)* and Sierra sweet-bay *(M. hartwegii* S. Wats.*)* are the only species that remain in the genus *Myrica* (Weakley 2000; Wilbur 1994). The other species formerly in the genus *Myrica* are grouped under a third genus which, depending on the authority, is either *Morella* Lour. (Weakley 2000; Wilbur 1994) or *Cerothamnus* Tidestrom (Small 1933). Radford and others (1968) also divide *Myrica* into 2 genera. However, in their view, sweet gale is removed from *Myrica* and placed in the genus *Gale* Adanson.

The newly standardized plant nomenclature of USDA (the PLANTS database of the National Resources Conservation Service), which is being followed in this publication, places the former *Myrica* species into 2 genera—*Myrica* and *Morella*. Both genera are included in this chapter on *Myrica* because the *Morella* nomenclature is not widely known (table 1). The reader should be aware that further division of *Myrica* is possible in the future and the above cited references should be consulted for more information.

Occurrence, growth habit, and uses. Bayberries—both *Myrica* and *Morella*—include about 35 to 50 species of

Table 1—*Morella* and *Myrica,* bayberry and wax-myrtle: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***Morella californica* (Cham. & Schlecht.) Wilbur** *Myrica californica* Cham. & Schlecht.	**California wax-myrtle,** California bayberry, Pacific bayberry	Pacific Coast from Washington to California
***Morella cerifera* (L.) Small** *Myrica cerifera* L. *Myrica pusilla* Raf. *Cerothamnus ceriferus* (L.) Small *C. pumilus* (Michx.) Small *Morella pumila* (Michx.) Small	**southern wax-myrtle,** southern bayberry waxberry, candleberry	New Jersey to S Florida, W to Texas & N to Arkansas (swampy or sandy soils with low pH)
***Morella faya* (Ait.) Wilbur** *Myrica faya* Ait.	**candleberry-myrtle**	Canary Islands, Madeira, & Portugal
***Morella pensylvanica* (Mirbel) Kartesz** *Myrica pensylvanica* *Cerothamnus pensylvanica* (Mirbel) Moldenke *M. caroliniensis* auct. non Mill.	**northern bayberry** bayberry, candleberry	Alaska to Newfoundland, S to Pennsylvania, W to Wisconsin, Washington, & Oregon; isolated areas of Tennessee & North Carolina (swampy soils) Coastal plain from Newfoundland & Nova Scotia S to North Carolina
***Myrica gale* L.** *Gale palustris* Chev. *Myrica palustris* Lam.	**sweet gale,** bog-myrtle, meadow-fern	

deciduous or evergreen shrubs and trees (Bornstein 1997; Huxley 1992; LHBH 1976). Six are native to North America; of these only California wax-myrtle, southern wax-myrtle, sweet gale, and northern bayberry are of any horticultural significance. Another species—candleberry-myrtle, which is native to the Canary and Madeira Islands—was introduced into Hawaii and has achieved considerable ecological impact (Walker 1990).

The evergreen California wax-myrtle and southern wax-myrtle can be maintained as shrubs or allowed to grow to 10.5 m in height, whereas candleberry-myrtle, also evergreen, matures at a shorter height of 7.5 m. The deciduous sweet gale and the deciduous or semi-evergreen, multi-stemmed northern bayberry are species that attain heights of 1.5 and 2.7 m, respectively (LHBH 1976).

Species of bayberry have both ecological and landscape significance. Their ability to associate with symbiotic nitrogen-fixing bacteria—*Frankia* Brunchorst spp.—makes them well adapted for land-reclamation efforts. California wax-myrtle, candleberry-myrtle, and northern bayberry have been used for this purpose, as they establish and grow well in near-sterile soils (Everett 1981; Walker 1990). Candleberry-myrtle performs so well under these conditions that it is now considered a noxious weed in Hawaii, becoming a co-dominant species in areas of the Hawaii Volcanoes National Park (Walker 1990). Southern wax-myrtle and northern bayberry are well suited to coastal marine environments because they will tolerate soils high in salt that may be saturated with water or prone to drought (Bir 1992). Both species are extremely versatile and can be used as shrubs or trained to grow as attractive multi-stemmed small trees.

Bayberries are valued also for their ornamental attributes. California wax myrtle has lustrous dark green foliage and attractive purple fruits (Everett 1981). The foliage of southern wax-myrtle and northern bayberry is pleasantly aromatic when crushed. Birds are attracted to the wax-covered fruits of these species, and the wax is used to scent candles and soaps (Fordham 1983). Medicinal properties as well as ornamental characteristics were the rationale for introducing candleberry-myrtle into Hawaii (Walker 1990). Sweet gale also has been used for medicinal purposes, as well as flavoring beer in Europe (Everett 1981).

Geographic races and hybrids. Individual plants of southern wax-myrtle, which inhabit dry, sandy soils, tend to be more rhizomatous and ultimately attain a smaller size with smaller morphological characteristics than individuals growing in fertile soils (Bornstein 1997). These plants are commonly referred to as *Morella cerifera* var. *pumila* Michx. (*M. pusilla* Raf.) and are usually < 1 m in height; they occur on dry, sandy pinelands and prairies from Texas to North Carolina and Florida (Elias 1971). However, it is uncertain if these differences are genetic or environmentally influenced, and therefore assignment of varietal status is uncertain (Bornstein 1997). Leaf pubescence of sweet gale can be quite variable and is reflected in 2 varieties—*M. gale* var. *subglabra* (Chev.) Fern. and *M. gale* var. *tomentosa* C. DC. (Elias 1971; Kartesz 1994). Other authors, however, do not recognize these as valid varieties (Bornstein 1997). Few selections of particular species have been reported in the literature. However, one—*Morella cerifera* 'Emperor'—is distinguished by elongated, deeply serrate leaves (Brackin 1991).

Flowering and fruiting. Flowers of bayberries are small and inconspicuous. Time of flowering is variable, depending on the species (table 2). Male inflorescences consist of catkins usually < 2 cm long; female inflorescences are ovoid and sessile up to 1 cm in length (Huxley 1992). Fordham (1983) reported that southern wax-myrtle, sweet gale, and northern bayberry are all dioecious. However, there are reports of monoecious forms of sweet gale. Even more interesting is the phenomenon that individual plants of sweet gale have been observed altering their sex from year to year (Everett 1981). Plants of California wax-myrtle are monoecious (Krochmal 1974). Fruit maturation generally occurs in late summer to fall (table 2). Fruits are small spherical drupes usually covered with a wax coating (figures 1 and 2) that ranges in color from gray-green to purple (Huxley 1992). Fruits of sweet gale, however, are surrounded by 2 wing-like bracts and form a catkin by clustering around a central axis (Fordham 1983).

Figure 1—*Morella cerifera*, southern wax-myrtle: wax-coated drupe (**left**) and cleaned drupe (**right**).

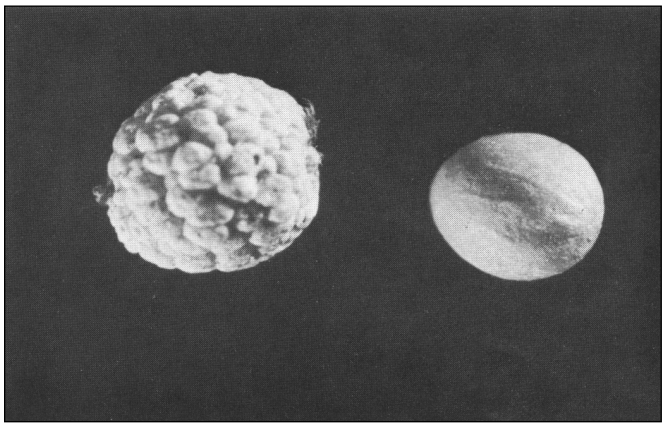
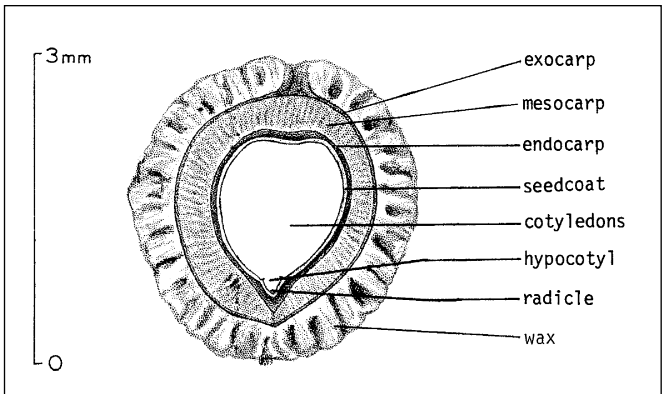


Table 2—*Morella* and *Myrica,* bayberry and wax-myrtle: flowering and fruiting characteristics

Species	Flowering	Fruit ripening	Color of ripe fruit	Diam of ripe fruit (mm)	Cleaned seeds/wt /kg	Cleaned seeds/wt /lb
Morella californica	May–June	Sept	Brownish purple with grayish white wax	6	48,000	22,000
Morella cerifera	Mar-June	Aug–Oct	Light green with pale blue wax	3	185,000	84,000
Morella faya	Variable	Aug–Nov	Red to purple	5	—	—
Myrica pensylvanica	Apr–July	Sept–Oct	Covered with grayish white wax	4	121,000	55,000
Myrica gale	Mar–Apr	Oct	Lustrous & dotted with resin	3	—	—

Sources: Fordham (1983), Huxley (1992), Krochmal (1974), Krüssmann (1984), Schwintzer and Ostrofsky (1989), Walker (1990).

Figure 2—*Morella cerifera*, southern wax-myrtle: longitudinal section of a drupe.



Collection of fruits, seed extraction and cleaning. Ripe drupes can be harvested by stripping branches by hand or shaking them from the branches onto ground sheets. After harvest, they should be handled as seeds (Krochmal 1974). Therefore, seed extraction and cleaning are often unnecessary except as mentioned below.

Seed storage. Fordham (1983) suggested that drupes should be stored intact to avoid desiccation of their seeds; drupes of northern bayberry stored in this manner remained viable for 9 months at room temperature (Krochmal 1974). Most evidence, however, suggests that bayberry seeds are orthodox and should be dried to low moisture contents and stored at low temperatures. Dirr and Heuser (1987) recommend that wax be removed before long-term (10 to 15 years) dry storage at 1 to 3 °C. Seeds of sweet gale air-dried at room temperature for 28 days following collection and stored dry at 5 °C remained viable for 6 years (Schwintzer and Ostrofsky 1989). Optimum moisture contents for storage of bayberry seeds are not known, but similar seeds of other orthodox species store well at 6 to 10% moisture.

Pregermination treatments and germination tests. All species of bayberry discussed herein require pregermination treatments for optimum germination. Those species with wax-covered drupes require that the wax be removed. This can be accomplished by abrasion with a screen or with a warm water soak (Fordham 1983). Following wax removal, stratification (moist-prechilling) for approximately 90 days at 5 °C is necessary to overcome dormancy. However, stratification is ineffective if wax remains (Fordham 1983). Fruits of sweet gale, which lack a wax coating, will germinate in low percentages without stratification. However, best germination occurs following 6 weeks stratification at 5 °C (Schwintzer and Ostrofsky 1989). Seeds of candleberry-myrtle also germinate without any pregermination treatments. However, a fleshy mesocarp and stony endocarp are inhibitory to germination. Removal of the mesocarp and scarification of the endocarp will significantly increase germination (Walker 1990).

Fordham (1983) investigated seed germination of southern wax-myrtle. Seeds were subjected to 4 treatments: no stratification with no wax removal; stratification at 5 °C for 90 days with no wax removal; no stratification with wax removal; and stratification with wax removal. Germination for the first 3 treatments was very poor (6, 17, and 6%, respectively), whereas that for the fourth treatment was significant (data not available).

Schwintzer and Ostrofsky (1989) conducted an extensive study on seed germination of sweet gale. Among factors investigated were the effects of stratification, light, and gibberellic acid (GA) treatment. Some germination (38%) was noted with no stratification or GA treatment. However, stratification for 3, 6, or 12 weeks at 5 °C significantly increased germination with the highest (66%) occurring following 6 weeks of stratification. Without stratification, GA treatment at 500 ppm (0.05%) stimulated germination (48%).

However, germination was reduced when GA was used in combination with stratification. Seeds did not germinate in the dark. Germination was about 12% when seeds were exposed to light for a single 16-hour photoperiod (80 μmol/m²/sec) and then placed in darkness for 28 days. Maximum germination (about 35%) occurred following exposure to 4 such photoperiods.

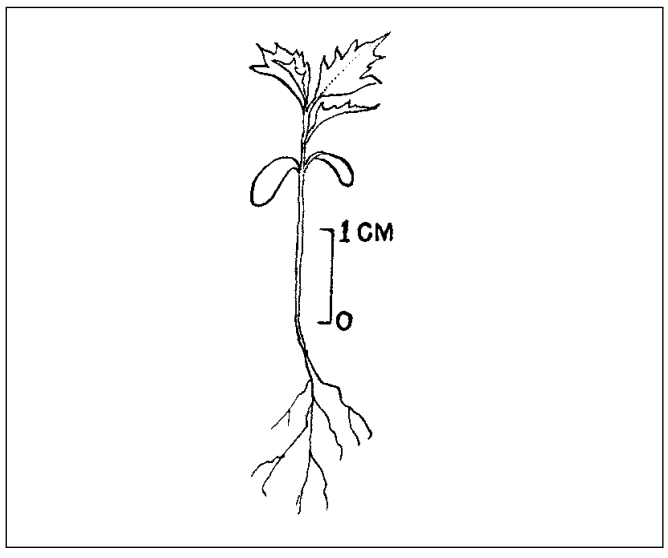
Hamilton and Carpenter (1977) investigated effects of scarification, stratification, and exogenous growth regulator treatment on seed germination of northern bayberry. After their wax was removed, seeds were either scarified with coarse sandpaper or not. Seeds were then soaked in 0, 100 (0.01%), 500 (0.05%), or 900 ppm (0.09%) GA_3 or 6-furfurylamino purine (kinetin) at 0, 25 (0.0025%), or 100 ppm (0.01%) for 24 hours at 22 °C. Following scarification and growth regulator treatments, seeds were sown in flats containing a 1:1 peat/perlite (v/v) medium. Then, flats were placed in sealed polyethylene bags for stratification at 5 °C for 0, 15, or 30 days. After stratification, flats were removed from the bags and placed in a greenhouse at 25 °C for germination periods of 20, 40, 60, or 80 days. Kinetin had no effect on germination unless seeds were scarified and stratified for 30 days. When seeds were scarified and stratified, germination after 80 days was 4, 20, and 28% for seeds treated with 0, 25, or 100 ppm kinetin. Highest germination of scarified seeds followed by stratification for 0 or 15 days was 4 and 8%, respectively. GA_3 proved more effective in promoting germination. Germination after 80 days for scarified seeds was 8, 25, 69, and 65% for seeds treated with 0, 100, 500, or 900 ppm GA_3, respectively. Reducing the length of stratification significantly decreased germination. Germination of nonscarified seeds was similar to scarified seeds following 0 or 15 days of stratification. However, germination was enhanced provided seeds were scarified followed by stratification for 30 days.

Walker (1990) studied the effects of various environmental factors on germination of candleberry-myrtle. He found that storage periods >10 weeks at 20 °C significantly reduced germination. He also noted that germination of seeds collected after passage through the digestive tract of birds (normal method of dissemination) did not differ significantly in comparison to seeds collected directly from trees. Irrigating seeds with water steeped with litter of native woody species and candleberry-myrtle (leachate), densely shading seeds (>55% shade), and covering sown seeds with 0.5 cm of medium all reduced germination. Germination was promoted by removal of the fleshy mesocarp.

Nursery practice and seedling care. For field production, seeds can be sown in fall or spring. Fall-sowing should be sufficiently late to avoid germination before winter, and seedbeds should be mulched. Spring-sowing should follow a period of stratification at 5 °C for 90 days (Krochmal 1974). If container production is desired, seeds may be sown indoors in early spring, and the seedlings repotted before moving outdoors for further growth. Germination is epigeal (figure 3) (Young and Young 1992).

Asexual propagation has been successful to varying degrees depending on species. Blazich and Bonaminino (1984) reported that terminal stem cuttings of southern wax-myrtle, in a transitional growth stage between softwood and semi-hardwood, rooted in high percentages. Cuttings treated with solutions of indolebutyric acid (IBA) at 0, 1,000 (0.1%), 2,000 (0.2%), or 4,000 ppm (0.4%) resulted in rooting of 87, 97, 87, and 90%, respectively. Cutting propagation of northern bayberry is more challenging. However, softwood cuttings can be rooted successfully when treated with a solution of 5,000 ppm (0.5%) IBA (Dirr and Heuser 1987). Most bayberry species produce root suckers and can be propagated by division as well as by root cuttings (Dirr and Heuser 1987).

Figure 3—*Morella californica*, California wax-myrtle: 1-month-old seedling.



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N

Hydrophyllaceae—Waterleaf family

Nama lobbii Gray
woolly nama

Eamor C. Nord and Andrew T. Leiser

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Other common names. Lobb fiddleleaf.

Growth habit, occurrence, and use. There are 2 perennial species in this genus, both low-growing, suffruticose plants native to California, Nevada, and Utah. Only the sub-shrub woolly nama—*Nama lobbii* Gray—has potential for revegetation use, as it can provide a rather persistent, dense groundcover. The other species—Rothrock fiddleleaf, *N. rothrockii* Gray—furnishes only a sparse cover that dies back to the roots each year.

Woolly nama is native to the Sierra Nevada and Cascade ranges in east central and northern California, and western Nevada at elevations of 1,220 to 2,100 m within ponderosa (*Pinus ponderosa* Dougl. ex Laws.) or Jeffrey (*P. jeffreyi* Grev. & Balf.) pine and California red fir (*Abies magnifica* A. Murr.) forests. It occurs in sunny, exposed locations with slightly to moderately acid soils derived mostly from volcanic mud flows and decomposed granites. Plants 15 to 60 cm tall are generally sparse and widely scattered (McDonald and Oliver 1984). However, where the tree or associated shrub overstory is removed, such as by logging or other mechanical means, woolly nama spreads rapidly to form dense crowns up to 1.5 m in diameter on individual plants (McDonald and Fiddler 1995). Fast-growing roots that extend up to 5 m or more in a single year contain a profusion of adventitious buds that sprout to form new plants.

Woolly nama has many characteristics that make it desirable for revegetation on adapted sites. The low growth habit helps reduce fire hazards in brush-cleared areas, and its abundant, aggressive sprouting habit together with dense foliage provides good groundcover. It is known to offer strong competition and thus reduce growth of young conifers within plantations (McDonald and Oliver 1984). Although it is not regarded as a serious weed pest in areas where it occurs naturally, care should be exercised to prevent introduction and possible spread of this plant into cultivated croplands, mainly because of its aggressive rooting habits, which enable the plant to withstand cultivation.

Flowering and fruiting. The numerous small purple flowers are borne in reduced terminal cymes or in axillary angles along slightly erect stems; they appear from May to September. The fruit is a capsule containing 10 to 12 oval, angular, very dark brown seeds up to 1.5 mm long (figures 1 and 2). The capsules mature in late August, September, and October. In a test of a cleaned seedlot, seeds measured 1 to 1.3 mm in diameter; 85% of the seeds in the lot were filled and there were about 2,000 seeds/g (56,875/oz).

Collection, extraction, and storage. Mature seeds may be hand-stripped or flailed directly into containers, or seed heads together with some foliage may be harvested mechanically during late September and thereafter until snow covers the ground. One means is to use a rotary lawnmower equipped with a collection bag and set at maximum height that clips and gathers the material, which is later dried and threshed. The seeds may be extracted by threshers or hammermills, and cleaned with aspirators or air-screen cleaners. A collection made in the Tahoe basin, using this type of equipment, yielded over 1.8 kg (4 lb) of clean seeds from about 59 kg (130 lb) of dry clippings (Nord and Leiser 1974). Only half of the total number of seeds was released from capsules during clipping and drying, and the remaining seeds had to be extracted and separated by a hammermill and South Dakota Seed Blower. No precise data are available on longevity of woolly nama seeds, but they are presumed to be orthodox in storage behavior and should remain

Figure 1—*Nama lobbii*, woolly nama: seed.

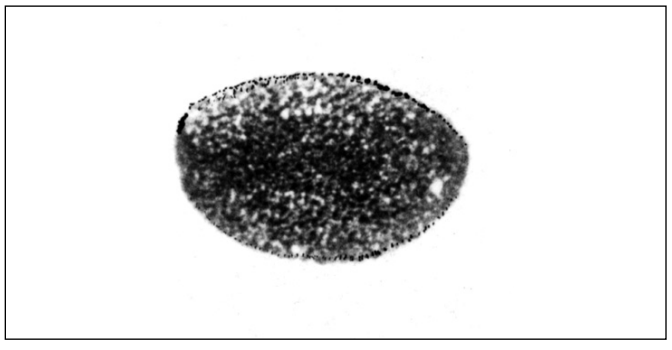
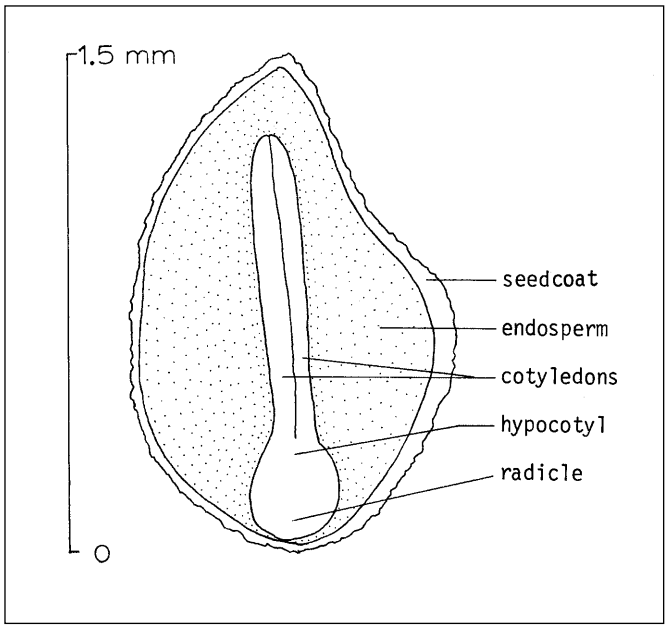


Figure 2—*Nama lobbii*, woolly nama: longitudinal section through a seed.



viable for a number of years when stored dry at low temperatures.

Germination. Woolly nama seeds exhibit what apparently is seedcoat dormancy. Stratification has no effect, but when the seedcoats are removed, up to 60% of the seeds will germinate. The dormancy may be due to a chemical that is found in the seedcoat. Extracts of the colored leachate obtained from seeds kept under intermittent mist contained an anionic polyphenol that may inhibit germination (Nord and Leiser 1974). Leaching woolly nama seeds for 3 days under intermittent mist for 3 seconds at 2-minute intervals, followed by soaking in 200 ppm gibberellic acid, yielded 39% germination. Other treatments in which gibberellic acid was used yielded as much as 30% total germination, but sulfuric acid, thiourea, hydrogen peroxide, and hot water treatments were not effective in improving germination. In laboratory tests , the first observed germination was at 12 days and germination continued intermittently thereafter throughout a 4-month period (Nord and Leiser 1974).

Because of the very low and slow germination, it is most unlikely that woolly nama can establish itself satisfactorily from direct field seeding unless seeds are treated in some manner to break dormancy. This appears to be the case even in native stands, where seedling plants are rarely found; presumably most natural establishment or spread of this species comes from root segments transported during some form of soil disturbance.

Nursery and field practice. The best method known to prepare the seeds for sowing calls for leaching the seeds under intermittent mist or running water for 2 to 3 days, soaking in gibberellic acid that is constantly agitated, and air-drying thoroughly. The seeds should not be rinsed or washed. Soaking for 2 hours in 200 ppm or stronger gibberellic acid solution is suggested if seeds are to be sown within a few days after treatment. If seeding is to be delayed for more than about 10 days and soil moisture conditions are unpredictable, stronger solutions and longer soak times (probably up to 500 ppm for periods up to 24 hours) should be used to reduce risks of leaching should rains occur before seeds germinate. Seeding should be done in the late fall or very early spring to take advantage of the most favorable moisture conditions for germination and seedling establishment. Seeds may be sown separately or mixed with rice hulls as a diluent and carrier at a depth of about 12 mm ($^1/_2$ in) on properly prepared, firm seedbeds where competing vegetation has been previously removed.

The plant makes its best development on medium-textured, well-drained soils that are neutral to moderately acid in reaction. The plants are susceptible to gopher damage to the roots in southern California, but they appear to be immune from damage to the foliage by animals, including rabbits, which often damage or destroy many other shrub or herbaceous species.

Rooting either stem cuttings or root sections of woolly nama has not been too successful. In several trials, only 30% of stem cuttings rooted, and none survived when transplanted into pots. Root cuttings failed to regenerate new plants, although some fresh shoots became green and grew slightly (Nord and Goodin 1970).

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Berberidaceae—Barberry family

Nandina domestica Thunb.

nandina

Laura G. Jull and Frank A. Blazich

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Other common names. heavenly-bamboo, sacred-bamboo, *nanten*.

Occurrence, growth habit, and uses. *Nandina* is a monotypic genus indigenous from India to central China (Huxley and others 1992; Krüssmann 1985; Ohwi 1984). It was introduced into Japan from China before the sixteenth century (Coats 1992). The species is a broadleaf evergreen, upright, flat-topped shrub reaching a height of 1.5 to 2.4 m with a spread of 1.0 to 1.5 m that can spread by root suckers into large colonies (Dirr 1990; Whitcomb 1996). Plants are characterized by numerous, unbranched stems with horizontal branches. However, with age, they tend to become leggy and open, unless pruned properly (Flint 1997). The species is hardy to USDA Zone 6 (Dirr 1990) and will remain evergreen in USDA Zones 7–8. It becomes deciduous when exposed to colder temperatures (Gibson 1982).

In Japan, nandina is called *nanten*,"sacred-bamboo," as fruiting twigs are sold in winter to decorate altars, both in temples and private homes (Coats 1992; Krüssmann 1985; Richards and Kaneko 1988). There, nandina is planted close to the entrances of homes because the plant is used to comfort family members who have bad dreams. The wood is aromatic and very close grained; it is considered by the Japanese to be flavorful and suitable for toothpicks (Coats 1992). The plant is reputed to have medicinal properties effective in treatment of various ailments (Ikuta 1994).

Nandina is cultivated commonly in the United States because of several desirable landscape attributes. The new, finely dissected leaves are bronze to red, becoming blue-green with age, and turning a dull purple to bright red in winter (Flint 1997). Flowers occur in large panicles held above the foliage and are followed in the fall by showy, bright red berries produced in clusters that persist throughout the winter. The stems give the appearance of bamboo (Flint 1997). Plants are adaptable to many different soils; they tolerate sun, shade, and drought; and they are pest free (Dirr 1990; Whitcomb 1996).

Geographic races and hybrids. Nandina has been in cultivation for centuries. China and Japan are considered as sources of dwarf selections. Cultivars with fern-like foliage, distorted branchlets, and white, yellow, or crimson fruits occur in the nursery trade (Dirr 1990).

Flowering and fruiting. Nandina will flower and produce fruit in heavy shade to full sun (Dirr 1990). Plants fail to set fruit if planted singly, so it is best to plant groupings of several plants to ensure cross pollination (Gibson 1982). Inflorescences are erect, terminal, 20- to 38-cm-long white panicles that appear from May to June. Individual flowers are perfect, 6 to 13 mm across, and pinkish in bud, opening to white with yellow anthers. The fruits are globular, bright red berries that are 8 mm in diameter with 2 seeds; they ripen in the fall and persist through the winter (Dirr 1990).

Collection of fruits, seed extraction, and cleaning. Fruits should be harvested when mature in the fall. Removal of the fleshy pulp is recommended and is accomplished easily by maceration (Dirr and Heuser 1987; Gibson 1982). After fruits are soaked in water for 24 hours and macerated, the seeds (figures 1 & 2) can be separated from the fleshy pulp (Newman 1991).

Seed storage. Due to the presence of a rudimentary embryo, seeds should be stored under slightly moist conditions at 4 °C, then sown in late spring or summer to obtain uniform and rapid germination (Dehgan 1984; Hartmann and others 1997). Seeds held in cold storage for 9 to 10 months germinate as well as those sown immediately after seed extraction and do so without appreciable loss in viability (Afanasiev 1943; Dirr and Heuser 1987).

Pregermination treatments. Seeds exhibit delayed germination due to a rudimentary embryo and slow rate of embryo development (Dirr and Heuser 1987). The rudimentary embryo is formed after flowering in August and September and during fruit enlargement in winter. However, further development is arrested during spring and summer months (Afanasiev 1943), although embryo maturation can

Figure 1—*Nandina domestica*, nandina: seeds.

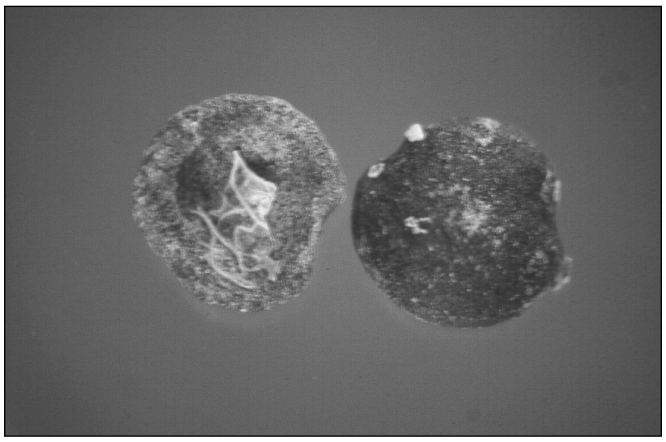
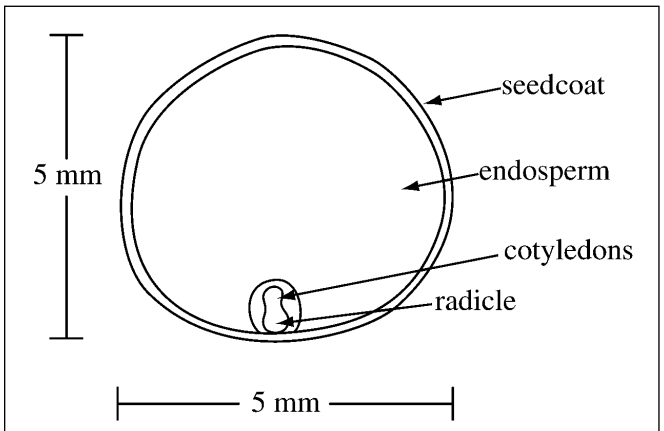


Figure 2—*Nandina domestica*, nanadina: longitudinal section of a seed.



occur during cold storage (Hartmann and others 1997). Embryo development also can occur regardless of whether seeds are stored at high or low temperatures or in moist or dry environments (Dirr and Heuser 1987).

Seeds of nandina have a tendency to germinate only during late fall or early winter, regardless of the sowing date (Afanasiev 1943; Hartmann and others 1997). Attempts to overcome this response—by cold stratification, treatment with various chemical compounds, increased oxygen pressure during germination, or varying the time of planting—have all been unsuccessful (Afanasiev 1943). Afanasiev concluded that cold stratification neither hastened embryo development nor improved germination. To speed embryo development, Dirr and Heuser (1987) recommend warm stratification of seeds for several months, followed by cold stratification for several months. In contrast, Hartmann and others (1997) reported that cold stratification was not necessary for seed germination.

Dehgan (1984) further investigated seed germination of nandina. Seeds were placed under dry or moist conditions at 4 or 30 °C for 0, 6, or 12 weeks. Another group of seeds was first treated with 1,000 ppm (0.1%) gibberellic acid (GA_3) for 24 or 48 hours followed by cold stratification at 4 °C or warm stratification at 30 °C for 0, 6 or 12 weeks. Results demonstrated that cold stratified seeds sown in a greenhouse in February had the greatest germination (78%) with the shortest germination time (3 weeks). Seeds that were cold-stratified for 12 weeks germinated more rapidly and uniformly compared to those stratified for 6 weeks. Neither GA_3 treatment nor warm stratification (30 °C) resulted in greater germination than nontreated seeds. Alternating periods of cold–warm, warm–cold, or warm stratification alone had little effect on increasing germination.

Germination tests. At present, optimum conditions for seed germination of nandina have not been defined. Two years are required for germination if seeds are sown in the fall (Dirr 1990). Dirr and Heuser (1987) reported 65% germination of seeds sown immediately following collection. However, time of actual germination was not reported.

Nursery practice. Although seeds can be germinated, commercial propagation of nandina is typically accomplished by vegetative means. If sexual propagation is desired, nandina seeds should be sown 6 mm ($^1/_4$ in) deep in a moist, sterile medium at 21 °C. The medium needs to be covered with polyethylene film and the container placed in bright light. Germination tends to be slow and generally occurs in about 60 days (Gibson 1982; Hartmann and others 1997). Seedlings tend to be relatively uniform (Whitcomb 1996).

Stem cuttings can be rooted anytime of year (except during the spring flush) with success rates of 80 to 90% (Barr 1987; Hartmann and others 1997). Auxin treatment of cuttings is beneficial (Barr 1987; Dirr and Heuser 1987). However, rooting tends to be slow (Bean 1976). Once stems have hardened, which is indicated by a reddening of the foliage, they become more difficult to root (Dirr and Heuser 1987; Gwaltney 1983). In addition, division of side shoots and removal of suckers that appear at the bases of plants have been successful, especially on dwarf cultivars (Dirr and Heuser 1987; Gwaltney 1983; Hartmann and others 1997). This is best accomplished in spring before growth begins.

Micropropagation protocols for nandina are currently being used commercially (Briggs and McCulloch 1983; Dirr 1990). *In vitro* techniques have been used to eliminate viruses from nandina (Smith 1983).

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Aquifoliaceae—Holly family

Nemopanthus mucronatus (L.) Loes.

mountain-holly

John C. Zasada and C. S. Schopmeyer

Dr. Zasada retired from the USDA Forest Service's North Central Research Station; Dr. Schopmeyer (deceased) retired from the USDA Forest Service's Research National Office

Growth habit, occurrence, and use. Mountain-holly is a deciduous, branchy shrub occasionally attaining small tree stature that occurs in swamps, bogs, and poor fens from Newfoundland to Minnesota and south to Virginia and Indiana. Heights at ages 5, 10, 20, 30, and 40 years for plants in a shrub-dominated peatland in New York were 1.4, 2.0, 3.5, 4.0, and 4.5 m, respectively (LeBlanc and Leopold 1992). It is regarded as an obligate wetland species: 99% of the plants grow in wetlands (Begin and others 1990; Curtis 1959; Reed 1988; Vitt and Slack 1975). It is typically found on acidic to mildly acidic soils in the shrub zone adjacent to bog mats (Cram 1988).

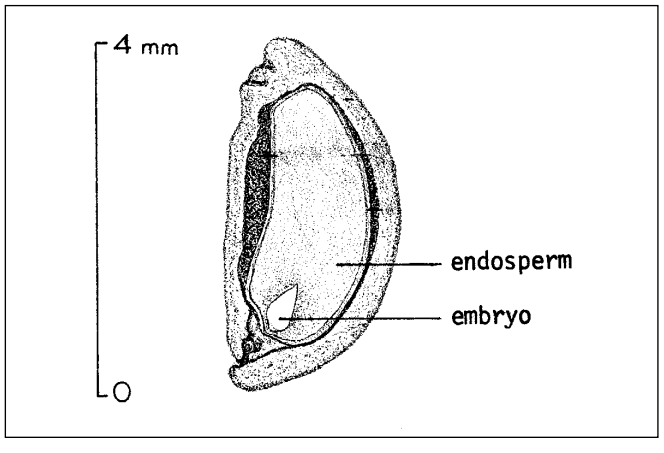
Nemopanthus is a monospecific genus and is closely related to *Ilex* spp. Similarities between *Ilex* and *Nemopanthus* in anatomical characteristics provide a basis for combining the 2 genera, but at this time it is maintained as a separate genus (Baas 1984). Information from Bonner (1974) for *Ilex* seeds is relevant to *Nemopanthus*. The species was introduced into cultivation in 1802.

Flowering, fruiting, and seed collection. This species is mainly dioecious, with some monecious individuals (Farrar 1995). Flowering occurs in early May to June; fruits ripen as early as July, continuing into August; animals disperse the seeds (Gorchov 1990). The fruit is a scarlet, dull-red berrylike drupe, 0.6 to 2.5 cm in diameter, containing 4 to 5 bony nutlets (Rehder 1940), although Gorchov (1990) found a mean of 2.9 seeds/fruit. The latter are somewhat crescent shaped and are bone colored, with 1 rib on the back (figure 1). Because the fruits are somewhat persistent, they may be collected as late as mid-October (Schopmeyer 1974).

Extraction and cleaning of seeds. Seeds in small lots can be prepared by rubbing the fruits through a #10 soil screen (0.7mm) and then floating off the pulp and empty seeds. There are about 1,600 berries in 0.45 kg (1 lb) of fruit. The number of cleaned seeds per weight (3 samples) ranged from 68,355/kg (31,000 to 66,000/lb), with an average of 99,225/kg (45,000/lb). Seed purity in one sample was 96% and average soundness in 4 samples was 80% (Schopmeyer 1974).

Germination. Seeds are doubly dormant and require a period of after-ripening before the immature embryo will develop (figure 1) (Dirr and Heuser 1987). Consequently, germination is very slow. In 3 tests, germination began several months after sowing and continued for about 2 years, when germination capacities of 14 to 66% were observed

Figure 1—*Nemopanthus mucronatus*, mountain-holly: longitudinal section through a nutlet showing small immature embryo (**left**) and nutlet (**right**)



(Adams 1927; Schopmeyer 1974). Cold stratification alone did not increase germination rate (Adams 1927; Nichols 1934). Dirr and Heuser (1987) recommended 5 months of warm followed by 3 months of cold stratification. Propagation by greenwood cuttings is feasible (Bailey 1937; Dirr and Heuser 1987).

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Nyssaceae—Sour-gum family

Nyssa L.

tupelo

Franklin T. Bonner

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Growth habit and use. The 4 deciduous, arboreal species of tupelo—the genus *Nyssa*—native to North America (table 1) are valued for pulp, veneer, specialty wood products, wildlife food, and honey production. Water tupelo, black tupelo, and swamp tupelo were cultivated in North America before 1750 (Bonner 1974; Brown and Kirkman 1990).

Flowering and fruiting. The minute, greenish white flowers that appear in spring (table 2) may be either perfect or staminate and pistillate; flowers may be borne separately on different trees. Fruits of the tupelos are thin-fleshed, oblong drupes about 10 to 38 mm long (figure 1). Their colors range from red to blue-black when they ripen in the autumn (table 2). Each fruit contains a bony, ribbed, usually 1-seeded stone (figures 2 and 3). Seeds of water tupelo range in color from white to dark brown or gray, and some are pinkish white. Seeds of all colors have germinated equally well (Bonner 1974). Trees of Ogeechee tupelo will bear fruit when they are about 5 years old (Kossuth and Scheer 1990), and 2-year-old stump sprouts of both swamp

Table 1—*Nyssa,* tupelo: nomenclature, occurrence, and height

Scientific name & synonym(s)	Common name(s)	Occurrence	Height at maturity (m)
***N. aquatica* L.** *N. uniflora* Wangenh.	**water tupelo,** tupelo-gum, sourgum, cotton-gum, swamp tupelo	Coastal Plain from Virginia to N Florida & Texas N to Missouri & S Illinois	24–30
***N. biflora* Walt.** *N. sylvatica* var. *biflora* (Walt.) Sarg. *N. sylvatica* var. *ursina* (Small) Wen & Stuessy	**swamp tupelo,** blackgum, swamp, black-gum	Coastal Plain, chiefly from Delaware to S Florida & E Texas, N to W Tennessee	40
***N. ogeche* Bartr. ex. Marsh.** *N. acuminata* Small	**Ogeechee tupelo,** Ogeechee-lime, sour tupelo, sour tupelo-gum, white tupelo	Coastal Plain from South Carolina to NW Florida	12–15
***N. sylvatica* Marsh.**	**black tupelo,** blackgum, sourgum, tupelo-gum, pepperidge	Maine W to Michigan & Missouri, S to E Texas & S Florida	15–18

Source: Little (1978).

Table 2—*Nyssa,* tupelo: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Color of ripe fruits	Fruit drop
N. aquatica	Mar–Apr	Sept–Oct	Dark purple	Oct–Dec
N. biflora	Apr–June	Aug–Oct	Blue-black	Sept–Dec
N. ogeche	Mar–May	July–Aug	Red	Nov–Dec
N. sylvatica	Apr–June	Sept–Oct	Blue-black	Sept–Nov

Sources: DeBell and Hook (1969), Kossuth and Scheer (1990), Radford and others (1964), Vande Linde (1964).

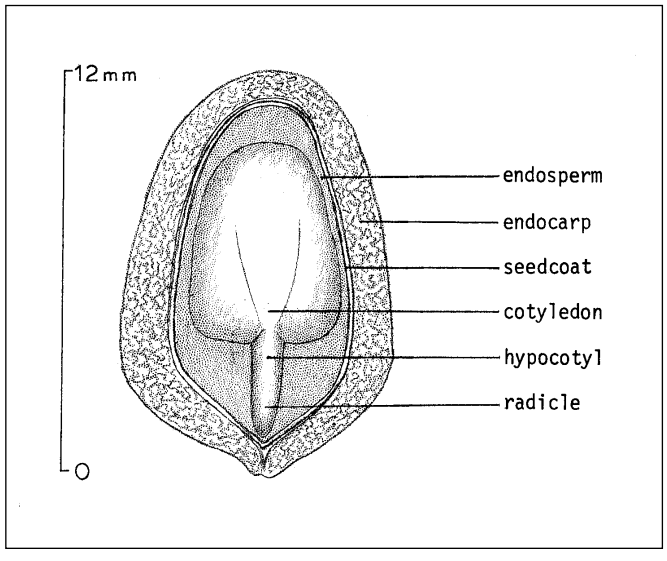
Figure 1—*Nyssa*, tupelo: fruits of *N. aquatica*, water tupelo (**upper left**); *N. sylvatica*, black tupelo (**upper right**); *N. ogeche*, Ogeechee tupelo (bottom).

Figure 2—*Nyssa,* tupelo: stones (seeds) of *N. aquatica*, water tupelo (**upper left**); *N. ogeche*, Ogeechee tupelo (**upper right**); *N. sylvatica*, black tupelo (**lower right**); *N. biflora*, swamp tupelo (**lower right**).

tupelo and water tupelo have produced viable seeds (Priester 1979). Major seed production can be expected when trees reach a dbh of about 20 cm, and all of the tupelos typically fruit abundantly each year (Johnson 1990; Kossuth and Scheer 1990; McGee and Outcalt 1990).

Collection, extraction, and storage. Ripe tupelo fruits may be picked from the ground, from standing trees, or from freshly felled logging tops. Newly shed fruits of water tupelo with exocarps intact will float for as long as 100 days, and they may be skimmed from the top of the water or picked from drift piles (Johnson 1990; Schneider and Sharitz 1988). Ogeechee tupelo fruits that are partially

Figure 3—*Nyssa sylvatica*, black tupelo: longitudinal section through a seed.



dried may float also (Kossuth and Scheer 1990), but fruits of the other tupelos do not (McGee and Outcalt 1990). External fruit color is the best index of maturity in the field (table 2). To extract the seeds, the fruits should be run through a macerator with running water to float off the pulp. Small samples may be de-pulped by rubbing the fruits over a large-meshed screen, such as hardware cloth. For water tupelo, observed numbers of fruits per weight have been from 340 to 600/kg (155 to 270/lb). Fifty kilograms (100 lb) of black tupelo fruits should yield 12 kg (25 lb) of cleaned seeds (Bonner 1974). Seed weights are listed in table 3.

Water tupelo seeds are orthodox in storage behavior. They can be stored for at least 30 months in polyethylene bags at either 3 or –10 °C, if seed moisture contents are <20% or <10%, respectively (Bonner and Kennedy 1973). Seeds of black tupelo can be stored satisfactorily over 1 winter in cold, moist stratification in sand or in just cold storage (Vande Linde 1964). Removal of the pulp did not appear to be essential for retention of viability in either condition. There are no published storage data for other tupelo species, but it is probable that the same methods would be successful for them also.

Pregermination treatment. Tupelo seeds exhibit moderate embryo dormancy, and they benefit from cold, moist stratification. Treatment in moist sand and in plastic bags without medium have been used successfully (Bonner 1974; DeBell and Hook 1969). Good germination has been reported after only 30 days of stratification, but periods up

to 120 days may be needed for some seedlots (Bonner 1974; DuBarry 1963).

Germination tests. Official seed testing prescriptions for tupelos in North America (AOSA 1993) call for a temperature regime of 8 hours at 30 °C in light and 16 hours at 20 °C in the dark. Testing should be on moist blotters or creped cellulose wadding for 21 days (water tupelo) or 28 days (black tupelo). Stratification for 28 to 30 days should precede the test. Germination of stratified seeds has been tested in several other media (table 4), and each of these probably would be satisfactory for seeds of all tupelo species.

Nursery practice. Although untreated seeds may be sown in the fall (Heit 1967) spring-sowing of stratified seeds is recommended, particularly in the South. They may be broadcast or drilled in rows, with 50 seeds/m (15/ft) for water tupelo. Seeds should be planted 12 to 25 mm ($^1/_2$ to 1 in) deep or sown on the bed surface and rolled into the soil and mulched (Bonner 1974; Vande Linde 1964). Mulching with 2 to 3.5 cm (.8 to 1.4 in) of sawdust is recommended for water tupelo and with 6 mm ($^1/_2$ in) of sawdust or 1 cm (.4 in) of pine straw for swamp tupelo. After sowing, the seeds and mulch must not be allowed to dry excessively.

Table 3—*Nyssa,* tupleo: seed weights

Species	Collection place	Cleaned seeds/weight: Range /kg	Range /lb	Avg /kg	Avg /lb	Samples
N. aquatica	—	—	—	1,000	456	—
N. biflora	South Carolina	—	—	5,320	2,415	10
N. ogeche	—	2,300–3,100	1,040–1,420	2,700	1,230	2
N. sylvatica	—	4,100–8,820	1,850–4,000	7,280	3,300	5
	North Carolina	5,750–8,500	2,610–3,860	7,450	3,380	10
	Midwest	—	—	5,500	2,492	2+

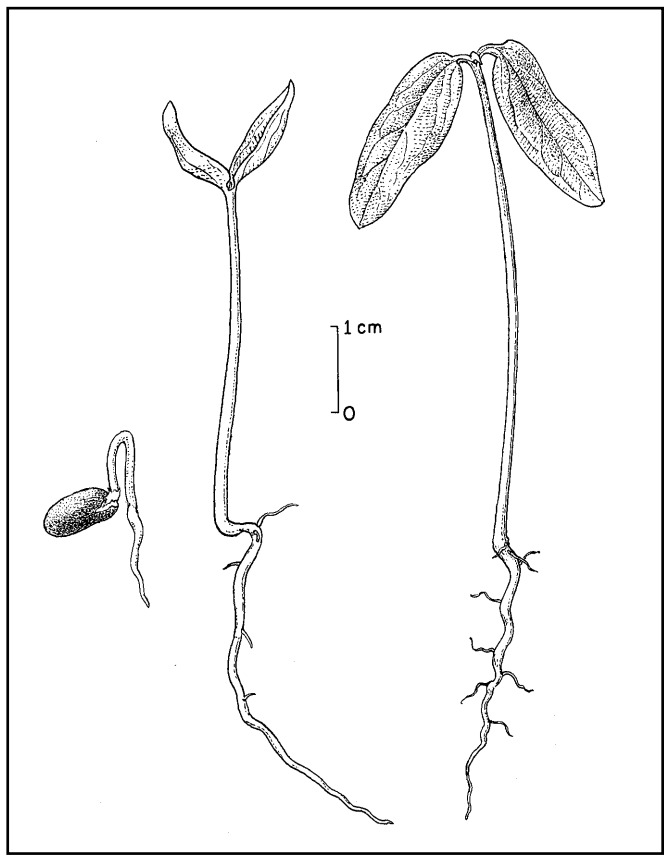
Sources: Bonner (1974), Earle and Jones (1969).

Table 4—*Nyssa,* tupelo: germination test conditions and results on stratified seeds

Species	Daily light (hr)	Germination test conditions: Medium	Temp (°C): Day	Night	Days	Germination rate: Amt (%)	Days	Germination %: Avg (%)	Samples	Purity (%)
N. aquatica	8	Kimpak	30	20	27	87	18	97	5	100
	0	Water in petri dish	29	29	28	57	14	79	24	—
N. biflora	ND	Sand	—	—	60	—	—	51	—	—
N. ogeche	8	Kimpak	30	20	70	69	12	85	1	—
N. sylvatica var. *sylvatica*	8	Kimpak	30	20	27	—	—	71	8	99

Sources: Bonner (1974), Debell and Hook (1969).
ND = natural daylength in a greenhouse.

Figure 4—*Nyssa sylvatica*, black tupelo: seedling development at 1, 4, and 39 days after germination.



Shading with tobacco shade cloth can help keep beds moist and aid the newly emerged seedlings (Vande Linde 1964). Germination is epigeal (figure 4). Desirable seedbed densities for water and black tupelos are 100 to 150 seedlings/m^2 (9 to 14/ft^2) (Williams and Hanks 1976. Vegetative propagation of tupelos is possible by softwood cuttings and grafting (Dirr and Heuser 1987).

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Rosaceae—Rose family

Oemleria cerasiformis (Torr. & Gray ex Hook. & Arn.) Landon

osoberry

William I. Stein

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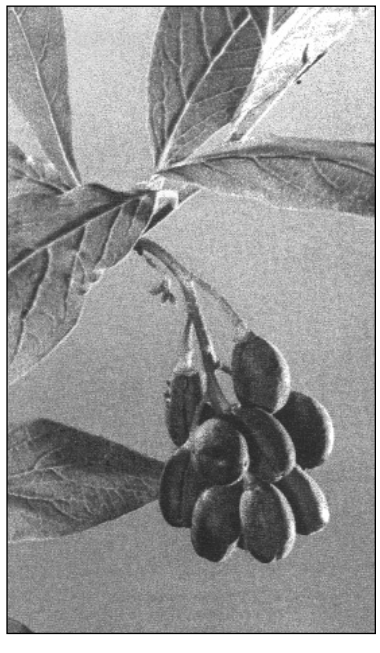
Other common names. Indian plum, squaw-plum, Indian peach.

Growth habit, occurrence, and uses. The genus *Oemleria* contains a single species—osoberry, *Oemleria cerasiformis* (Torr. & Gray ex Hook. & Arn.) Landon. Osoberry was described originally as *Nuttalia cerasiformis,* then identified for decades as *Osmaronia cerasiformis* (Hunt 1970) until an earlier legitimate name was rediscovered about 30 years ago (Landon 1975).

Osoberry is a deciduous, generally multiple-stemmed shrub that is 1.5 to 5 m or taller and sometimes develops into a small tree (Abrams 1944; Hitchcock and others 1961). A plant may have 10 or more stems and can produce new stems throughout its lifetime. Individual stems 7 m tall and 50 years of age have been observed (Allen and Antos 1993). Osoberry's native range is from the Pacific Coast eastward into the Cascade Mountains and the Sierra Nevada from southwest British Columbia southward to California, extending to Tulare County in the Sierras and northern Santa Barbara County in the coastal ranges (Hitchcock and others 1961; McMinn 1970). It is most widely distributed from the Willamette Valley northward to Vancouver Island on stream terraces, alluvial soils, and other moist to moderately dry locations, especially in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) woodlands and open Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests. Based on a sampling of osoberry stands at 56 locations, Antos and Allen (1990b) concluded that its geographical distribution is related to (1) a fairly mild maritime climate, (2) moist areas over much of its range, (3) an inability to tolerate low light levels or wet soils, and (4) a need for disturbance to allow seedling establishment. It is most common at elevations below 250 m but occurs up to 1,700 m in the southern part of its range (Antos and Allen 1990b; Munz and Keck 1959). Two varieties were described in 1905—*lancifolia* in British Columbia and *nigra* in Washington (Hitchcock and others 1961)—but their recognition is now uncertain.

Ripening osoberry fruits are highly attractive to birds such as cedar waxwings (*Bombycilla cedrorum*), and ripe fruits are readily eaten by both birds and mammals (Dayton 1931; Dimock and Stein 1974). The fruits were eaten in small quantities fresh, cooked, or dried by Native American peoples in the Pacific Northwest; twigs and bark were used for several medicinal purposes (Gunther 1945; Mitchem 1993; Pojar and Mackinnon 1994). Flavor of the fruits apparently varies by locality, from sweet to bitter (Dayton 1931). Its attractiveness as an ornamental includes flushing of light green leaves and white flowers much earlier than other plant associates, handsome variegated appearance as scattered leaves throughout the crown turn yellow in early summer, and colorful clusters of fruit (figure 1) that soon disperse or are eaten by wildlife.

Figure 1—*Oemleria cerasiformis*, osoberry: ripe and near-ripe fruits; their color changes from reddish to purple when fully ripe.



Flowering and Fruiting. Anatomical and natural population studies have confirmed strongly that osoberry is dioecious, with male and female plants similar in size, growth form, morphology of vegetative structures, and microhabitats occupied (Allen and Antos 1988, 1993, 1999; Antos and Allen 1990a; Sterling 1964). Flowering period in osoberry is relatively short and varies with latitude and elevation from January to May concurrent with leaf development (Allen 1986; Haskin 1967; Hitchcock and others 1961; McMinn 1970). Both male and female plants flower frequently except in low light; male plants are generally more abundant and may have up to 3 times as many flowers as female plants (Allen 1986; Allen and Antos 1988, 1993). Male plants start flowering earlier than female plants but reach peak abundance and finish flowering later (Allen 1986). First flowering has occurred 2 years after germination on male plants raised from seed (Allen and Antos 1993). The 5-petaled flowers are white, fragrant, and borne on drooping racemes (figure 2). Osoberry pollen is sculptured and distinctive among Rosaceae pollens studied in western Canada (Hebda and others 1991).

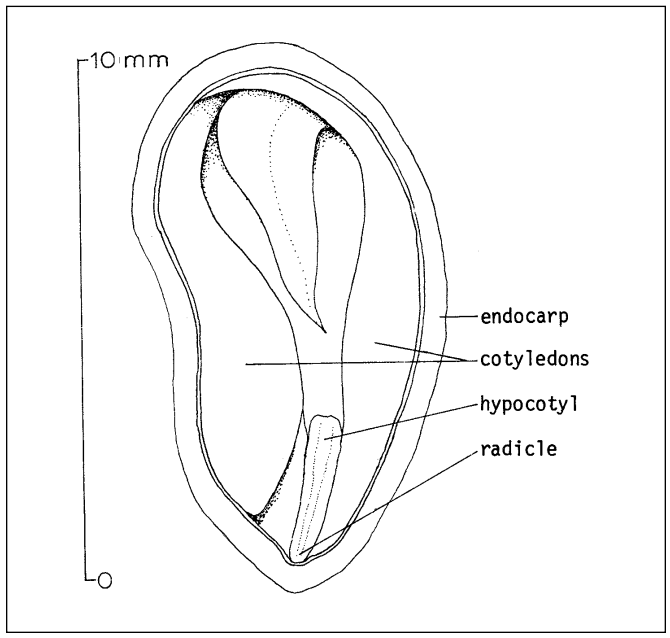
Pistillate flowers may yield up to 5 thin-fleshed, single-seeded drupes per flower, but generally fewer than 60% of pistils on a plant bear fruit; production from 10 to 20 of pistils has been reported (Antos and Allen 1994, 1999). Higher light levels favorably influence fruit set; exposure to light is gained by early flowering before deciduous associates leaf out (Allen and Antos 1988). Fruits develop and ripen in 10 to 12 weeks near Victoria, British Columbia (Antos and Allen 1994). Developing fruits become peach colored, then reddish, and finally deep blue-black under a whitish bloom when ripe (figure 1). In the Pacific Northwest, dispersal by gravity, birds, and mammals may begin in May and be nearly finished in July (Dimock and Stein 1974), substantially earlier than the August 1 to September 15 collection period listed for California by Mirov and Kraebel (1939).

Collection, extraction, and storage. Clusters of the ripe 1-seeded drupes can be stripped readily from the shrubs by hand. Fruits in small collections are de-pulped easily by rubbing them against a submerged screen or by running them through a macerator followed by repeated washings to float off the loosened pulp. Fruit biomass is about half pulp and half seed (ovendry weight); the seeds have a much higher nitrogen concentration (Antos and Allen 1990a, 1994). Osoberry seeds have a bony endocarp (Abrams 1944) and lack endosperm (figures 3 and 4). Air-drying is needed to minimize molding in cool dry storage.

Figure 2—*Oemleria cerasiformis*, osoberry: white flowers are borne on drooping racemes.

Figure 3—*Oemleria cerasiformis*, osoberry: seeds have a bony endocarp.

Figure 4—*Oemleria cerasiformis*, osoberry: longitudinal section through a seed shows folded cotyledons



About 11 kg (25 lb) of seeds (cleaned and air-dried for 24 hours) can be obtained from 45 kg (100 lb) of fresh drupes, based on 7 samples (Dimock and Stein 1974). Cleaned seeds air-dried for 4 weeks averaged 10.2/g (4,630/lb) for 12 samples from western Washington. Heavier seed weights have been reported from other parts of the osoberry's range—4.0/g (1,800/lb) in California (Mirov and Kraebel 1939) and 9.2/g (4,175/lb) in British Columbia (Antos and Allen 1994). Seeds generally are full, 98 to 100% in 4 samples (Dimock and Stein 1974).

Pregermination treatments and germination tests. Lengthy cold moist stratification is needed to overcome dormancy in fresh osoberry seeds (Dimock and Stein 1974; Mirov and Kraebel 1939). In a comparison of stratification periods at 3.3 °C in peat moss followed by 21 days at alternating 30 to 20 °C day/night temperatures, Dimock and Stein (1974) found that 60 days of stratification barely triggered germination, whereas 120 days were required for nearly complete germination. Osoberry seeds are capable of germinating at 3.3 °C during lengthy stratification—84% of total germination in 120 days, full germination in 180 days (table 1). Over 90% germination is obtainable from good seeds. Germination is epigeal (figure 5).

Nursery practice. Osoberry was introduced to cultivation by Theodor Hartweg in 1848 (Hunt 1970). It has been propagated primarily from seeds but also from suckers and cuttings. It lacks rhizomes or stolons, but some layering occurs naturally when woody debris presses stems to the ground (Antos and Allen 1990b). Tips of branches have been propagated vegetatively in a frame with bottom heat (Mirov and Kraebel 1939).

Though fruits ripen and are disseminated naturally by early summer, the seeds rarely, if ever, germinate within the year of dispersal (Dimock and Stein 1974). However, in the following year, they may germinate as early as mid-February. Seeds collected in July, cleaned, and stored at room temperature until sown outdoors in flats in late December began germinating in March in Victoria, British Columbia; second-year germination started in early February and varied from 0 to 70% of total germination for individual seedlots (Allen and Antos 1995). Total germination ranged from 1 to 96% among the 25 lots of 100 seeds each representing 5 plants at each of 5 collection areas in British Columbia and Washington.

Figure 5—*Oemleria cerasiformis*, osoberry: seedlings at 40 and 120 days after germination.

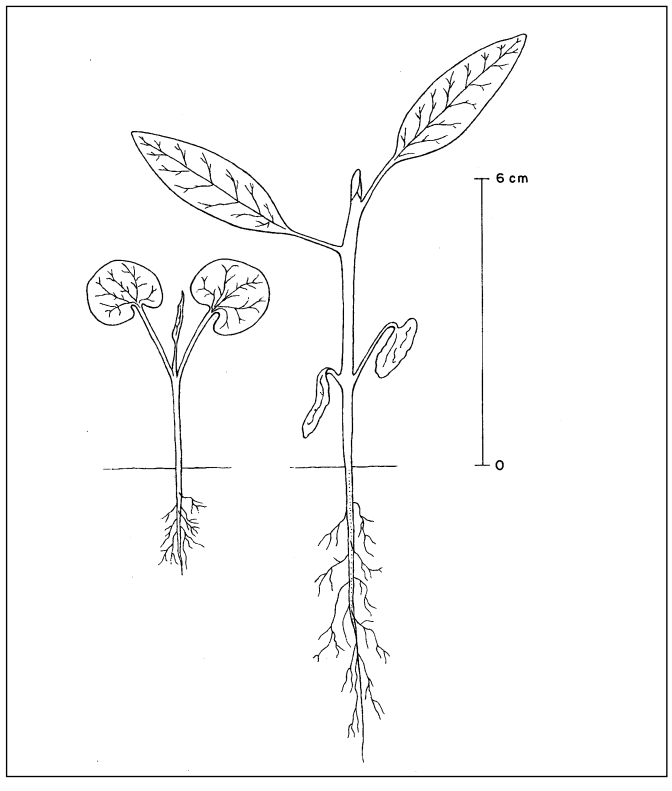


Table 1—*Oemleria cerasiformis,* osoberry: effect of stratification on germination

Stratification at 3.3 °C (days)	Germination during stratification (%)	Additional germination during 21 days at 30/20 °C (%)	Total germination (%)
60	0	1	1
90	21	37	58
120	80	14	94
160	94	0	94
180	95	0	95

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Oleaceae—Olive family

Olea europaea L.

olive

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Growth habit. Olive is a member of the Oleaceae, the family that contains the genera *Fraxinus* (ash), *Forsythia* (golden bell), *Forestiera (F. neomexicana,* the California "wild-olive"), *Ligustrum (*privet), and *Syringa* (lilac) as well as *Olea* (olive). Commercial olives belong to the species *Olea europaea* L. There are about 20 species of *Olea* found in tropical and subtropical regions of the world, but only *O. europaea* L. produces edible fruit.

Olive is a long-lived evergreen tree; some specimens have been reported to live for 1,000 years. The wood resists decay, and when the top of the tree is killed by mechanical damage or environmental extremes, new growth arises from the root system. Whether propagated by seed or cuttings, the root system generally is shallow, spreading to 0.9 or 1.2 m even in deep soils. The above-ground portion of the olive tree is recognizable by the dense assembly of limbs, the short internodes, and the compact nature of the foliage. Light does not readily penetrate to the interior of an olive tree unless the tree is well managed and pruned to open light channels toward the trunk. If unpruned, olives develop multiple branches with cascading limbs. The branches are able to carry large populations of fruit on terminal twigs, which are pendulous and flexible—swaying with the slightest breeze.

Olive leaves are thick, leathery, and oppositely arranged. Each leaf grows over a 2-year period. Leaves have stomata on their lower surfaces only. Stomata are nestled in peltate trichomes that restrict water loss and make the olive relatively resistant to drought. Some multicellular hairs are present on leaf surfaces. Olive leaves usually abscise in the spring when they are 2 or 3 years old; however, as with other evergreens, leaves older than 3 years are often present.

Flower bud inflorescences are borne in the axil of each leaf. Usually the bud is formed on the current season's growth and begins visible growth the next season. Buds may remain dormant for more than a year and then begin growth, forming viable inflorescences with flowers a season later than expected. When each leaf axil maintains a developing inflorescence, there are hundreds of flowers per twig. Each inflorescence contains between 15 and 30 flowers, depending on developmental processes for that year and the cultivar.

The flowers are borne on the inflorescence and are small, yellow-white, and inconspicuous. Each contains a short, 4-segmented calyx and a short-tubed corolla containing 4 lobes. The 2 stamens are opposite on either side of the 2-loculed ovary that bears a short style and capitate stigma. Two types of flowers are present each season: perfect flowers, containing stamen and pistil, and staminate flowers, containing aborted pistils and functional stamens. The proportion of perfect and staminate flowers varies with inflorescence, cultivar, and year. Large commercial crops occur when 1 or 2 perfect flowers are present among the 15 to 30 flowers per inflorescence. As a rule, more staminate flowers than pistillate flowers are present.

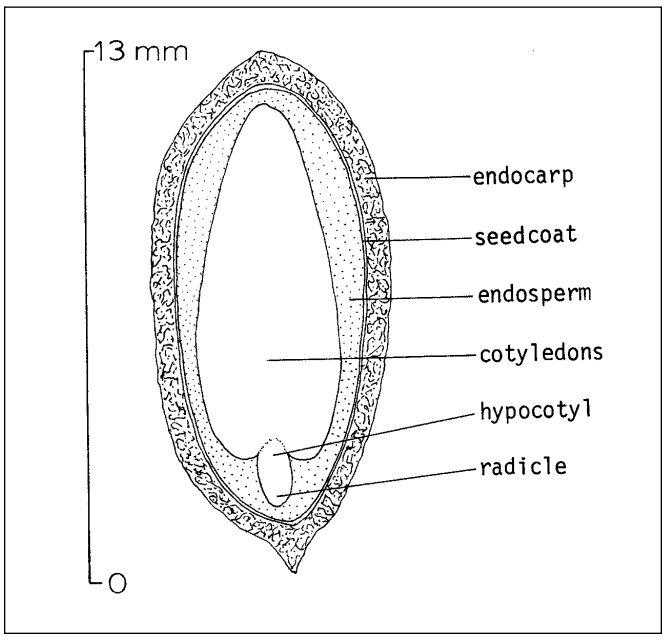
The perfect flower is evidenced by its large pistil, which nearly fills the space within the floral tube. The pistil is green when immature and deep green when open at full bloom. Staminate flower pistils are tiny, barely rising above the floral tube base. The style is small and brown, greenish white, or white, and the stigma is large and plumose as it is in a functioning pistil.

The olive fruit is a drupe, botanically similar to almond, apricot, cherry, nectarine, peach, and plum fruits. The olive fruit consists of carpel, and the wall of the ovary has both fleshy and dry portions. The skin (exocarp) is free of hairs and contains stomata. The flesh (mesocarp) is the tissue eaten, and the pit (endocarp) encloses the seed. Fruit shape and size and pit size and surface morphology vary greatly among cultivars.

The mature seed (figure 1) is covered with a thin coat that covers the starch-filled endosperm (figure 2). The latter surrounds the tapering, flat leaflike cotyledons, short radicle

Figure 1—*Olea europaea,* olive: stone.

Figure 2—*Olea europaea*, olive: longitudinal section through a stone.



(root), and plumule (stem). Seed size and absolute shape vary greatly with cultivar.

The seed undergoes most of its development starting in July and ending in about September. The fruit is horticulturally mature in September or October (ready for the California black-ripe or green-ripe process), and physiologically mature in January or February. The seed is horticulturally mature by October, and if harvested and stratified at that time it will achieve maximum germination (Lagarda and others 1983a). When the fruit is physiologically mature by January, seed germination is greatly reduced.

Occurrence. The origin of olive is lost in prewritten history. The wild olives *Olea chrysophylla* Lam. and *O. europaea* L. var. *oleaster* most probably yielded the domesticated form *O. europaea* L. These wild types are known to have existed in the region of Syria about 6,000 years ago (Zohary and Spiegal-Roy 1975). From the eastern Mediterranean, olive trees were spread west throughout the Mediterranean area and into Greece, Italy, Spain, Portugal, and France. In 1560, the Spanish Conquistadors carried olive cuttings and seeds to Peru. From there or independently, olive was found in Mexico at Jesuit missions. The Franciscan padres carried olive and other fruits from San Blas, Mexico, into California. Sent by Jose de Galvez, Father Junipero Serra established Mission San Diego de Acala in 1769. Though oil production began there in the next decade, the first mention of oil was written in the records of Mission San Diego de Alcala in 1803 as described by Father Lasuen.

Use. By the late 1800s, olive oil production in California was sufficient to supply markets outside of California. By the 1900s, California olive oil production had met the competition from imported olive oil and American vegetable oil and, in an effort to survive, the canning olive industry was born. During the 20th century, the California canning olive occupied a strong market position in America, with olive oil as a salvage industry. Currently, a renewed emphasis in health benefits of monosaturated olive oil has lead to a resurgence of olive oil production in California.

The olive tree has been used widely for shade around homes and as a street tree in cities. Its distribution is only limited by cold weather in the winter, as temperatures below –9.4 °C are lethal (Denney and others 1993).

Varieties. Several hundred varieties of olive are known and can be found at the World's Olive Variety Collection in Cordoba, Spain (del Rio and Caballero 1994). A smaller collection exits at the United States Germplasm Repository at Winters, California. Varieties differ by features of the tree shape, leaves, and fruit. Canning varieties possess larger fruit than do oil varieties. Any of the varieties are useful for landscape purposes. The varieties grown in California for canning are 'Manzanillo', 'Mission', 'Sevillano', 'Ascolano', and 'Barouni'.

Flowering and fruiting. Floral initiation occurs by November (Pinney and Polito 1990), after which, flower parts form in March. Unlike deciduous fruits with a short induction-to-initiation cycle, induction in olive may occur as early as July (about 6 weeks after full bloom), but initiation is not easily seen until 8 months later in February. Complex microscopic and histochemical techniques reveal evidence of floral initiation by November, but the process of developing all the flower parts starts in March. Some olive cultivars,

such as those grown in Crete, southern Greece, Egypt, Israel, and Tunisia, bloom and fruit heavily with very little winter chilling; whereas those originating in Italy, Spain, and California require substantial chilling for good fruiting.

In experiments with the cultivars grown in California, optimum flowering occurred when the temperature fluctuated daily between 15.5 to 19 °C maximum and 2 to 40 °C minimum. Trees held at a constant temperature of 13 °C also bloomed profusely but had poor pistillate flower formation. If temperatures did not rise above 7.5 °C or fall below 15.5 °C, trees did not bloom. At 13 °C, both chilling and warmth are sufficient for flowering but not for complete flower development. In contrast to flower buds, vegetative buds of olive seem to have little if any dormancy, growing whenever the temperatures are much above 21 °C. In addition to winter chilling, inflorescence formation requires leaves on the fruiting shoots. Therefore, it is important to prevent defoliation. The occasional occurrence of hot, dry winds during the blooming period has been associated with reduced fruit set. Winds or heat increase the amount of natural abscission.

Prolonged, abnormally cold weather during April and May, when the olive flower buds should be developing rapidly, can have a detrimental effect on subsequent flowering, pollination, and fruit set. Such weather occurred in California in the spring of 1967, delaying bloom by several weeks and leading to flower abnormalities and a crop of only 14,000 tons, the lightest in modern California history. In California, fruit on the tree by July 1, as a rule, continue on to maturity.

At full bloom, flowers are delicately poised for pollination, when some 500,000 flowers are present in a mature tree; a commercial crop of 7 metric tons/ha (3 tons/ac) or more can be achieved when 1 or 2% of these flowers remain as developing fruit. By 14 days after full bloom, most of the flowers destined to abscise have done so. By that time, about 494,000 flowers have abscised from a tree that started with 500,000 flowers.

Olives are polygamo-monoecious. The flowers are born axially along the shoot in panicles. The panicles of ‘Barouni’, ‘Manzanillo’, ‘Mission’, and ‘Sevillano’ carry an average of 12 to 18 flowers; ‘Ascolano’ average 20 flowers. Perfect flowers, those with both pistillate and staminate parts, normally consist of a small calyx, 4 petals, 2 stamens and filaments supporting large pollen-bearing anthers, and a plum-green pistil with a short thick style and a large stigma. Perfect flowers are borne apically in an inflorescence, and within the typical triple-flower inflorescence the middle flower is generally perfect. Imperfect flowers are staminate, with the pistil either lacking or rudimentary. Flowers with abortive anthers also occur and are common in ‘Sevillano’.

Cultivars vary, but most abscission occurs soon after full bloom and final fruit set nearly always occurs within 6 weeks of full bloom. Further fruit abscission can result from pest infestation and environmental extremes. When trees have an inflorescence at nearly every leaf axil a commercial crop occurs with 1 to 2% fruit set; with a small population of inflorescence, a commercial crop may require 10% fruit set.

“Shotberries” (parthenocarpic fruits) occur randomly and for reasons not clearly understood. When shotberries occur, they may be seen in clusters on each inflorescence. Here the interfruit competition for raw materials differs from that of normal olive fruits. Shotberries mature much earlier than normal fruit and may be more prevalent when conditions favor a second large crop in succession.

The endocarp (pit) enlarges to full size and hardens by 6 weeks after full bloom. At that time, the endosperm begins to solidify and embryo development takes place, leading to embryo maturity by September. The mesocarp (flesh) and exocarp (skin) continue their gradual growth. The fruits begin changing from the green color to yellow-white (straw) and accumulate anthocyanin from the distal or base end. The purple to black color eventually bleeds into the mesocarp, signaling fruit overmature for the California black-ripe or green-ripe processing. As has been reported for most other fruit crops, trees with few fruits mature their crops earlier than trees with many fruits.

Collection, extraction, storage, and germination of seeds. For seed production, the fruits should be harvested when ripe, but before they turn black. This period extends from late September to mid-November, depending on the cultivar (Largarda and others 1983a&b). Pits are removed from the flesh of the fruit with macerators. Pits can be stored in a dry place for years or planted directly, but germination is slow and uneven. Pregermination treatments are designed to overcome both seedcoat (mechanical) and embryo dormancies. Mechanical or chemical scarification is used to treat mechanical dormancy. In scarification, the endocarp can be cracked mechanically or clipped at the radicle end, with care taken not to damage the embryo. Clipping just the cotyledonary end of the endocarp does not improve germination. Good germination results can be obtained using a seed cracking device before subsequent handling procedures (Martin and others 1986). Pits may be soaked in concentrated sulfuric acid to soften the endocarp. Soaking time depends on the thickness of the endocarp; typical soaking times for ‘Manzanillo’ are between 24 and 30 hours. The

Table 1—*Olea europaea,* olive: fruit and seed data

	Fruits/wt		Seed wt/metric ton of fruit		Seeds/weight	
	/kg	/lb	kg	lb	/kg	/lb
Small	706	320	778	353	4,410	2,000
Medium	198	90	584	265	1,654	750
Large	99	45	485	220	992	450

acid bath is followed by 1 to 2 hours of rinsing in water (Crisosto and Sutter 1985).

The pits can be planted directly after the endocarp treatments. Pits should be planted at a depth about 2 to 3 times their diameter. Seeds planted outdoors in December do not germinate until the following spring. Pits can also be planted in pots or seedbeds in a greenhouse maintained at a 21 to 24 °C daytime temperature. Germination takes up to 3 months. It is critical that the seeds do not dry out after germination begins. The number of fruits and seeds per weight for 3 commercial size classes are listed in table 1.

Germination is quicker and more uniform when treatments to overcome internal dormancy are carried out in addition to scarification. The most successful of these treatments on a commercial scale is stratification. Pits are scarified as described above and then soaked in water at room temperature for 24 hours. The pits are mixed with moist sand or vermiculite and then placed in the dark in a controlled environment. The temperature is kept at 15 °C for 30 days. Stratification is thought to reduce abscisic acid (which inhibits germination) within the embryo or seedcoat. After stratification, pits can be planted outdoors if the weather is suitable; severe weather can cause losses. Pits can be planted in a greenhouse maintained at a 21 to 27 °C daytime temperature. Bottom heat is necessary. Germination should occur within 1 month. Transplanting seedlings from the greenhouse to the nursery should include steps to harden the seedlings, such as partial shade provided by a lathhouse. Adequate irrigation and fertilization are recommended to ensure continued rapid growth.

Nursery practice and seedling care. Virtually all olive trees are produced from rooted cuttings. Seed handling difficulties, low germination percentage, and slow initial seedling growth rate make seedling production impractical.

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Fabaceae—Pea family

Olneya tesota Gray

olneya

Robert Becker

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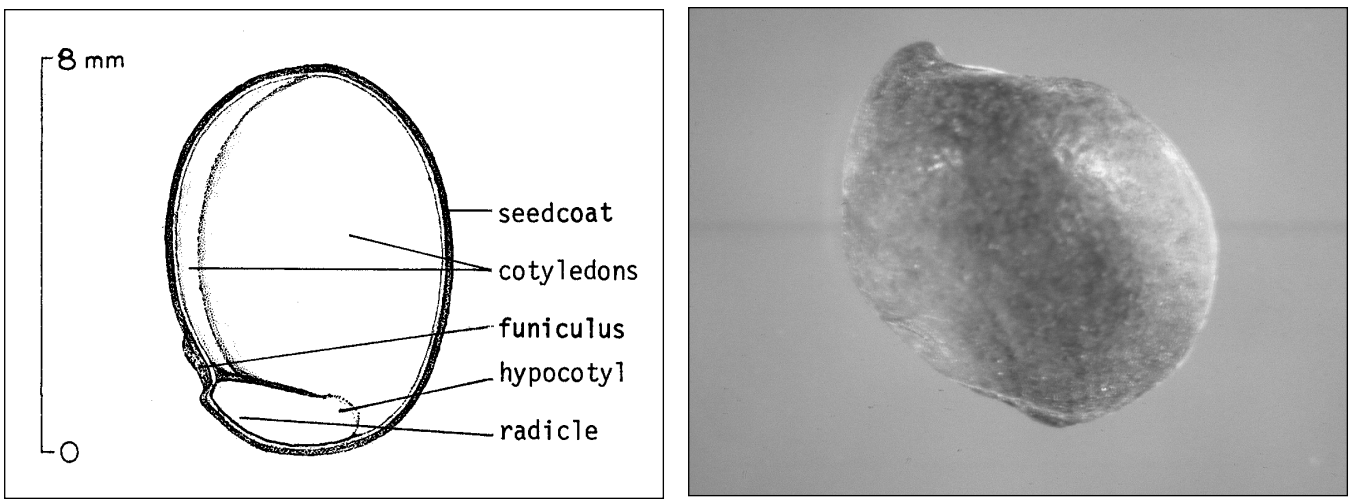
Other common names. ironwood, desert ironwood, *palo fierro, tesota*.

Growth habit, occurrence, and uses. Olneya is a long-lived, multi-trunked, broad-crowned, deciduous tree, 5 to 10 m high, that is commonly found at elevations below 600 m in desert washes and valleys of the Sonora Desert in California, Arizona, Baja California, Baja California Sur, and Sonora (Munz 1974; Shreve and Wiggins 1964). It will grow in areas receiving less water than is required to support mesquite (*Prosopis* spp.) (Felker 1981), has a frost tolerance similar to that of citrus, and will nodulate and fix nitrogen (Felker and Clark 1981). Olneya provides browse for cattle and habitat for native animals; it serves as a nurse plant for cacti and other plants (Nabhan and Carr 1994; Suzan and others 1994). It was also a food source for early cultures of Native Americans (Felger and Moser 1985). The seeds contain large amounts of canavanine, an arginine analog that is a potent growth inhibitor (Becker 1983). The wood is very dark, used for carvings, and will not float, its density being 1.22. The tree is threatened by introduced pasture grasses, urbanization, and illegal harvesting for charcoal and artists' wood.

Flowering and fruiting. Flowering occurs from April to June (Munz 1984; Shreve and Wiggins 1964). The pinkish to pale rose-purple flowers, 8 to 9 mm long, produce a legume (pod) that may contain 1 to 2, or sometimes 3 or 4 or more seeds. The legume is light brown, rounded, and hairy, and measures 4 to 6 cm in length (Munz 1984; Shreve and Wiggins 1964). The seeds are chestnut brown to blackish, shiny, ovoid, and 8 to 9 mm long (figure 1) (Irving and Becker 1985).

Collection and storage of fruits. Legumes on the tree may be picked in June or July or fallen legumes and seeds may be hand-gathered. The legumes dehise easily (Felker 1981). Many seeds are infested with insect larvae when collected, so the seeds should be stored cold or fumigated. Seed

Figure 1— *Olneya tesota*, olneya: longitudinal section through a seed (**left**) and exterior view (**right**).



counts on 2 samples were 4,400 and 4,850 seeds/kg (2,000 and 2,200/lb) (Krugman 1974), with a reported yield of 8 kg (17.6 lbs) of seeds/tree (Felker 1981).

Germination and nursery practice. Fresh seeds germinate readily when soaked for 12 to 24 hours in water; stored seeds may require longer soaking. Mild scarification before soaking is often helpful (Emery 1964; Krugman 1974). Seeds can be broadcast sown in the spring and covered with 6 mm ($^1/_2$ in) of soil or sand. Small seedlots can be germinated in planting flats or small containers and then transplanted. Seeds will rot easily, so extra care must be taken in watering (Everett 1957; Krugman 1974). Initial germination is prompt when soaked or watered, often occurring within 18 to 24 hours of sowing (Everett 1957; Krugman 1974). Seedlings appear within 6 days after sowing (Krugman 1974).

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Betulaceae—Birch family

Ostrya virginiana (P. Mill.) K. Koch

eastern hophornbeam

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Other common names. hophornbeam, American hophornbeam, hornbeam, leverwood, ironwood.

Growth habit, occurrence, and uses. Three of the 8 species of the hophornbeam genus—*Ostrya*—are native to the United States; of these, eastern hophornbeam is the most common (Little 1979). It is a small deciduous tree that attains a maximum height of about 18 m and occurs throughout the eastern half of North America, ranging from Nova Scotia and southeastern Manitoba in Canada south to eastern Texas and northern Florida. It also occurs in the mountains of Mexico, El Salvador, and Honduras (Little 1979). Small trees often occur in the understory on a wide variety of sites ranging from deep, moist soils to dry and gravelly or rocky slopes (Metzger 1990).

The heavy, hard, durable wood has been used for fence posts, tool handles, and other specialty items (Schopmeyer and Leak 1974). Eastern hophornbeam also provides food and cover for many birds and some mammals. The seeds are a preferred food for sharp-tailed grouse (*Pedioecetes phasianellus*) and wild turkey (*Meleagris gallopavo*), and the buds and catkins are important winter foods for ruffed grouse (*Bonasa umbellus*) (Metzger 1990). This tree is sometimes planted as ornamental because of its attractive foliage and fruit clusters (Brown and Kirkman 1990), but it does not grow very rapidly. It was first cultivated in 1690 (Rehder 1940).

Flowering and fruiting. The flowers are monoecious. Staminate catkins, 2.5 to 4 cm in length, develop on the branch tips in late summer and overwinter in a dormant state. Pistillate catkins are small, inconspicuous, and 6 mm long; they appear with the leaves in the spring. Both flowers mature and open in March and April in the South and May and June in the North (Brown and Kirkman 1990; Metzger 1990). The fruit is a strobile, usually 2.5 to 7.5 cm long (figure 1), consisting of involucres that each enclose a single nut (figure 2) about 7 mm long and 4 mm in diameter (Brown and Kirkman 1990; Sargent 1965). The fruits ripen from the end of August in Michigan to October in the South. Nuts are dispersed after ripening when the strobiles fall apart. The buoyancy of the papery sacs aids dispersal by wind (Metzger 1990). Trees do not produce seeds abundantly until they are about 25 years old (Schopmeyer and Leak 1974). Seed production in the northern part of the range has averaged 124,000 seeds/ha (50,200/ac) (Metzger 1990).

Figure 1—*Ostrya virginiana*, eastern hophornbeam: strobile

Collection, extraction, storage. The strobiles may be hand-picked from the trees when they are a pale greenish brown in color. At this stage, they are not yet dry enough to fall apart. When completely ripe, they are light gray to greenish brown (Schopmeyer and Leak 1974). The fruits should be thoroughly dried before seeds are extracted by thrashing or rubbing the dried fruits over screens. Seeds can be separated from the chaff with air-screen cleaners or fractionating aspirators or by fanning. One hectoliter of fruit will yield about 2.5 kg of seed (1 bu yields 2 lb). The number of seeds per weight (5 samples) ranged from 55,100 to 77,200/kg (25,000 to 35,000/lb), with an average of 66,100/kg (30,000/lb). Purities (percentages) in the high 90s are easily obtained with good cleaning. The proportion of sound seeds will vary widely, especially due to insect dam-

Figure 2—*Ostrya virginiana*, eastern hophornbeam: longitudinal section through a seed (**left**) and intact seeds (**right**).

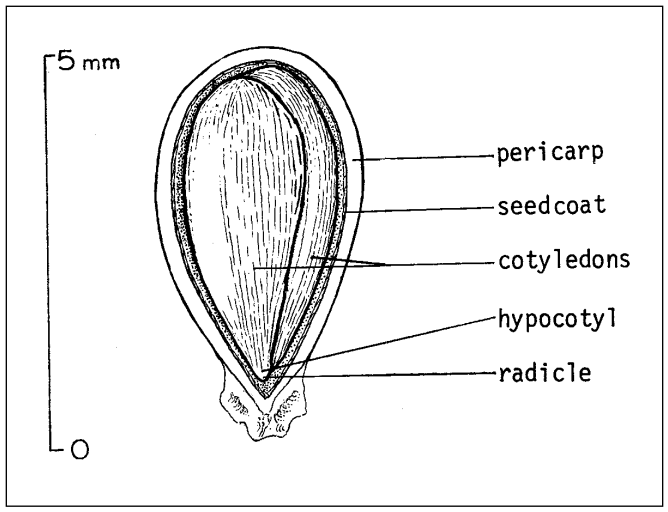
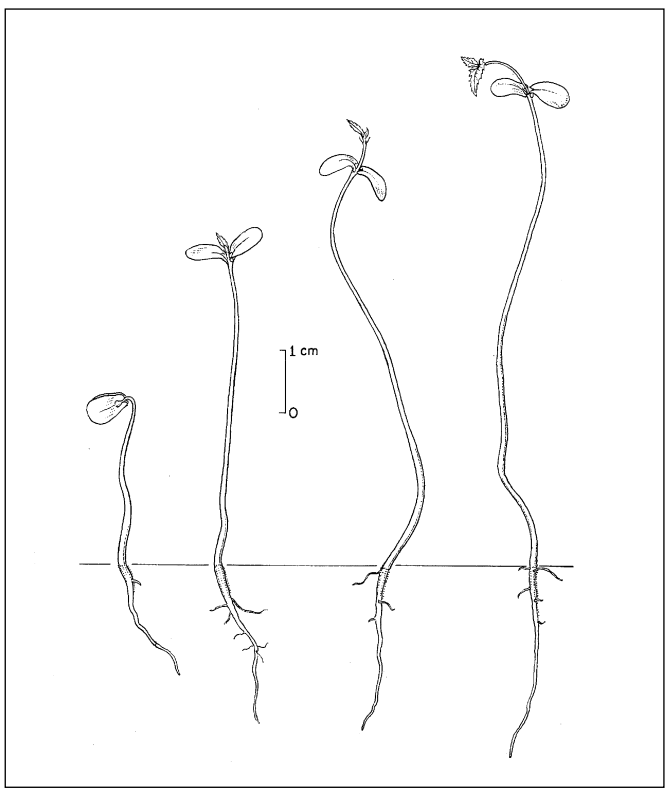


Figure 3—*Ostrya virginiana*, eastern hophornbeam: seedling development at 2, 4, 23, and 27 days after germination.



age, but 80% has been reported (Schopmeyer and Leak 1974). There are no storage test data for eastern hophornbeam, but the seeds have the ability to survive at least 1 year in the soil and should have good storage potential.

Pregermination treatments and germination tests. Seeds have a hard seedcoat and an internal dormancy that is difficult to overcome. Warm incubation, followed by cold stratification may be best. Three months of warm, followed by 3 to 5 months of cold produced germination of 81 to 92% (Dirr and Heuser 1987). Germination is epigeal (figure 3). Tetrazolium staining can be used to estimate viability. Official seed testing organizations do not include eastern hophornbeam in their recommendations.

Nursery practice. Either fall- or spring-sowing is feasible, but fall-sowing should take place soon after seeds are collected. In Iowa, seeds collected when they were slightly immature (August) and sown immediately germinated 100% the following spring (Titus 1940). Seeds should be covered with 6 mm ($^1/_4$ in) of firmed soil. Fall-sown beds should be covered with burlap, straw, or other suitable mulch, and uncovered when germination begins. Stratified seeds may be sown in the spring as soon as the soil can be worked, and the beds should be mulched or watered to keep them moist until germination starts (Schopmeyer and Leak 1974).

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Ericaceae—Heath family

Oxydendrum arboreum (L.) DC.

sourwood

Frank A. Blazich and Mark C. Starrett

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Synonym. *Andromeda arboreum* L.

Other common names. sorrel-tree, lily-of-the-valley tree.

Growth habit, occurrence, and uses. Sourwood is a medium-sized, deciduous tree that develops a graceful, pyramidal shape when mature (Dirr 1990). The plant typically grows 9 to 15 m tall in the wild but seldom attains such height outside its native range (DeWolf 1987). This species is indigenous to the eastern United States, extending from Pennsylvania southward into northern Florida, and west to Indiana and Louisiana (Rehder 1986). Sourwood often is found on ridges of gravelly soil adjacent to streams and is hardy to USDA Zone 5 (Dirr 1990). The species has several attributes that create an outstanding specimen plant. It has slender, drooping branches of dark green foliage that contrast sharply with pendulous terminal panicles of white flowers in mid-summer, when few other plants are flowering. In addition, the brilliant scarlet fall foliage is without comparison amongst plants indigenous to the United States (DeWolf 1987). Sourwood should be grown in full sun to attain maximum flower production and the most vibrant fall color. However, the tree will also grow in partial shade (DeWolf 1987). Sourwood prefers an acidic (pH 4.0 to 5.5), moist, well-drained soil high in organic matter (DeWolf 1987; Dirr 1990). Sourwood is best suited for suburban or rural landscapes, as it will not tolerate air pollution occurring in urban areas (DeWolf 1987). Lastly, sourwood honey is highly prized, as is the wood, which is used for tool handles and in crafts (Duncan and Duncan 1988).

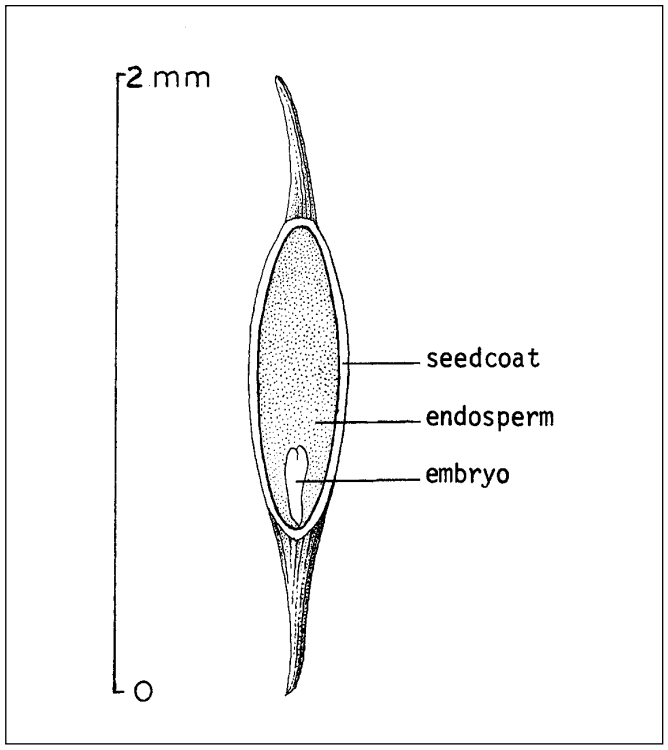
Geographic races and hybrids. Sourwood is monotypic, that is, the only species of its genus. No hybrids are described in the literature.

Flowering and fruiting. Fragrant, 6-mm-wide, white, urn-shaped flowers are borne profusely on 15- to 25-cm, pendulous, terminal panicles (Bridwell 1994; Dirr 1990). Flowers open in late June or July and provide a dramatic, mid-summer show. The floral display can completely shroud the dark green foliage in a white, lacy veil (Dirr 1990). Fruits are ovoid-pyramidal, dry, 5-chambered, dehiscent capsules, borne in clusters, each capsule about 5 to 7 mm long (Bailey 1977; Dirr 1990; Radford and others 1968). Seeds are 2 mm long, 0.5 mm wide, and gray to brown when mature (figure 1) (Olson and Barnes 1974).

Collection of fruits, seed extraction, cleaning, and storage. Capsules and seeds ripen in September and October and can be collected at that time (Olson and Barnes 1974). Capsules are removed from the plant, lightly beaten, and then rubbed to open them completely (Dirr and Heuser 1987). Next, seeds are shaken from the capsules. Viability can be poor if seeds are not graded rigorously. Use of an air-column blower is recommended to remove chaff and empty seeds (Barton and Bonaminio 1986). Lots of cleaned, pure seeds average 8,200 seeds/g (230,000/oz) (Olson and Barnes 1974). The seeds are apparently orthodox in storage behavior and may remain viable for several years if stored dry in a sealed container at 4.5 °C (Blazich 1996).

Pretreatment and germination tests. Seeds germinate readily after harvest and no pretreatments are necessary (Dirr and Heuser 1987; Fordham 1960). Germination is epigeal (figure 2). Seeds of sourwood require light for maximum germination (Barton and Bonaminio 1985). A 30-day test of seeds collected in Yadkin Co., North Carolina, demonstrated that germination in total darkness at 25 °C was minimal (5%) (Barton and Bonaminio 1985). However, a daily photoperiod of $^1/_2$ hour resulted in 29% germination and daily photoperiods ≥ 4 hours resulted in maximum germination (58%). In another test, seeds were placed at 20, 22.5, 25, 28 °C, or at 9/15-hour thermoperiods of 25/15 or 30/20 °C (Barton and Bonaminio 1985). Seeds received 1 hour of light daily at each temperature. After 21 days, the highest germination occurred at 25/15 °C and 30/20 °C, with germination of 50 and 64%, respectively. Germination began faster at 30/20 °C. These studies utilized cool-white fluorescent lamps as the light source, at 4.3 klux (about 55 μmol/m^2/sec). Under particular conditions, stratification (moist prechilling) also may be used to stimulate germination (Barton and Bonaminio 1986).

Figure 1—*Oxydendron arboreum*, sourwood: seeds in longitudinal section (**left**) and external view (**right**).



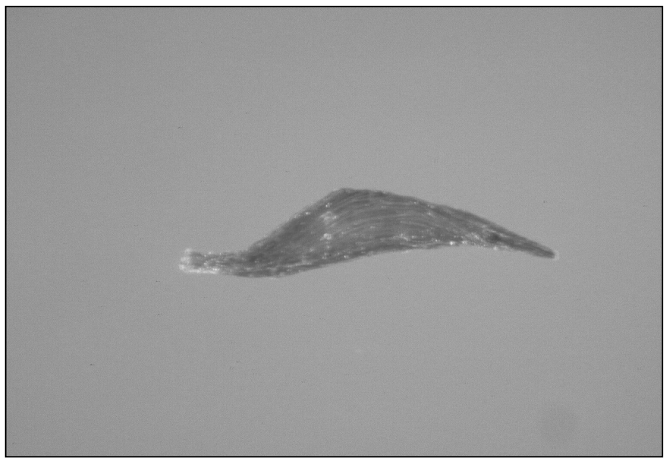
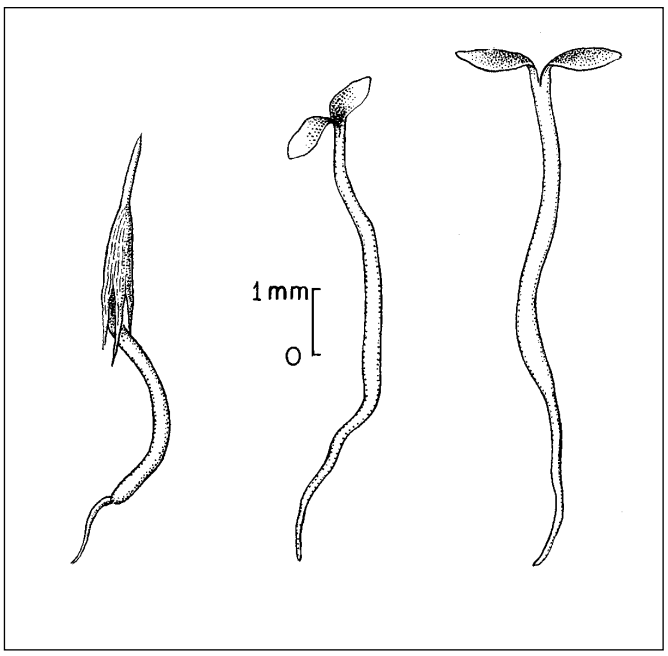


Figure 2—*Oxydendron arboreum*, sourwood: seedlings of sourwood at 2, 6, and 8 days after germination.



Nursery practice. Johnson (1978) described a commercial method for seed propagation, in which seeds are sown in November soon after harvest. Seeds are spread lightly on the surface of a flat containing fine milled sphagnum and vermiculite (1:1, by vol.) and misted. Then, the flat is wrapped in a clear plastic bag, with supports to keep the bag from touching the surface of the medium, and placed under continuous light, provided by cool-white fluorescent lamps. Typically, the germination medium is maintained at 22 °C using bottom heat. The medium surface should never be allowed to dry. Seeds germinate within 2 weeks, and seedlings develop rapidly. At the 2- to 3-leaf stage, seedlings can be transplanted into peat pots or individual containers containing an acidic, organic medium. After 6 months, seedlings can be potted into 3.8-liter (1-gal) containers containing a well-drained, acidic, organic medium. Growth of 0.6 m (2 ft) can be obtained in 9 months following this production protocol. Blazich and others (1994) reported that commercial production of seedlings of sourwood may be accelerated by utilizing a pine bark medium and a day/night cycle of 26/22 °C or 30/26 °C with long-day conditions.

Stem cuttings are reported as difficult to root (Dirr and Heuser 1987). However, sourwood can be propagated vegetatively by micropropagation (Banko and Stefani 1989).

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P

Fabaceae—Pea family

Paraserianthes falcataria (L.) I. Nielsen

peacock-plume

John A. Parrotta and Franklin T. Bonner

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Synonyms. *Albizia falcataria* (L.) Fosberg

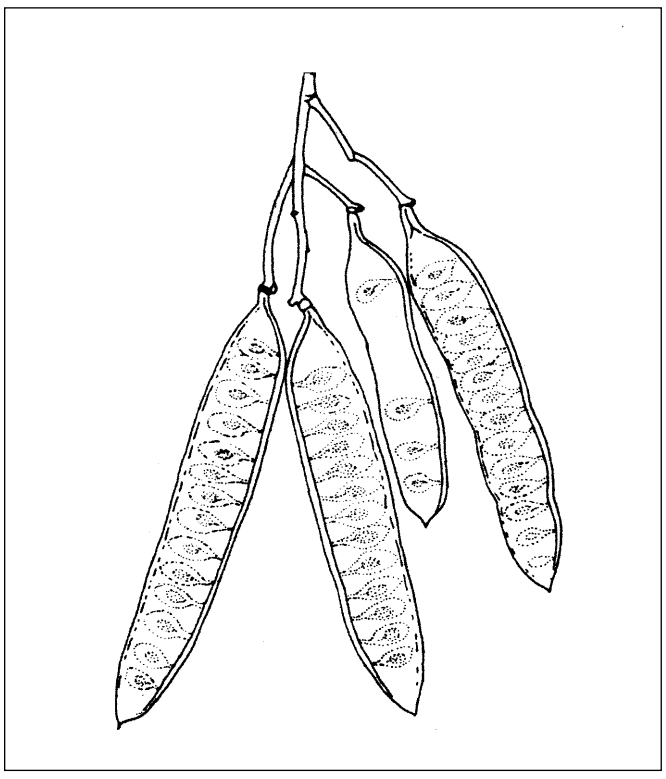
Other common names. Molucca-albizia, *batai, sau,* peacock's plume.

Growth habit, occurrence, and uses. Peacock-plume is a large deciduous tree that may reach 30 m in height and 1.2 m in bole diameter. It has a large spreading crown and light gray, smooth bark with small corky warts. This fast-growing native of the Moluccan Islands of Indonesia in the South Pacific has been widely planted throughout many tropical regions of the world and has become naturalized in many of them. The species was introduced into Hawaii in 1917 for ornamental and timber purposes (Rock 1920). The wood is lightweight; moderately weak in bending and compressing strength, and moderately soft and limber (Desch 1941; Gerhards 1966). It has been used for core-stock veneer, pallets, boxes, shelving, and internal furniture parts (Little and Skolmen 1989). In Asia, the wood has been used for fuel, matches, and pulp (Khullar and others 1992). Its lack of resistance to decay and termites, however, limits the value of the wood (Little and Skolmen 1989).

Flowering and fruiting. The flower clusters of peacock-plume are large, lateral panicles 8 to 25 cm in length that are borne at the branch tips. The numerous flowers are long (13 mm), stalkless, and greenish yellow to whitish in color. The legumes (pods) are narrow and flat; they measure 10 to 15 cm long and about 2 cm wide (figure 1). Each legume may contain 12 to 20 oblong, flattened, dark brown seeds, about 6 mm in length (Little and Skolmen 1989; Little and Wadsworth 1964; Wick and Walters 1974). In Hawaii, peacock-plume flowers in April and May, with legumes maturing in June to August (Wick and Walters 1974); in India, legumes mature in May and June (Khullar and others 1992).

Collection, extraction, and storage. The legumes can be picked from the tree after they turn from green to straw color or from the ground by shaking the branches. After being dried in the sun, the legumes should be run through a macerator or flailed by hand to extract the seeds. Debris can be removed with aspirators or air-screen cleaners or by simple winnowing. Empty, immature, and damaged seeds can removed by water flotation or by careful blowing in seed aspirators. There are usually 38,000 to 44,000 cleaned seeds/kg (17,000 to 20,000/lb) (Khullar and others 1992; Parrotta 1990; Wick and Walters 1974). Seeds of peacock-plume are orthodox in nature and can be easily stored when dried to about 8 to 10% moisture content. Dried seeds can be stored for at least 2 years in sealed containers at room temperature, but refrigeration at 3 to 5 °C should be used for longer storage (Parrotta 1990). There are no data on the long-term storage potential of these seeds.

Figure 1—*Paraserianthes falcataria,* peacock-plume: legumes (from Little and Skolmen 1989).



Germination. Seeds of peacock-plume exhibit seed-coat dormancy that can be overcome with acid scarification, mechanical scarification, or hot-water soaking (Khullar and others 1992; Wick and Walters 1974). The first 2 methods have often produced slightly better results, but hot water soaking is less likely to damage the seeds. Ten to 15 minutes in concentrated sulfuric acid, followed by washing and then 15 minutes of soaking in water has been recommended (Wick and Walters 1974). In hot-water soaking, seeds are immersed in boiling water for 1 to 3 minutes, then soaked in cool water at room temperature for 24 hours immediately before sowing (Parrotta 1990). In a similar method, seeds are immersed in boiling water that is then removed from the heat source and allowed to cool at room temperature; the seeds should remain in the water for 24 hours. Proper treatment with any of these methods should produce germination of 70 to 99% within 10 days (Khullar and others 1992; Parrotta 1990; Wick and Walters 1974). Germination is epigeal.

Nursery practice. In Hawaii, peacock-plume seeds are sown at densities of 300 to 400 seeds/m^2 (28 to 37/ft^2) and covered with about 6 to 12 mm ($^1/_4$ to $^1/_2$ in) of soil. Seedlings are usually thinned to the desired seedbed density at maturity of 200 to 250/m^2 (20 to 25 seedlings/ft^2) and outplanted at 8 to 12 months of age (Wick and Walters 1974). Container seedlings and stumped seedlings can also be used to establish this species (Parrotta 1990).

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P

Fabaceae—Pea family

Parkinsonia L.

palo verde

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Growth habit, occurrence, and uses. There are 3 noteworthy species of *Parkinsonia* grown in the United States. Two of these—blue palo verde and yellow palo *verde*—were formerly in the genus *Cercidium* but they are now considered to be in *Parkinsonia* (table 1). Palo verde is a thorny, green-barked shrub/small tree that can reach a height of 11 m (Vines 1960). The name is of Spanish-Mexican origin and refers to the very noticeable green (*verde*) color of the smooth trunk of this drought-resistant tree of the hot southern deserts (Jaegar 1940). The open-crowned trees have alternate, bipinnate leaves on slightly zig-zag green twigs (Little and Wadsworth 1964). The species are widely distributed in tropical America and widely planted in the southwestern United States and the Old World tropics (Little 1979; Little and Wadsworth 1964). Palo verde was introduced into Puerto Rico from the southwestern United States and is now naturalized (Francis and Liogier 1991). Blue palo verde and yellow palo verde are 2 closely related species, commonly found on the edges of washes, more occasionally in the washes, and scattered in the *bajadas* (Bainbridge and Virginia 1989). Both species drop their leaves when drought-stressed and only the green, thorny branches remain.

The 3 species serve as shelter for animals and rodents (Dean and Milton 1991), and the leaves and legumes (pods) as browse for livestock, rodents, rabbits, other mammals, and many species of birds (Bainbridge and Virginia 1989; Jaeger 1940; Little and Wadsworth 1964; Vines 1960). In the past, the legumes were a fairly important food for Native American inhabitants of the Sonoran Desert (Ebeling 1986; Felger and Moser 1985; Vines 1960). They were picked from July to August and dried; the beans were removed, ground in mortars into flour, and used in mush or cakes (Bean and Saubel 1972). The flowers of palo verde serve as a primary source of forage for megachilid bees in India (Jain and Kapil 1980; Sihag 1982), but the species is considered a weed in Australia (Pearce 1984).

Flowering and fruiting. Palo verdes have fragrant 5-petaled, showy, yellow flowers that form in loose racemes 5 to 20 cm long (Little and Wadsworth 1964). Blossoms appear in late March to June and occasionally in August to November after rains. In the past, these trees have been referred to as *fluvia de oro* or "fountain of gold" by Spanish Americans because of their incredible flower show after a generous rainy season. The fruits are 5 to 10 cm long, pointed legumes that contain 1 to 8 oblong, glossy, yellow-brown

Table 1—Parkinsonia, palo verde: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. aculeata* L.**	**palo verde,** Jerusalem-thorn, horsebean, *retama, palo de ray, palo rayo*	South to trans-Pecos Texas & S Arizona; widely distributed in tropical America; Puerto Rico
***P. florida* (Benth. ex Gray) S. Wats** *Cercidium floridum* Benth. ex Gray	**blue palo verde**	SW US
***P. microphylla* Torr.** *Cercidium mycrophyllum* (Torr.) Rose & I.M. Johnston	**yellow palo verde**	SW US

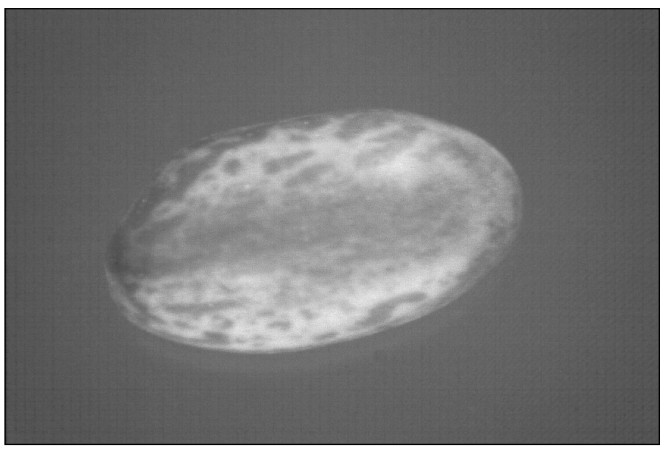
Sources: Bainbridge and Virginia (1989), Little (1979), Little and Wadsworth (1964).

seeds (figures 1 and 2) (Delorit and Gunn 1986; Vines 1960). Both flowers and legumes can occur throughout the year. The fruits are ripe when the legume turns yellow-brown and the seeds rattle (Bainbridge and Virginia 1989). Most legumes of blue palo verde contain only 1 seed (Siemens and Johnson 1995).

Collection, storage and germination. Seed collection should be timely because harvesting by animals and birds quickly reduces seed availability. Legumes dehisce upon drying, and small quantities of seeds can be hand-cleaned. A disc mill, meat grinder, or hammermill can be used to clean larger quantities. Reports on seeds per weight for palo verde range from 12,345 to 13,300/kg (5,600 to 6,000/lb) (Francis and Rodrıguez 1993; Little and Wadsworth 1964). The seeds are obviously orthodox, since Everitt (1983) found no reduction in seed viability after 2 years storage at room temperature.

Some form of seed scarification is necessary in order to achieve rapid and uniform germination. Francis and Rodrıguez (1993) germinated mechanically scarified seeds of palo verde on blotter paper and reported that 59% had germinated after 2 days. Everitt (1983) found that soaking seeds in concentrated sulfuric acid for 45 minutes increased germination from 1% to over 50%. Germination rose to over 87% at continuous temperatures of 15 to 35 °C, or at alternating temperatures of 10/20, 15/25, or 20/30 °C. Although percentage germination and radicle length were little affected by pH, results were enhanced if seeds were buried 1 to 7 cm (0.4 to 2 $^{3}/_{4}$ in) rather than left on the surface. Zodape (1991) reported germination of over 80% of seeds soaked in concentrated sulfuric acid. However, Bainbridge and Virginia (1989) found a negative effect of certain abrasion methods—they can create a dust on the seeds that encourages mold growth during germination.

Figure 1—*Parkinsonia aculeata*, palo verde: seed.



Although the seedcoat serves as a barrier to overcome when germinating, it also serves as a protective shield against insect infestation. Janzen (1977) found that the cause of mortality of larvae of the southern cowpea weevil—*Callosobruchus maculatus* F.—in palo verde seeds was not seed toxicity but rather the inability of the larvae to emerge through the seedcoat. Johnson and Siemens (1991) reported a field survival rate of less than 0.1% for *Stator* spp. larvae on palo verde seeds, also attributed to seedcoat density. Bainbridge and Virginia (1989) found that freezing the seeds will kill bruchid beetles, which are a major seed pest.

Nursery practice and seedling care. Palo verde seedlings are capable of fast root growth, for example, 35 cm (13.8 in) in 60 days, and may require air- or root-pruning. Young seedlings are susceptible to various damping-off diseases. Washing seeds with dilute hydrogen peroxide or dilute sodium hypochlorite (1:3 laundry bleach with water) before scarification may reduce problems with fungal disease (Bainbridge and Virginia 1989). Seedlings can be grown in a variety of deep, narrow containers. Pots that allow for uninterrupted taproot growth, such as the "tall pot," a 76-cm (30-in) PVC pipe used at the U.S. Department of the Interior National Park Service's Joshua Tree National Park (JTNP) seem to work well for revegetation projects. Soil mix should be sandy and drain well. Mychorrhizal inoculation is not required; however, use of VA-mycorrhizae may be desirable for planting in washes that are usually deficient in soil phosphorous (Virginia 1986).

Palo verde grown in the tall pots have been successfully outplanted without follow-up irrigation at JTNP (Rodgers and Miller 1995). Transplant studies determined that seedlings could be initially established with minimal irrigation. However, seedlings are tempting browse for small mammals, and plants are unlikely to survive without protective screening.

Direct seeding may be successful in the field, provided seeds are pretreated and sown after heavy rains or floods, when moisture and heat stress are low. In 1988, direct seeding trials were undertaken by Bainbridge and Virginia (1989) at the travertine site near the Salton Sea. Seeds were scarified, presoaked, and buried 6 to 12 mm deep in loose soil. Initial treatments of the first trial included control, supplemental water, supplemental water and screening, and supplemental water with screening and shade. After 7 months, only 1 tree was still alive, rated in good condition, in the plot with water and screen. A second trial in the same area in April used presoaked, scarified seeds planted at a density of 100 seeds/m^2 (9/ft^2). Plots were moistened before and after planting. No germination was observed, probably due

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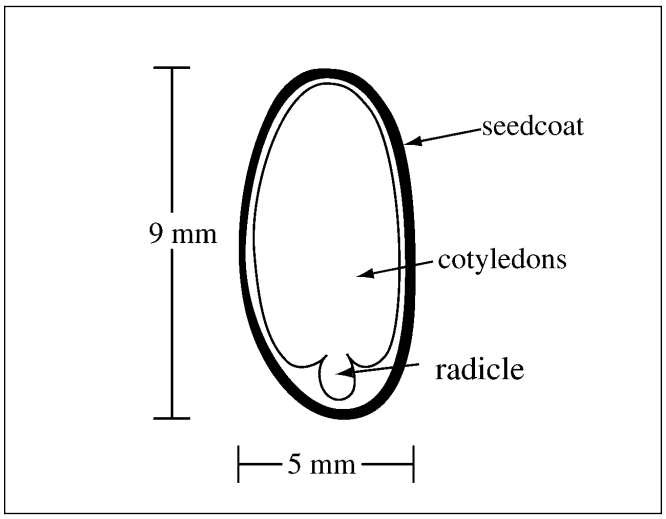
Figure 2—*Parkinsonia aculeata*, palo verde: longitudinal section of a seed.



to the late planting date. Results of both trials showed that seedlings in the 2-leaf stage are sensitive to both high winds and freezing; the best time for direct seeding appears to be in late January or early February. Subsequent trials suggest that the use of remote-site irrigation systems—pitchers, porous capsules, and wicks—can improve direct seeding success.

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Vitaceae—Grape family

Parthenocissus Planch.

creeper

John D. Gill, Franz L. Pogge, and Franklin T. Bonner

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Growth habit, occurrence, and use. About 10 species and many varieties of creepers are native to either eastern Asia or North America. Both of the species discussed here (table 1) are adapted to climbing; Virginia creeper may ascend to about 15 m above ground and Japanese creeper to about 18 m (Robinson 1960). In the 1974 edition of this Manual, thicket creeper—*P. inserta* (Kerner) Fritsch—was treated as a separate species, but it is now considered the same as Virginia creeper. Virginia and Japanese creepers prefer soils that are moist but otherwise grow well in a wide variety of soil types. They are at least moderately tolerant of shading but are most likely to occupy places such as the edges of clearings, fence rows, old walls, and other structures, and stream banks. Chief uses are as ornamentals or for wildlife habitat. The creepers have attractive bluish black fruits and handsome foliage that turns scarlet, crimson, or orange in the fall. They provide food for more than 39 species of wildlife as well as cover for many small birds and mammals (Fisher and others 1935). The creepers are also used for erosion control. Virginia creeper was first cultivated in 1622 and Japanese creeper was first imported about 1862 (Rehder 1949).

Flowering and fruiting. The flowers are small and greenish and are borne in rather inconspicuous, long-stemmed clusters. Flowers are usually perfect (bisexual), but some vines have both perfect and unisexual flowers. The periods of flowering and fruiting are listed in table 2. Seed dispersal is largely effected by birds and mammals. Ripe berries (figure 1) of both species are bluish black and usually contain 1 to 4 seeds per fruit (Rehder 1949). Seeds have small embryos (figures 2 and 3). Good seedcrops are borne frequently.

Collection, extraction, and storage. After their color has turned to bluish black, fruits can be hand-stripped from the vines. Leaves and other debris mixed with the fruits can be removed by screening or blowing. Seeds can be extracted

Table 1—*Parthenocissus,* creeper: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. quinquefolia* (L.) Planch.** *P. inserta* (Kerner) Fritsch *Pserda quinquefolia* (L.) Greene	**Virginia creeper,** woodbine	Maine to Manitoba & Florida, to Texas & Rocky Mtns, also California & Mexico
***P. tricuspidata* (Sieb. & Zucc.) Planch.** *Ampelopsis tricuspidata* Sieb. & Zucc.	**Japanese creeper,** Boston ivy	Japan & Central China; escaped from cultivation in Massachusetts & Ohio

Sources: Rehder (1949), Robinson (1960), Vines (1960).

Table 2—*Parthenocissus,* creeper: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Fruit drop
P. quinquefolia	June–Aug	July–Oct	Aug–Feb
P. tricuspidata	June–July	Sept–Oct	—

Sources: Fernald (1950), Gill and Pogge (1974), Rehder (1949), Van Dersal (1938).

Figure 1—*Parthenocissus quinquefolia*, Virginia creeper: cluster of berries.

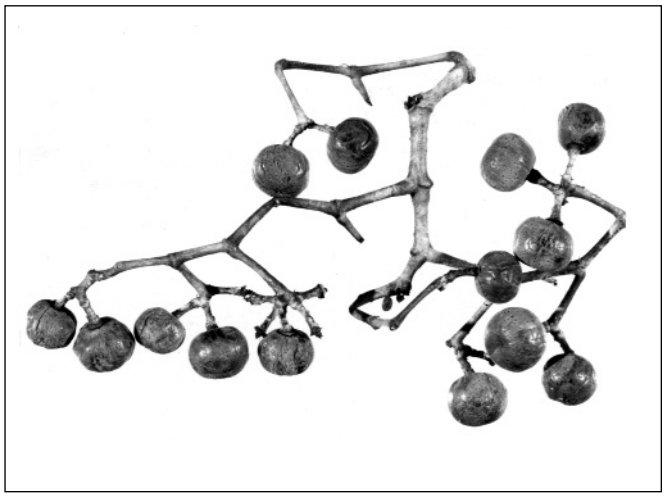


Figure 2—*Parthenocissus*, creeper: seeds of *P. quinquefolia*, Virginia creeper (**left**) and *P. tricuspidata*, Japanese creeper (**right**).

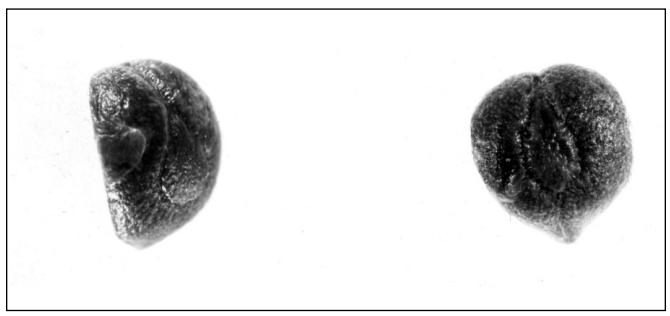
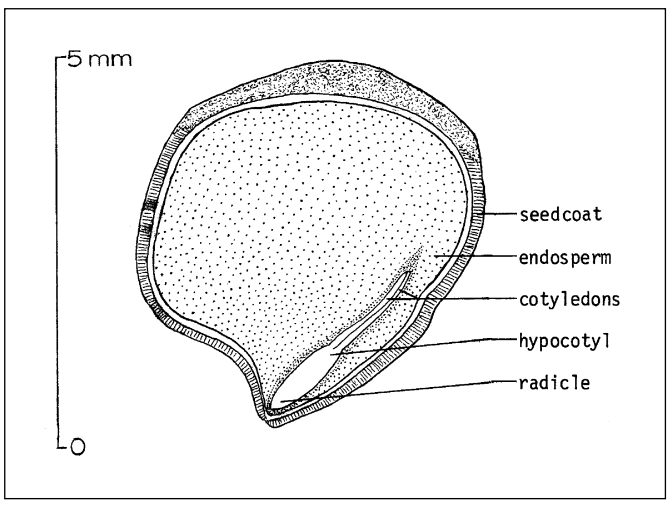


Figure 3—*Parthenocissus quinquefolia*, Virginia creeper: longitudinal section through a seed.



by running the fruits, with water, through a macerator or a hammermill and then floating off the pulp and empty seeds. Seeds in small lots can be extracted with laboratory blenders run at low speed. Extraction should be done carefully because the seedcoats are often soft and easily injured. An extraction method developed for the soft seeds of wild grapes (*Vitis* spp.) may be satisfactory for creepers also. In this method (Gill and Pogge 1974), the berries are placed in bags made of 14-mesh soil screen and a solid stream of water at a pressure of 2,800 kN (400 lb/in^2) is directed onto the berries. Most of the pulp and skins are washed through the screen. The remaining fragments are floated off in a pail of water, and the seeds are recovered from the bottom of the pail. After cleaning, the seeds should be thoroughly dried before storage. Soundness of cleaned seedlots has ranged from 44 to 99% (Swingle 1939). If seed cleaning is not convenient, whole berries can be dried and stored. Cleaned and dried seeds have been stored at room temperatures (Edminster 1947; Fisher and others 1935), but there are no known studies of seed longevity. These seeds are almost certainly to be orthodox in storage behavior, however, so they should keep well for several years at least if stored with low seed moisture (<12%) and at low temperatures (1 to 5 °C). Seeds of another species—*Vitis riparia* (Michx.)—in the same family showed no germination loss after storage for over 2 years in sealed containers at 5 °C (Gill and Pogge 1974).

Cleaned Virginia creeper seeds range from 21,600 to 57,800/kg (9,800 to 26,200/lb) and average 36,500/kg (16,560/lb). No seed yield data on Japanese creeper are available, but they are probably similar to those for Virginia creeper.

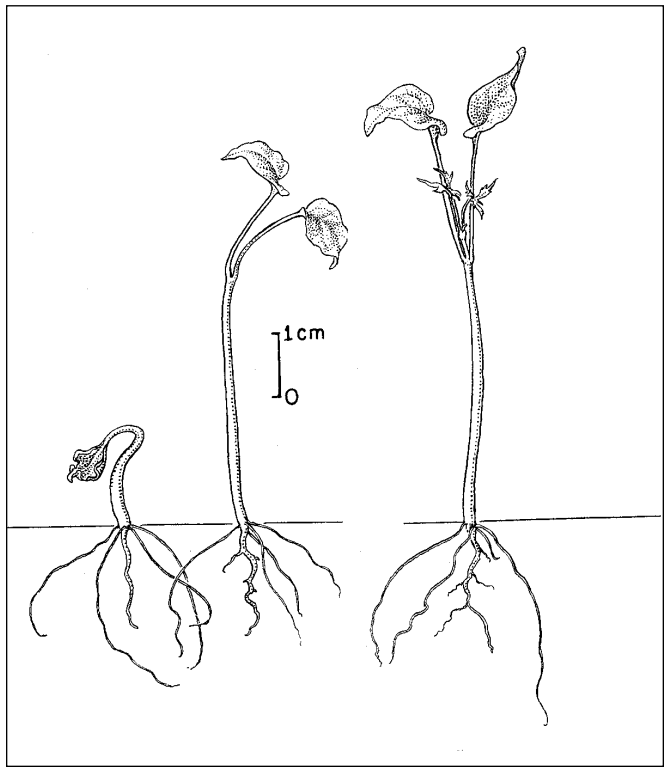
Germination. Natural germination takes place during the first or perhaps the second spring following dispersal and is epigeal (Fisher and others 1935) (figure 4). The seeds have an internal dormancy that can be overcome by moist stratification for about 60 days at 5 °C (Gill and Pogge 1974). Outdoor stratification in winter, during which the seeds become frozen, has also increased germination (Adams 1927; Howard 1915). There are no official germination test prescriptions for creepers, but tests can be made in sand flats at alternating temperatures of 20/30 °C. About 30 days is a sufficient test length for stratified seeds, but untreated seeds may require >150 days (Gill and Pogge 1974). Results from a small number of tests suggest that germination of stratified seeds should peak at about 15 days and reach 70 to 80% by 30 days. For untreated seeds, germi-

nation was less than 5% in 4 tests, but 45% in another that ran for 595 days (Adams 1927; Howard 1915; Gill and Pogge 1974). The excised embryo method has also been used to estimate viability (Flemion 1948; Heit 1955).

Nursery practice. Untreated seeds may be sown in the fall, but spring sowing of stratified seeds is recommended. Seeds should be sown in drills, and covered with about 1 cm ($^1/_2$ in) of soil or soil and mulch (Edminster 1947). For Virginia creeper, Edminster (1947) recommended sowing seeds at the rate of 750/m^2 (70/ft^2) with a target bed-density of 108/m^2 (10/ft^2), but these rates depend on viability, of course. Planting is recommended with either 2+0 or 1+0 stock that has a top height about 15 cm and a stem diameter of about 5 cm, measured 12 mm above the root collar (Edminster 1947).

Creepers can also be propagated vegetatively (Dirr and Heuser 1987). Virginia creeper softwood cuttings taken in June through August should root 100% without hormone treatment, and hardwood cuttings can also be rooted. Japanese creeper softwood cuttings should be treated with 8,000 ppm indolebutyric acid (IBA) in talc. Cuttings should not have tendrils, as buds will not form there.

Figure 4—*Parthenocissus quinquefolia*, Virginia creeper: seedling development at 1, 3, and 33 days after germination.



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P

Scrophulariaceae—Figwort family

Paulownia tomentosa (Thunb.) Sieb. & Zucc. ex Steud.

royal paulownia

Franklin T. Bonner

Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi.

Other common names. paulownia, empress tree, princess tree.

Growth habit, occurrence, and use. Royal paulownia—*Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud.—is a common sight along the sides of roads and railroad tracks, as well as near old house sites, in the Northeast and South. A native of eastern Asia, it has been widely planted in North America from Montreal to Florida and west to Missouri and Texas, as well as in some western states (Bonner 1990). It was introduced for its ornamental value in the 19th century and has escaped from cultivation in many localities. This deciduous tree reaches heights of 9 to 21 m at maturity. It has been planted extensively in the South for specialty wood products and for mine spoil reclamation in surface mine areas (Tang and others 1980).

Flowering and fruiting. The showy, violet or blue, perfect flowers appear in terminal panicles up to 25 cm long in April to May before the leaves emerge. The fruits are ovoid, pointed, woody capsules about 3 to 4 cm long (figure 1). They turn brown when mature in September and October and persist on the tree through the winter (Vines 1960). The trees start bearing seeds at 8 to 10 years of age and are very prolific (Bonner 1990).

Collection, extraction, and storage of seed. The dry fruits can be collected and opened by hand anytime before they disperse their seeds. They can also be collected when still a little green but must be dried completely for seed extraction. One proven extraction method is to place dried capsules in burlap bags and then crush them. Seeds and capsule fragments can then be separated by air (Carpenter and Smith 1979). The tiny, winged, flat seeds are about 1.5 to 3 mm long (figures 2 and 3) and are easily disseminated by wind when the capsules break open on the trees. Fruits collected in southeast Arkansas yielded the following data that appear to be typical for royal paulownia (Bonner and Burton 1974):

Fruits per volume	8,800/hl	3,100/bu
Seeds per fruit	2,033	—
Seeds per volume of fruit	2.8 kg/hl	2.2 lb/bu
Seeds per weight	6,200/g	175,770/oz
Percent moisture content (fresh weight)	7%	—

Royal paulownia seeds are orthodox in storage behavior. Carpenter and Smith (1979) reported that samples stored dry at 4 °C germinated 85% or more after 3 years but the rate of germination declined somewhat. Long-term storage performance has not been studied and is therefore unknown.

Germination. Royal paulownia seeds exhibit little or no dormancy, but light is necessary for timely germination of fresh seeds (Borthwick and others 1964; Toda and Isikawa 1952). Moist stratification at 3 or 4 °C for up to 8 weeks effectively removes the light requirement (Barnhill and others 1982; Carpenter and Smith 1981). Fresh seedlots from the 1974 Arkansas collection mentioned above had a germinative capacity of 90% in 19 days (4 samples) when tested on moist Kimpak with alternating temperatures of 20 and 30 °C. Eight hours of light were supplied during the

Figure 1—*Paulownia tomentosa*, royal paulownia: capsule.

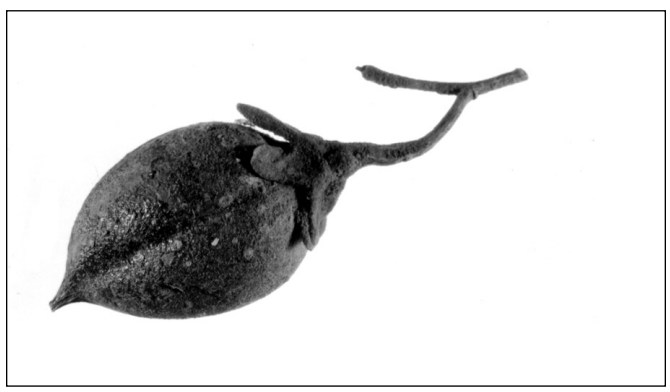


Figure 2—*Paulownia tomentosa*, royal paulownia: winged seed.

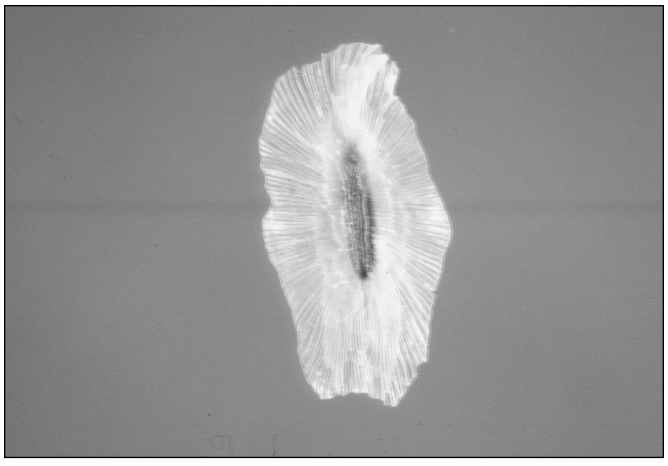
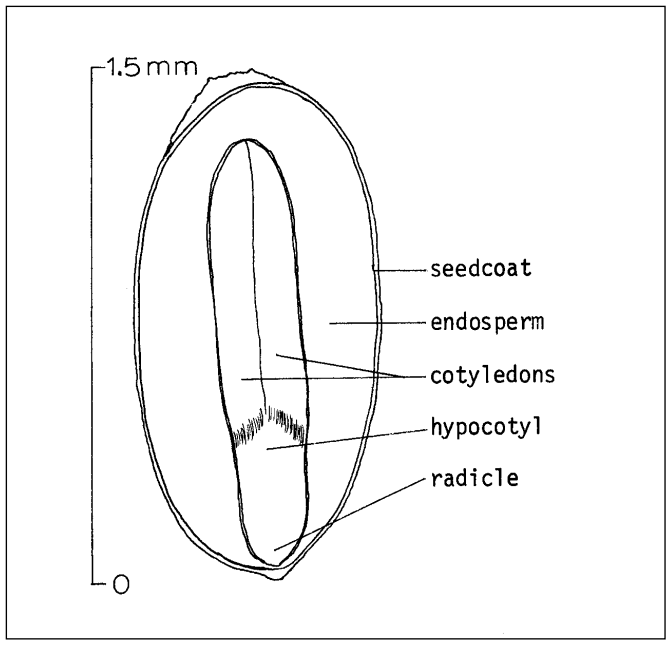


Figure 3—*Paulownia tomentosa,* royal paulownia: longitudinal section through a seed.



30 °C cycle. Germination rate was 86% in 9 days (Bonner and Burton 1974). Excellent germination in the laboratory has also been obtained at a constant 20 °C (Carpenter and Smith 1979) and at alternating temperatures of 10/20 °C (Barnhill and others 1982). Stratification is beneficial at these lower temperatures.

Nursery practice. Royal paulownia seeds should be broadcast on the surface of nursery beds or planted at a depth of about 3 mm ($^1/_8$ in) with mechanical drills. A desirable bed density is approximately 100 seedlings/m^2 (9/ft^2). Unstratified seeds sown in the fall should be mulched; seeds sown in the spring should have been stratified (Williams and Hanks 1976). Container production systems have also been developed for this species (Beckjord 1982; Immel and others 1980).

Vegetative propagation is relatively easy with lateral root cuttings, and successful tissue culture techniques are also available (Tang and others 1980; Dirr and Heuser 1987).

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P

Scrophulariaceae—Figwort family

Penstemon Schmidel

penstemon, beardtongue

Susan E. Meyer

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Growth habit, occurrence, and use. The genus *Penstemon* comprises about 230 species of perennial herbs and subshrubs, most of which are found in western North America. Although most of the species are herbaceous, there are many more subshrubby species than are treated here. Several shrubby species from California that were formerly included in the genus *Penstemon* have been transferred to the closely related genus *Keckiella* Straw. In the previous edition of the Seed Manual, Hylton (1974) treated these species under the name *Penstemon*.

Subshrubby penstemon species occur in most vegetation types of the western United States, from warm desert shrublands to alpine fell-fields (table 1). They are most often found on well-drained, rocky or sandy, infertile soils with sunny exposure. Some species, such as Bridges penstemon, are widely distributed and of wide ecological amplitude, whereas others, such as crevice penstemon, are restricted both geographically and ecologically. Many penstemons are pioneer plants that occupy natural disturbances such as rockslides, making them useful for erosion control along roadsides and for mined land reclamation. They are used to some extent as browse by domestic and wild ungulates, and the seeds are used by rodents, birds, and ants. But perhaps the most important use for penstemons is in ornamental horticulture. Many of the penstemons are among our most outstandingly beautiful wildflowers, and the subshrubby species are no exception (Nold 1999). They are easily grown in cultivation, and many species have found their way into garden catalogues specializing in plants for low-maintenance landscapes. One named variety that is commercially available is shrubby penstemon 'Purple Haze'. Some of the warm-desert species are not hardy in cultivation in the North, although some of these, for example, crevice penstemon, can be successfully grown in containers.

Table 1—*Penstemon*, penstemon, beardtongue: habitat and geographic distribution

Scientific name(s)	Common name(s)	Habitat*	Geographic distribution
***P. ambiguus* Torr.**	**moth penstemon,** bush penstemon, gilia beardtongue	Sandy soil; desert shrubland, pinyon–juniper	S Nevada to S Utah, Kansas, & Oklahoma
***P. fruticosus* (Pursh) Greene**	**shrubby penstemon,** bush penstemon	Shallow soils; spruce–fir, lodgepole pine	N Rocky Mtns from British Columbia to Idaho
***P. leonardii* Rydb.**	**Leonard penstemon,** Leonard's beardtongue	Sagebrush–grassland to aspen–conifer	SE Idaho to S Utah
***P. linarioides* Gray**	**toadflax penstemon**	Sagebrush–grassland to ponderosa pine	Utah & Colorado to Arizona & New Mexico
***P. petiolatus* Brandeg.**	**crevice penstemon,** petiole beardtongue	Limestone crevices; warm desert shrubland	E Mojave Desert
***P. platyphyllus* Rydb.**	**sidehill penstemon,** broadleaf beardtongue	Mountain brush; aspen–conifer	Wasatch Mtns, N Utah
***P. rostriflorus* Kellogg** *P. bridgesii* Gray	**Bridges penstemon**	Warm desert shrubland to alpine	Widespread in W US
***P. sepalulus* A. Nels.**	**littlecup penstemon,** littlecup beardtongue	Sagebrush–grasssland to aspen–conifer	Wasatch Mtns, N Utah

Source: Cronquist and others (1984).
* May include forest type.

Flowering and fruiting. Penstemon flowers are borne in elongate racemes that are often held above the leafy stems, though this habit is often less pronounced in the subshrubby species. The flowers consist of a 5-toothed cuplike calyx, a tubular or snapdragon-like corolla made of 5 fused petals, 5 stamens mounted on the interior of the corolla tube, and a superior 2-chambered ovary that contains many ovules. One of the 5 stamens is sterile, that is, it has no anther, and is often covered with long hairs and exserted from the corolla, hence the name "beardtongue." The flowers are pollinated by a variety of insects and hummingbirds, and flower form, color, and arrangement in each species reflect specialization to attract particular pollinators. Most penstemons flower in the spring or early summer, though some—for example, Bridges penstemon—are midsummer-flowering. Flowering is indeterminate, with the youngest flowers at the tip of each flowering stalk. After fertilization, the ovaries develop into 2-valved capsules that split open at the tip and sometimes along the sides. The numerous gray to black, angular seeds are dispersed by the shaking action of the wind.

Seed collection, cleaning, and storage. Penstemon seeds are usually harvested by hand-stripping or clipping the flowering stalks into containers. Capsules generally begin to split open from 6 to 8 weeks after the plants are in full flower, with those at the base of each stalk ripening first. Stalks can be clipped before the capsules start to open, as long as the seeds can be seen darkening through the ovary wall. If the stalks are clipped after the capsules begin to open, care must be taken to avoid excessive spillage during harvest. For most species, the window of opportunity for harvest is quite wide, as capsules are held upright on the plant and seeds are dispersed only gradually. The harvested material should be dried carefully to avoid molding, especially if it is collected when somewhat green. The capsules will open after harvest, and for small lots, the seeds can be shaken free and collected by screening. For commercial seedlots, processing with a hammermill or barley debearder, followed by a fanning mill, is the usual procedure. Seedlots can readily be cleaned to high purity (>95%).

Penstemon seeds are generally quite small, though size varies considerably among species (table 2). Viability at harvest is usually high (table 2). Damage by seed beetles and other insects during ripening is common, but unfilled and damaged seeds are usually removed in cleaning, so that yield rather than seed quality of the cleaned lot is affected. Penstemon seeds are orthodox in storage behavior, as they keep well in warehouse storage if maintained at moisture contents of 8 to 11%. There is little loss of viability during 5 years, and seeds stored for 15 years may still show viability as high as 50% (Stevens and others 1981, 1996).

Seed germination and testing. The germination requirements of penstemon seeds vary widely, both among and within species (Kitchen and Meyer 1991; Meyer and others 1995). Some species have seeds that are germinable without pretreatment and unaffected by chilling, whereas other species have seeds that are nondormant and negatively affected by chilling, and still others have seeds with a positive requirement for chilling (table 3). In general, seeds of species of the desert Southwest and coastal and cis-montane California are the least likely to have a chilling requirement, whereas those from the Great Basin, Rocky Mountains, and Sierras are more likely to require chilling. Within a species (Bridges penstemon, for example), the length of the chilling requirement is positively correlated with the length of time seeds are likely to spend under snow cover in winter (Meyer 1992; Meyer and Kitchen 1994; Meyer and others 1995).

Table 2—*Penstemon*, penstemon, beardtongue: seed data

Species	Seeds/weight				Mean % viability	Samples
	Mean		Range			
	/g	/oz	/g	/oz		
P. ambiguus	1,000	28,000	820–1,270	23,000–36,000	90	6
P. fruticosus	3,500	98,000	3,230–3,850	90,000–108,000	68	4
P. leonardii	1,250	35,000	900–2,220	25,000–62,000	84	8
P. linarioides	810	23,000	720–900	20,000–25,000	84	4
P. petiolatus	2,700	77,000	2,640–2,800	74,000–78,000	98	2
P. platyphyllus	1,460	42,000	1,390–1,590	39,000–45,000	95	3
P. rostriflorus	2,260	64,000	1,560–2,940	44,000–82,000	87	14
P. sepalulus	1,700	48,000	1,350–2,000,	38,000–56,000	85	6

Source: Meyer (2002).

Table 3—*Penstemon*, penstemon, beardtongue: germination data after 0 to 24 weeks of chilling*

Species	0 wk	4 wk	8 wk	12 wk	16 wk	24 wk	Samples
P. ambiguus	35	21	19	10	16	31	3
P. fruticosus	6	19	14	19	40	83	4
P. leonardii	0	1	22	82	80	80	2
P. linarioides	0	0	1	6	12	10	2
P. petiolatus	100	—	—	100	100	100	1
P. platyphyllus	1	55	66	99	97	100	7
P. rostriflorus	18	17	54	83	—	98	3
P. sepalulus	3	25	37	83	86	100	2

Sources: Kitchen and Meyer (1991), Meyer (2002), Meyer and others (1995).
* Germination percentage for seeds subjected to 0 to 24 weeks of chilling at 1 to 2 °C followed by 4 weeks of incubation at 10/20 °C.

The germination requirements of penstemon seeds generally change very little in dry storage; dormancy status is affected only by conditions during time spent in the imbibed state (Meyer and others 1995). For species and populations from middle elevations in the West, there is rarely a natural dormancy-breaking treatment that will remove dormancy in all seeds of a lot. For those that respond positively to chilling, this is manifest as a fraction that will not respond to chilling of any duration. These seeds form a persistent seedbank under natural conditions, and it is not known how they eventually become germinable. Treatment with gibberellic acid can remove seed dormancy or shorten the chilling requirement for many (but not all) species of penstemon (Kitchen and Meyer 1991). This method may or may not be feasible in a production setting, depending on the degree to which gibberellic acid affects seedling quality. Penstemon seeds germinate best at cool temperatures, and germination at temperatures higher than 20 °C may be completely suppressed, a fact to keep in mind when attempting to produce plants from direct sowing in the greenhouse (Allen and Meyer 1990). Light usually has little effect (Meyer and others 1995).

The quality of penstemon seeds may be evaluated using tetrazolium (TZ) staining, a germination test with chilling or gibberellic acid, or a combination of these. A general seed-testing rule for the genus has been adopted by the Association of Official Seed Analysts (Kitchen and others 1999). This test calls for 2 separate procedures. In the first procedure, seeds are placed on blotters saturated with 500 ppm gibberellic acid, chilled at 2 to 5 °C for 60 days, and incubated at 15 or 10/20 °C for 14 days. Post-test viability of ungerminated seeds is then determined with TZ staining. This procedure is used to determine total viability for the seedlot, and TZ staining on non-incubated seeds may be substituted. In the second procedure, seeds are incubated at 15 or 10/20 °C in the light for 28 days. This second procedure is used to determine the size of the nondormant fraction.

Tetrazolium staining is carried out by allowing the seeds to imbibe water for 24 hours, piercing their seedcoats with a needle, immersing them in 1% TZ for 12 hours at room temperature, and then bisecting them longitudinally for evaluation. The embryo is a small, sausage-shaped body embedded in the copious endosperm. Non-viable embryos usually do not stain at all but remain a yellowish color. Even light pink staining indicates a viable embryo, as evidenced by comparisons with maximum germination percentages for numerous seedlots (Kitchen and Meyer 1991). A simple cut test can be used in place of TZ staining for recently harvested seeds, as the presence of a firm, white, viable embryo is quite evident.

Field planting and nursery practice. Most penstemon species can be established from direct seeding. Seeds should be broadcast on a firm seedbed and lightly covered, raked, or pressed in. Planting should take place in late fall or early winter for most species, except in the summer rainfall areas of the Southwest, where seeds of nondormant species should be sown just before summer rains. Nondormant species may be spring-seeded in the North but may require supplemental water to establish. Penstemons are susceptible to fusarium wilt diseases in cultivation and should not be fertilized or overwatered. They are more likely to survive in coarse, rapidly draining soils that have not previously been used for agriculture. The young seedlings cannot survive heavy competition from weeds or aggressive perennial grasses.

Penstemons may also be readily produced from seeds in container culture. They grow well in a coarse medium in elongated containers such as those used to produce conifer seedlings. Seeds of nondormant species may be direct-sown, whereas chilled seeds or germlings may be planted for those

species with seeds that require chilling. The seedlings will be ready for hardening-off and outplanting in 3 to 4 months, but they can be held much longer if necessary. Survival of outplanted stock is usually high, as long as plants are watered-in well at the time of transplanting and care is taken to eliminate air pockets around the roots. Plants both from direct seeding and outplanting usually flower the second year, and individuals of the subshrubby species can live for 10 years or more. If seed stalks are not clipped, most plants will readily self-seed.

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P

Rosaceae—Rose family

Peraphyllum ramosissimum Nutt.

squaw-apple

Janene Auger and Justin G. Smith

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Growth habit and occurrence. Squaw-apple—*Peraphyllum ramosissimum* Nutt.— the sole member of its genus, is an intricately and rigidly branched deciduous shrub growing to 2 m tall from numerous, gray-barked basal stems. Leaves are simple, linear-oblanceolate, entire or minutely serrulate, and alternate but fascicled on secondary growth at the ends of short lateral spurs. Squaw-apple occurs mainly in well-drained soils on dry foothill and mountain slopes and is associated with several community types, including oak–sagebrush, mountain brush, pinyon–juniper, and the lower edges of ponderosa pine forests (Hitchcock 1961; Shaw and Monsen 2004; Welsh and others 1987). On a microhabitat scale, squaw-apple often grows in mixed-species clumps. The overall range distribution extends from Grant and Baker Counties in north-central Oregon, south to northeastern California, and east through Nevada, southern Idaho, Utah, western Colorado and northwestern New Mexico (Harrington 1954; Hitchcock and others 1961; Welsh and others 1987). Dayton (1931) reports an altitudinal distribution of 915 m in Oregon to 2,740 m towards the southern range limit.

Uses. Wildlife known to eat squaw-apple fruits and seeds or both in Utah include grouse and wild turkeys (family Phasianidae), deer mice (*Peromyscus maniculatus*), chipmunks (*Eutamias* spp.), ground squirrels (*Spermophilus* spp.), and American black bears (*Ursus americanus*) (Auger and others 1995). Deer (*Odocoileus* spp.) browse squaw-apple lightly during the fall and winter (Shaw and others 2004; Smith 1974), and small birds use the intricately branched shrubs as cover even when leaves are not present (Shaw and Monsen 2004). Livestock also browse squaw-apple, and opinions vary widely on its forage value. In central Utah, squaw-apple is said to be almost worthless; in western Colorado, it is considered poor to fair; in eastern Oregon and northeastern California, it is commonly considered fair to moderately good sheep and cattle browse in the spring; and finally, in southwestern Utah, squaw-apple ranks as a valuable browse (Dayton 1931; Plummer and others 1968; Smith 1974). On ranges grazed by cattle during late winter and very early spring, individual plants may be severely hedged (Smith 1974). Even though squaw-apple grows slowly, Monsen and Davies (1985) suggest that it can persist in native plant landscaping for arid environments.

Flowering and fruiting. The regular, perfect flowers with their pinkish, spreading, showy petals open in May and June and appear singly or in clusters of 2 to 5. Data from Utah suggest that flowering intensity is greatest for individual plants larger than 1 m in both height and crown (Auger and others 1995). Squaw-apple is pollinated by a variety of insects, and seed production does not appear to be pollen-limited (Auger and others 1995). The fruits, which ripen from late June to early August, are yellowish red, bitter-tasting pomes measuring 8 to 18 mm in diameter, each containing 1 to 8 plump seeds (figure 1). Seeds consist of a brown, leathery testa entirely filled with embryo (figure 2). At 1,070 m in northeastern Oregon, most of the fruits have either dropped or been partially eaten by birds by mid-August (Smith 1974). At 2,500 m in east-central Utah, initiation of fruit removal precedes ripening, and again, most fruits usually have been consumed by mid-August (Auger and others 1995).

Figure 1—*Peraphyllum ramosissimum*, squaw-apple: seeds.

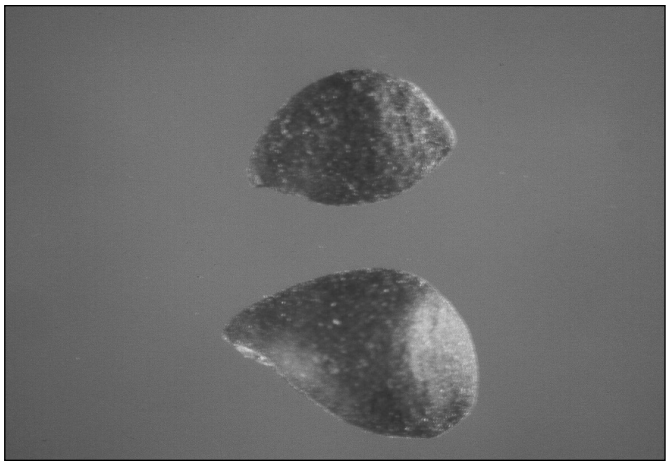


Figure 2—*Peraphyllum ramosissimum*, squaw-apple: longitudinal sections through a seed.

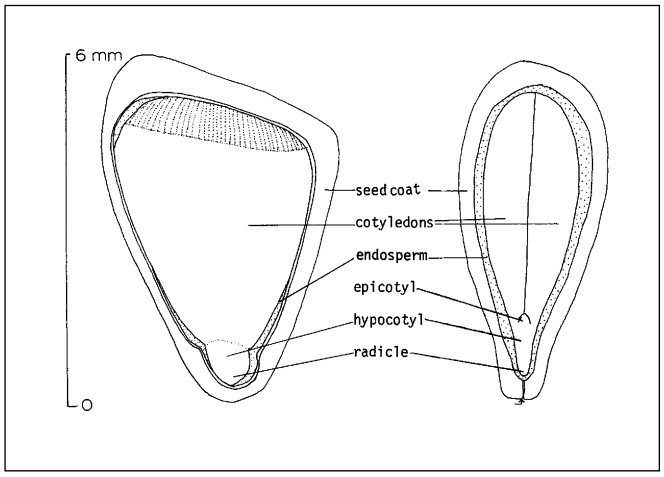
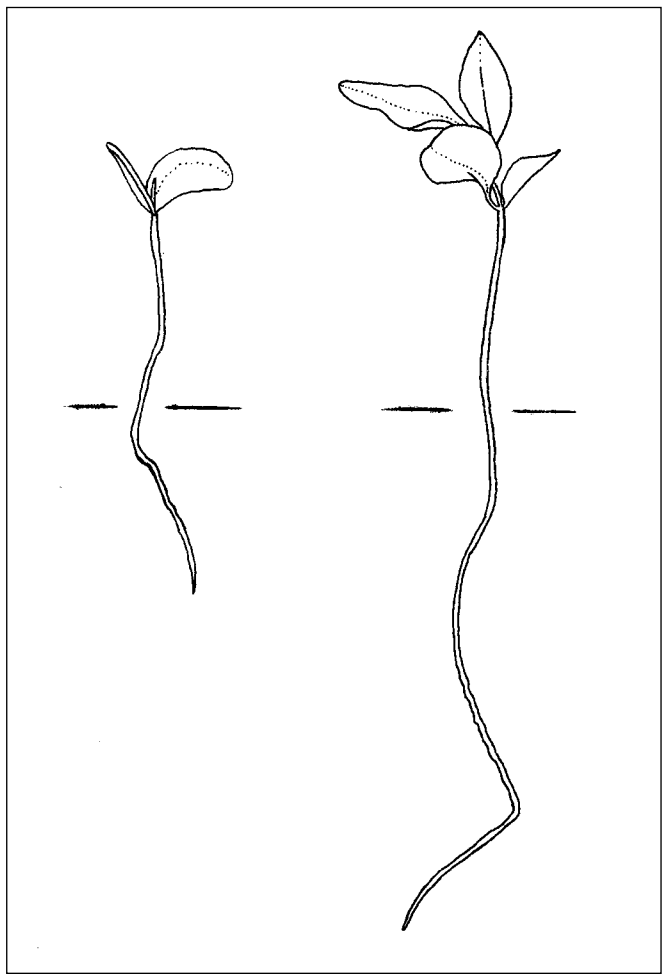


Figure 3—*Peraphyllum ramosissimum*, squaw-apple: germinating seedlings.



Collection, extraction, and storage. Ripe fruits are easily picked from the shrubs. Seeds can be extracted by mashing the fruits in water and floating off the pulp. Any remaining debris may be removed using a fanning mill after the seeds are dry. Seeds stored in a dry, cool, ventilated metal container remained viable up to 5 years (Plummer and others 1968). The yield of pure seeds from 45.5 kg (100 lb) of fresh fruits ranges from 3.0 to 4.7 kg (6.5 to 10.3 lb), and the number of pure seeds per weight ranges from 52,360/kg (23,750/lb) (Plummer and others 1968) to 110,870 (50,290/lb) (Auger and others 1995; Smith 1974). When individual fruits were examined from 2 squaw-apple stands in Utah, filled seeds averaged 71 and 58% of the lot (Auger and others 1995); in another seedlot, fill value was 68% (Smith 1974).

Germination. Germination of squaw-apple seeds is epigeal (figure 3) and may occur during cold stratification both in the laboratory and the field. For 1 seedlot, the percentage viability of filled seeds (tetrazolium method) was 79.8% (Auger 1994). Dormancy is embryo-induced. Embryos excised from unstratified seeds and placed on blotters did not germinate when incubated at 10/20 °C (12/12 hours, day/night). Excised embryos required 49 days—the same as intact seeds—before beginning to germinate during cold stratification (Auger 2002). Tests at the USDA Forest Service's Eastern Tree Seed Laboratory (now the National Seed Laboratory) (Smith 1974) indicated that stratification of seeds in a plastic bag for about 45 days at 3 °C maximizes total germination while minimizing germination occurring during stratification.

For a seedlot collected at 2,500 m, viable seeds treated to 70 days of stratification at 1 °C followed by incubation at 10/20 °C (12/12 hours, day/night), showed 79% total germination (Auger 1994). This represented a 71% difference in value for seeds stratified only 35 days. Viable seeds from the same lot kept in low-temperature stratification (1 °C) showed 50% germination by day 82 and about 95% by day 120. Results from seeds collected the next year (1995) were similar. Smith (1974) reported somewhat lower germination percentages at longer chill durations. When seeds were tested at 30/20 °C (8/16 hours, day/night) after 0, 30, 60, and 90 days of cold stratification, germination of squaw-apple averaged 9, 9, 16, and 51% of total seeds.

Nursery practice. Squaw-apple is grown in nursery beds only occasionally, usually when requested for transplantation at age 1 to 2 years into native-plant gardens (Prag and Prag 1996). In the greenhouse, squaw-apple seedlings emerge in 6 to 12 days from seeds planted about 5 mm (0.2 in) deep and covered with a thin layer of fine sand (Smith 1974). Overwatering and transplantation during the growing season increase the risk of seedling mortality (Prag and Prag 1996). Establishment is rated fair and persistence is very good (Plummer and others 1968; Shaw and Monsen 2004).

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Lauraceae—Laurel family

Persea borbonia (L.) Spreng.

redbay

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Other common names. shorebay, swampbay, swampbay persea.

Growth habit, occurrence, and uses. There are about 150 species of *Persea*, almost all of which are tropical. The best-known is avocado—*P. americana* P. Mill. Only 1 species, redbay—*P. borbonia* (L.) Spreng.—is native to the continental United States (Little 1979). A variety of redbay, swampbay—*P. borbonia* var. *pubescens* (Pursh) Little—is considered by some to be a separate species (Brown and Kirkman 1990; Little 1979). Redbay is found mainly along streams and swampy sites, and occasionally dry woodlands, in the coastal plain from southern Delaware south to the Florida Keys and west to southern Texas and southwest Arkansas (Little 1979; Sargent 1965). It is a small to medium-sized tree that occasionally reaches heights of 18 to 21 m (Brown and Kirkman 1990). The wood is used locally for cabinets and boatbuilding. The fruits are eaten by birds, and the leaves are widely used to flavor soups and meat dishes (Brendemuehl 1990; Brown and Kirkman 1990). The tree is also planted as an ornamental because of its fruit and evergreen foliage.

Flowering and fruiting. Redbay's small (6 mm long), yellow, perfect flowers are borne in axillary panicles that appear from May to June. The fruits are oblong, dark blue, single-seeded drupes that are covered with a thin, fleshy tissue; the endocarp is firm, but pliant (figure 1). Average fruit size is 7 to 10 mm in diameter and 10 mm in length. Seed size is 0.5 to 1 mm less than fruits (figures 2 and 3). The fruits, which are borne on yellow-orange peduncles 12 to 25 mm long, mature in September to October (Brown and Kirkman 1990; Radford and others 1968; Vines 1960).

Collection, extraction, and storage. Redbay fruits can be easily collected by hand from the branches when the exteriors of the fruits turn dark blue or purple. Even though the fruits persist for a short while on the trees, early collection may be necessary to prevent predation by birds. Removal of the fleshy exocarp should not be necessary if seeds are to be planted immediately. If they are to be stored temporarily, removal of this tissue may help avoid damage from pathogens. There are about 3,680 seeds/kg (1,670/lb) (the sample came from Mississippi). Storage data are not available for redbay, so viability retention under typical storage conditions is unknown. Avocado, however, is considered to be recalcitrant in nature and difficult to store (King and

Figure 1—*Persea borbonia*, redbay: fruits.

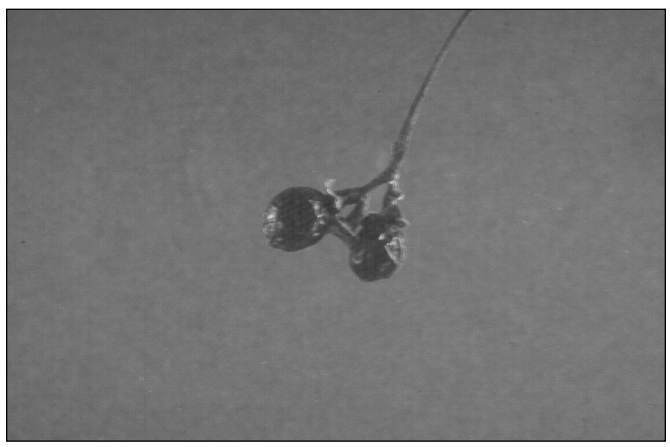

Figure 2—*Persea borbonia*, redbay: cleaned seed.

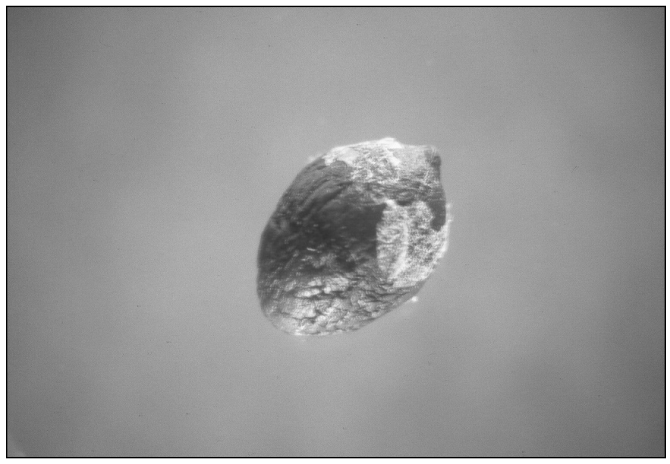

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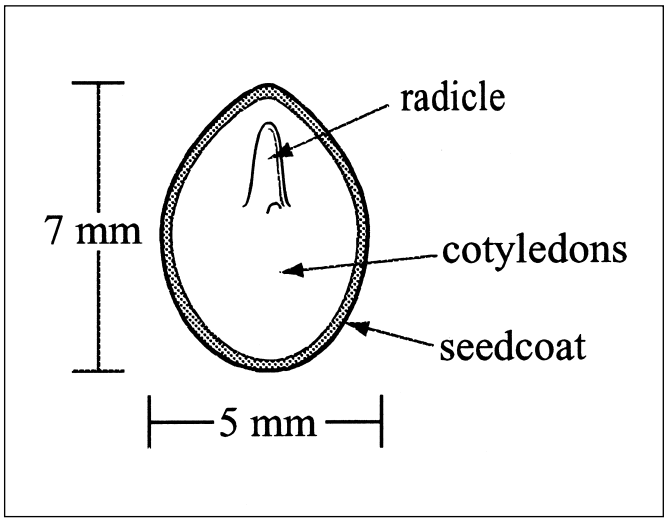
Figure 3—*Persea borbonia*, redbay: longitudinal section through a seed.



Roberts 1980), and redbay may be the same. Some research is clearly needed on this subject.

Germination tests and nursery practice. Redbay apparently has some type of seedcoat dormancy. Tests with 1 sample from Mississippi yielded 44% germination after 56 days for seeds that had part of their seedcoats removed with a longitudinal cut. Untreated seeds and seeds stratified for 28 days at 3 °C had zero germination in the same test. All seeds were germinated on moist blotter paper at alternating temperatures of 20 °C at night for 16 hours and 30 °C for 16 hours in the light. There are no recommended test procedures from official seed testing organizations for redbay. Germination is hypogeal (Brendemuehl 1990).

There are no specific directions for nursery production of redbay. Avocado is commonly propagated from seeds or cuttings (Vines 1960), and redbay may respond to similar practices.

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Rutaceae—Rue family

Phellodendron amurense Rupr.

Amur corktree

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Growth habit, occurrence, and use. Amur corktree—*Phellodendron amurense* Rupr.—is native to northern China, Manchuria, Korea, and Japan. This small to medium deciduous tree—25 to 50 feet tall—has been cultivated in the Far East and eastern Europe. It was introduced into the United States around 1865, and its thick, corky bark and massive, irregular branches have made it of special interest for landscape and environmental plantings in the northern and western United States (Blackburn 1952; Everett 1964; Hoag 1965; Lewis 1957). In tests in Kansas, however, the tree did not perform well and was not recommended for general use (Hensley and others 1991). It is a potential source of industrial cork (Izmodenov 1972; Ota and others 1965), important as a nectar-bearing species in bee-keeping areas of the Russian Far East (Necaev and Pelemenev 1965), and of possible importance for the insecticidal properties of its fruit oils (Schechter 1943). In Byelorussia it is considered a "soil builder" when mixed with Scots pine—*Pinus sylvestris* L. (Letkovskij 1960). It tolerates a wide range of soil conditions, pH, drought, and pollution; it is easily transplanted and generally free of pests.

Flowering and fruiting. The species is dioecious, and female plants develop tend to have a bushier form than males (Hensley and others 1991). Small, yellowish green flowers, in large clusters of terminal panicles, appear in May and June (Krecetova 1960; Rehder 1940; Schechter 1943). Climate affects the time of day when flowers open, pollination, and the longevity of flowers (Starshova 1972).

Fruits are subglobose drupes about 1 cm in diameter (figure 1), green to yellowish green, turning black when ripe in September and October (Read 1974). They remain on the terminal panicles long after the leaves have dropped. Fruits are borne singly on short stalks (figure 1) and are very oily and aromatic. Each fruit usually contains 2 or 3 full-sized seeds and 3 or 4 aborted seeds (Read 1974). Seeds are brown to black, 5 mm long, 2 mm wide, and about 1 mm thick (figures 2 and 3); they have a moderately hard, stony coat (Gorokhova 1981; Read 1974).

Figure 1—*Phellodendron amurense*, Amur corktree: fruit cluster.

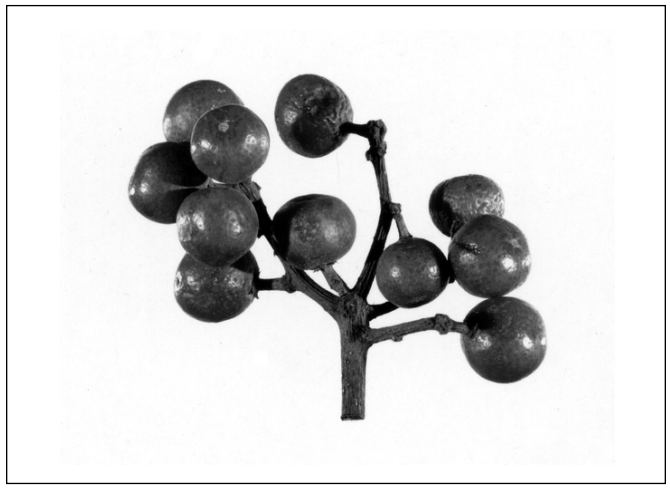
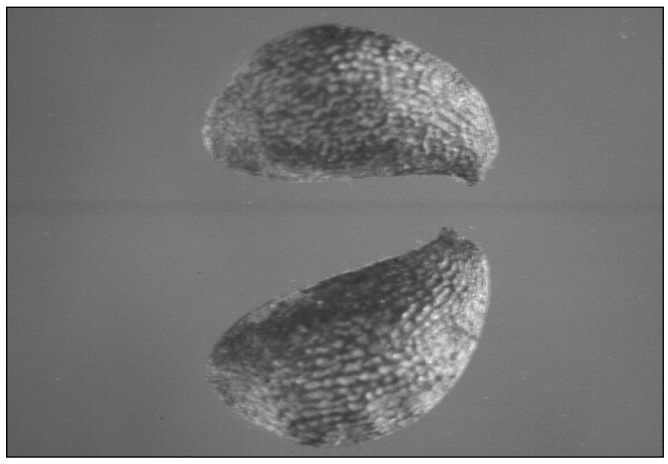
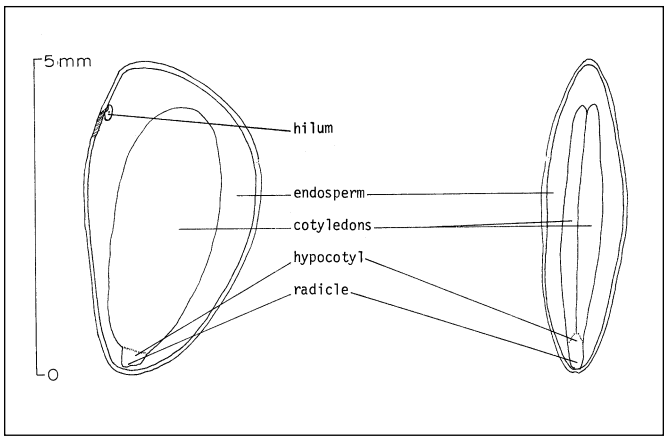


Figure 2—*Phellodendron amurense*, Amur corktree:



Minimum seed-bearing age is 7 to 13 years, both within the natural range and where the species has been introduced (Atkimockin 1960; Gorokhova 1981; Maljcev 1950; Read 1974; Starshova 1972). No data are available on the frequency of seedcrops. Severe drought had no marked effect on the

Figure 3—*Phellodendron amurense*, Amur corktree: longitudinal section through 2 planes of a seed.



morphology of fruits and seeds, but appeared to reduce seed quality (Gorokhova 1986).

Collection, extraction, and storage. The terminal panicles of fruit may be harvested with pruning shears in late September through October after leaf fall. After that, although many fruits remain tightly on the tree, some will have fallen. Fruits should be spread out in shallow layers to prevent heating and mildew during air-drying. Fruits may be soaked in water and seeds squeezed from the fleshy matter by hand; large lots can be run through a macerator and separated from the pulp by flotation. Fresh fruits weigh about 57 kg/hl (44 lb/bu) and yield about 0.9 kg (2 lb) of cleaned seeds (Read 1974). Based on seeds from 2 different lots, 1 kg contained 58,960 to 80,000 (26,800 to 36,363/lb) and 96,800 to 105,600 (44,000 to 48,000/lb) cleaned seeds (Read 1974; Swingle 1939). Seeds collected from plants growing in the natural range had similar seed weights (Gorokhova 1981).

Germination. Fresh seeds germinate well without pretreatment (Dirr 1990; Read 1974). However, there are a number of reports of greatly improved germination following stratification. Stratification is recommended for seeds stored any length of time (Dirr and Heuser 1987). Germination for a seedlot (for which the handling and storage history was not described) was best following cold moist, underground stratification for 166 days (Timm 1989). In another study, seeds stratified for 8 weeks had a higher germination rate and the same germination percentage as seeds stratified 4 weeks; germination of unstratified seeds was less than half that of stratified seeds (Mukai and Yokoyama 1985). Based on the information available, it is recommended that seeds be stratified if the history of collection, handling, and storage is not documented. Seeds of other *Phellodendron* spp. vary in their requirements for stratification (Dirr and Heuser 1987; Lin and others 1994).

Seeds germinate best at alternating temperatures. Both Lin and others (1979) and Mukai and Yokoyama (1985) reported germination of 3% or less at constant temperatures and 75 to 90% at alternating temperatures. The best temperature regimes were 35/5 °C and 35/15 °C (day length and high temperature for 8 hours).

Nursery practice and natural regeneration. In its natural range, natural regeneration sometimes occurs in dense groups. Although the corktree has been reported to sucker from its roots (Dirr and Heuser 1987), this dense regeneration is believed to be from seeds present in the forest floor (Soludukin 1977). Light fire or disturbances that result in drying and warming of the forest floor are believed to promote this development. There was no indication regarding the longevity of the seeds in the forest floor environment, however the endocarp is moderately hard and might facilitate longevity under these conditions (Soludukin 1977).

In the nursery, untreated seeds may be sown in the fall (Read 1974) or stratified through winter for spring-seeding (Yerkes 1945). It is suggested that the best time for spring sowing is when the mean daily soil temperature has reached 8 to 10 °C (Antonyuk 1987). Trees may also be propagated vegetatively by root cuttings or shoot cuttings (Bailey 1947; Dirr and Heuser 1987).

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P

Hydrangeaceae—Hydrangea family

Philadelphus L.

mock orange

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Growth habit, occurrence, and use. The mock oranges—*Philadelphus* spp.—have been placed in several families: Saxifragaceae (Harrington 1954), Hydrangeaceae (Hitchcock and others 1961), and more recently, the Philadelphaceae (Hickman 1993). Hydrangeaceae, however, is the most widely accepted placement (Cronquist and others 1997; USDA NRCS 2001). There are about 50 to 65 species of mock orange, occurring primarily in temperate and subtropical areas of the Northern Hemisphere. Four or five species are native to the United States. Two of these—Lewis mock orange (*Philadelphus lewisii* Pursh) and littleleaf mock orange (*P. microphyllus* Gray)—occur in the western United States and are used in wildland as well as in ornamental plantings (table 1). Both western species are erect to rounded, multi-stemmed, deciduous shrubs with opposite, entire or nearly entire leaves and fragrant white flowers (Hickman 1993; Munz amd Keck 1973; Welsh and others 1987).

Lewis mock orange, the state flower of Idaho, was named for Captain Meriwether Lewis, who collected the plant in 1806. It is an extremely variable plant, growing from 1.5 to 3 m tall and producing leaf blades that are 25 to 75 mm long. The species is distributed from British Columbia to California and eastward into Montana (table 1). It exhibits wide ecological amplitude, growing in riparian areas and on cliffs, talus slopes, and rocky hillsides from the big sagebrush (*Artemisia tridentata* Nutt.) zone to ponderosa pine (*Pinus ponderosa* Dougl.) and lodgepole pine (*Pinus contorta* Dougl.) forests at elevations from sea level to 2,440 m (Hitchcock and others 1961; Hopkins and Kovalchik 1983).

Littleleaf mock orange is a smaller plant, ranging from 0.9 to 2 m in height and producing leaf blades 8 to 25 mm long. It is distributed from Utah to central Mexico (table 1) and grows in pinyon–juniper, mountain brush, aspen (*Populus tremuloides* Michx.), lodgepole pine, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and white fir (*Abies concolor* Lindl.) communities (Hitchcock 1943; Welsh and others 1987).

Both species furnish excellent cover and habitat for wildlife. Lewis mock orange provides good browse for deer (*Odocoileus* spp.) and elk (*Cervus elaphus*), especially on some winter ranges (Kufeld 1973; Leege 1968; Marchant and Sherlock 1984; USDA Forest Service 1937). It is usually not grazed heavily by livestock, but in some areas it does receive fair amounts of use (Leege 1968; USDA Forest Service 1937). Plants resprout and are often more palatable following fire (Leege and Hickey 1971; USDA Forest

Table 1—*Philadelphus*, mockorange: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. lewisii* Pursh** *P. californicus* Benth. *P. gordonianus* Lindl. *P. columbianus* Koehne *P. gordonianus* var. *columbianus* Rehd.	**Lewis mock orange,** Indian arrowwood, syringa*, wild mock orange	British Columbia, SW Alberta, Washington, Oregon, Idaho N of the Snake River, Montana E of the Continental Divide, & N California
***P. microphyllus* Gray** *P. nitidus* A. Nels. *P. stramineus* Rydb.	**littleleaf mock orange,** little-leaf mock orange, desert mockorange	Idaho, Nevada, Utah, SE Wyoming, W Colorado, SE California, Arizona, New Mexico, W Texas, N Mexico

Sources: Conquist and others (1997), Davis (1952), Hickman (1974), USDA ARS (2002), Welsh and others (1987).

* This common name, although widely used, creates some confusion, as it also the generic name of the lilacs, to which the mock orange bears some resemblance.

Service 1937). Quail (*Callipepla* spp.) and squirrels consume Lewis mock orange seeds (Van Dersal 1938). Mule deer (*O. hemionus*) browse littleleaf mock orange (Patton and Ertl 1982).

Mock oranges are valuable plants for revegetating disturbances on steep, rocky, unstable slopes within their native ranges (Stevens and others 2004). Seedlings or larger stock are recommended for planting such sites. Mock oranges are also useful for planting in drier areas of degraded riparian zones.

Mock orange species and their cultivars are used as ornamentals. Lewis mock orange was first cultivated in 1823 or 1884, and littleleaf mock orange in 1883 (Rehder 1940). Both are used as borders, screens, and hedges or as isolated specimens in sunny areas. They can also be used for low-maintenance landscaping and in recreational area plantings (Kruckeberg 1982, Sutton and Johnson 1974, Wright 1980). They do well on a wide variety of soils and require little maintenance. Plants grow vigorously, flower reliably, and are generally free of insect and disease problems.

Native Americans used stems of Lewis mock orange for making arrows (USDA FS 1937). Flowers are used in preparing perfumes and teas (Taylor 1972).

Genetic variation and hybridization. Natural variability in mock orange floral and vegetative characteristics is extensive and has contributed to development of the complex synonymy for each species (Cronquist and others 1997; Hickman 1993; Hitchcock and others 1961; Holmgren and Reveal 1966; Hu 1955; Rydberg 1905). This variability has been exploited to develop numerous hybrids (Rehder 1940; Rydberg 1905) and several ornamental cultivars (Wright 1980). 'Waterton' Lewis mock orange, selected from the Waterton Lakes area of Alberta, is a hardy, bushy shrub with flowers scattered over the crown of the plant (Taylor 1972). The *P. lemoinei* (*P. coronarius* × *P. microphyllus*) group of hybrids exhibit the pineapple scent and beauty of their littleleaf mock orange parent (Sutton and Johnson 1974; Wright 1980).

Flowering and fruiting. Mock orange flowers are white, fragrant, and showy, with 4 (5) petals and numerous stamens. They are produced in few-flowered cymes at the ends of shoots formed the previous year. Western species flower from May to July (Hitchcock and others 1961; Munz and Keck 1973; Orme and Leege 1980). Fruits are woody, turbinate, loculicidal capsules that mature in late summer (figure 1); those of Lewis mock orange dehisce in September or October (Marchant and Sherlock 1984; Orme and Leege 1980). The seeds are dispersed by wind and gravity.

Seeds of both species are slender, 3 mm long, pale brown, and caruncular with a thick, brown seedcoat (Hurd 1995; Taylor 1972) (figures 1 and 2). The embryo is cylindrical and well developed (figure 2). A thin layer of endosperm adheres to the seedcoat. Lewis mock orange plants grown from seed may begin flowering in the second or third year (Everett 1957).

Figure 1—*Philadelphus lewisii,* Lewis mock orange: capsules and cleaned seed.

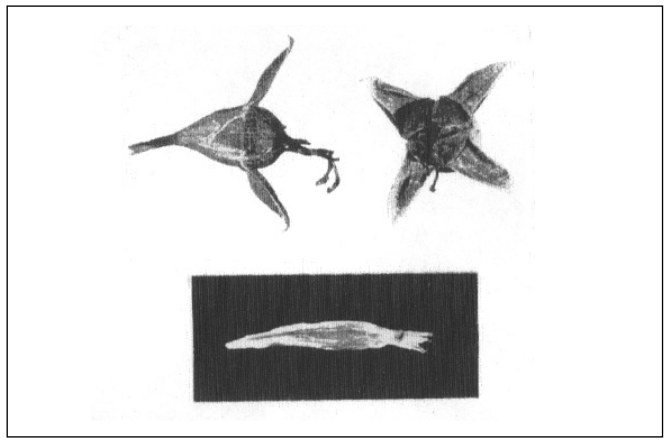
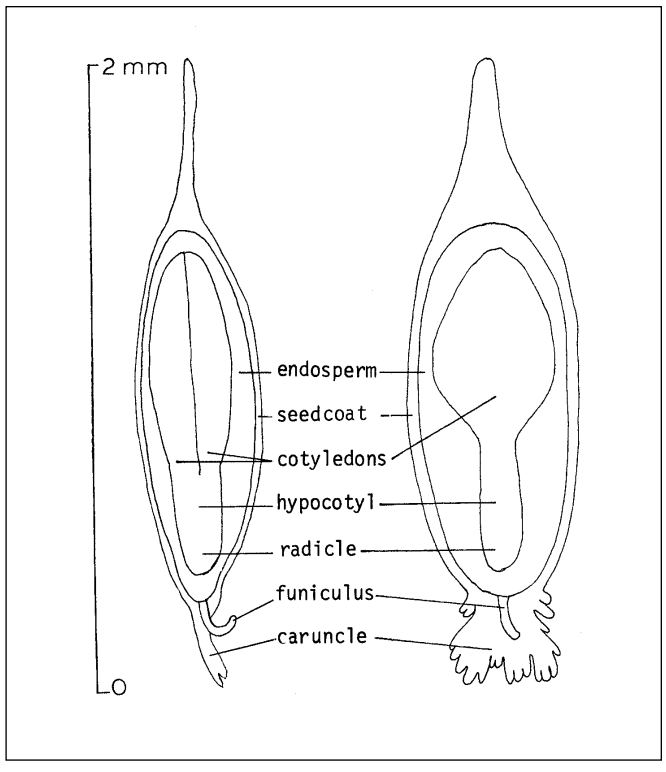


Figure 2—*Philadelphus lewisii*, Lewis mock orange: longitudinal sections of a seed.



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Collection, cleaning, and storage of seeds. Mock orange seeds are collected in late summer by hand-stripping the capsules after they have turned dark brown and the valves have just begun to open (Stevens and others 2004). After drying, seeds are extracted by crushing the capsules with a barley de-bearder, or if most capsules have opened, seeds are separated from coarse debris using an aspirator or air-screen machine (Glazebrook 1941). Shaking or crushing the dried capsules and screen to remove debris cleans small lots. The number of cleaned seeds of Lewis mock orange was estimated at 11,600,000/kg (5,300,000/lb), with a range of 7,700,000 to 18,000,000 (3.5 to 8 million/lb) (Glazebrook 1941; Hurd 1995; Mirov and Kraebel 1939; Swingle 1939). Fill of cleaned seedlots varies with rigor of cleaning. Acceptable purity for commercial seed purchases is 95% and acceptable germination is 65% (Jorgensen 2004).

Seeds of Lewis mock orange can be sown as soon as they are ripe or placed in storage for later planting. Reports of longevity vary, but the seeds appear to be orthodox in storage behavior. Refrigerated storage has been recommended (Marchant and Sherlock 1984). Taylor (1972) reported that dry seeds could be stored in airtight containers in a cool place for 1 year.

Germination. Seeds of Lewis mock orange reportedly require light for germination (Dirr and Heuser 1987), but exposure to continuous light or darkness may be inhibitory (Glazebrook 1941). Germination is enhanced by 20 to 75 days of wet prechilling at 0 to 5 °C (Dirr and Heuser 1987; Marchant and Sherlock 1984; Stickney 1974). Germination seeds from 2 sources that were chilled for 8 weeks at 5 °C and incubated at 22 to 26 °C was 64% (Glazebrook 1941) and 52% (Mirov and Kraebel 1939). Without prechilling, germination of seeds from 4 Idaho and Oregon collections incubated at 15 or 20/10 °C (8/16 hours) for 28 days was 12% or less (Shaw 1995) (table 2). A 28-day prechill at 3 to 5 °C improved germination with the increase greater when seeds were incubated at 15 °C compared to 20/10 °C (table 2).

Littleleaf mock orange is readily propagated from seeds (Sutton and Johnson 1974; Swingle 1939). Germination of untreated seeds collected in New Mexico was 12 times greater when they were incubated at 15 compared to 20/10 °C (8/16 hours) for 28 days (Shaw 1995) (table 2). Prechilling for 28 days at 3 to 5 °C improved germination if seeds were subsequently incubated at 20/10 °C, but decreased germination if they were incubated at 15 °C (table 2). Germination of both species is epigeal.

Nursery practice. Bareroot stock of Lewis mock orange may be produced by fall-seeding untreated seeds or by spring-seeding prechilled seeds (Stevens and others 2004). Uniformity of seed spacing may be improved by diluting the small seeds with rice hulls. Seeds should be covered very lightly. Seedlings develop rapidly and can be transplanted as 1-year-old stock.

Container stock may be grown from seeds (Atthowe 1993). Seedlings should be provided with shade for the first month and not watered excessively, as they are fragile and susceptible to damping-off (Taylor 1972). The 3-leaf stage should be attained before seedlings are transferred to larger containers.

Table 2—*Philadelphus,* mock orange: germination test conditions and results

Species, seed source, & elevation	Seed fill (%)	Viability (%)	Wet prechill (days)	Percentage germination 15 °C	Percentage germination 20/10 °C
P. lewisii					
Banks, ID (830 m)	98	96	0	1	1
	98	96	28	57	16
Craters of the Moon National	100	92	0	12	6
Monument, ID (1,680 m)	100	92	28	41	23
Grant Co., OR (1,020 m)	100	90	0	8	5
	100	90	28	47	33
Idaho City, ID (1,650 m)	99	96	0	2	2
	99	96	28	34	33
P. microphyllus					
Sandoval Co., NM (2,380 m)	98	63	60	5	
	98	63	28	44	20

Sources: Shaw (1995).
Note: Seeds were prechilled at 3 to 5 °C and then incubated at 15 or 20/10 °C (8/16 hours) for 0 or 28 days. The percentage germination was then determined. For 28 days of incubation, seeds were exposed to 8 hours of light (PAR=350 μMol/m^2/sec) each day. Exposure corresponded to the high temperature period of the alternating temperature regime. Viability is based on the percentage of viable seeds to germinate normally.

Mock orange is easily propagated from softwood or hardwood cuttings, rooted suckers, divisions, or layers (Hartmann and others 1990; Macdonald 1986; Sutton and Johnson 1974). Softwood cuttings harvested in midsummer root readily under a mist system. Root production is enhanced by treatment with 1,000 ppm indole butyric acid (IBA) (Dirr and Heuser 1987; Marchant and Sherlock 1984). Hardwood cuttings may be harvested and planted in fall or early spring (Hartmann and others 1990; Macdonald 1986). These should be treated with 2,500 to 8,000 ppm IBA. Both types of cuttings can also be rooted in a cold frame (Macdonald 1986; Marchant and Sherlock 1984).

Field practice. Mock orange seeds may be broadcast seeded on a rough seedbed and covered lightly or spot-seeded on prepared seedbeds (Stevens and others 2004). Seeds may also be surface-planted using a seeder that presses the seeds into the soil surface. Best results are obtained if seeds are planted in well-drained sites free of herbaceous competition. Seeds may be mixed with other shrub seeds that require surface or shallow planting.

Mock orange seedlings quickly develop a fibrous root system and transplant easily as bareroot or container stock (Everett 1957; Sutton and Johnson 1974). Youtie (1991, 1992) obtained good survival of Lewis mock orange planting stock grown from cuttings and planted on a disturbed site in the Columbia River Gorge. Plant growth is reportedly slow for Lewis mock orange (Taylor 1972) and moderate to rapid for littleleaf mock orange (Sutton and Johnson 1974).

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P

Rosaceae—Rose family

Physocarpus (Camb.) Raf.

ninebark

Andrew Youngblood, John D. Gill, and Franz L. Pogge

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Growth habit, occurrence, and use. The genus *Physocarpus* includes about 6 species of deciduous, spiraea-like shrubs with exfoliating bark, alternate and lobed leaves resembling *Ribes*, and small white to pinkish flowers in corymbs. The common name, ninebark, probably refers to the use of the plant in a number of medicinal cures (Stokes 1981) or the numerous layers of bark that peel off (Strausbaugh and Core 1978). Five species are native to North America, and one is introduced from Asia (table 1). Three subspecies of dwarf ninebark—*P. alternans* ssp. *alternans, P. a.* ssp. *annulatus* J.T. Howell, and *P. a.* ssp. *panamintensis* J.T. Howell—are recognized (USDA NRCS 2001). Although the genus is not wide-spread, certain species may be locally abundant because of root sprouting. Atlantic ninebark and common ninebark, 2 varieties of *opulifolius* — the specific epithet refers to *Viburnum opulus,* an introduced species from Europe (Stokes 1981)—are the most common species in the eastern United States and are found along streams, riverbanks, and moist hillsides. Atlantic ninebark grows to 1.5 m, whereas common ninebark may be twice that height. A dense, compact cultivar of Atlantic ninebark named 'Nugget' produces golden yellow foliage in the spring that matures to orange-bronze (Higginbotham 1990). Of the western species, dwarf ninebark is found mostly in rocky canyons and low-elevation forests of California and grows to 1 m in height; mountain ninebark is found from foothill forests to mountain tops of the central and southern Rocky Mountains and grows to 1 m in height; mallow ninebark is found in rocky canyons and low-elevation open forests throughout the Rocky Mountains and grows to 2 m; and Pacific ninebark is found in moist to wet lowlands or foothills mostly west of the Cascade Range and grows to 3 m. A prostrate and rhizomatous cultivar of Pacific ninebark named 'Tilden Park' grows to a height of 1.5 m (Straley 1989).

Ninebark species and cultivars generally are hardy, do best in full sunlight or thin shade, and tolerate a wide variety of soil types (Krüssmann 1985). They are used primarily as ornamentals in landscaping or for watershed protection. Most of the species have been cultivated in the United States for nearly 100 years (table 1). In the wild, mallow ninebark sprouts prolifically from the root crown after spring and fall fires (Lea and Morgan 1993). Although the genus is reported to be remarkably free from insects and diseases (Everett 1981; Gill and Pogge 1974), at least 17 flower-eating, 63 leaf-and-stem-eating, and 4 seed-eating insects have been identified on common ninebark, including the flower-specialist mirids *Plagiognathus punctatipes* Knight and *Psallus physocarpi* Henry and seed-specialist torymids *Megastigmus gahani* Milliron and *M. physocarpi* Crosby (Wheller and Hoebeke 1985).

Flowering and fruiting. Flowers are complete, regular, and clustered together in terminal corymbs consisting of a few in mountain and mallow ninebarks, 3 to 6 in dwarf ninebark, and many in Pacific and common ninebarks. Flowers are from 0.5 to 1 cm in diameter, the corolla mostly white, sometimes pinkish to light pink in Pacific and mountain ninebarks. The 5 sepals are densely stellate pubescent to tomentose, except in Pacific ninebark, where they are sometimes glabrous (Krüssmann 1985). Flowers of Pacific ninebark appear in April through June, those of mountain ninebark appear in May through June, and those of mallow and common ninebarks in June.

The fruits are small, firm-walled, inflated follicles (figure 1); the generic name *Physocarpus* is derived from the Greek *physa* ("bladder" or "bellows") and *karpos* ("fruit"), referring to the bladder-shaped follicles (Stokes 1981). Follicles range in size from 5 mm in dwarf ninebark to 11 mm in Pacific ninebark. They are solitary in dwarf ninebark and sometimes mountain ninebark; paired in mallow ninebark and sometimes mountain ninebark; and

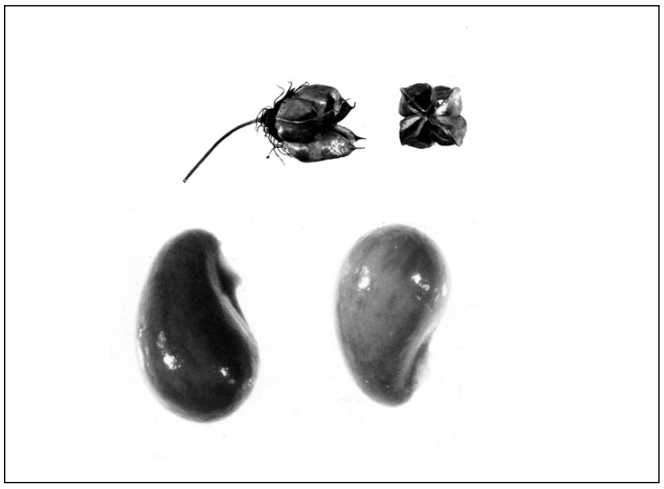
Table 1—*Physocarpus,* ninebark: nomenclature, occurrence, and first cultivation

Scientific name & synonyms	Common name	Occurrence	First cultivated
***P. alternans* (M.E. Jones) J.T. Howell** *Neillia monogyna* var. *alternans* Jones *Opulaster alternans* Heller	**dwarf ninebark**	California to Nevada	—
***P. amurensis* (Maxim.) Maxim.** *Spiraea amurensis* Maxim.	**Amur ninebark**	Manchuria & Korea	1856
***P. capitatus* (Pursh) Kuntze** *Spiraea capitatus* Pursh	**Pacific ninebark**	Alaska, British Columbia, Montana, south to California	1827
***P. malvaceus* (Greene) Kuntze** *Neillia malvacea* Greene *Opulaster malvaceus* (Greene) Kuntze ex Rydb. *Opulaster pauciflorus* (Torr. & A. Gray) Heller *Opulaster pubescens* Rydb. *P. pubescens* (Torr. & A. Gray) Piper *P. pubescens* (Rydb.) A. Nels. *P. pauciflorus* Piper ; *Spiraea opulifolia* L.	**mallow ninebark**	British Columbia to Montana, south to Oregon, Utah, & Wyoming	1897
***P. monogynus* (Torr.) Coult.** *Opulaster hapmanii* Rydb. *Opulaster monogynus* Kuntze *P. torreyi* (S. Wats.) Maxim.	**mountain ninebark**	South Dakota to Texas, Arizona, Nevada	1889
***P. opulifolius* (L.) Maxim.** *Opulaster alabamensis* Rydb. *O. australis* Rydb. *O. opulifolius* (L.) Kuntze; *O. stellatus* Rydb. *Spiraea opulifolia* L.	**common ninebark**	Maine to Minnesota, S to Tennessee & Florida	1687
***P. opulifolius* (L.) Maxim. var. *intermedius* (Rydb.) Robins.** *Opulaster intermedius* Rydb. *P. intermedius* (Rydb.) Schneid. *P. missouriensis* Daniels; *P. ramaleyi* A. Nels.	**Atlantic ninebark** Missouri	Quebec to North Dakota, S to Colorado, Arkansas, &	1908

number 3 to 5 in Amur, Pacific, common, and Atlantic ninebarks. When mature, the follicles tend to be brown, reddish, or coppery in color, glabrous in common ninebark and sometimes Pacific ninebark, otherwise stellate-pubescent. Follicles burst open at both sutures when mature. They seldom fall of their own weight but are easily dislodged by wind or snow. Some fruits may persist until the end of winter (Gill and Pogge 1974). Each follicle may contain several seeds, which are shiny and pyriform (figures 1 and 2). Seed ripening is indeterminate and does not always result in good fill (Link 1993).

Collection, extraction, and storage. Ripe fruits can be picked from the shrubs or shaken onto dropcloths, dried either naturally or with artificial heat, and then threshed with a hammermill, and cleaned. Seeds of common and Atlantic ninebark are extracted by dry maceration followed by hand-screening to remove debris and follicle fragments (Yoder 1995). Yields are about 1,650 clean seeds/g (46,800/oz) for mallow ninebark (Link 1993), 1,550 clean seeds/g (43,750/oz) for Pacific ninebark (USDA NRCS 2001), and

Figure 1—*Physocarpus opulifolius*, common ninebark: follicles (**above**) and seeds (**below**).



1,000 to 3,650 clean seeds/g (28,350 to 103,500/oz) for common ninebark (Gill and Pogge 1974). Viability is usually less than 50%. The seeds are orthodox and may be stored for at least 5 years when cool and dry (Link 1993).

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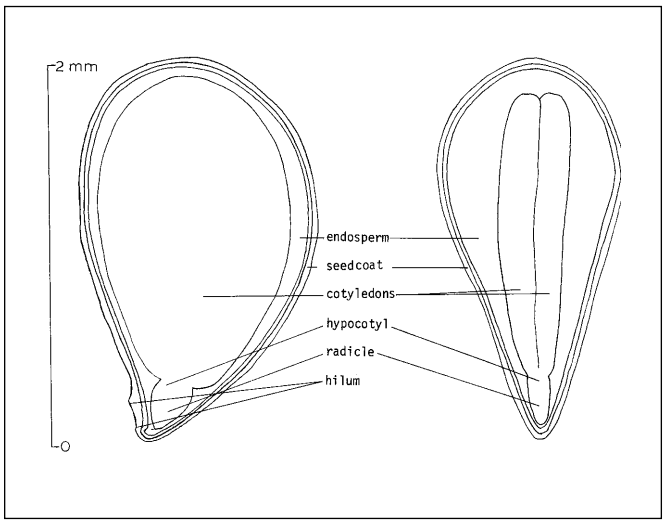
Figure 2—*Physocarpus malvaceus*, mallow ninebark: longitudinal sections through a seed.



Nursery practices. Mallow ninebark seeds may be planted in the fall or planted in the spring after 30 days of prechilling (Link 1993). Seeds of common ninebark and Atlantic ninebarks are sown in raised beds either in the fall or in the spring after 60 days of prechilling (Yoder 1995). Seeds are mixed one part seeds to three parts (by volume) dry, sifted sawdust to provide bulk and facilitate even distribution; sown at a depth of about 3 mm ($^1/_8$ in); and mulched with a layer of sawdust about 6 mm ($^1/_4$ in) thick (Yoder 1995). The ninebarks are easily propagated by softwood cuttings planted under mist, or hardwood cuttings planted in the field (Everett 1981; Dirr and Heuser 1987).

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Pinaceae—Pine family

Picea A. Dietr.

spruce

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Growth habit, occurrence, and use. The spruce genus—*Picea*—includes 40 to 50 species of evergreen conifers native to the temperate and boreal regions of the Northern Hemisphere, occurring in Europe, Asia Minor, the Caucasus, Siberia, China, Japan, the Himalayas, and North America (table 1). The genus evolved from primordial ancestors in the northeastern mainland of Asia, with present-day Korean spruce likely the most primitive species. Most North American species probably arose through eastward migrated and mutation of Ezo spruce (Wright 1955). More recent work suggests a strong relation between the Old World Serbian spruce and the New World black spruce (Fowler 1980). At least 12 species occur in China (Li and others 1990). Seven species are native in North America, excluding the rare and localized occurrence of Chihuahua spruce—*P. chihuahuana* Martinez—in northwest Mexico (Rushforth 1986; Patterson 1988). The genus name is derived from the Latin *pix* or *picis,* "pitch", referring to the resinous qualities of the trees (Everett 1981) or of a pitch pine, probably Scots pine (*Pinus sylvestris* L.) (Little 1979).

The genus includes medium to tall conifers that range in height at maturity from 9 to over 70 m. Crowns of most species appear conical in outline. The generally small branches occur in whorls with common internodal branches. The needle-like leaves are borne on peg-like projections (pulvini) on the twigs, have angled or flattened cross section, and persist for several years. Needles fall readily from twigs on drying. The slender boles gradually taper along their entire length, sometimes from a buttressed base. The thin and scaly bark sometimes has furrows at the base of old trees. The generally shallow root systems have many long, stringy, and tough rootlets. Open-grown trees retain live branches to the ground, and in black spruce and sometimes Norway, Ezo, and white spruces, layering occurs when branch tips come in contact with moist soil, take root, and develop into full-size trees (Nienstaedt and Zasada 1990; Nikolov and Helmisaari 1992; Stone and McKittrick 1976; Viereck and Johnston 1990).

Members of the spruce genus grow on various soils and at all elevations up to treeline in the more northern latitudes. In more southern latitudes, spruce species usually inhabit cold, wet, or shallow soils of bogs or higher elevations on mountain slopes. Shade-tolerant spruce species often replace stands of birch (*Betula*), quaking aspen (*Populus tremuloides* Michx.), or other pioneer species on disturbed areas (Dallimore and Jackson 1967). Nursery and greenhouse cultivation currently provide seedlings and transplants of 7 North American and 8 introduced species for forestry or horticultural purposes in the United States (table 1).

The strong, light-weight, light-colored, fine-grained, even-textured, long-fibered wood of Engelmann, white, black, red, and Sitka spruces result in high-value timber. However, the restricted range, occurrence in inaccessible locations, and propensity for developing knots limits the commercial timber value of Brewer spruce (Thornburgh 1990). Specialty products have included violin faces and piano soundboards from Engelmann, white, red, and Sitka spruces; aircraft parts from Engelmann and Sitka spruces; and house logs from Engelmann and white spruces. The occurrence of most species at high elevations and on steep slopes or wet soils makes them important watershed protectors. The genus also provides important winter shelter for wildlife in the higher latitudes. Although some animals such as snowshoe hare (*Lepus americanus*), porcupine (*Erethizon dorsatum*), and black bear (*Ursus americanus*) may sometimes browse on spruce foliage or inner bark, neither wild or domestic animals prefer spruce as a food source (Alexander and Shepperd 1990; Blum 1990; Dallimore and Jackson 1967; Harris 1990; Nienstaedt and Zasada 1990; Viereck and Johnston 1990).

Tolerance of extreme exposure to wind and cold temperatures makes spruce especially well-suited to some shelterbelt planting. White, Norway, blue, and Sitka spruces have been widely used for this purpose. The relatively shallow root systems of Engelmann, white, blue, red, and Sitka spruces make these species susceptible to windthrow, how-

Table 1—*Picea,* spruce: nomenclature and occurrence of native and cultivated species in North America

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. abies* (L.) Karst.** *P. excelsa* Link	**Norway spruce**	Native of Fennoscandia, W Europe to Ural Mtns of central Russia; widely planted in NE & central US
***P. asperata* Mast.** *P. crassifolia* Kamarov	**dragon spruce,** Chinese spruce	Native of NW China; occasionally cultivated in US
***P. breweriana* S. Wats.**	**Brewer spruce,** weeping spruce	NW California & SW Oregon
***P. engelmannii* Parry ex Engelm.** *P. columbiana* Lemmon *P. glauca* ssp. *engelmann* (Parry ex Engelmann) T.M.C. Taylor *P. engelmanii* var. *glabrata* Goodman	**Engelmann spruce,** mountain spruce	Rocky Mtns from British Columbia S to Arizona & New Mexico; Cascade Range in Washington & Oregon
***P. glauca* (Moench) Voss** *P. alba* (Aiton) Link *P. alba* var. *albertiana* (S. Brown) Beiss. *P. albertiana* S. Brown; *P. canadensis* B.S.P. *P. canadensis* var. *albertiana* (S. Brown) Rehder *P. glauca* var. *albertiana* (S. Brown) Sarg. *P. glauca* var. *posildii* Raup *P. nigra* var. *glauca* Carr.	**white spruce,** Canadian spruce, skunk spruce, cat spruce, Black Hills spruce, western & white spruce, Alberta spruce, Porsild spruce	Norton Sound to Gulf of Alaska, E across Canada from British Columbia SW Alberta to Labrador, Newfoundland; also in Black Hills of South Dakota
***P. glehnii* (Fr. Schmidt) Mast.**	**Sakhalin spruce**	Native to Sakhalin & Hokkaido; planted in NE US to Newfoundland
***P. jezoensis* (Siebold & Zucc.) Carr.** *P. ajanensis* (Lindley & Gordon) Fischer ex Carr. *P. kamchatkensis* LaCassagne *P. komarovic* Vasiljev *P. microsperma* (Lindley) Carr.	**Ezo spruce,** yeddo spruce, yezo spruce	Native of SE Russia, Shantar Islands, Kamchatka Peninsula, Sakhalin Island, S to NE China, N Korea, & N Japan
***P. koraiensis* Nakai**	**Korea spruce,** Koyama spruce	N Korea, NE China, & Sikhote-Alin Mtns of SE Russia
***P. mariana* (Mill.) B.S.P .**	**black spruce,** bog spruce, swamp spruce, eastern spruce	Alaska to Labrador, Newfoundland; NE & N central US
***P. obovata* Ledeb.** *P. abies* var. *obovata* Lindquist	**Siberian spruce**	From White Sea & Kola Peninsula E across Russia to Sea of Okhotsk
***P. omorika* (Pancic) Purk.**	**Serbian spruce**	SE Europe
***P. pungens* Engelm.** *P. commutata* Horton *P. parryana* Sarg.	**blue spruce,** Colorado spruce, Colorado blue spruce	Rocky Mtns in Wyoming, Utah, & Colorado, scattered in Arizona & New Mexico
***P. rubens* Sarg.** *P. australis* Small *P. nigra* (Ait.) Link var. *rubra* (Du Roi) Engelm. *P. rubra* (DuRoi) Link (not A. Dietrich)	**red spruce,** West Virginia spruce, eastern spruce, yellow spruce, he-balsam	Nova Scotia, S Quebec, New York, & S in Appalachian Mtns to North Carolina
***P. sitchensis* (Bong.) Carr.** *P. sitchensis* Bong. *P. falcata* (Rafin.) Suringar *P. menziesii* (D. Don) Carr. *Abies falcata* Rafin. *A. menziesii* (D. Don) Lindley *Pinus menziesii* Douglas	**Sitka spruce,,** coast spruce, tideland spruce, yellow spruce, Alaska spruce	Gulf of Alaska & Kodiak Island to N California
***P. smithiana* (Wall.) Boss.** *P. morinda* Link *P. ramaleyi* A. Nels.	**Himalayan spruce,** west Himalayan spruce	N India & Pakistan

Sources: USDA ARS (2005), NRCS (2001).

ever, especially when growing on sites with moist soils or high water tables. The conical form and dense, persistent branches of spruce species make them highly desirable for environmental plantings. All 7 North American species and the introduced Norway, Ezo, dragon, and Serbian spruces are planted as ornamentals. Many cultivars featuring variations or extremes in crown height, shape and symmetry, or thickness; rate of height growth; branch angle and degree of twig droop; and needle color exist (Everett 1981, Huxley 1992). In general, spruce species do not tolerate droughty

sites but do thrive on slightly acidic and moist but well-drained soils. Of all the species, Serbian spruce may best tolerate industrial air pollution (Dallimore and Jackson 1967).

Geographic races and superior strains. The wide ranges and diverse environments to which the spruce species have adapted provide an array of individual, ecological, and geographic variations. Natural hybridization and introgression commonly occur where ranges of compatible species overlap. Hybridization between white spruce and Sitka spruce (first reported by Little 1953 as *P.* × *lutzii)*, occurs in British Columbia and throughout the Kenai Peninsula in Alaska (Copes and Beckwith 1977). This hybrid has demonstrated a genetically based resistance to attack by the Sitka spruce weevil—*Pissodes strobi* Peck—which causes severe height growth and stem form reduction in Sitka spruce (Mitchell and others 1990). Hybridization between white spruce and Engelmann spruce occurs in northern Montana and British Columbia (Daubenmire 1974). Artificial crosses of Engelmann spruce with Sitka spruce and with blue spruce suggest the close relatedness of these North American species (Fowler and Roche 1977). Electrophoresis has yet to clearly identify hybrids of Engelmann spruce and blue spruce along a 1,200-m elevational transect in the front range of the Colorado Rocky Mountains, where the species grow together. Morphological similarity between the 2 species, such as number of bud scales, number of stomatal rows, and location of resin sacs, however, suggests either convergent evolution or the influence of environmental variation on the morphological characters (Mitton and Andalora 1981). Natural introgression between the maritime Sitka spruce and the more interior complex of white and Engelmann spruces occurs in a portion of British Columbia, and the hybrid fraction was estimated by restriction fragment length polymorphisms of the nuclear ribosomal RNA genes (Sutton and others 1994). Differences in monoterpene composition from black spruce oleoresin (including

α–pinene, 3-carene, and terpinolene) vary among geographic origins in an east–west pattern, except for seeds from sources in New England that have close affinity in monoterpene composition to red spruce (Chang and Hanover 1991). Natural introgression of black spruce into red spruce may result in greater height and diameter growth in New Brunswick, yet the hybrid performed unpredictably in managed stands (Fowler and others 1988).

Early crosses within the genus have provided a thorough background in potential crossability of the genus, including specimens from artificial crosses between nonsympatric species (Wright 1955). Analysis of morphological characteristics and monoterpene composition from artificial crosses between white, red, and blue spruces later verified the hybridity of the seedlings, evaluated the utility of spruce hybrids, and clarified the evolutionary relation among members of the genus (Bongarten and Hanover 1982). Height growth of Englemann spruce × Sitka spruce hybrids proved unsuitable for reforestation purposes in the north central interior of British Columbia (Kiss 1989). Hybrids of black spruce and Serbian spruce out-performed the black spruce parents in height and diameter growth and can be produced sexually en masse in seed orchards (Fowler 1980).

Seed source identification and provenance testing of native as well as exotic spruce species are important in selecting suitable races for various purposes. Seeds intended for use in artificial reforestation usually are collected from "superior" trees growing in the same area that is to be replanted. Measurements of phenology and growth—both adaptive characters closely related to survival and optimal utilization of the growing season—indicated a clinal variation pattern with photoperiod and temperature as primary factors in 100 seed sources of black spruce from natural stands in Alaska to Newfoundland. A 1° shift in latitude changed the seedlings' total height 2 to 11% (Morgenstern 1978). On a smaller scale, clinal variation in black spruce in the maritime provinces resulted in 3 overlapping breeding zones (Park and Fowler 1988). Within the range of black spruce, extensive gene flow between stands discourages formation of distinctive provenances. Phenotypic characteristics of cones, needles, twigs, percentage survival, and growth generally differ more within-populations than between-populations (Fowler and Mullin 1977; Parker and others 1983; Thomson and others 1990). In Alberta, black spruce populations growing on strongly contrasting environments, such as uplands adjacent to peatlands, exhibited similarity in isozyme variability (Wang and MacDonald 1992). In contrast, populations near the margins of the range, such as coastal regions in Newfoundland, better reflected provenance effects (Khalil 1984; Yeh and others 1986).

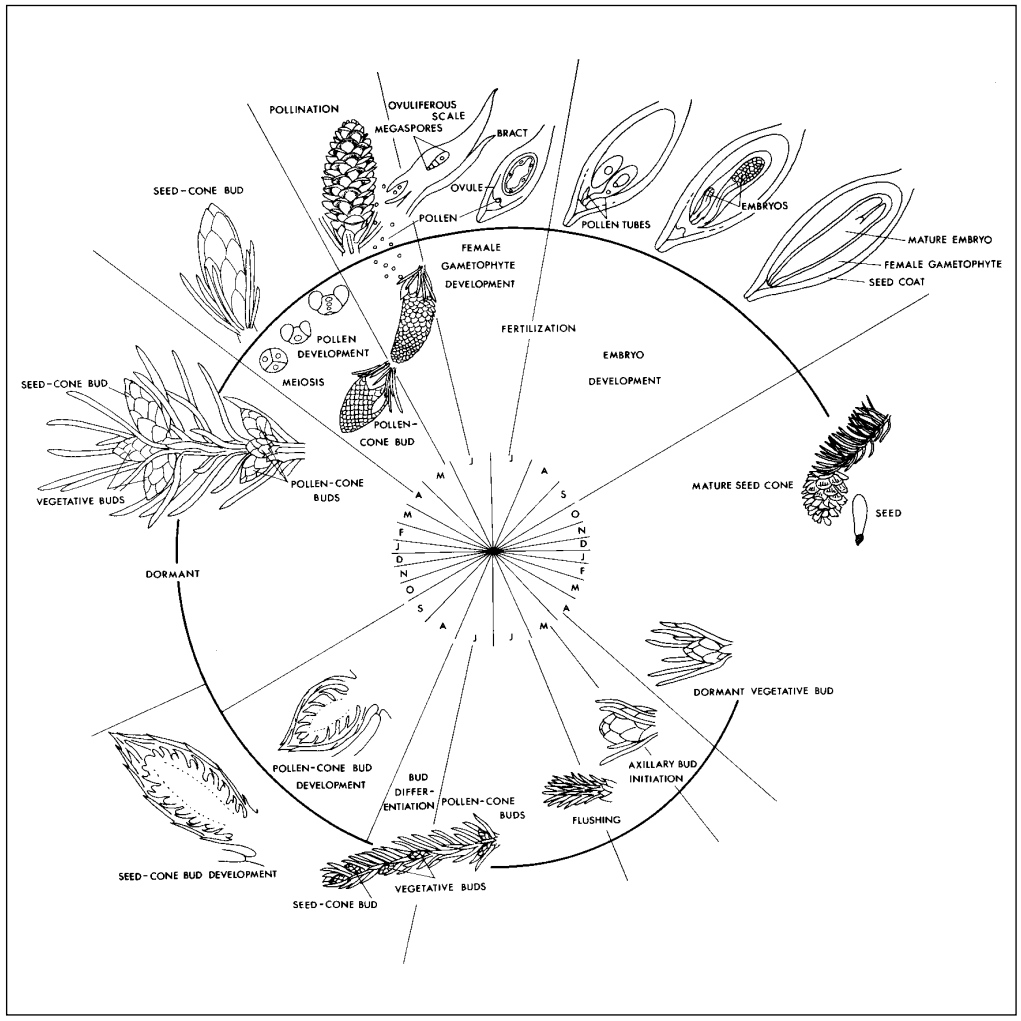
Genetic variation of Engelmann spruce may correlate with latitude and elevation; the species grows at 762 to 1,067 m in British Columbia and as high as 3,658 m in the southern Rocky Mountains (Alexander 1987). After 10 years, seedlings from more northern and lower elevation sources grew better than those from other sources within this wide geographical and elevational distribution when planted together at 2,930 m in central Colorado (Shepperd and others 1981). Lack of genetic variation of red spruce at the provenance level suggests a single broad seed and breeding zone for the maritime provinces (Fowler and others 1988). Genetic variation in natural populations of blue spruce has received considerable attention and seems to conform to a discontinuous (rather than clinal) pattern with extensive stand-to-stand and individual-tree variation

(Diebel and Fechner 1988; Fechner 1985; Hanover 1975). Provenance research in genetic variation of white spruce indicates that distinct populations have evolved within broad ecological regions, thereby resulting in differences in rate of juvenile growth, response to calcium nutrition, wood density, late-season initiation of needle primordia, nuclear volume, DNA content, branch to bud morphology, optimal temperature for seed germination, terpene biochemistry, and isoenzymes (Alden 1985). A range-wide provenance study planted in Minnesota showed large differences for tree height at ages 9 and 19 among populations with relatively poor performance by northern and western populations. Yet, no apparent geographic pattern existed in allozyme variation due to high outcrossing rates and strong inbreeding depression (Furnier and others 1991).

Norway spruce, perhaps the most intensively studied non-native species, shows strong latitudinal and elevational gradients. Seeds from northern latitudes and higher elevations weigh less than seeds from southern latitudes and lower elevations (Heit 1968; Tyszkiewics 1968). Seed source also influences mineral nutrient content of seeds (Youngberg 1951) and early growth of seedlings in nursery beds (Heit 1968). Seed source of Serbian spruce can affect the crown shape and susceptibility to frost (Dirr and Heuser 1987).

Flowering and fruiting. The reproductive cycle in spruce takes 2 years; timing of various processes has been studied in detail for Engelmann spruce (Harrison and Owens 1983), white spruce (Owens and Molder 1977; 1984) (figure 1), and Sitka spruce (Owens and Molder 1976). Production of cones and filled seed varies with (1) the number of central or fertile ovuliferous scales formed in the cone-primordium; (2) the success of pollination and fertilization; (3) the degree of self-pollination; and (4) the loss to seed-eating animals and disease organisms (Caron and Powell 1989). Male and female strobili arise in spring in axils of elongating shoots, usually on different branches of the same tree. Bisexual cones occasionally occur; in interior Alaska, white spruce bisexual cones with the female portion at the apex are more common than those with the male portion at the apex (Zasada and others 1978). The pendant, yellow,

Figure 1—*Picea glauca*, white spruce: reproductive cycle (from Owens and Molder 1984, used with permission of the author and publisher).



bright purple, or crimson male strobili have ovoid to cylindrical shape and uniform distribution over the crown. Each scale (microsporophyll) bears 2 pollen sacs (microsporangia) and are spirally arranged on a central axis. Male strobili dry out and fall off soon after pollen-shedding.

The timing of female strobili differentiation is similar for most species of spruce that have been studied; female strobili become anatomically determined at the end of the period of bud-scale initiation and the end of lateral shoot elongation (Owens 1986). Female strobili arise near the apex of shoots on upper branches in crowns of Engelmann, Sitka, and white spruces; the seed-cone zone in black spruce occurs on the most vigorous 1-, 2-, and 3-year-old branches at the top of the tree (Caron and Powell 1992). Initially the female strobili are erect, yellowish green, crimson, or purple; cylindrical; and 5 to 20 mm in diameter. The ovuliferous scales are spirally arranged on a central axis and each bears 2 ovules (megasporangia) at the base. Each species has a characteristic number of spirals per cone, and the number of seeds per cone depends in part on the pitch and diameter of the spirals as well as the length of the cones (Fogal and Alemdag 1989). The size of the preceding cone crop and climatic conditions at the time of cone bud differentiation influence the number of reproductive buds formed in white spruce (Zasada and others 1978). Checking female strobili in the fall preceding the seed year provides an early means of predicting potential size of the cone crop (Eis 1973).

Female strobili receive pollen when fully open, a period that lasts only a few days. Fechner (1974) determined that female strobili of blue spruce become receptive 1 to 5 days after the first pollen release, depending on elevation, and that cones tip over and become pendent within 3 to 4 weeks of initial receptivity. Fertilization may follow pollination within a few days or may be delayed until after cones become pendent (Fechner 1974); cones mature in late summer or autumn, depending on summer growing conditions (table 2). Embryo development (figure 2) of white spruce seeds in Alaska generally proceeds rapidly during July after completion of shoot, stem, and cone growth, although on any specific date, embryo length, percentage of embryo length, cotyledon length, and relative cotyledon length will differ among trees within a stand (Zasada 1988). Embryos of white spruce–Englemann spruce hybrids in British Columbia typically fill the embryo cavity well before the seeds mature (Eremko and others 1989). Cotyledon number between species differs from 4 to 15 (Dallimore and Jackson 1967) and may be under strong maternal control (Diebel and Fechner 1988).

The size of a cone crop for individual trees and stands tends to follow the phenomenon of alternate bearing, with heavy crops followed by light or no crops, because cones develop in terminal positions on the shoots, leaving fewer available locations for flower production the year after a

Table 2—*Picea,* spruce: height, seed-bearing age, and phenology of flowering and fruiting

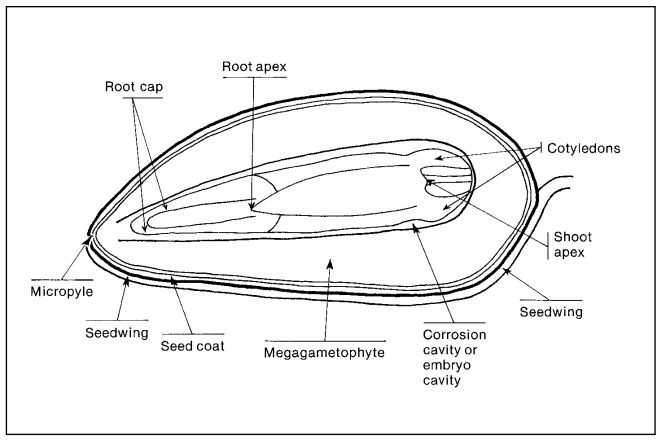
Species	Mature height (m)	Minimal seed-bearing age (yr)	Flowering	Cone ripening	Cone size (cm)	Dispersal	Years between large seedcrops	Preripe cone color	Ripe cone color
P. abies	30–60	40–60	Apr–June	Sept–Nov	10–18	Sept–Apr	4–13	—	Brown
P. asperata	45	—	—	—	8–13	—	—	—	—
P. breweriana	25–30	20–30	—	Sept–Oct	—	Sept–Oct	2	Green	Dark brown, black
P. engelmannii	25–30	15–40	May–June	Aug–Sept	3–6	Sept–Oct	2–6	Green	Brown
P. glauca	15–30	30	May	Aug	3–5	Aug–May	2–13	Green	Pale brown
P. glehnii	30	—	—	—	6	—	—	—	Shiny brown
P. jezoensis	30–45	20–25	—	—	5–8	—	2–4	Crimson	Brown
P. koraiensis	18	—	—	—	—	—	—	Green	Brown
P. mariana	9–27	10	May–June	Sept	2–4	Oct*	4	Green	Purple–brown
P. obovata	—	—	—	Sept	—	—	12–13	—	—
P. omorika	30	—	May	—	5	—	—	Bluish black	Cinnamon brown
P. pungens	21–50	20	Apr–June	—	7–10	—	1–3	Green	Pale brown
P. rubens	21–30	30–50	Apr–May	Sept–Oct	—	Oct–Mar	3–8	Green	Brown
P. sitchensis	18–73	20	May	Aug–Sept	—	Aug–Sept	3–4	Yellow-green	Brown
P. smithiana	61	20	Apr–May	Oct–Nov	10–18	Oct–Nov	—	Bright green	Brown

Sources: Alden (1955), Alexander (1987), Alexander and Shepperd (1984), Edwards (1980), Fechner (1985), Nikolov and Helmisaari (1992), Safford (1974), Zasada and Viereck (1970).

* Cones of *P. mariana* are semi-serotinous and release seeds throughout the year for several years.

P

Figure 2—*Picea glauca*, white spruce: diagrammatic longitudinal section of a mature seed at dispersal, showing seedcoat, gametophyte, and fully developed embryo (from Alden 1985, used with permission of the author and publisher).



good crop (Edwards 1986; Fechner 1985). Annual production of cones and seeds differs considerably, however, with the intervals between good cone crops ranging from 2 years in Brewer spruce to as long as 13 years in white and Norway spruces (table 2). Between 1969 and 1994, Engelmann spruce in central Colorado produced good cone crops in 8 of the 26 years (Shepperd 1995). Between 1957 and 1978, irregular production of white spruce cones and seeds in interior Alaska varied with environmental factors such as temperature during cone initiation; nutrient deficiencies; and losses to insects, diseases, and squirrels (Zasada 1980; Zasada and Viereck 1970).

At maturity, the pendent cones open to shed seeds during autumn and winter (table 2). Persistent cone scales on mature cones may have rounded, pointed, irregular, notched, or reflexed ends. Most species shed cones at the end of the season, but some cones may remain on the tree throughout the next growing season. Cones should be harvested before inclement weather reduces workers' productivity or losses to squirrels increase (Curran and others 1987). Cones may be collected before they are fully ripe and, if artificially ripened, release seeds with maximal germination capacity (Edwards 1980). Cones may be collected from standing trees, slash, or animal caches, although cones that have been in contact with the forest floor may acquire seed-killing fungi. Seeds generally reach maturity before cones show their characteristic ripe color (table 2). Time of ripening varies among cones on an individual tree and among trees in a single stand (Fechner 1974; Jensen and others 1967; Zasada 1988). Various measures of estimating seed maturity have emphasized (1) physical attributes such as color and firmness of cones; (2) moisture content and specific gravity of cones; (3) color of testa and brittleness of seeds (Crossley 1953; Edwards 1980); (4) a cone moisture content of 30% or less for Norway spruce; (5) specific gravity between 0.78 and 0.95 (Winston and Haddon 1981; Zasada 1973) and a soft "spongy feel" of cones when squeezed in the fingers for white spruce; or (6) dark brown or black testa and seeds that "snap" when cut with a sharp instrument. All of these indicate that cones are sufficiently ripe for harvest.

Morphological characteristics of seed maturity for white spruce embryos show 75 to 95% complete embryo development by the end of the growing season, depending on site characteristics of the stand. Continued embryo development in seeds of cones collected in high latitude forests at this stage of seed maturity requires careful handling of the cones (Zasada 1988). Changes in sugar content provide a biochemical measure of maturity in ripening seeds of Norway and Sitka spruces (Jensen and others 1967). Computation of average daily temperature and growing degree-day summations also indicates seed maturity. Zasada (1973) recommends 625 growing degree-days (above a threshold of 5 °C and summed from pollination date) as a minimal time for white spruce embryos in interior Alaska to fully develop; this heat sum is reached in early August. Other optimal growing degree-day sums include 912 for white spruce in Ontario (Winston and Haddon 1981) and 955 for white spruce and 1,050 for black spruce in Newfoundland (Curran and others 1987). Maximal cone maturity in blue spruce, measured as seed germinability, occurs 6 weeks before natural seed release for low-elevation trees and 4 weeks before natural seed release for high-elevation trees (Fechner 1974).

Recent work has expanded the understanding of seed production in relation to crown structure and cone size. Cones of black spruce on trees of intermediate crown class initially produce almost twice as many seeds as those of either the dominant or the co-dominant trees, but disperse their seeds at a much faster rate during the first 5 to 6 seed-bearing years (Payandeh and Haavisto 1982). The number of black spruce seeds per cone and number of filled seeds per cone relate to cone size: cones in New Brunswick averaged from 26 to 30 mm long with 10 to 37 filled seeds per cone (Caron and Powell 1989) and the most common size of black spruce cones in Ontario averaged 20 to 28 mm long with potential yields of 74 to 94 seeds per cone and 38 to 44 filled seeds per cone (Haavisto and others 1988). Cones of white spruce from Ontario averaged 39 to 47 mm in length and contained an average of 46 to 62 filled seeds per cone; regression models developed from these results estimate the number of sound seeds per cone as a function of seeds per cone section, cone length, and cone diameter (Fogal and Alemdag 1989).

Attempts to enhance seed yields in seed orchard programs have been hampered by the relatively long period of tree growth before flowering begins. Documented minimal seed-bearing age (table 2) for most species ranges from 10 to 60 years, although crops of sufficient quantity to warrant collection may not occur until much later. Efforts to stimulate flowering in younger trees have involved girdling of the

bole, nitrogen fertilization, and root pruning. Top-pruning of grafted white spruce in seed orchards, done to maintain the cone-bearing branches at a height within reach of a short ladder, may also increase cone production and decrease the cost of cone collection (Nienstaedt 1981).

Several lines of research have attempted to define the physiological processes and procedures for large-scale stimulation of flowering to either shorten the length of breeding programs or to increase production of cones and seeds. Application of gibberellins A_4, A_7, and A_9 stimulated female cone production in grafted Norway spruce clones, although the response differed by year and clone (Dunberg 1980). Gibberellin $A_{4/7}$ applied in the top 2 branch whorls of mature Sitka spruce grafts increased female flowering and seed production (Tompsett and others 1980); girdling in combination with stem injections of gibberellin $A_{4/7}$ in grafted clones of Sitka spruce may stimulate pollen-cone production (Philipson 1985a); and top-pruning and stem injection of gibberellin $A_{4/7}$ may increase cone production in the lower crown and increase the ease of cone collection (Philipson 1985b). Heat and drought also promote flowering, although by a different induction mechanism. Potted grafts of Engelmann spruce produced high numbers of both male and female cone buds after exposure to high temperature within heated polyethylene-covered houses when the exposure occurred during the late stage of slow shoot elongation, whereas drought during the period of rapid shoot elongation after vegetative bud burst enhanced female cone production (Ross 1985). Optimal daytime temperature is 22 to 25 °C (Ross 1988a). In contrast, polyhouse temperatures that frequently exceed 30 °C during the pollination sequence of Engelmann spruce resulted in accelerated pollen shed, increased underdevelopment of pollen cones, and reduced yields of seed (Ross 1988b). These results suggest a need for a year's rest between treatments to allow time for cone maturation and vegetative replenishment of shoots. Repeated injection of gibberellin $A_{4/7}$ into container-grown grafts of Sitka spruce in a polyhouse during May and June effectively stimulated flowering (Philipson 1992). Application of gibberellin $A_{4/7}$ also stimulated flowering of white spruce (Ho 1988b; Marquard and Hanover 1984), even though white spruce has been classed as recalcitrant because of its sporadic flowering and usually nominal response to gibberellin $A_{4/7}$ alone (Pharis and others 1986). Stem injection of gibberellin $A_{4/7}$ in combination with nondestructive girdling greatly increases flowering in mature white spruce trees (Pharis and others 1986) and grafted clones (Ross 1992). Whole-tree spraying of branches at relatively high concentrations (800 mg/liter gibberellin $_{4/7}$) during May through July promoted cone production the next year (Ho 1988b). In the Great Lakes region, elongating shoots sprayed in May produced more male and female strobili than shoots sprayed in June (Cecich 1985). Flowering of white spruce responded to heat similar to that of Engelmann spruce by enhanced pollen-cone production after subjecting potted grafts to 30 °C for 10 hours, whereas seed-cone production was enhanced after 5 hours at 20 °C (Ross 1991). Seed-cone production of black spruce also has been stimulated by application of gibberellin; the greatest increase occurred with 200 mg/liter of gibberellin $A_{4/7}$ sprayed repeatedly on young grafts during the period of rapid shoot elongation (Ho 1991). Seed-cone production also may be enhanced in field-grown seed orchards by applying a foliar spray of 400 mg/liter gibberellin $A_{4/7}$ during the period before lateral shoot elongation and bud-type differentiation (Ho 1988a), and in seed orchards of seedling origin by applying a foliar spray of 200 to 800 mg/liter gibberellin $A_{4/7}$ (Hall 1988). Attempts with several species to promote male flowering preferentially by the synthetic auxin naphthalene acetic acid (NAA) have been inconclusive (Hall 1988; Ross 1992).

Spruce seeds are small (2.5 to 5.0 mm long), oblong to acute at the base, with a single well-developed wing that is 2 to 4 times the length of the seed (figure 3). Wind is the primary agent for dispersal (Dobbs 1976; McCaughey and Schmidt 1987; Youngblood and Max 1992; Zasada and Lovig 1983). Dispersal of white spruce seeds begins in late August and extends throughout winter; however, seeds released before mid-October have higher viability because they tend to come from well-developed central cone scales, whereas seeds released either earlier or later tend to come from less-developed basal and apical scales (Dobbs 1976; Youngblood and Max 1992; Zasada and others 1978). Cones of red spruce release seeds in a similar manner. The semi-serotinous cones of black spruce remain partially closed, and disperse seeds for several years as the cone scales flex with repeated wetting and drying (Haavisto and others 1988; Viereck and Johnston 1990). Seed viability decreases only slightly during the first 3 years, then decreases rapidly to about 5% in cones up to 12 years old, and may remain almost constant for older cones (Payandeh and Haavisto 1982). Nonlinear equations have been developed to model dispersal of filled seeds into openings for Engelmann spruce (Alexander 1986; McCaughey and Schmidt 1987), white spruce (Dobbs 1976; Youngblood and Max 1992) and black spruce (Payandeh and Haavisto 1982). Once dispersed, spruce seeds remain viable for only a short period; Fraser

Figure 3—*Picea*, spruce: seeds with wings of *P. breweriana*, Brewer spruce; *P. engelmannii*, Engelmann spruce; *P. glauca*, white spruce; *P. mariana*, black spruce; *P. rubens*, red spruce; and *P. sitchensis*, Sitka spruce (**left to right**).

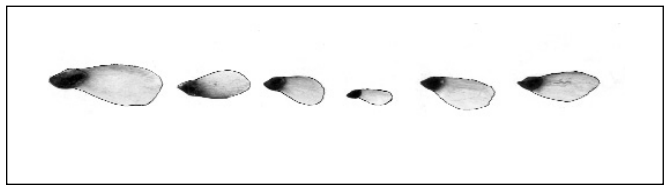


Table 3—*Picea,* spruce: common cone- and seed-damaging insects

Insect species	Common name	Damage	Affected species*
Choristoneura occidentalis Freeman	western spruce budworm	Larvae feed externally on cones	***P. engelmannii***
Dasineura canadensis Felt	spruce cone gall midge	Larvae form gall on cone scale	***P. glauca***
Dasineura rachiphaga Tripp	spruce cone axis midge	Larvae mine through scales into axis	***P. engelmannii, P. glauca***, *P. sitchensis,P. mariana*
Dioryctria abietivorella Grote	fir cone moth	Larvae mine & riddle cone	***P. mariana, P. glauca***, *P. engelmannii, P. pungens,*
Henricus fuscodorsanus Kearfott	cone cochylid	Larvae feed on scales & seeds	***P. sitchensis, P. glauca***
Hylemya anthracina Czerny	spruce cone seed maggot	Larvae tunnel around cone axis	***P. mariana, P. glauca, P. engelmannii, P. sitchensis***
Laspeynesia youngana Kerfott	spruce seed moth	Larvae feed on seeds	***P. engelmannii, P. glauca***, *P. mariana, P. pungens, P. rubens, P. sitchensis*
Mayetiola carpophaga Tripp	spruce seed midge	Larvae feed on seeds	***P. glauca***
Megastigmus atedius Walker	spruce seed chalcid	Larvae feed on seeds	All native *Picea*
Strobilomyia neanthracina Michelson	spruce cone maggot	—	***P. mariana***

Sources: Cameron and Jenkins (1988), Schmid and others (1981).

* Major hosts in **boldface type.**

(1976) reported that on a natural forest floor seedbed, black spruce seeds may lose viability completely after 16 months.

Cone and seed losses. Various agents destroy cones and seeds, including killing frosts, insects, diseases, birds, and mammals. Late frost during the spring may damage cones of white spruce; affected conelets become flaccid, die and turn black and do not produce seeds (Zasada 1971). Frost also commonly damages cones of Engelmann spruce (Cameron and Jenkins 1988).

Many insects feed on seeds and cone parts (table 3). Just 2 species—spruce cone seed maggot (*Hylemya anthracina* Czerny) and spruce seed moth (*Laspeyresia* × = *Cydia) youngana* Kearfott)—cause the most widespread damage (Cameron and Jenkins 1988; Hedlin 1973; Hedlin and others 1980; Schmid and others 1981). Insect populations fluctuate with cone crop abundance and differ among spruce communities having dissimilar stand structure (Fogal and Larocque 1992). Greater seed and cone losses usually occur in years of below-average cone production (Schmid and others 1981; Werner 1964). Above-average summer temperatures may ameliorate seed losses in Ontario from *Laspeyresia* by contributing to greater insect mortality and preventing prolonged insect diapause (Fogal 1990). Damage to cones and seeds by insects has been reduced by soil application of carbofuran (Cerezke and Holmes 1986) or stem implants of acephate (West and Sundaram 1992).

Basidiospore production of the inland spruce cone rust—*Chrysomyxa pirolata* Winter—coincides with the period when most spruce cones are receptive to pollen. This fungus sometimes causes severe damage to the cones of white, blue, Engelmann, and black spruces. Diseased cones contain fewer seeds, with reduced viability, and germinants may be abnormal (Summers and others 1986, Sutherland 1990). Coastal spruce cone rust—*Chrysomyxa monesis* Ziller—causes similar damage in Sitka spruce (Bega and Scharpf 1993). Pre-emergence seed losses caused by a soil-borne fungus—*Geniculodendron pyriforme* G.A. Salt—in Sitka spruce nurseries occur after cones come in contact with the ground during collection and cleaning of seeds (Sutherland and Woods 1978). Similarly, another fungus—*Caloscypha fulgens* (Pers.) Boudier—infects cones lying on the forest floor or in squirrel caches; spreads during stratification and presowing storage; and kills seeds of white, black, and Sitka spruces (Sutherland 1990). The seed-borne blight caused by *Sirococcus strobilinus* Preuss may damage seedlings of Engelmann, Sitka, and white spruces, and their hybrids (Sutherland and others 1981).

Many species of birds consume spruce seeds. Several finches (families Fringillidae and Estrildidae) feed almost exclusively on conifer seeds, including the common (red) crossbill (*Loxia curvirostra*), the two-barred (white-winged) crossbill (*L. leucoptera*), and the pine siskin (*Carduelis pinus*). Spruce seeds often provide an important winter food source for the American goldfinch—*C. tristis.* In addition,

the pine siskin and the pine grosbeak—*Pinicola enucleator*—may feed on reproductive buds (Benkman 1987; Clement and others 1993).

Pine squirrels (*Tamiasciurus hudsonicus fremonti*) harvest and cache Engelmann spruce cones (Alexander 1987). Red squirrels (*T. hudsonicus*) and northern red-backed voles (*Clethrionomys rutilus*) consume great quantities of seeds of white spruce during winter (Brink and Dean 1966; West and deGroot 1990; West and others 1980). Red squirrels also consume seeds of black spruce and clip twigs and terminals and eat reproductive and vegetative buds of red spruce (West 1989). In Newfoundland, the proportion of black spruce cones per tree harvested by red squirrels in years with small cone crops ranged from 64 to 96%, whereas in a year with a good cone crop, less than 1% of cones were taken (West 1989).

Extraction and storage of seeds. Spruce seeds require careful extraction and storage because cones often are collected before fully mature and seeds may continue to ripen within the cones (Caron and others 1990; Edwards 1980, 1986; Zasada 1973). Post-harvest ripening of prematurely collected cones, however, allows flexibility in collecting operations and extends the collection period by allowing the use of immature cones (Edwards 1986). Cones of white spruce may air-dry in half-filled burlap sacks or on open screens for a few weeks at 5 to 15 °C and 60 to 75% relative humidity (Alden 1985), or for up to 3 months at 5 °C and 75 to 90% relative humidity (Winston and Haddon 1981). Cones also may dry under field conditions of outside storage if ventilation is good (Caron and others 1990; Zasada 1973). Cones of Engelmann Sitka, and white spruces have been safely stored for up to 5 months without loss of seed quality (Edwards 1986).

Improper extraction, even from mature cones, will reduce viability of spruce seeds. Mature cones usually require additional drying with heat to fully flex the cone scales and ensure maximal seed recovery. Cones of Engelmann, Sitka, and white spruces require exposure to an air flow of gradually decreasing moisture content and increasing temperature in a convection kiln for 6 to 24 hours at 38 to 49 °C (Edwards 1986). Other workers suggest slightly lower maximal temperatures for white spruce (Alden 1985; Curran and others 1987). Kiln-drying requires careful monitoring of temperature because high temperature can cause physiological injury (Carmichael 1958). After drying, tumbling or shaking loosens seeds from opened cones. If cones fail to open fully, complete extraction of seeds may require remoistening and redrying followed by additional tumbling or crushing (Alden 1985; Edwards 1986).

Black spruce cones present a greater challenge for seed extraction because of the tightly bonded scales. The following special extraction procedure has been developed for these semi-serotinous cones (Haavisto and others 1988):

1. Cones are soaked in lukewarm water for 2 hours.
2. Cones are oven-dried at 40 °C for 20 to 22 hours.
3. Cones are tumbled in a revolving screened drum for 30 minutes.
4. Steps 1 to 3 can be repeated for up to 16 times for complete extraction of seeds.

The weakly bonded seedwings separate readily from the seeds with little abrasive action (Edwards 1986). For small seedlots, the seeds can be gently rubbed by hand inside a moistened cotton bag (Alden 1985; Caron and others 1990). For larger lots, wings and chaff are separated from seeds using any commercial seed-processing device: an oscillating screen scalper, a fanning mill, an air-screen cleaner, or a small rotating cement mixer, for example (Alden 1985; Edwards 1986; Stiell 1976). In some cases, seeds may need remoistening with a fine mist to aid in cleaning, after which they can be dried again. Air and gravity separators not only remove empty seeds, wings, and debris, but also sort seeds into different density fractions. Cleaned seeds are prepared for storage by conditioning with low heat to achieve 4 to 8% moisture content. The number of cleaned seeds per weight ranges from about 50,000 to almost 900,000/kg (110,200 to 1,984,200/lb) for the various species (table 4).

Because cone- and seed-crops differ between years, seeds collected during good to excellent years are stored for use during poor crop years. Seeds from most species of spruce seem fairly similar in longevity characteristics and storage requirements; seeds have been safely stored for 10 to 20 years at moisture content of 4 to 8% and temperatures between –10 and +3 °C (Wang 1974). Seeds of Norway spruce, stored at 0 to 2 °C and 6 to 8% moisture content in glass carboys sealed with cork and wax, retained high percentage germination for 17 years (Hill 1976). Seeds of white spruce stored at –18 to +3 °C and 7% moisture content for 7 years retained their initial percentage germination (Stiell 1976). To assure maximal seed longevity, the specified moisture content must be maintained during the entire storage period. Polyethylene bags (4- to 10-mil) make satisfactory storage containers. Seeds treated with rodent repellent have longevity characteristics similar to untreated seeds (Radvanyi 1980). For longer storage, metabolic processes are halted; Ahuja (1986) found that Norway spruce seeds stored in liquid nitrogen (–196 °C) retained full germinability, suggesting this as a long-term storage method.

Pregermination treatments. Seeds of most species of spruce germinate promptly without pretreatment, but seeds of black, blue, Brewer, Engelmann, Ezo, Norway, Sakhalin, Sitka, and white spruces may germinate more rapidly after a stratification treatment. Seeds of Norway spruce may be stratified by conditioning for 3 weeks at cold temperature and may be soaked in water for 24 hours (“priming”) before planting (Dirr and Heuser 1987). Seeds of red and white spruces stratified in newspaper and moist sand at 0 to 3 °C

Table 4—*Picea,* spruce: weight of cleaned seeds, methods of testing for laboratory germination, and additional directions

Species	Seeds/weight /kg	Seeds/weight /lb	Substrate	Test (days)	Additional directions
P. abies	105,600–462,300	47,000–209,700	TB	16	—
P. asperata	154,300–165,400	70,000–75,000	—	—	—
P. breweriana	112,500–163,200	51,000–74,000	—	—	Prechill
P. engelmannii	152,200–710,000	69,000–322,000	TB,P	16	Prechill; light; sensitive to excess moisture; if dormant, use KNO_3
P. glauca	298,000–884,200	135,000–401,000	TB	21	Prechill 14–21 days at 3–5 °C; light
P. glehnii	—	—	TB,P	14	Prechill 21 days at 3–5 °C
P. jezoensis	395,100–508,500	179,200–230,600	TB,P	14	Prechill 21 days at 3–5 °C
P. koraiensis	209,500–242,500	95,000–110,000	TB	21	Light
P. mariana	739,000–1,464,100	335,000–664,000	TB	—	Prechill or soak; light
P. omorika	277,000–377,500	125,600–171,200	TB	16	Light; sensitive to excess moisture
P. pungens	176,400–359,000	80,000–163,000	TB,P	16	Prechill
P. rubens	220,500–637,000	100,000–289,000	TB	28	Light
P. sitchensis	342,000–882,000	155,000–400,000	TB,P	21	Soak; prechill; light; sensitive to excess moisture; if dormant, use KNO_3
P. smithiana	53,000–88,200	24,000–40,000	—	—	—

Sources: Dirr and Heuser (1987), Jeglum and Kennington (1993), Nikolov and Helmisaari (1992), Safford (1974), Stein and others (1986), Willan (1985).
Note: TB = top of blotters; P = petri dishes covered with blotters, filter paper, or sand.

for 14 months showed only a slight loss of percentage germination; under these conditions black spruce lost about one-third of its percentage germination and germination of all 3 species declined to about 10% of the original capacity after 27 months (MacGillivary 1955). Prechilling, or cold stratification, may widen the range of temperatures over which seeds can subsequently germinate, increase the maximal percentage germination at some temperatures, and increase the rate of germination at almost any temperature (Gosling and Rigg 1990). Prechilling of white spruce seeds at 2 to 4 °C for 6 weeks results in high percentage germination (Caron and others 1990). Other researchers have prechilled white spruce seeds by soaking them in cold running water for 24 hours, blotting them dry, and then refrigerating them at 4 °C for 3 weeks (Chanway and others 1991). Storage of cones at 5 °C for 4 weeks, however, may eliminate any subsequent need for stratification of white spruce seeds (Winston and Haddon 1981). White spruce seeds from high-latitude sites in Alaska (> 55° latitude) do not undergo dormancy, and stratification is detrimental for mature seeds (Alden 1995). Before nursery sowing, Engelmann spruce seeds need to be primed for 24 hours, then prechilled for 6 to 8 weeks at 2 °C in loosely closed polyethylene bags (Tanaka and others 1986). Unstratified seeds of black spruce incubated for 24 days at 3 or 20 °C germinated completely within18 days with 14:10 (light:dark) hours of fluorescent light, whereas moist seeds prechilled for 24 hours at 3 °C in a polyethylene bag in the dark reached 95% germination within 12 days when incubated at 5 to 30 °C, regardless of lighting regime (Farmer and others 1984). Priming black spruce seeds for 5 to 6 days in water (until the radicles nearly emerge) and surface-drying before sowing accelerated germination by about 1 week (Malek 1992). Seeds of black spruce from high latitudes in Alaska, collected and immediately extracted in the spring, will germinate in 2 to 6 days after becoming fully imbibed with water; no dormancy exists and stratification is not required (Alden 1995). Dormancy of Sitka spruce seeds is broken and 95% germination is possible after priming for 72 hours (until seeds reach 30% moisture content), then chilling for 6 weeks in loosely closed polyethylene bags at 4 °C (Gosling and Rigg 1990).

Treating seedlots with various fumigants, insecticides, fungicides, and rodent repellents in storage or before sowing may reduce germination of seeds. Germination of white spruce seeds treated with a finely ground rodent repellent mixed with graphite declined slightly from that of untreated seeds after more than 5 years of storage (Radvanyi 1980). Aluminum powder, which is used as a lubricant on Sitka and white spruce seeds in bareroot nurseries in Canada, may decrease the percentage germination of treated seeds and reduce first-year survival of seedlings (Sutherland and others 1978). Embedding black spruce seeds in pellets may discourage their consumption by small mammals, depending

on the material surrounding the seeds (Martell 1981). As always, pesticide users should closely follow the manufacturer's recommended dosages.

Seedlots of all spruce species should meet the quality standards of 95% purity and 80% viability recommended by the International Seed Testing Association and the Association of Official Seed Analysts for most species. Many spruce seedlots contain a fairly high percentage of empty seeds when extracted from the cones. Failure to remove these empty seeds during the cleaning process can seriously affect germination test results. Methods of germination testing are summarized in table 4 (Safford 1974; Stein and others 1986). In all species, germination tests call for alternating temperatures of 20 °C for 16 hours and 30 °C for 8 hours (Stein and others 1986).

Germination and nursery practices. Germination of spruce seeds is epigeal (figure 4). Growers raise seedlings of spruce species in North America either as bareroot stock (2+0 or 3+0) in nursery beds or as container seedlings (1+0 or 2+0) in greenhouses. Nursery-grown transplants (2+2) of slow-growing species such as black spruce may have greater survivability (Mullin 1980). Seeds of blue, Engelmann, and Korean spruces may germinate at low temperatures in the fall and die over winter, making fall-sowing of these species in nursery beds highly risky (Heit 1968).

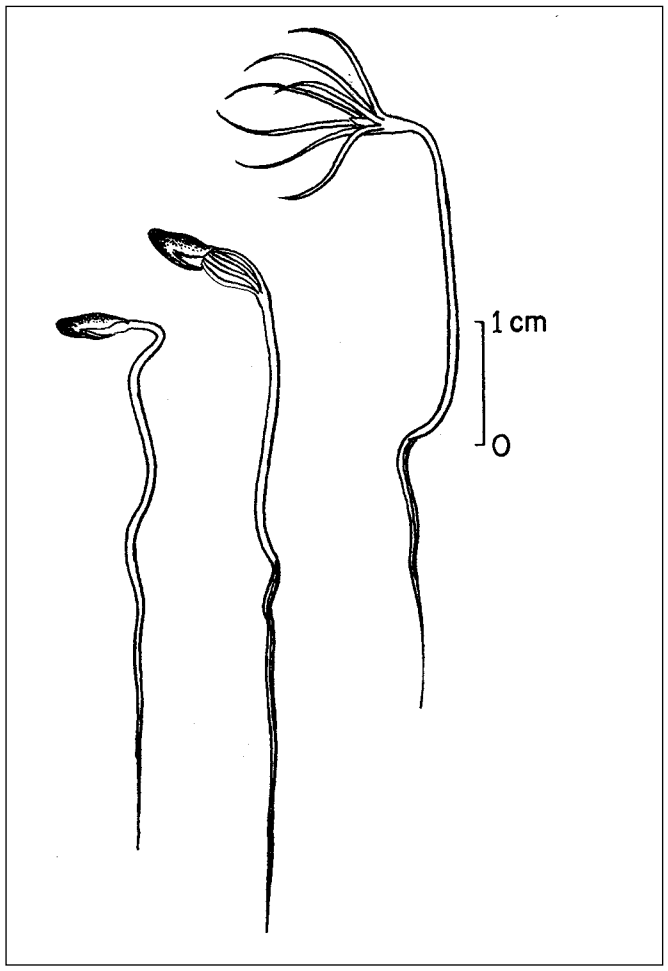
Under natural conditions, most species of spruce germinate on various media, including rotten wood, shallow duff, and mixtures of mineral and organic soil. Mineral soil makes an ideal seedbed because of greater water availability. Commercial growers raise white spruce seedlings with high stem caliper and stem height and heavy stem and root weights as container seedlings in either (1) a commercially prepared mixture composed of equal parts of sphagnum peat moss and vermiculite or (2) a mixture of equal parts of sphagnum peat moss, peat moss, and vermiculite (Lackey and Alm 1982). Germination of some seedlots of Sitka spruce has been improved by moistening the substrate with a 0.2% solution of potassium nitrate (Safford 1974).

Seeds of most species germinate promptly and completely under a wide range of temperatures either with or without light. Once germinated, seedlings in greenhouses require extended daylength to accelerate growth and prevent dormancy. Continuous fluorescent lighting providing about 150 μmol/m^2/sec photosynthetically active radiation at 25 °C allows continuous vigorous growth of blue spruce seedlings (Young and Hanover 1978). White spruce seedlings respond favorably to photoperiodic lighting intensities of about 414 to 4,150 μmol/m^2/sec, although Engelmann spruce has a much narrower response range of about 210 to 520 μmol/m^2/sec (Arnott and Macey 1985). Seedlings of white spruce also have been grown with photosynthetically active radiation at the seedling canopy level of about 300 μmol/m^2/sec in a 16-hour photoperiod at 23 °C and a night temperature of 17 °C (Chanway and others 1991). Failure of the lighting system for only a few days reduced the effectiveness of extended or intermittent photoperiod, leading to increased root rather than shoot growth in white spruce seedlings (Arnott and Simmons 1985). Under laboratory or greenhouse conditions, newly germinated seedlings of red spruce require a light period of at least 16 hours to prevent the onset of dormancy (Safford 1974).

In greenhouse management, imposing a reduced photoperiod will induce bud scale formation leading to dormancy and hardening-off in spruce seedlings. Without this stimulus, first- or second-year seedlings may not enter dormancy, regardless of temperature. Imposing nitrogen stress and moisture stress will also induce dormancy (Young and Hanover 1978). Once dormant, seedlings of most species require 4 to 6 weeks of cold treatment at 0 °C or lower to initiate new growth (Safford 1974).

Macro- and micro-nutrients introduced in the irrigation system commonly support spruce seedlings in accelerated growth conditions within a greenhouse (Landis and others 1989). In addition to fertilizer, addition of growth-promoting rhizobacteria such as *Bacillus* strains may stimulate the

Figure 4—*Picea pungens*, blue spruce: seedling development at 2, 5, and 7 days after germination.



P

emergence rate of white spruce seedlings, possibly through induction of root elongation and the formation of lateral and adventitious roots (Chanway and others 1991). In nurseries in the Great Lakes region, stunting of first-year white spruce seedlings—described as early cessation of growth, purple discoloration of foliage, and low foliage phosphorus concentration without a soil phosphorus deficiency—may result from poor mycorrhizal development after soil fumigation (Croghan and others 1987).

Ectomycorrhizae may play an important role in seedling establishment, and a growing number of researchers are investigating the formation of mycorrhizae on seedlings. Black spruce seedlings inoculated soon after emergence with fungal plugs of the ectomycorrhizae-forming *Laccaria bicolor* (Maire) Orton or *L. laccata* (Fries) Berkely & Broome showed more second-order lateral roots and greater seedling dry weight and height (Thomson and others 1990).

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Ericaceae–Heath family

Pieris floribunda (Pursh) Benth. & Hook.

mountain andromeda

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Synonym. *Andromeda floribunda* Pursh.

Other common names. mountain pieris, fetterbush, mountain fetterbush.

Growth habit, occurrence, and uses. Mountain andromeda—*Pieris floribunda* (Pursh) Benth. & Hook.—is a broadleaf, evergreen, erect shrub 1 to 2 m in height and of equal or greater spread (Kruse 1987). The plant forms a rounded or flat-topped shape when mature and is covered with dense medium green foliage (Sabuco 1990). This species is indigenous to the Appalachian Mountains of the United States, extending from West Virginia southward into northern Georgia (Judd 1982). Mountain andromeda has a limited and scattered distribution along the Blue Ridge Mountains in the southern Appalachians (Spongberg 1990). It is typically found on mountain balds at high elevations and is hardy to USDA Zone 4 (Dirr 1990; Radford and others 1968).

The species is rare in cultivation, due in part to difficulties in propagation. This handsome, evergreen shrub has several desirable landscape attributes: a dense, compact growth habit; white, upright inflorescences; a tolerance of higher soil pH (pH 7.5) than typical for species in the Ericaceae; a greater cold tolerance than shown by other species in *Pieris* D. Don; and resistance to leaf damage by lacebug—*Stephanitis takeyai* Drake and Maa. (Kruse 1987; Sabuco 1990). The plant is best suited for landscape use in lightly shaded sites with a well-drained soil high in organic matter (Kruse 1987).

Geographic races and hybrids. There is only 1 known interspecific hybrid of mountain andromeda—*Pieris* × 'Brouwer's Beauty'. The hybrid resulted spontaneously when a plant of *Pieris floribunda* was pollinated by nearby plants of Japanese andromeda—*Pieris japonica* (Thunb.) D. Don ex G. Don (Jaynes and Dunbar 1976). The resultant hybrid has morphological characteristics that are intermediate between both parents (Jaynes 1975). The interspecific hybrid has an increased numbers of flowers that may be attributed to the sterility of the plant (Jaynes 1975). Lack of seed-set apparently gives the cultivar added vigor, as well as improved flowering over mountain andromeda (Jaynes 1975).

Flowering and fruiting. Fragrant, white flowers are borne on upright panicles that open beginning in late March and last until early May. Inflorescences are held well above the leaves at the top of the shrub, where they can be seen easily (Sabuco 1990). The floral display will last from 4 to 6 weeks. After flowering and a flush of new vegetative growth, the plant develops the inflorescences for the next year. Decorative, greenish white flower buds are produced in midsummer and stand out from the foliage during the fall and winter (Hillier Nurseries 1994). These panicles of buds serve to extend the period of landscape interest of this shrub. Flowers are pollinated by small bees (Gibson 1901). Fruits are globular, dry, 5-chambered, dehiscent, capsules borne in clusters, each 1 about 3 mm in diameter (Bailey 1977). Seeds are 3 mm long and 1.5 mm wide, are flattened with 2 inconspicuous wings, and have a dark golden-yellow color (figures 1 and 2).

Collection of fruits, seed extraction, cleaning, and storage. Capsules and seeds ripen in mid- to late autumn and can be collected at that time (Kruse 1987). Capsules are removed from the plant, lightly beaten and rubbed to open them completely (Dirr and Heuser 1987), and then shaken to loosen the seeds. Viability can be poor if seeds are not graded rigorously. Use of an air column blower is recommended to remove chaff and empty seeds (Starrett and others 1992). When dried to a moisture content of 6% and cleaned, the number of pure seeds was 7,500/g (210,000/oz) (Starrett and others 1992).

Seeds of mountain andromeda are orthodox in storage behavior. They can be stored at room temperature if used within a year but can remain viable for several years if stored in a sealed container at 4.5 °C (Blazich and Starrett 1996).

Germination tests. There are no test methods prescribed for official seed tests of mountain andromeda, but

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Figure 1—*Pieris floribunda*, mountain andromeda: seeds.

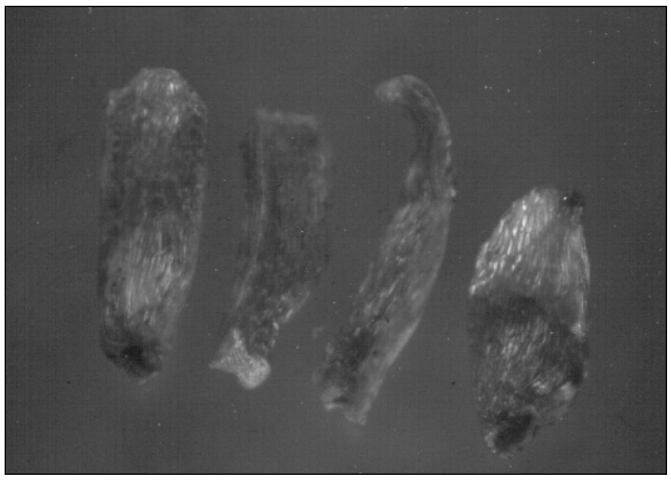
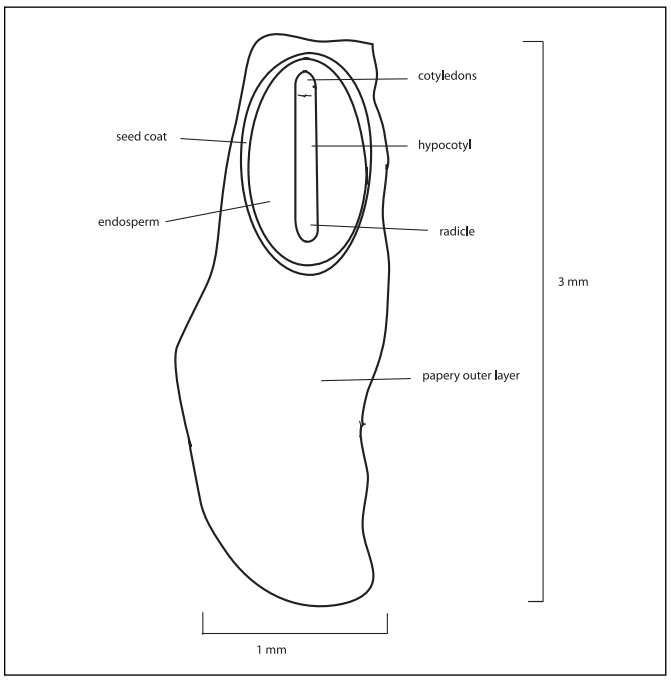


Figure 2—*Pieris floribunda*, mountain andromeda: longitudinal section of a seed.



the seeds germinate readily without pretreatment (Kruse 1987). Seeds do not require light for germination, but daily photoperiods as short as $^1/_2$ hour will maximize germination (Starrett and others 1992). A 30-day test of seeds from a source in the Blue Ridge Mountains of western North Carolina demonstrated that a daily photoperiod as short as 1/2 hour at 25 °C or an 8/16-hour thermoperiod of 25/15 °C resulted in 90% germination (Starrett and others 1992). Photoperiods of longer duration did not significantly improve germination of seeds from this source, regardless of temperature (Starrett and others 1992). The germination study of Starrett and others (1992) utilized cool-white fluorescent lamps as the light source, which provided a photosynthetic photon flux (400 to 700 nm) of 69 μmol/m^2/sec (5.3 klux). Germination is epigeal.

Nursery practice. Typically, a germination medium is warmed to 24 °C via bottom heat (Bir 1987). Seeds are sown on the surface of a steam-pasteurized medium such as pine bark sifted through a 6-mm ($^1/_4$-in)-mesh screen and irrigated slightly. The surface of the germinating medium should never be allowed to dry completely (Bir 1987). Once seeds have germinated, seedlings have very slow initial growth. The authors have observed that seedlings will often produce 1 true leaf above the cotyledons and then fail to exhibit any further growth for several weeks. Current practice is to fertilize seedlings at the first-true-leaf stage with a half-strength solution of a 15-45-5 ($N:P_2O_5:K_2O$) complete fertilizer (Bir 1987). After 2 weeks, nursery workers then shift the seedlings to a full-strength fertilizer with weekly application until they transplant the seedlings into liner flats or pots (Bir 1987).

Mountain andromeda can also be propagated vegetatively by rooting stem cuttings (Dirr and Heuser 1987) and by micropropagation (Starrett and others 1993). However, stem cuttings are reportedly difficult to root (Leach 1976).

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Pinaceae—Pine family

Pinus L.

pine

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Growth habit, occurrence, and use. The genus *Pinus* comprises about 100 species and numerous varieties and hybrids. It is one of the largest of the conifer genera, and one of the most important and widely distributed genera of forest trees in the Northern Hemisphere. Globally, the genus spans latitudes from Alaska to Nicaragua, Scandinavia to North Africa, and Siberia to Sumatra and inhabits a diversity of sites at altitudes ranging from sea level to timberline (Critchfield and Little 1966). Various pines exemplify the extremes of coastal and subalpine habitats in different regions of the world, including shore and whitebark pines in western North America; Italian stone and Swiss stone pines in Europe; and Japanese black and Siberian stone pines in Asia (table 1).

Some of the pines occur naturally over vast geographic ranges; others occur only in narrow or highly restricted ones. Those of limited natural range include Canary Island pine in the Canary Islands off the western coast of North Africa; Monterey pine in 3 distinct but quite small coastal areas of central California; and Torrey pine, with its total population of a few thousand trees, in 2 isolated island and coastal areas of southern California. The natural range of Scots pine, the most widespread of all the pines, crosses Eurasia, extending from Scotland and the Iberian Peninsula to eastern Siberia and northern Mongolia.

Evergreens of diverse heights, the pines supply major amounts of the world's most valuable timber and wood fiber, continue to yield the bulk of naval stores, and produce seeds that are valuable food sources for humans and wildlife. Pines are widely planted to protect watersheds, form shelterbelts and windbreaks, and provide wildlife habitats; they also are being increasingly planted to improve environments in rural and urban areas.

Sixty-seven species and varieties of pines are planted in or are known to have potential in the United States (table 1). Forty-three of these pines are native to the United States, and at least 13 of them are native to Mexico. Two are native solely to Mexico; one is native to the Caribbean region; 12 are indigenous to Europe, North Africa, and the Near East; and 12 are native to Asia.

Most of these pines grow tall, but some do not, and a few are shrubby in form (table 2). Eastern white, ponderosa, and sugar pines often surpass 61 m in height at maturity; Parry and Mexican piñyons and Japanese stone pines, by contrast, rarely attain 9, 8, and 2.5 m in height, respectively.

Pines are widely planted in the United States. Most survive and grow well in plantations within their areas of seed origin but largely fail outside their ranges. Nevertheless, successful plantations outside the native range have extended the geographic distributions of many pines in the United States, particularly those of jack, slash, Rocky Mountain ponderosa, Monterey, red, eastern white, loblolly, and Virginia pines (Fowells 1965; Harris and Harrar 1946; Wright 1962). Still, abundant plantation experience has also shown that the eastern pines, and especially the southern ones, survive and grow poorly in the western United States, and reciprocally, that western pines perform poorly in the eastern United States (Krugman and Jenkinson 1974; Schmitt and Namkoong 1965).

Many exotic pines have been introduced into the United States and, depending on region, have survived and grown well. Some have regenerated extensively and at least 4—namely Japanese red and Japanese black pines from Asia and Austrian and Scots pine from Europe—have naturalized in parts of New England and the Great Lakes region (Krugman and Jenkinson 1974; York and Littlefield 1942).

Many pine species have been successfully planted outside their native range, in various regions and on other continents around the world. The best of a host of known thriving introductions include the following species: Canary Island pine in North Africa and South Africa; Caribbean pine in Australia, Fiji, and South Africa; lodgepole, Austrian, eastern white, and Scots pines in Europe; slash, longleaf, maritime, and loblolly pines in Australia, New Zealand, China, and South Africa; Aleppo pine in South America; Khasi pine in East Africa; Merkus pine in Borneo and Java; bishop and

Table 1— *Pinus,* pine: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. albicaulis* Engelm.**	**whitebark pine**	Subalpine; Sierra Nevada–Cascade Ranges; coastal ranges & Rocky Mtns; S British Columbia, adjacent Alberta S to central California, N Nevada; Idaho, Montana, to NE Oregon, W Wyoming
***P. aristata* Engelm.** *P. balfouriana* var. *aristata* (Engelm.) Engelm.	**bristlecone pine,** foxtail pine, hickory pine	Subalpine; E central California, Nevada, Utah, N Arizona; central Colorado & N New Mexico
***P. arizonica* Engelm.** *P. ponderosa* var. *arizonica* (Engelm.) Shaw	**Arizona pine,** Arizona ponderosa pine, Arizona yellow pine	Sierra Madre Occidental; NW Durango, central Mexico, N into SE Arizona, SW corner New Mexico
***P. armandii* Franch.**	**Armand pine**	Mid-high elevations of mtns in central China to SW China, N Burma, E Tibet; Hainan, Taiwan; Japan (N Ryuku Islands)
***P. attenuata* Lemmon** *P. tuberculata* Gord.	**knobcone pine**	Rocky slopes & ridges of Klamath Mtns, coastal ranges & Sierra Nevada in SW Oregon & California; Baja California Norte
***P. balfouriana* Grev. & Balf.**	**foxtail pine,** Balfour pine	Subalpine California; central, S Klamath Mtns, S Sierra Nevada
***P. banksiana* Lamb.** *P. divaricata* (Ait.) Dum.-Cours.	**jack pine,** scrub pine, banksiana pine, black/gray pine, Hudson Bay pine	Canada, NE US: S Mackenzie to central Alberta, E through Ontario to Nova Scotia, S through Great Lakes region to SW Wisconsin, Michigan to NW Indiana; upstate New York, New Hampshire, Maine
***P. brutia* Tenore** *P. halepensis* var. *brutia* (Ten.) Elwes & Henry	**Calabrian pine**	Crete, Cyprus, Lebanon, W Syria, Turkey to NE Greece, Black Sea; Caucasus Mtns; N Iraq
***P. canariensis* C. Smith**	**Canary Island pine,** Canary pine	Dry slopes of Canary Islands (Hierro, La Palma, Tenerife, Gomera, & Gran Canaria), Spain
***P. caribaea* Morelet** *P. bahamensia* Griseb. *P. hondurensis* Loock	**Caribbean pine**	W Bahamas; W Cuba, Isle of Pines; Caribbean Central America, Belize S to Nicaragua
***P. cembra* L.** *P. montana* Lam.	**Swiss stone pine,** cembrian pine, arolla pine	High elevations in Alps & Carpathian Mtns; N Italy, SE France, Switzerland, Austria, W tip of Yugoslavia; Romania, SW Ukraine, NW [Czecho]slovakia
***P. cembroides* Zucc.**	**Mexican piñyon,** nut pine, pinyon	Semiarid, low elevations of Sierra Madre Oriental & Occidental; Puebla, Tlaxcala N in E, W Mexico to SE Arizona, SW New Mexico, SW Texas; S Baja California Sur, Mexico
***P. clausa* (Chapman ex Engelm.) Vasey ex Sarg.**	**sand pine,** scrub pine, spruce pine	Sandy plains; throughout central Florida to coastal NE & S Florida; also W Florida Panhandle W into Baldwin Co., coastal Alabama
***P. contorta* var. *bolanderi* (Parl.) Vasey**	**Bolander pine**	Coastal N California: acid podsol soils of Mendocino White Plains in Mendocino Co.
***P. contorta* var. *contorta* Dougl. ex Loud.**	**shore pine,** coast pine, beach pine, lodgepole pine	Pacific Coast mtns, low elevations down to sea level; California north coastal ranges N to Yakutat Bay, SE Alaska
***P. contorta* var. *latifolia* Engelm. ex S. Wats.**	**Rocky Mountain lodgepole pine,** black pine	Rocky Mtns & intermountain region; Colorado & Utah N through W Canada to central Yukon; Black Hills, South Dakota
***P. contorta* var. *murrayana* (Grev. & Balf.) Engelm.**	**Sierra Nevada lodgepole pine,** tamarack pine	Subalpine; Sierra Nevada–Cascade Ranges, transverse–peninsular ranges; California to Baja California Norte, W Nevada, Oregon N to SW Washington
***P. coulteri* D. Don** *P. ponderosa* ssp. *coulteri* (D. Don) E. Murr	**Coulter pine,** nut pine, big-cone pine	Mtns; California south coastal ranges S through transverse–peninsular ranges to N Baja California Norte
***P. densiflora* Sieb. & Zucc.**	**Japanese red pine**	Mtns, low-mid elevations in Japan (Honshu to Kyushu), South Korea, E North Korea to SE Manchuria, adjoining Chabarovsk, Siberia
***P. echinata* P. Mill**	**shortleaf pine,** southern yellow pine, oldfield pine	Coastal plains, Piedmont, Appalachian Mtns, Ozark Plateau; tip SE New York S to NW Florida, W to E Texas, E Oklahoma, SE Missouri, S Ohio
***P. edulis* Engelm.** *P. cembroides* var. *edulis* (Engelm.) Voss	**piñyon,** Colorado pinyon, nut pine, two-needle pinyon	Semiarid regions; Arizona, Utah, Colorado, New Mexico; crosses into W Oklahoma, SW Texas, & SE California

Table 1— *Pinus,* pine: nomenclature and occurrence (continued)

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. elliottii* var. *densa* Little & Dorman**	**South Florida slash pine**	Sandy plains of central to S Florida, E & W Florida coasts; lower Florida Keys
***P. elliottii* var. *elliottii* Engelm.** *P. caribaeu* Morelet	**slash pine,** pitch pine, swamp pine, yellow slash pine, Honduras pine	Coastal plains of lower South Carolina S to central Florida, W to S Mississippi, SE Louisiana
***P. engelmannii* Carr.** *P. latifolia* Sarg. *P. apacheca* Lemmon	**Apache pine,** Arizona longleaf pine	Sierra Madre Occidental; Aguascalientes, SW Zacatecas N through W Mexico into SE Arizona, SW corner of New Mexico
***P. flexilis* James**	**limber pine,** Rocky Mountain white pine	Subalpine; Sierra Nevada, Great Basin ranges, Rocky Mtns; New Mexico N to Alberta, Canada; W in Idaho, Utah, Nevada, into S California
***P. gerardiana* D. Don** *P. aucklandii* Lodd. *P. chilghoza* Ehh.	**chilgoza pine,** Gerard pine	Himalayas, dry valleys; E Afghanistan, contiguous N Pakistan, N India
***P. glabra* Walt.**	**spruce pine,** cedar pine, bottom white pine	Coastal plains of E South Carolina to N Florida, W to S Mississippi, SE Louisiana
***P. halepensis* P. Mill.** *P. alepensis* Poir.	**Aleppo pine,** Jerusalem pine	Mediterranean region: E Spain, SE France, Italy, S Adriatic Coast to Greece; NE Libya; Israel, Morocco to N Tunisia; Pantalleria, Sicily; W Jordan N to extreme S central Turkey
***P. heldreichii* Christ** *P. heldreichii* var. *leucodermis* (Ant.) Markgr. *P. eucodermis* Ant. *P. nigra* var. *leucodermis* (Ant.) Rehd.	**Heldreich pine,** Balkan pine, Bosnian pine, graybark pine	High elevations of Balkan Peninsula, Albania to SW Yugoslavia, extreme N Greece, SW to SW Bulgaria, & SW Italy
***P. jeffreyi* Grev. & Balf.** *P. ponderosa* var. *jeffreyi* (Grev. & Balf.) E. Murr.	**Jeffrey pine**	Sierra Nevada–Cascade & Klamath Mtns, coastal & transverse–peninsular ranges of California to SW Oregon, Baja California Norte, W Nevada
***P. kesiya* Royle & Gordon** *P. khasya* Royle *P. insularis* Endl.	**Khasi pine,** Benguet pine	High elevations of E India, SE Tibet, Burma, SW Yunnan to N Thailand, Laos, S Vietnam, W Luzon, Philippines
***P. koraiensis* Sieb. & Zucc.**	**Korean pine,** cedar pine	Mtns of South Korea to North Korea through E Manchuria, S Chabarovsk, Siberia; Japan (central Honshu & Shikoku)
***P. lambertiana* Dougl.**	**sugar pine,** *piño real*	Sierra Nevada–Cascade & Klamath Mtns, coastal & transverse–peninsular ranges of California to N Oregon, Baja California Norte, W Nevada
***P. leiophylla* var. *chihuahuana* (Engelm.) Shaw** *P. chihuahuana* Engelm.	**Chihuahua pine,** yellow pine, *piño real*	Sierra Madre del Sur, trans–Mexico volcanic belt, Sierra Madre Occidental; Oaxaca, Vera Cruz W to Michoacán; N in W Mexico to SE Arizona, SW New Mexico
***P. merkusii* Junghuhn & Vriese ex Vriese**	**Merkus pine,** Tenasserim pine	Mtns, low elevations of SE Burma, N Thailand, Cambodia, Laos, Vietnam, Hainan, N Sumatra, Philippines (W Luzon & N Mindoro)
***P. monophylla* Torr. & Frém.** *P. cembroides* var. *monophylla* (Torr. & Frém.) Voss	**singleleaf piñyon,** nut pine, pinyon, piñon	Semiarid mtns of NW Arizona, W Utah to SE Idaho, W through Nevada to E California, S to Baja California Norte
***P. monticola* Dougl. ex D. Don**	**western white pine,** Idaho white pine, silver pine	Sierra Nevada, Cascade & coastal ranges; Klamath & Rocky Mtns; California, W Nevada, Oregon through Washington, N Idaho, NW Montana, Vancouver Island, S British Columbia, SW corner Alberta
***P. mugo* Turra** *P. montana* Miller	**Swiss mountain pine,** mugho (or mugo) pine, dwarf mountain pine	Subalpine areas in central & S Europe: Pyrenees, Alps, Carpathian Mtns, Balkan Mtns; Austria, Switzerland, N Italy, E France; N to Germany, Czech Republic & Slovakia into S Poland, E into W Ukraine, Romania; Yugoslavia to N Albania, W Bulgaria; central Italy; S France, NE Spain
***P. muricata* D. Don** *P. remorata* Mason	**bishop pine**, prickle-cone pine, Santa Cruz Island pine	Coastal mtns; California Coast Ranges, Santa Rosa & Santa Cruz Islands; Baja California Norte, Cedros Island, Mexico
***P. nigra* Arnold** *P. nigra* var. *austriaca* (Hoess) Aschers. & Graebn.	**Austrian pine,** European black pine, black pine	S Europe, Mediterranean, Asia Minor; Spain to Corsica, Italy, Sicily; Yugoslavia to E Austria, SW Romania, Bulgaria, Albania, Greece, Turkey; Black Sea Coast in Ukraine, Russia; Cyprus; NE Morocco; N Algeria

Table 1— *Pinus,* pine: nomenclature and occurrence (continued)

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. palustris* P. Mill.** *P. australis* Michx. f.	**longleaf pine,** southern pine, longstraw pine	Coastal plains of SE Virginia to central Florida, W to N Louisiana, E Texas
***P. parviflora* Sieb. & Zucc.** *P. pentaphylla* Mayr *P. himekomatsu* Miyabe & Kudo	**Japanese white pine**	Mtns of Japan (Kyushu, Tsushima, Shikoku, Honshu, Sado, & S Hokkaido); South Korea (Ullung Island)
***P. patula* Schiede ex Schtdl. & Cham.**	**Mexican weeping pine**	Sierra Madre Oriental, Mexico; central Oaxaca N to Querétaro, SW Tamaulipas; Guatemala, El Salvador, Honduras, Nicaragua
***P. peuce* Griseb.** *P. excelsa* var. *peuce* (Griseb.) Beissn.	**Balkan pine,** Macedonian pine, Greek stone pine	High elevations of Balkan Peninsula: SW Yugoslavia, E Albania, SW Bulgaria, extreme N Greece
***P. pinaster* Aiton** *P. maritima* Poir.	**maritime pine,** cluster pine, pinaster pine	SW Europe & Mediterranean Basin: Iberian Peninsula, SE France + Corsica; W Italy + Sardinia & Pantalleria; Morocco, coastal E Algeria
***P. pinea* L.**	**Italian stone pine,** umbrella pine, stone pine	Iberian Peninsula& Mediterranean Coast of France, W Italy, Albania, Greece, Turkey; NE Turkey; Lebanon; Ibiza, Majorca; Sardinia, Sicily; Corfu, Crete, & Cyprus
***P. ponderosa* var. *ponderosa* P. & C. Lawson.**	**Pacific ponderosa pine,** western yellow pine, bull pine, rock pine, blackjack pine	Sierra Nevada–Cascade Mtns, coastal & transverse–peninsular ranges, Klamath Mtns; California to W Nevada, N through Oregon, Washington, Idaho, W Montana, to S British Columbia
***P. ponderosa* var. *scopulorum* Engelm.**	**Rocky Mountain ponderosa pine,** western yellow pine, blackjack pine	Rocky Mtns, Sierra Madre Oriental; Montana, SW North Dakota S in Wyoming, Colorado, New Mexico, trans–Pecos Texas to Coahuila, San Luis Potosi; E to central Nebraska; W in Utah, Arizona to Nevada
***P. pumila* Regel** *P. cembra* var. *pumila* Pall.	**Japanese stone pine**, dwarf Siberian pine	NE Asia; E Siberia, Lake Baikal, Lena River regions E to Bering Sea & Sea of Okhotsk; N Mongolia; E Manchuria to South Korea; Sakhalin; Kamchatka, Kuril Islands to central Honshu, Japan
***P. pungens* Lamb.**	**Table Mountain pine,** hickory pine, mountain pine, prickly pine	Appalachian Mtns of SW Pennsylvania, W Maryland through E West Virginia, W Virginia to E Tennessee, W North Carolina, extreme NE Georgia
***P. quadrifolia* Parl. ex Sudworth**	**Parry piñyon,** nut pine, pinyon	Semiarid, low elevations of San Jacinto Mtns, SW California, S to Sierra San Pedro Mártir, Baja
***P. radiata* D. Don** *P. insignis* Dougl.	**Monterey pine,** radiata pine, insignis pine	Coastal central California, in Año Nuevo Point, Monterey, & Cambria areas; Cedros Island & N Guadalupe Island, Mexico
***P. resinosa* Soland.**	**red pine,** Norway pine, hard pine, pitch pine	Great Lakes region, Appalachian Mtns; SE Manitoba E to Nova Scotia, N Newfoundland; S to Wisconsin, N Illinois, Pennsylvania, New Jersey; NE West Virginia
***P. rigida* P. Mill.**	**pitch pine,** hard pine, bull pine	Appalachian Mtns in N Georgia, Kentucky, E Tennessee N through Pennsylvania, Delaware to SE Ontario, & central Maine
***P. roxburghii* Sarg.** *P. longifolia* Roxb.	**Chir pine,** longleaf Indian pine	Himalayas, monsoon belt; N Pakistan E through N India, Nepal, Sikkim, Bhutan
***P. sabiniana* Dougl. ex Dougl.**	**Digger pine,** bull pine, gray pine	Dry slopes, low-mid elevations; California, in S Klamath Mtns, coastal ranges, Cascade Mtns–Sierra Nevada
***P. serotina* Michx.** *P. rigida* var. *serotina* (Michx.) Clausen	**pond pine,** marsh bay pine, pocosin pine	SE US, coastal plains of central & N Florida N to lower New Jersey, W to central & SE Alabama
***P. sibirica* Du Tour** *P. cembra* var. *sibirica* Loud.	**Siberian stone pine**	Ural Mtns of Russia, E across central Siberia to Stanovoy Mtns, S through Sayan Mtns, Lake Baikal region to N Mongolia
***P. strobiformis* Engelm.** *P. flexilis* var. *reflexa* Engelm. *P. reflexa* (Engelm.) Engelm. *P. ayacahuite* var. *brachyptera* Shaw	**southwestern white pine,** border limber pine, Mexican white pine	Sierra Madre Occidental & Oriental; S Rocky Mtns; Durango, central Mexico N to E Arizona, SW San Luis Potosi N to extreme W Texas, N through New Mexico to SW Colorado

Table 1— *Pinus,* pine: nomenclature and occurrence (continued)

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. strobus* var. *chiapensis* Martínez**	**Chiapas white pine**	Mtns of S Mexico (Chiapis) & Guatemala
***P. sylvestris* L.**	**Scots pine,** Scotch pine	Eurasia: Scotland, Scandinavia, Germany, France, & Spain E to Turkey, Caucasus Mtns; Central & E Europe through Ural Mtns, N Kazakhstan, Siberia to Sea of Okhotsk, N Mongolia, N Manchuria
***P. taeda* L.**	**loblolly pine,** Arkansas pine, North Carolina pine, oldfield pine	Coastal Plains, Piedmont; Delaware S to central Florida; W through Georgia, S Tennessee, Gulf Coast states to SE corner Oklahoma, E Texas
***P. thunbergiana* Franco** *P. thunbergii* Parl.	**Japanese black pine**	Maritime Japan (Honshu to N Ryukyu Islands), South Korea (Cheju Island)
***P. torreyana* Parry ex Carr.**	**Torrey pine,** Soledad pine, Del Mar pine	Maritime S California (NE Santa Rosa Island) & coastal bluffs of San Diego County
***P. virginiana* P. Mill**	**Virginia pine,** scrub pine, Jersey pine, spruce pine	Piedmont & Appalachian Mtns; Long Island, New York to Chesapeake Bay, S to N Georgia, central Alabama; W to Ohio, S Indiana, W Kentucky, Tennessee, NE Mississippi
***P. wallichiana* A.B. Jacks.** *P. excelsa* Wall. *P. griffithii* McClelland *P. nepalensis* de Chambr.	**blue pine,** Bhutan pine, Himalayan pine	Himalayas, mid-high elevations: NE Afghanistan, N Pakistan, N India E through Nepal, Bhutan, NE India, S Tibet to N Burma, NW Yunnan
***P. washoensis* Mason & Stockwell**	**Washoe pine**	W edge of Great Basin; E slope Mt Rose, W Nevada; Bald Mtn Range in N Sierra Nevada; S Warner Mtns, NE California

Sources: Critchfield and Little (1966), Gardner and Berenson (1987), Griffin and Critchfield (1976).

ponderosa pines in Australia and New Zealand; Mexican weeping pine in South Africa; and Monterey pine in Australia, New Zealand, Spain, South Africa, and South America. Nine of these 17 pines are native to North America (Leloup 1956; Magini and Tulstrup 1955; Mirov 1967; Wright 1962).

Geographic races. Abundant field experience and provenance research have shown that genetic adaptation mandates sowing seeds and outplanting seedlings grown from seeds from the proper source. Seed origin critically controls a species' ability to survive and grow in a particular environment. Pines that have extensive natural ranges (and even some with highly restricted ones) have evolved geographic races that are distinct both morphologically and physiologically (Callaham 1963). The resultant genetic—that is, seed-source—differences make each race the best suited for growth and survival in a particular environment.

As a general rule, seeds from pines growing in moist regions are smaller than those from sources in dry regions and seeds from moist regions normally produce seedlings that are faster growing and less deeply rooted than those from dry regions. Seeds from southern sources differ from those from northern sources. Seeds from northern sources often require longer moist chilling times than seeds from southern ones to release seed dormancy and enable germination. Trees from southern sources grow faster, are able to grow for a longer time during the growing season, and are more prone to winter freezing damage and less prone to damage from hard frosts in late spring and early autumn than are trees from northern sources (Krugman and Jenkinson 1974; Squillace and Silen 1962; Wells 1969; Wright 1962).

Detailed data on geographic races are ample for some pines and still lacking for many others. In some cases, our knowledge of races in pines native to the United States derives from species introduction trials and provenance tests in other countries. We have recapped the knowledge on geographic variation for the following 52 pines, all of those for which sufficient information was available.

Pinus aristata—Bristlecone pines in western and eastern parts of the range differ sufficiently in chemical composition and morphological traits that some suggest calling western populations *P. longaeva* D.K. Bailey and eastern populations *P. aristata* (Bailey 1970; Zavarin and Snajberk 1973). This very low crossing ability between western and eastern populations supports the naming of 2 distinct species (Critchfield 1977).

Pinus attenuata—For knobcone pine, differences in nursery and morphological traits tend to define 2 major groups, 1 north and 1 south of the Monterey County–San Luis Obispo County line in California. Seed weight generally increases from north to south. Seeds with northern origins

Table 2 —*Pinus,* pine: mature tree height, earliest cultivation, seed bearing age, and interval between large cone crops

Species	Mature tree height (m)	Year first cultivated	Age at onset seed bearing (yr)	Years between cone crops
P. albicaulis	6–33	1852	20–30	3–5
P. aristata	6–15	1861	20	102
P. arizonica	23–27	—	15–20	2–3
P. armandii	18–37	1895	20	—
P. attenuata	5–15	1847	5–8	1
P. balfouriana	11–18	1852	20	5–6
P. banksiana	17–30	1783, earlier	3–15	3–4
P. brutia	20–30	—	7–10	1
P. canariensis	30	—	15–20	3–4
P. caribaea	18–30		—	—
P. cembra	10–23	1746	25–30	6–10
P. cembroides	5–8	1830	—	5–8
P. clausa	5–24	1832	5	1–2
P. contorta				
var. *contorta*	6–12	1855	4–8	1
var. *latifolia*	8–46	1853	5–10	1
var. *murrayana*	15–30	—	4–8	1
P. coulteri	9–23	1832	8–20	3–6
P. densiflora	21–37	1854	20–30	2
P. echinata	2–30	1726	5–20	3–10
P. edulis	3–12	1848	25–75	2–5
P. elliottii				
var. *densa*	8–26	—	8–12	1–5
var. *elliottii*	24–30	—	7–10	3
P. engelmannii	15–21	—	28–30	3–4
P. flexilis	6–24	1861	20–40	2–4
P. gerardiana	15–24	1839	—	—
P. glabra	24–27	—	10	—
P. halepensis	15–24	1683	15–20	1
P. heldreichii	18–30	1865	—	—
P. jeffreyi	18–55	1853	8	2–4
P. kesiya	30–46	—	5–10	1
P. koraiensis	27–46	1861	15–40	1–5
P. lambertiana	30–69	1827	40–80	3–5
P. leiophylla var. *chihuahuana*	9–24	—	28–30	3–4
P. merkusii	18–30	—	10–20	1–2
P. monophylla	6–15	1848	20–25	1–2
P. monticola	27–61	1851	7–20	3–7
P. mugo	2–12	1779	10	1
P. muricata	12–27	1846	5–6	2–3
P. nigra	20–50	1759	15–40	2–5
P. palustris	24–37	1727	20	5–7
P. patula	18–34	—	12–15	—
P. parviflora	5–30	1861	—	4–5
P. peuce	10–30	1863	12–30	3–4
P. pinaster	27–37	1660, earlier	10–15	3–5
P. pinea	14–23	Long history	—	—
P. ponderosa				
var. *ponderosa*	18–70	1826	16–20	2–5
var. *scopulorum*	15–35	—	6–20	2–5
P. pumila	0.3–2.5	1807	—	—
P. pungens	9–18	1804	5	—
P. quadrifolia	5–9	1885	—	1–5
P. radiata	2–46	1833	5–10	1

Table 2 —*Pinus,* pine: mature tree height, earliest cultivation, seed bearing age, and interval between large cone crops (continued)

Species	Mature tree height (m)	Year first cultivated	Age at onset seed bearing	Years between cone crops
P. resinosa	21–46	1756	20–25	3–7
P. rigida	6–30	1759, earlier	3–4	4–9
P. roxburghii	46–55	1807	15–40	2–4
P. sabiniana	12–24	1832	10–25	2–4
P. serotina	12–24	1713	4–10	1
P. sibirica	40	1837	25–35	3–8
P. strobiformis	8–38	1840	15	3–4
P. strobus	24–67	1705	5–10	3–10
P. sylvestris	24–40	Long history	5–15	4–6
P. taeda	27–34	1713	5–10	3–13
P. thunbergiana	30–40	1855	6–40	—
P. torreyana	8–18	1853	12–18	1
P. virginiana	15–30	1739	5	1
P. wallichiana	15–46	1827	15–20	1–2
P. washoensis	18–46	—	15–20	2–5

Sources: Altman and Dittmer (1962), Bailey (1970), Bates (1930), Britton and Shafer (1908), Carlisle and Brown (1968), Cooling (1968), Dallimore and Jackson (1967), Day (1967), den Ouden and Boom (1965), Dimitroff (1926), Duff (1928), Fowells (1965), Fritts (1969), Goor (1955), Harlow and Harrar (1950), Iroshnikov (1963), Iroshnikov and others (1963), Jacaline and Lizardo (1958), Krugman and Jenkinson (1974), Little EL (1941a, 1950), Loock (1950), Luckhoff (1964), Magini and Tulstrip (1955), McIntyre (1929), Mirov (1956), NBV (1946), Otter (1933), Pearson (1931), Poynton (1961), Pravdin (1963), Rehder (1940), Rohmeder and Loebel (1940), Rossi (1929), Sargent (1905, 1965), Sudworth (1908), Troup (1921), Veracion (1966), Wahlenberg (1946), Wakeley (1954), Wakeley and Barnett (1968), Wappes (1932), Wellner (1962).
Note: See table 3 for cone ripening and seed dispersal dates and table 4 for cone ripeness criteria.

require longer stratification times (3 weeks or more) than seeds with southern origins (less than 3 weeks). Seedlings from northern sources tend to be more frost resistant than seedlings from southern sources. Trees in the northern part of the species' range are somewhat larger than those in the southern part. The source differences appear to be clinal and largely reflect the species' latitudinal distribution (Brown and Donan 1985; Newcomb 1962).

Pinus balfouriana—Foxtail pine seeds of northern origin in California (Lake Mountain, in the eastern Klamath Mountains) are longer than those of southern origin (Mineral King, in the southern Sierra Nevada). Seeds of northern origin have persistent wings, and seeds of southern origin have detachable wings (Mastrogiuseppe 1968).

Pinus banksiana—Jack pine seeds from various sources differ in seed size, cone traits, seedling and tree growth, tree form, and susceptibility to insect and disease damage (King 1971; Yeatman 1974). Cone serotiny in Minnesota changes from closed cones in the north to chiefly open cones in the south (Rudolph and others 1959). Seeds tend to be larger from trees growing in warmer parts of the range (Fowells 1965), and seedlings from lower latitudes show less winter needle coloration than those from higher latitudes (Stoeckeler and Rudolf 1956). In Canada, height growth was greater for seeds from areas with longer growing seasons; height growth of selections moved north was better than that of those moved south (Holst 1962). Growth in provenance tests follows a largely clinal pattern that is linked to environmental gradients of latitude and length and temperature of the growing season at seed origin (Rudolph and Laidly 1990; Rudolph and Yeatman 1982).

Pinus brutia—Calabrian pine has 2 known varieties, both in the northernmost parts of its range. The var. *pithyusa* Stev. occurs along the north central and northeast shores of the Black Sea and var. *eldarica* Medw. occurs in the central Caucasus Mountains (Magini and Tulstrup 1955). Trees from an Afghanistan source related to var. *eldarica* outgrew trees of var. *pithyusa*, had good form, and were both frost and drought hardy in California (Harris and others 1970; Krugman and Jenkinson 1974). Altitudinal variation in a number of seed and seedling traits is manifested in Greece and in Turkey (Isik 1986; Panetsos 1986).

Pinus canariensis—Canary Island pine is native only to the Canary Islands, where it is found at 640 to 2,195 m above sea level (Magini and Tulstrup 1955). Seedlings grown from seeds from the various islands and an array of elevations showed marked differences in winter cold hardiness when grown at the USDA Forest Service's Institute of Forest Genetics nursery near Placerville, California. Seedlings from a seed source at 1,220 m on Tenerife Island showed more cold damage than those from a source at 1,890 m there. Seedlings from a source from 1,890 m on Palma Island, however, were badly damaged, suggesting that

sources on different islands differ in their susceptibility to cold (Krugman and Jenkinson 1974).

Pinus caribaea—Caribbean pine has 3 geographic variants. The var. *caribaea*, native to Cuba and the Isle of Pines, has persistent seed wings. The others do not. The var. *bahamensis* Barr. & Golf., in the Bahama Islands, has the smallest seeds, and var. *hondurensis* (Seneclauze) W.H.G. Barret & Golfari has the largest. In tests in South Africa, var. *caribaea* outgrew var. *hondurensis* from mainland Central America (Luckhoff 1964; Styles and Huges 1983).

Pinus cembra—Swiss stone pine has several recognized cultivars (Dallimore and Jackson 1967; den Ouden and Boom 1965). No distinct geographic races have been described, but there is genetic variation in needle width and in height growth (Holzer 1975)

Pinus cembroides—Mexican piñyon has 2 known varieties at the species' northernmost limits. The var. *bicolor* Little occurs in southeastern Arizona and southwestern New Mexico. The var. *remota* occurs on the Edwards Plateau of southwestern Texas and has very thin seedcoats (Little 1968).

Pinus clausa—Sand pine has 2 geographic races that are distinguished primarily on the basis of cone characteristics (Brendemuehl 1990). The wider ranging var. *clausa* (Ocala sand pine) occurs in central and eastern Florida and bears closed cones. The var. *immuginata* Ward (Choctawhatchee sand pine) occurs in the western Florida Panhandle and bears cones that ripen in September and shed seeds in October (Krugman and Jenkinson 1974; Little and Dorman 1952a). The varieties differ in important physiological traits. Seedlings grown from Choctawhatchee seed sources show higher survival rates after planting, better growth form, and greater resistance to root rot (Burns 1975).

Pinus contorta—Lodgepole pine has 5 highly differentiated geographic races that differ morphologically and ecologically (Critchfield 1980; Lotan and Critchfield 1990). The races include 4 recognized varieties—*bolanderi, contorta, latifolia, and murrayana*—and 1 poorly known race (not named). The var. *bolanderi* (Bolander pine) is restricted to the narrow strip of highly acid podsol soils (the Mendocino White Plains) that parallels the coast in Mendocino County in northern California and bears serotinous cones similar to those of the interior var. *latifolia* (Rocky Mountain lodgepole pine). Both the var. *contorta* (shore pine) and the var. *murrayana* (Sierra Nevada lodgepole pine) bear cones that open at maturity or shortly thereafter. The open cones of var. *contorta* persist indefinitely, whereas those of var. *murrayana* do not. The fifth race is endemic to ultramafic soils in the low coastal mountains in Del Norte County in northern-most California. Its cones are heavier and more reflexed than those of any other race and often are serotinous. The var. *murrayana* produces the largest seeds, and var. *latifolia* has seeds that germinate twice as fast at 10 to 20 °C as those of coastal origins (Critchfield 1957). In provenance tests in northern Europe, seedlings of var. *contorta* grew faster but were less winter hardy and more branchy than those of var. *latifolia* from the Rocky Mountains and interior British Columbia (Edwards 1954–55).

Seed-source differences exist within varieties. Seeds from high-elevation populations in central British Columbia germinated fastest at 20 °C; those low-elevation populations germinated faster at temperatures above 20 °C (Haasis and Thrupp 1931). Trees from southern seed sources commonly grow faster than those from northern sources (Critchfield 1980).

Pinus coulteri—Coulter pine has no known races but grows in isolated stands on fertile to very poor soils at altitudes ranging from 152 to 2,134 m in central California to northern Baja California. Seeds from the species' northernmost populations, at Mount Diablo, the north end of the southern coastal range, are judged to have the poorest form, with greater branching than those from any other source (Zobel 1953).

Pinus densifloria—Japanese red pine is widely planted and shows hardy growth in the Great Lakes region, New England, and southern Ontario (Krugman and Jenkinson 1974). Cultivars have been described (Ouden and Boom 1965).

Pinus echinata—Shortleaf pine shows wide geographic and racial variation (Dorman 1976; Lawson 1990). Tree growth and survival in a rangewide seed source test in the southern United States showed that seeds from sources east of the Mississippi River were superior to northern sources and that those from northern sources should be planted in the northernmost parts of the species' range (Little 1969; Wells 1969, 1973, 1979; Wells and Wakeley 1970). Important differences in tree height, bole diameter at breast height, and stem volume were found among the various sources planted in Oklahoma (Tauer and McNew 1985). An Arkansas source performed the best in an Oklahoma test, surpassing even a local source (Posey and McCullough 1969).

Pinus edulis—Piñyon has 2 forms (Ronco 1990). The single-needle form, var. *fallax* Little, ranges near 1,830 m in the mountains of central and eastern Arizona, in the Grand Canyon, and in parts of New Mexico. Seeds of var. *fallax* tend to be larger and have a thicker seedcoat than seeds of

the 2-needle form, var. *edulis*. Moreover, the var. *fallax,* unlike the more widespread var. *edulis*, seldom produces seeds in quantity (Little 1968).

Pinus elliottii—Slash pine has 2 distinct varieties (Lohrey and Kossuth 1990). Geographic variation in the widespread var. *elliottii* is clinal in numerous form and growth traits (Dorman 1976; Frampton and Rockwood 1983; Gansel and Squillace 1976). Seeds from northeast Florida sources are susceptible to ice damage and are less resistant to drought than those from northern and western sources. The var. *densa* (Little & Dorman) Gaussen in south Florida germinates faster than the var. *elliottii*, shows a grasslike seedling stage with crowded needles, and has heavy wood with wide summer growth rings (Kraus 11963; Little and Dorman 1952b, 1954; Squillace 1966, Wells 1969).

Pinus flexilis—Limber pine generally shows genetic variation in a north–south pattern, but the overall variability for any one trait is small (Steele 1990; Steinhoff and Andresen 1971). Seedlings of southern origins grow faster than those of northern origins (Steinhoff 1964).

Pinus halepensis—Aleppo pine is distributed extensively around the Mediterranean basin and shows broad geographic variation in seed germination, seedling growth, trunk straightness, branch size and angle, and cone shape (Falusi and others 1983; Giordano 1960). Two elevational ecotypes are known in Israel, and others are expected in other parts of the species' range (Karschon 1961; Magini and Tulstrup 1955).

Pinus heldreichii—Heldreich pine is viewed as a timberline tree by some and has 4 varieties. The var. *leucodermis* (Ant.) Markgr. ex Fitschen, the main variety, grows on drier sites and on soils formed on limestones (Dallimore and Jackson 1967). The var. *heldreichii* forms open forests in mountains at 915 to 1,524 m of elevation (Ouden and Boom 1965). The other, minor varieties are var. *longiseminis* and var. *pancici* (Vidacovic 1991).

Pinus jeffreyi—Jeffrey pine has 2 distinct distributions, one linked to climatic and altitudinal factors and the other to ultramafic soils, edaphic factors that signal geographic races (Jenkinson 1990). Seedlings from sources from east of the crest of the Sierra Nevada grow more slowly and are more drought resistant and cold hardy than those from sources west of the Sierra crest (Haller 1957). Seeds from high-elevation sources in the Sierra Nevada grew more slowly than those from lower elevations when planted in the western Sierra Nevada but showed ranking changes when planted in the northern California coastal range (Callaham and Liddicoet 1961; Callaham and Metcalf 1959). Seasonal patterns of seedling top and root growth capacity (RGC) vary with region and altitude of seed origin (Jenkinson 1980). Allele frequencies in populations on ultramafic soils in the Klamath Mountains of southwest Oregon and northwest California differ from those in the Sierra Nevada and transverse–peninsular ranges (Furnier and Adams 1986). Trees derived from populations on ultramafic soil in the Sierra Nevada, with allele frequencies similar to those of Klamath Mountains sources, show resistance to dwarf mistletoe (Scharpf and others 1992). New Zealand provenance tests showed that trees grown from a seed source at 514 m in the northern California coastal range—at low altitude, undoubtedly one on ultramafic soil—were distinct from those from a Sierra Nevada source in having higher resistance to needle blight, faster tree growth on moister sites, and higher wood density (Burdon and Low 1991).

Pinus kesiya—Khasi pines of Philippine seed origin had greater vigor and better form than those of Burmese, Indian, or Vietnamese origins in tests in what is now northern Zimbabwe (Magini and Tulstrup 1955; Savory 1962).

Pinus koraiensis—Korean pines from Siberia, mainland China, and Korea should likely be considered a geographic race distinct from those of Japanese origins (Krugman and Jenkinson 1974). Several horticultural cultivars have been identified (Vidacovic 1991).

Pinus lambertiana—Sugar pine, the tallest and largest of all pines, grows on diverse sites at altitudes from near sea level to more than 3,000 m and ranges through California into north central Oregon, west Nevada, and Baja California Norte. It is one of the more genetically variable pines (Kinloch and others 1996; Kinloch and Scheuner 1990). Pronounced differences among rangewide seed sources in seedling growth and in tree growth and survival were demonstrated in common garden tests in nurseries in the western Sierra Nevada and on cleared sites at low and high altitudes in the western Sierra Nevada and sites in coastal and inland regions of southwest Oregon. Genetic variation in adaptive traits is associated with altitude, latitude, and geographic region of seed origin (Harry and others 1983; Jenkinson 1996; Jenkinson and McCain 1993, 1996). Differences in xylem resin monoterpenes distinguish stands in the Cascade Range–Sierra Nevada from stands in the transverse–peninsular ranges of southern California (Smith and Green 1996). Gametic frequency of the dominant allele for resistance to white pine blister rust increases clinally from zero in the Oregon Cascade Range to 0.08 in the southern Sierra Nevada, then declines in the transverse–peninsular ranges to zero in the Sierra San Pedro Mártir in Baja California Norte (Kinloch 1992).

Pinus leiophylla var. *chihuahuana*—Chihuahua pine shows both good and poor growth forms. Trees of good form grow up to 24 m in height. Trees of poor form have short, crooked boles and many branches (Magini and Tulstrup 1955).

Pinus merkusii—Merkus pine shows distinct races on the Asian mainland and on Sumatra. Seeds of mainland origins are larger than seeds of Sumatra origins. Trees of mainland origins pass through a grasslike stage and tend to develop a straight, cylindrical bole, but they do not grow so tall as trees of Sumatran origins. Sumatran origins tend to sinuous growth and may reach 61 m in height (Cooling 1968). Some classify these races as 2 distinct species, placing *P. merkusiana* Jungh & Vriese on the Asian mainland and *P. merkusii* on Sumatra (Cooling and Gaussen 1970).

Pinus monophylla—Singleleaf piñyon grows over a wide geographic and altitudinal range, and differences in growth form, foliage color, and cone production are commonly observed among trees on identical sites (Meeuwig and others 1990). No variety has been named, but variants have partly or mostly 2 needles per fascicle, rather than the typical 1 needle per fascicle (Little 1968).

Pinus monticola—Western white pine varies by geographic region and elevation of seed origin. Seeds of northern Idaho sources are smaller than seeds of Washington and California sources, and progenies of high-elevation sources grow faster at high elevation than those of low-elevation sources (Squillace and Bingham 1958; USDA Forest Service 1948). Idaho populations differ from California populations, but populations in northern Idaho differ little from those in coastal Washington and western British Columbia (Rehfeldt and others 1984; Steinhoff 1981). Adaptation to different geographic, climatic, topographic, and edaphic conditions reflects phenotypic plasticity more than selective genetic differentiation (Graham 1990; Rehfeldt 1979; Steinhoff 1979).

Pinus mugo—Swiss mountain pine has many horticultural varieties, with growth forms ranging from the sprawling shrubs of var. *pumilio* (Haenke) Zenari to the small trees of var. *rostrata* (Antoine) Hoopes (den Ouden and Boom 1965; Vidacovic 1991). Varieties differ in seed size and germination capacity (Rafn 1915), and seedlings of sources from low elevations are not cold hardy at high elevations (Wappes 1932).

Pinus muricata—Bishop pine populations north of Fort Ross in the northern coastal range of California differ from those south of Fort Ross in tree growth form, foliage color, and cone shape. Trees of northern sources tend to grow larger and have fuller, more compact crowns than trees of southern sources (Duffield 1951). In tests in Australia, trees of northern sources maintained better growth rate and form than trees of southern sources (Fielding 1961).

Pinus nigra—Austrian pine has an extensive, disjunct distribution; the species encompasses a host of recognized varieties and cultivars (Magini and Tulstrup 1955; Rafn 1915; Van Haverbeke 1990; Vidacovic 1991). The var. *caramanica* (Loudon) Rehder in Cyprus, Turkey, and the Crimea tends to have the largest seeds, 38,500 to 45,760/kg (17,500 to 20,800/lb); var. *corsicana* (Loudon) Hyl. in Corsica has the smallest seeds, 61,600 to 79,000/kg (28,000 to 36,000/lb). The Corsican variety has notably better wood than typical Austrian pine, the var. *austriaca* (Hoess) Aschers. & Graebn. in the eastern Alps and on the Balkan Peninsula. Planted stands of the var. *calabrica* C.K. Schneid. in Belgium are believed to represent one of the more cold-hardy varieties. Other distinct varieties include the var. *cebennensis* (Godr.) Rehder in the Pyrenees of France, the var. *hispanica* in Spain, and the ssp. *mauritanica* (Maire & Peyerimh.) Heywood in Morocco and Algeria. Physiological traits delimit 3 regional seed source groups (Magini and Tulstrup 1955): (1) Western sources in France and Spain have often proved to be both drought resistant and indifferent to soil type. (2) Central sources in Corsica and Italy grow well and have good form, but all need high humidity and grow poorly on limestone soils. (3) Eastern sources in the Balkan and Crimean regions appear to grow well on poorer limestone soils.

In provenance tests in the north central United States, trees grown from seed sources in the eastern half of the species' natural range were the fastest growing and most winter hardy, but those from western Europe were more susceptible to frost damage (Wheeler and others 1976). A disease-resistant seed source from Yugoslavia had the fastest growing trees in a provenance test in eastern Nebraska (Read 1976; Van Haverbeke 1986b).

Pinus palustris—Longleaf pines of different geographic origins differ in seedling survival, height growth, and cold resistance. Southeastern and central Louisiana seed sources performed poorly and southern Florida sources failed outside their area of seed origin. Trees from central Gulf Coast seed sources grow well throughout the Gulf Coast region and are expected to outgrow those from other sources on coastal plains sites from Louisiana to northern Florida and Georgia (Boyer 1990; Fowells 1965; Snyder and others 1977; Wells 1969). Longleaf pines grown from seed sources west of the Mississippi River are more susceptible to brown spot needle blight than are those from Gulf Coast sources east of the Mississippi River (Dorman 1976; Lantz and Kraus 1987).

Pinus parviflora—Japanese white pine is thought to consist of 2 geographical varieties that merge in central Honshu (Critchfield and Little 1966). Several horticultural forms of the species are cultivated (Krüssmann 1960).

Pinus patula—Mexican weeping pine grows rapidly and has been widely introduced. It grows well in Australia, New Zealand, and East Africa and has become an important source of wood in the summer-rainfall areas of South Africa (Leloup 1956; Loock 1950; Magini and Tulstrup 1955). Two varieties are known. The typical var. *patula* bears closed cones and has entirely black seeds. The var. *longepedunculata* ssp. *tecumumanii* Loock, found in the Mexican states of Oaxaca and Chiapas, opens cones quickly at maturity and yields seeds that are black with brown marks (Loock 1950).

Pinus peuce—Balkan pine of the best quality in Europe is believed to come from seed sources in the Rila and Pirin Mountains of Bulgaria (Müller 1932). Two distinct varieties have been identified, one in the mountains near Rodopes, Bulgaria, and the other in the western part of the species' range near Prokletije, Albania (Vidacovic 1991).

Pinus pinaster—Maritime pine has 5 major races. The highly variable French or Atlantic race typically inhabits coastal sands. The Portuguese race also inhabits coastal sands, but surpasses the French race in tree form, growth rate, and drought resistance. It grew well in tests in South Africa and western Australia and appears to have dormant seeds (Hopkins 1960; Wright 1962). The Iberian Mountains race is continental and slow growing (Resch 1974). The Corsican race occurs mainly in the mountains. In the Moroccan race, trees grown from seeds of mountain origins differ from near-coastal ones, as trees grown from seeds of mountain origins fail when they are planted in coastal areas. Trees of more southern origins are highly susceptible to frost damage. Trees of mountain origins are believed to be frost resistant (Magini and Tulstrup 1955).

Pinus ponderosa—Ponderosa pine, one of the most widely ranging pines in North America, has 2 distinct varieties: Pacific (var. *ponderosa*) and Rocky Mountain (var. *scopulorum*) Engelm. (Oliver and Ryker 1990). The varieties differ in a host of traits, including needle length and number per fascicle, xylem resin monoterpenes, cone and seed size, seed isozymes, seed dormancy and germination rate, seasonal patterns of seedling top and root growth capacity (RGC), seedling and tree survival, growth rate, stem form, drought tolerance, cold hardiness, disease resistance, and susceptibility to hail (Callaham 1962; Conkle and Critchfield 1988; Eldridge and Dowden 1980; Fowells 1965; Hoff 1988; Jenkinson 1976, 1980; Larson 1966; Read 1980, 1983; Read and Sprackling 1981; Rehfeldt 1986a&b; Smith 1977; Squillace and Silen 1962; Van Haverbeke 1986a; Wang 1977; Weidman 1939; Wells 1964).

Interpretation of this vast genetic diversity suggests that there are 5 major geographic races, including 3 in var. *ponderosa* and 2 in var. *scopulorum* (Conkle and Critchfield 1988). In var. *ponderosa,* the Pacific race occurs west of the crest of the Cascade Range–Sierra Nevada from northern Oregon to the transverse ranges in southern California; the southern California race ranges through the transverse–peninsular ranges; and the North Plateau race ranges along the east side of the Cascade Range–Sierra Nevada and extends east to the Continental Divide in Montana. In var. *scopulorum*, the Rocky Mountain race occurs in the northeast part of the species' range and joins the southwest race along a broad and ill-defined front in southern Colorado, Utah, and Nevada.

Provenances within varieties and races differ in a host of traits. Seeds from sources in the Pacific Northwest, Rocky Mountain, and Southwest differed in germination rate at different temperatures (Callaham 1962). In Oregon and Washington, growth rate generally increased with seed origin from east to west, and from south to north in eastern parts of the range. Seeds from sources from eastern and southeastern parts of the range produced seedlings showing the slowest growth (Squillace and Silen 1962). In northern Arizona, seedlings from eastern and southeastern sources grew well, but those from northern and western sources and the southernmost one failed (Larson 1966). Northern sources of var. *scopulorum* showed comparatively good growth and frost resistance, while southern sources were slower growing but also frost resistant (Weidman 1939). In California, seedlings of var. *ponderosa* from sources west of the crest of the Cascade Range–Sierra Nevada grow faster but are more subject to frost injury than those from east of the crest (Krugman and Jenkinson 1974). Important differences exist between sources in adaptation to ultramafic soils on the west slope (Jenkinson 1974, 1977), and the seasonal pattern of seedling RGC in the nursery depends on climatic region and altitude of seed origin in the Cascade Range–Sierra Nevada and transverse–peninsular ranges (Jenkinson 1976, 1980).

Tree growth rate increased with decrease in source elevation in early years in plantations at low, middle, and high elevations in the western Sierra Nevada, but in later years, performances of high-elevation sources at high elevation overtook those of low-elevation sources and neared those of mid-elevation sources. Wind and snow damage reduced the superiority of mid- and low-elevation sources. Wood specific gravity increased with decrease in source elevation in all

plantations (Callaham and Liddicoet 1961; Conkle 1973; Echols and Conkle 1971; Namkoong and Conkle 1976). Elevational differentiation in growth also exists in Idaho populations (Rehfeldt 1986a). New Zealand provenance tests confirm and elaborate the complex combination of differences between discrete races and clinal variation, particularly for the Pacific and North Plateau races and show that the patterns of differentiation vary according to the traits assessed (Burdon and Low 1991).

Pinus pungens—Table Mountain pine has no distinct races. Seed weight and cone length and width appear to decrease with increase in seed source elevation and decrease in source latitude. Stands in which most cones open the first and second year after they ripen are found in the northern end of the species range. Cone serotiny is commonest in the southern part of the range (Della-Bianca 1990; Zobel 1969).

Pinus radiata—Monterey pine, native to just 5 limited areas, is the most widely introduced of all pines (Critchfield and Little 1966; McDonald and Laacke 1990). Rapid growth and valuable timber and pulp qualities have made it a major timber species in plantation forestry in Australia, New Zealand, Chile, Argentina, Uruguay, Spain, South Africa, and Kenya. The varieties from native mainland sources—Año Nuevo, Monterey, and Cambria—situated on the central California coast are faster growing than the 2-needled var. *binata* (S. Wats.) Lemm., isolated on Cedros and Guadalupe Islands, Mexico, in the Pacific Ocean west of Baja California Norte.

Cambria populations have the largest cones and seeds, and Monterey populations the smallest ones (Forde 1964). Seedlings from Año Nuevo and Monterey seed sources grew better than those from Cambria sources in Australia (Fielding 1961). Moran and others (1988) found little genetic differentiation among the native populations, which indicates that most of the genetic variation occurs within stands. Cedros and Guadalupe Island populations are more resistant to western gall rust than those on the mainland, and Año Nuevo populations are more resistant than the Monterey and Cambria ones (Old and others 1986).

Pinus resinosa—Red pine is one of the least variable pines and one of the most widely planted species in the northern United States and Canada. It has no described varieties or subspecies, yet northern and southern races may exist (Rudolf 1990; Wright and others 1972). Differences in height growth, tree form, and wood quality appear among sources in the Great Lakes region, New England, and West Virginia. Seeds usually are smaller, lammas frequency is less, and frost resistance is higher in northern sources than in southern ones (Fowler and Lester 1970; Wright 1962).

Pinus rigida—Pitch pine lacks distinct races but exhibits differences between populations in cone serotiny, tree growth, and form (Kuser and Ledig 1987; Ledig and Fryer 1974; Little and Garrett 1990). In a test of Atlantic Coastal Plain provenances, trees from southern seed sources grew faster than trees of northern sources, but adaptation of all sources decreased with distance from seed origin. Throughout most of the species' range, pitch pine promptly opens cones and sheds seeds at maturity, but in southern New Jersey, pitch pine mostly bears closed cones that open only at irregular intervals. The latter populations developed in areas that have a history of wild fire (Andresen 1963; Fowells 1965).

Pinus roxburghii—Chir pine has no reported varieties, but seeds from sources in different regions of India show differences in tree growth, wood quality, and oleoresin yield and quality (Dogra 1987).

Pinus sabiniana—Digger pine has no distinct races or varieties but shows genetic differences between populations and geographic regions in cone shape and size, seed size and germination traits, seedling growth traits, and adaptation to highly infertile (serpentinite) soil (Griffin 1962; Powers 1990). Larger cones are more frequent in the northern coastal ranges and Klamath Mountains than in the Sierra Nevada. Seeds from stands in milder climates germinate faster after cold, moist stratification than seeds from stands in colder climates. Seedlings of southern origins grow for a longer time during the growing season than those of northern origins (Griffin 1964, 1965, 1971).

Pinus serotina—Pond pine has no distinct races (Bramlett 1990). Slight differences were found between trees from the coastal plain and trees from drier inland areas. Cone serotiny is greater in southern and coastal populations than in northern and Piedmont populations (Smouse 1970).

Pinus sibirica—Siberian stone pine showed important growth and morphological differences in a series of seed-source studies in Russia (Pravdin and Iroshnikov 1982). Differences in growth rate, branching habit, and seed fat content between certain populations have also been reported. No varieties are recognized, but distinct forms exist: the form *coronans* has a wide, dense crown, is fairly drought resistant, and extends from sea level to 2,012 m; the form *humistrata* is a dwarf form found on mountain summits and ridges; and the form *turfosa* grows on peat (Pravdin 1963).

Pinus strobus—Eastern white pine in Canada and the United States is the typical var. *strobus*. One of the more wide ranging and widely planted American trees, it is geographically variable and is separated by a discontinuity of more than 1,932 km from its variant in southern Mexico and

Guatemala, the var. *chiapensis* Martinez (Chiapas white pine) (Critchfield and Little 1966; Wendel and Smith 1990). Within the var. *strobus,* seeds from western sources are lighter than those from eastern sources, and seeds from southern sources require longer times in stratification than seeds from northern ones (Fowler and Dwight 1964; Krugman and Jenkinson 1974; Mergen 1963). Seedlings grown from eastern seed sources had blue-green foliage in fall; seedlings of northwestern sources had yellow-green foliage (Wright and others 1963). Trees from sources in the southern Appalachian Mountains tend to grow faster and continue shoot elongation longer in autumn than trees from northern seed sources (Fowler and Heimburger 1969; Wright 1970). Artificial freezing studies and field observations in the northern Great Lakes region showed that seedlings from northern sources are less sensitive to cold than seedlings from southern sources (Krugman and Jenkinson 1974; Mergen 1963). Geographic differences in flower production, winter injury, susceptibility to blister rust, and sensitivity to air pollution are also known (Wendel and Smith 1990; Wright and others 1979). Horticultural varieties have been described (Waxman 1977).

Pinus sylvestris—Scots pine is the most widely planted introduced pine species in the United States, especially in the Northeast, Great Lakes region, central states, and the Pacific Northwest. It is now is naturalized in parts of New England and the Great Lakes region (Skilling 1990). The pine with the greatest natural range of all the pines, it grows in a host of different ecological situations, was involved in the first comparative seed source trials of pine, and is likely the most intensively studied of all pines. Its geographic varieties conservatively number from 21 to 52, and numerous forms and ecotypes have been described. Abundant variation exists within varieties, and seed sources differ in many traits, including flowering; needle, cone, and seed color; seed size, dormancy, and germination rate; root system structure, seedling and tree growth rate and form, and susceptibility to heat, cold, and drought (Brown 1969; Genys 1976; Giertych 1976; Pravdin 1964; Read 1971; Steven and Carlisle 1959; Wright 1962; Wright and others 1966). Seed size decreases from south to north, ranging from 97,240 seeds/kg (44,200/lb) in Spain to 279,400/kg (127,000/lb) in Lapland (Heit 1969). Seeds from sources in the extreme northern parts of the range and certain areas in Greece and Turkey show the highest seed dormancy (Heit 1969). Incompletely developed embryos explain part of the dormancy of northern sources (Kamra 1969). Growth rate typically decreases and cold hardiness increases from south to north. Trees from Finnish and Russian sources survived better in prairie conditions in Canada than did trees from more southern sources (Cram and Brack 1953). In Michigan, trees from certain French sources grew 3 times taller than trees from northern sources from Finland and Siberia, but northern sources were more cold hardy than southern ones (Wright 1962; Wright and others 1966). Needles of trees with origins in Asia Minor, the Balkans, southern France, and Spain remained green in winter, whereas those with Siberian and Scandinavian origins turned yellow. In Sweden, seeds from sources at north latitudes or high elevations germinated well over a wider range of temperatures than did seeds from sources at south latitudes or low elevations, and seedlings trees of southern sources grew faster and later in autumn than trees of northern sources (Kamra and Simak 1968). Trees from introduced sources produced better trees than did local sources in some European localities (Vidacovic 1991).

Pinus taeda—Loblolly pine, commercially the most important forest tree in the southern United States, has repeatedly demonstrated important geographic variation in seedling and tree survival, growth rate, cold hardiness, drought hardiness, and disease resistance (Baker and Langdon 1990; Dorman 1976; Dorman and Zobel 1973). Local seed sources have often proved to be the best. Seedlings from southern sources are more prone to cold damage than those from northern ones, and seedlings grown from seeds from west of the Mississippi River are more drought tolerant and disease resistant than those from most sources east of the Mississippi. Seedlings from Maryland sources tend to grow less than those from other sources when planted in different areas (Wells 1969; Wells and Wakeley 1966). Trees of southern sources outgrew trees of northern sources in South Africa (Sherry 1947).

Pinus thunbergiana—Japanese black pine of inland origin show better growth form than those of coastal origin (Krugman and Jenkinson 1974).

Pinus torreyana—Torrey pines with mainland California origins in a planting on the California mainland had a single trunk and grew taller than trees with a Santa Rosa Island origin, which were bushy and branched freely. Trees from the Santa Rosa Island source produced larger cones (Haller 1967). The populations differ morphologically and biochemically as well (Ledig and Conkle 1983).

Pinus virginiana—Virginia pine has no known varieties or races, but populations in the Talledega Mountains of central Alabama and on deep sands of the mid-Atlantic Coast conceivably are distinct ecotypes (Carter and Snow 1990; Dorman 1976; Kellison and Zobel 1974). Seeds from local sources or sources from locations with climate similar to

that of the planting site generally yield the best survival and growth rates. Southern seed sources produce fast-growing trees on southern sites but on northern sites these trees grow slowly and suffer winter injury (Dorman 1976; Genys 1966; Genys and others 1974). Genetic variation in growth rate, stem form, wood traits, and monoterpene content in Kentucky and Tennessee occurs mainly among and within stands, rather than among geographic origins (Carter and Snow 1990).

Pinus wallichiana—Blue pine ranges through the Himalayan region in discontinuous distribution from eastern Afghanistan to eastern-most India, north Burma, and adjoining China. Although no distinct varieties have been reported, at least 7 broad provenances have been proposed, including 4 in the western Himalayas and 3 in the eastern Himalayas (Dogra 1987).

Pinus washoensis—Washoe pine ranges in limited areas along the western edge of the Great Basin in western Nevada and northern California, notably on the east slope of Mount Rose in the Carson Range in Nevada, in the Bald Mountain Range in the northern Sierra Nevada, and in the South Warner Mountains and several intervening areas in northeastern California (Critchfield 1984; Critchfield and Allenbaugh 1965; Niebling and Conkle 1990; Smith 1981). Closely related in appearance to and often wrongly identified as Pacific ponderosa pine, this rare pine ranges at higher altitudes than ponderosa pine, the same as Jeffrey pine. Washoe pine flowers in July, and its male and developing second-year female cones are purple to purplish black. The latter mature in August–September, turn to a dull purple, purplish brown, or light brown, and open in September. Cones are assessed and processed like those of Pacific ponderosa pine. Stored seeds germinate quickly after 60 days of moist, cold stratification (Jenkinson 1980; Krugman and Jenkinson 1974).

Hybrids. Pine hybrids are myriad. More than 260 first- and second-generation hybrids—as well as backcrosses, crosses between varieties of the same species, and crosses that involve 3 or more different species—either occur naturally or have been produced artificially (Critchfield 1963, 1966a, 1977, 1984; Critchfield and Krugman 1967; Krugman and Jenkinson 1974; Little and Righter 1965; Mirov 1967; Vidacovic 1991; Wright 1962). We provide no yield statistics for hybrids because such data are highly variable. Yields of sound seeds depend on species and individual trees, as well as on the environmental conditions under which the cross is made.

Natural hybrids are common, and we list but few of the many known. *P. palustris* × *taeda* (Sonderegger pine) occurs frequently in Louisiana and east Texas and is the best-known southern pine hybrid (Baker and Langdon 1990; Chapman 1922). Most natural hybrids occur infrequently in the overlaps of their parent species' ranges. Some of the better-known examples include the following:

- *P. contorta* var. *murrayana* × *banksiana* in western Canada (Zavarin and others 1969)
- *P. ponderosa* × *jeffreyi, P. jeffreyi* × *coulteri*, and *P. radiata* × *attenuata in California* (Critchfield and Krugman 1967; Mirov 1967)
- *P. flexilis* × *strobiformis* in north central Arizona and north central New Mexico (Steinhoff and Andresen 1971)
- *P. taeda* × *echinata* in east Texas
- *P. taeda* × *serotina* throughout the species' common range in southern United States (Critchfield 1963; Smouse 1970; Wright 1962)

The hybrid *P. densiflora* × *thunbergiana*, natural in Japan, has formed spontaneously in plantations of its parent species in Michigan (Krugman and Jenkinson 1974). In Europe, Scots pine crosses occasionally with Austrian pine and with mugo pine where the species are planted near one another (Wright 1962), and Austrian pine crosses with Heldreich pine var. *leucodermis* where they overlap in Herzegovina (Vidacovic 1991).

Several pine hybrids have been produced in relatively large numbers by controlled pollination methods. They include *P. rigida* × *taeda* in Korea where the hybrid is important in plantation forestry (Hyun 1962), and *P. attenuata* × *radiata*, tested in California and Oregon (Griffin and Conkle 1967). Many other pine hybrids have been produced in small numbers and tested for fitness in various parts of the United States (Burns and Honkala 1990).

Flowering and fruiting. Reproductive structures in certain pines first form when the trees are 5 to 10 years old, as in knobcone, jack, sand, lodgepole, and Monterey pines, among others (table 2). In other pines, reproductive structures form when the trees are 25 to 30 years old (as in Swiss stone and Siberian stone pines; piñyon; and Apache and Chihuahua pines) or 40 years old (as in sugar pine).

Pines are monoecious. Male and female "flowers"—properly strobili (microsporangiate and megasporangiate strobili)—are borne separately on the same tree. Male strobili predominate on the basal part of new shoots, mostly those on older lateral branches in the lower crown. Female strobili occur most often in the upper crown, chiefly at the apical ends of main branches in the position of subterminal

Table 3—*Pinus,* pine: phenology of flowering and fruiting

Species	Location	Flowering	Cone ripening	Seed dispersal
P. albicaulis	California	July	Aug–Sept	Not shed †
P. aristata	Arizona	July–Aug	Sept–Oct	Sept–Oct
P. arizonica	Arizona	May	Sept–Oct	Oct
P. armandii	California	Apr–May	Aug	Aug–Sept
P. attenuata	California	Apr	Jan–Feb	Closed cone‡
P. balfouriana	California	July–Aug	Sept–Oct	Sept–Oct
P. banksiana	Great Lakes	May–June	Sept	Sept§
P. brutia	California	Mar–May	Jan–Mar	Closed cone‡
P. canariensis	California	Apr–May	Sept	Sept–Oct
P. caribaea	Cuba	Jan–Feb	July–Aug	Sept
P. cembra	Germany	May	Aug–Oct	Not shed†
P. cembroides	California	May–June	Nov–Dec	Nov–Dec
P. clausa	Florida	Sept–Dec	Sept	Sept§
P. contorta				
var. *contorta*	California	May–June	Sept–Oct	Fall§
var. *latifolia*	Rocky Mtns	June–July	Aug–Sept	Sept–Oct §
var. *murrayana*	California	May–June	Sept–Oct	Sept–Oct
P. coulteri	California	May–June	Aug–Sept	Octê
P. densiflora	California	Apr	Aug–Sept	Sept–Oct
P. echinata	South Carolina	Mar–Apr	Oct–Nov	Oct–Nov
P. edulis	Arizona	June	Sept	Sept–Oct
P. elliottii				
var. *densa*	Florida	Jan–Apr	Aug–Sept	Sept–Nov
var. *elliottii*	Florida	Jan–Feb	Sept–Oct	Oct
P. engelmannii	Arizona	May	Nov–Dec	Nov–Feb
P. flexilis	California, Montana	June–July	Aug–Sept	Sept–Oct
P. gerardiana	India, California	May–June	Sept–Oct	Nov
P. glabra	Mississippi	Feb–Mar	Oct	Oct–Nov
P. halepensis	France	May–June	Sept	Fall §
P. heldreichii	Italy, California	May–July	Aug–Sept	Sept–Oct
P. jeffreyi	California	June–July	Aug–Sept	Sept–Oct
P. kesiya	Philippines	Jan–Mar	Oct–Jan	Feb–Mar
P. koraiensis	Japan	May–June	Sept	Oct
P. lambertiana	California	June–July	Aug–Sept	Aug–Oct
P. leiophylla var. *chihuahuana*	California	May–June	Nov*	Dec–Jan
P. merkusii	Thailand	Jan	Apr–Jun	May–Jul
P. monophylla	California, Nevada	May	Aug	Sept–Oct
P. monticola	Idaho	June–July	Aug	Aug–Sept
P. mugo	Europe	May–June	Oct	Nov–Dec
P. muricata	California	Apr–June	Sept	Midwinter §
P. nigra	Ontario, Canada	May–June	Sept–Nov	Oct–Nov
P. palustris	SE US	Feb–Mar	Sept–Oct	Oct–Nov
P. parviflora	Japan	May–June	Sept	Nov
P. patula	Mexico, California	Feb–Apr	Dec	Midwinter §
P. peuce	Europe	May	Fall	Fall
P. pinaster	Europe, California	Apr	Nov–Dec	Dec–Jan §
P. pinea	Europe	May–June	Late summer*	Late summer
P. ponderosa				
var. *ponderosa*	California	Apr–June	Aug–Sept	Aug–Sept
var. *scopulorum*	South Dakota, Colorado	May–June	Aug–Sept	Sept–Jan
P. pumila	Russia	July	—	Fall or not shed †
P. pungens	West Virginia, California	Mar–Apr	Fall	Fall §
P. quadrifolia	California	June	Sept	Sept–Oct
P. radiata	California	Jan–Feb	Nov	Midwinter §

Table 3—*Pinus,* pine: phenology of flowering and fruiting (continued)

Species	Location	Flowering	Cone ripening	Seed dispersal
P. resinosa	Great Lakes, California	Apr–June	Aug–Oct	Oct–Nov
P. rigida	New Jersey	May	Sept	Fall §
P. roxburghii	India	Feb–Apr	Winter	Apr–May§
P. sabiniana	California	Mar–Apr	Oct	Oct II
P. serotina	SE US	Mar–Apr	Sept	Spring §
P. sibirica	Russia	May	Aug–Sept	Not shed †
P. strobiformis	Arizona	June	Sep	Sept–Oct
P. strobus	NE US	May–June	Aug–Sept	Aug–Sept
P. sylvestris	Great Britain, California	May–June	Sept–Oct	Dec–Mar
P. taeda	SE US	Feb–Apr	Sept–Oct	Oct–Dec
P. thunbergiana	Japan, Long Island	Apr–May	Oct–Nov	Nov–Dec
P. torreyana	California	Feb–Mar	Jun–Jul*	Sept II
P. virginiana	E US	Mar–May	Sept–Nov	Oct–Nov §
P. wallichiana	India	Apr–June	Aug–Oct	Sept–Nov
P. washoensis	Nevada, California	July	Aug–Sept	Sept

Sources: Andreev (1925), Britton and Shafer (1908), Carlisle and Brown (1968), Cocozza (1961), Cooling (1968), Critchfield (1966b), Dallimore and Jackson (1967), Dimitroff (1926), Dorman and Barber (1956), Duffield (1953), Fowells (1965), Goor (1955), Jacaline and Lizardo (1958), Krugman and Jenkinson (1974), Lamb (1915), Letourneux (1957), Little EL (1938a & b, 1940), Little S (1941, 1959); Loiseau (1945), Loock (1950), Luckhoff (1964), Mikhalevskaya (1960), Mirov (1962), NBV (1946), Ohmasa (1956), Pearson (1931), Rehder (1940), Rohmeder and Loebel (1940), Sargent (1905), Snow (1960), Sudworth (1908), Tkachenko (1939), Troup (1921), Veracion (1964), Vines (1960), Wahlenberg (1946).

* Cones and seeds mature in the third year.
† Seeds are dispersed when the detached cones disintegrate.
‡ Cones open after several years, if at all. Seed dispersal normally requires fire.
§ Many cones remain closed for several months or years.
II Cones are massive, open slowly, and shed seeds over several months.

or lateral buds. Exceptions to this general scheme are common. Trees of knobcone, jack, sand, and Monterey pines are multinodal in the bud, and female strobili occasionally arise in secondary whorl positions. Trees of knobcone, Monterey, and Virginia pines usually produce female strobili in all parts of the crown. In temperate climates, the earliest stages of male and female strobili can be detected in the developing buds in summer or fall. Male strobili appear from 1 to several weeks before the female strobili (Fowells 1965; Gifford and Mirov 1960; Krugman and Jenkinson 1974; Mirov 1967).

Male and female strobili of the southern and tropical pines emerge from buds in late winter, as in slash pine × var. *densa* and var. *elliottii)* and spruce and longleaf pines (table 3). Strobili of other pines emerge from the winter bud in early spring or in late spring and early summer.

Male strobili are arrayed in indistinct spirals in clusters that range from 13 to 51 mm in length (Dallimore and Jackson 1967; Pearson 1931; Shaw 1914; Sudworth 1908). Immature male strobili are green or yellow to reddish purple; mature male strobili at the time of pollen shed are light brown to brown. In most pines, male strobili fall soon after ripening.

Female strobili emerge from the winter bud shortly after the male strobili and are green or red to purple (Dallimore and Jackson 1967; Fowells 1965; Pearson 1931; Sudworth 1908). At the time of pollination, they are nearly erect and range from 10 to 38 mm long and sometimes longer. After pollination, the female strobili close their scales, begin a slow development, and grow to nearly one-eighth to one-fifth the length of mature cones at the end of their first growing season. Cone development continues through the winter where temperatures are favorable, as in knobcone and ponderosa pines at low elevations in the Sierra Nevada of California and south Florida slash pine (Krugman and Jenkinson 1974; Wakeley 1954).

Fertilization occurs in spring or early summer, about 13 months after pollination, and the young cones begin to grow rapidly. New shoot growth leaves the developing cones in a lateral position. As they mature, the developing cones gradually change color from green or purple to yellow, light brown, reddish brown, or dark brown (table 4).

Cones and seeds of most pines mature rapidly in late summer or fall of the second year (table 3). Cones of a few pines mature in late winter of the second year or in early spring of the third year, as in knobcone, Calabrian, and Merkus pines (Boskok 1970; Cooling 1968; Krugman and Jenkinson 1974). Seeds of knobcone and Calabrian pines mature in fall, about 16 to 18 months after pollination, but their cones do not develop fully until late winter (Boskok

Table 4—*Pinus*, pine: cone ripeness criteria

Species	Pre-ripe color	Ripe color
P. albicaulis	Dark purple	Dull purple to brown
P. aristata	Green to brown-purple	Deep chocolate brown
P. arizonica	Green	Green-brown to dull yellowish buff or brown
P. armandii	Green	Yellowish brown
P. attenuata	Greenish brown	Lustrous tawny yellow to light brown
P. balfouriana	Deep purple	Dark brown, red-brown, or russet-brown
P. banksiana	Green	Lustrous tawny yellow to brown
P. brutia	Green	Yellow to reddish brown
P. canariensis	Yellow-green	Nut brown
P. caribaea	Green	Yellow-tan, light brown to reddish brown
P. cembra	Greenish violet	Purplish brown
P. cembroides	Green	Yellowish to reddish brown or lustrous brown
P. clausa	Green	Dark yellow-brown
P. contorta		
var. *contorta*	Purple-green	Lustrous light yellowish brown to yellow-brown
var. *latifolia*	Purple-green	Light brown
var. *murrayana*	Purple-green	Clay brown
P. coulteri	Green	Shiny brown to yellowish brown
P. densiflora	Green	Dull tawny yellow to brown
P. echinata	Green	Green to light brown or dull brown
P. edulis	Green	Light yellow-brown
P. elliottii		
var. *densa*	Green	Brown
var. *elliottii*	Green	Brown-yellow to brown
P. engelmannii	Brownish purple-green	Light brown
P. flexilis	Green	Lustrous yellowish brown to light brown
P. gerardiana	Green	Brown
P. glabra	Green	Green
P. halepensis	Green	Lustrous yellowish brown or reddish brown
P. heldreichii	Yellow-green	Yellowish or light brown to dull brown
P. jeffreyi	Dark purple to black	Dull purple to light brown
P. kesiya	Green	Bright brown to dark brown
P. koraiensis	Green	Yellowish brown
P. lambertiana	Green	Lustrous greenish brown to light brown
P. leiophylla		
var. *chihuahuana*	Green	Light brown
P. merkusii	Green	Light brown
P. monophylla	Green	Shiny deep russet brown
P. monticola	Green to purple-black	Yellowish beige-brown to reddish, dark brown
P. mugo	Violet purple	Lustrous tawny yellow to dark brown or cinnamon brown
P. muricata	Green to purple	Shiny light chestnut brown
P. nigra	Yellowish green	Shiny yellow brown to light brown
P. palustris	Green	Green to dull brown
P. patula	Green	Yellow ochre to nut brown
P. parviflora	Yellow-green	Leathery-woody brownish red to reddish brown
P. peuce	Green to yellow	Tawny yellow to light brown
P. pinaster	Purplish	Lustrous light brown
P. pinea	Green	Shiny nut brown
P. ponderosa		
var. *ponderosa*	Green to yellow-green, rarely purple	Lustrous brownish green or yellow-brown to russet brown
var. *scopulorum*	Green	Purplish brown
P. pumila	Green to violet-purple	Dull reddish or yellowish brown
P. pungens	Deep green to brown	Lustrous light brown
P. quadrifolia	Green	Yellowish or reddish brown
P. radiata	Green	Lustrous nut brown to light brown
P. resinosa	Green	Purple with reddish-brown scale tips to nut brown
P. rigida	Green	Lustrous brown or light yellow-brown
P. roxburghii	Green to brown	Light brown
P. sabiniana	Green to light brown	Reddish to red-brown or chestnut brown

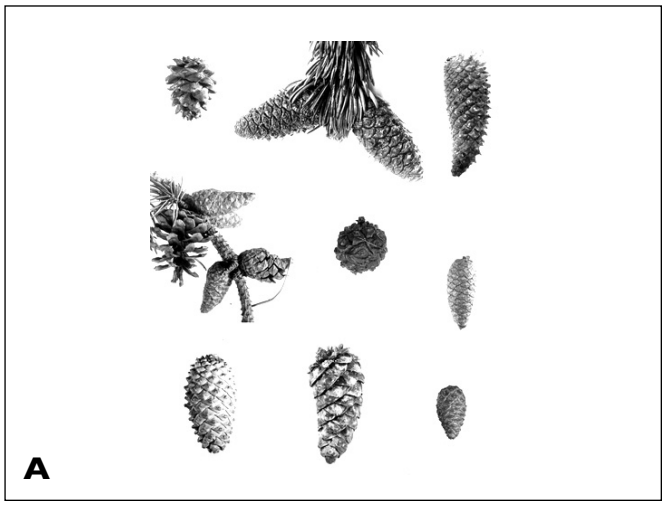
Table 4—*Pinus,* pine: cone ripeness criteria (continued)

Species	Pre-ripe color	Ripe color
P. serotina	Green to yellow	Lustrous light yellow to brown
P. sibirica	Green	Violet to light gray or brown
P. strobiformis	Green	Greenish brown to dark brown
P. strobus	Green	Yellow green to light brown
P. sylvestris	Green	Dull tawny yellow, greyish or dull brown, or cinnamon brown
P. taeda	Green	Green, shiny light or dull pale reddish brown
P. thunbergiana	Deep lustrous purple	Nut brown or reddish brown
P. torreyana	Green to dark violet	Shiny deep chestnut brown to chocolate brown
P. virginiana	Green	Lustrous dark purple to reddish and dark brown
P. wallichiana	Green	Tawny yellow to light brown
P. washoensis	Purple to purplish black	Dull purple to purplish brown or light brown

Sources: Bailey (1939), Barnett and McLemore (1967b), Britton and Shafer (1908), Cerepnin (1964), Cooling (1968), Dallimore and Jackson (1967), den Ouden and Boom (1965), Fowells (1965), Jacaline and Lizardo (1958), Krugman and Jenkinson (1974), Little EL (1940, 1950), Lizardo (1950), Loock (1950), Luckhoff (1964), McIntyre (1929), McLemore (1961a&b), Pravdin (1963), Rehder (1940), Sargent (1965), Sudworth (1908), Troup (1921), Wahlenberg (1946), Wakeley (1954).
Note: See table 2 for intervals between large cone crops and table 3 for cone ripening and seed dispersal dates.

Figure 1A —*Pinus,* pine: mature cones, collected before seed dispersal, of *P. albicaulis*, whitebark pine (**upper left**); *P. aristata*, bristlecone pine (**upper center**); *P. attenuata*, knobcone pine (**upper right**); *P. banksiana*, jack pine (**center left**); *P. cembroide*s, Mexican piñyon (**center middle**); *P. clausa*, sand pine (**center right**); *P. engelmannii*, Apache pine (**bottom left**); *P. flexilis*, limber pine (**bottom center**); *P. leiophylla* var. *chihuahuana*, Chihuahua pine (**bottom right**).

Figure 1B —*Pinus*, pine: mature cones, collected before seed dispersal, of *P. monophylla*, singleleaf piñyon (**upper left**); *P. arizonica*, Arizona pine (**upper center**); *P. ponderosa* var. *scopoulorum*, Rocky Mountain ponderosa pine (**upper right**); *P. rigida*, pitch pine (**center left**); *P. pungens*, Table Mountain pine (**center middle**), *P. serotina*, pond pine (**center right**); *P. strobiformus*, southwestern white pine (**bottom left**); *P. sylvestris*, Scots pine (**bottom center**); *P. virginiana*, Virginia pine (**bottom right**).



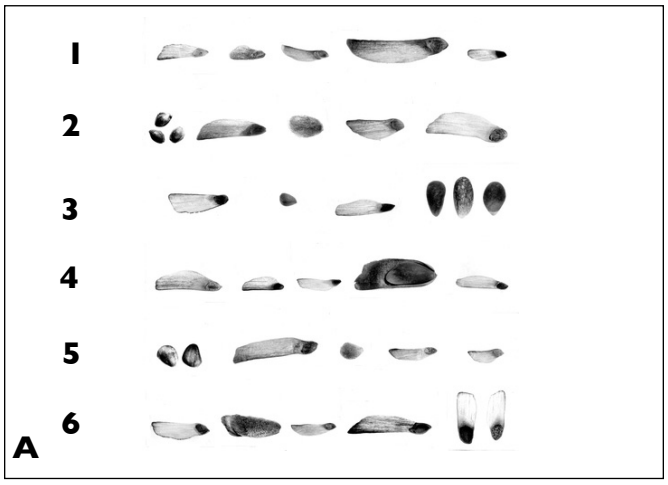
1970; Krugman and Jenkinson 1974). Seeds and cones of Italian stone and Chihuahua pines require 3 years to ripen (Dallimore and Jackson 1967; Little 1950). Seeds of Torrey pine are said to take 3 years to mature, but evidence suggests that the seeds of this pine mature in 2 years, whereas the cones require 3 years (Krugman and Jenkinson 1974).

Intervals between large cone crops vary and apparently depend on species and environment (table 2). Some pines consistently produce large cone crops. Others show cyclic or erratic patterns of 2 to 10 years between large crops.

Mature cones of pines vary greatly in size (figure 1). At one extreme, cones of mugo pine range from 2.5 to 5.1 cm in length and weigh about 1.7 g. At the opposite extreme, cones of sugar pine range from 30 to 64 cm in length and weigh from about 0.45 to 0.91 kg. Cones of Digger and Coulter pines, the California big-cone pines, often weigh more than 0.91 kg (Dallimore and Jackson 1967; den Ouden and Boom 1965; Sudworth 1908).

Mature cones consist of overlapping woody scales, each bearing 2 seeds at the base on its upper surface. In most

Figure 2A—*Pinus*, pine: seeds (although most are shed naturally from their cones, some are shed wingless) of **ROW 1, left to right**: *P. albicaulis*, whitebark pine; *P. aristata*, bristlecone pine; *P. armandii*, Armand pine; *P. attenuata*, knobcone pine; *P. balfouriana*, foxtail pine. **ROW 2, left to right:** *P. banksiana*, jack pine; *P. brutia*, Calabrian pine; *P. cembroides*, Mexican piñyon; *P. clausa*, sand pine. **ROW 3, left to right:** *P. contorta* var. *murrayana*, Sierra Nevada lodgepole pine; *P. coulteri*, Coulter pine; *P. densiflora*, Japanese red pine; *P. echinata*, shortleaf pine. **ROW 4, left to right:** *P. edulis*, piñyon; *P. elliottii* var. *elliottii*, slash pine; *P. engelmannii*, Apache pine; *P. flexilis*, limber pine; *P. gerardiana*, chilgoza pine. **ROW 5, left to right**: *P. glabra*, spruce pine; *P. halepensis*, Aleppo pine; *P. heldreichii*, Heldrich pine; *P. kesiya*, Khasi pine; *P. jeffreyi*, Jeffrey pine. **ROW 6, left to right:** *P. koraiensis*, Korean pine; *P. lambertiana*, sugar pine; *P. leiophylla* var. *chihuahuana*, Chihuahua pine; *P. merkusii*, Merkus pine; *P. monophylla*, singleleaf piñyon.



pines, cones open on the tree shortly after ripening and seeds are rapidly dispersed (table 3). As the cone drys, the cone scales separate by differential contraction of 2 tissue systems. One system consists of woody strands of short, thick-walled, tracheid-like cells that extend from the cone axis to the scale tip, and the other has thick-walled sclerenchyma cells in the abaxial zone of the scale (Allen and Wardrop 1964; Thompson 1968). In species with massive cones—Coulter, Chir, Digger, and Torrey pines—the scales separate slowly and seeds are shed over a period of several months (Sudworth 1908; Troup 1921).

In pines with serotinous cones—including knobcone, jack, Calabrian, sand, Rocky Mountain lodgepole, Aleppo, bishop, maritime, Table Mountain, and Monterey pines—some or all of the mature cones remain closed for several to many years, or they open on the tree only at irregular intervals (Dallimore and Jackson 1967; Fowells 1965; Sudworth 1908). Besides their closed-cone habit, jack, sand, lodgepole/shore, and pitch pines have forms whose cones open promptly at maturity (Fowells 1965;, Krugman and Jenkinson 1974; Rudolph and others 1959). The closed-cone habit results from 3 factors: an extremely strong adhesion between adjacent, overlapping cone scales beyond the ends of the winged seeds (LeBarron and Roe 1945, Little and Dorman 1952a); cone structure; and the nature of the scale tissue systems described. The scales appear to be bonded by a resinous substance. The melting point of this resin seal is between 45 and 50 °C for Rocky Mountain lodgepole pine (Critchfield 1957). Heat, especially that of fire, melts the resin so that the cones open. Still other pines, such as whitebark, Japanese stone, Swiss stone, and Siberian pines, shed partly opened or unopened cones, and their seeds are dispersed only when the cones disintegrate on the ground (Dallimore and Jackson 1967; Mirov 1967; Pravdin 1963; Sudworth 1908).

Cones that open on the tree are usually shed within a few months to a year after the seeds are shed. Pines such as knobcone, Rocky Mountain lodgepole, and pitch pine, how-

Figure 2B—*Pinus*, pine: seeds (although most are shed naturally from their cones, some are shed wingless) of **ROW 1, left to right:** *P. monticola*, western white pine; *P. muricata*, bishop pine; *P. nigra*, Austrian pine; *P. palustris*, longleaf pine; *P. patula*, Mexican weeping pine. **ROW 2, left to right:** *P. peuce*, Balkan pine; *P. pinaster*, maritime pine; *P. pinea*, Italian stone pine; *P. arizonica*, Arizona pine; *P. ponderosa* var. *ponderosa*, ponderosa pine. **ROW 3, left to right:** *P. ponderosa* var. *scopulorum*, Rocky Mountain ponderosa pine; *P. pumila*, Japanese stone pine; *P. pungens*, Table Mountain pine; *P. quadrifolia*, Parry piñyon. **ROW 4, left to right:** *P. radiata*, Monterey pine; *P. resinosa*, red pine; *P. rigida*, pitch pine; *P. sabiniana*, Digger pine; *P. serotina*, pond pine. **ROW 5, left to right:** *S. sibirica*, Siberian stone pine; *P.* × *sondereggeri*, Sonderegger pine; *P. strobiformis*, southwestern white pine; *P. strobus* var. *strobus*, eastern white pine; *P. sylvestris*, Scots pine. **ROW 6, left to right:** *P. taeda*, loblolly pine; *P. torreyana*, Torrey pine; *P. virginiana*, Virginia pine; *P. wallichiana*, blue pine; *P. washoensis*, Washoe pine.

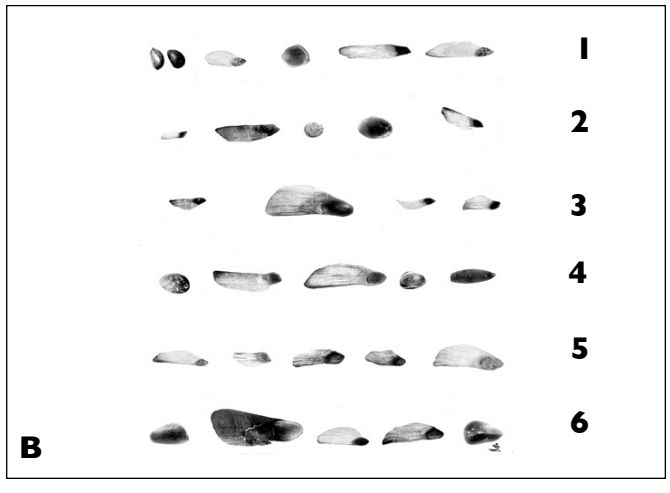
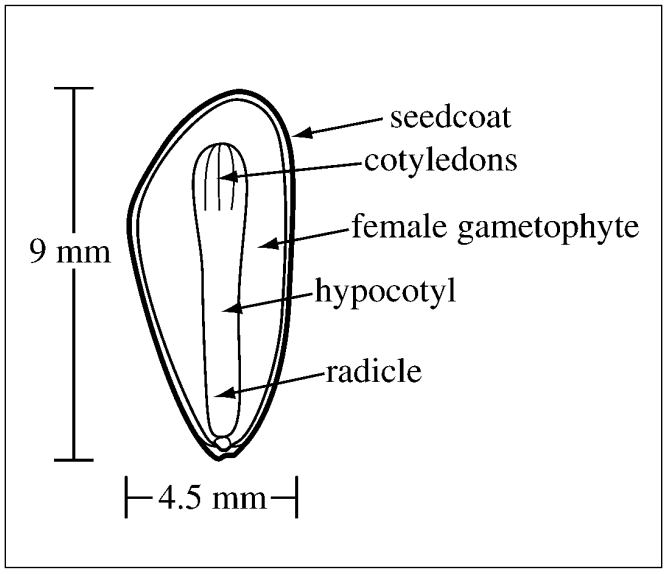


Figure 3—*Pinus ponderosa,* ponderosa pine: longitudinal section through a mature seed.



ever, may retain opened cones on the trees for up to 5 years or indefinitely (Fowells 1965; Sudworth 1908).

Mature seeds vary widely in size, shape, and color (figure 2). De-winged seeds vary from 1.6 to 2.5 mm in length for jack pine and range up to more than 19 mm long for Digger pine. Seeds are cylindric in shape for chilgoza pine, ovoid for Balkan pine, convex on the inner side and flat on the outer side for Italian stone pine, pear-shaped for Japanese stone pine, variously triangular for Table Mountain pine, and ellipsoid for Monterey pine (Dallimore and Jackson 1967; den Ouden and Boom 1965; Uyeki 1927). Mature seedcoats may be reddish, purplish, grayish brown, or black, and are often mottled. Depending on species, the seedcoats can be thin and papery, or thick and hard, or even stony (Dallimore and Jackson 1967; Shaw 1914; Sudworth 1908).

The seedcoat of the mature seed encloses a whitish food-storage tissue—female gametophyte tissue, the conifer analog of endosperm—which in turn encases the embryo (figure 3). A brown papery cap, the remnant of the nucellus, is attached to the micropylar end of the food-storage tissue. A thin, brown, membranous skin, the remnant inner layer of the ovules integument, covers the papery cap and the food-storage tissue.

Seeds of most pines have a membranous seedwing (figure 2). Seedwings detach readily in the hard pines (except for Canary Island, Italian stone, and Chir pines) but adhere firmly in the soft pines (except bristlecone and certain sources of foxtail pine). In nut pines such as Mexican, singleleaf, and Parry piñyons and chilgoza pine, the wings or modified wings may stay attached to the cone scale when the seeds are shed. In pines such as whitebark, Armand, Swiss stone, limber, chilgoza, Korean, Japanese stone, Siberian, and southwestern white pines, seedwings are rudimentary or nonexistent (Mirov 1967; Shaw 1914; Sudworth 1908; Troup 1921; Uyeki 1927).

Cone collection. Cones should be collected from trees that are free of disease and have superior growth and form characteristics. Larger cones generally contain more seeds, but normally all cones are collected except those with obvious disease and insect damage. Dominant, widely spaced trees with full crowns produce the most seeds per cone, given that other trees supply sufficient amounts of viable pollen. Seed yields tend to be low when trees are isolated and incur limited amounts of pollen from other trees. Spacing among trees in seed orchards is regulated to produce large crowns and plenty of pollen. With proper irrigation and fertilization, 20-year-old loblolly pine orchards in the South can average around 100 kg of seeds/ha (88 lb/ac) of orchard (Bonner 1991). Most pines growing in dense, young stands produce few or no seeds. Pines that commonly form fire thickets, such as knobcone, jack, sand, pitch, and pond pines, are prominent exceptions (Fowells 1965).

Ripe cones can be collected from standing trees, newly felled trees, and animal caches. To avoid large yields of immature seeds, collections from animal caches should be made in late fall, after seeds have matured (Schubert and others 1970). Because the mature cones of most pines open and shed seeds promptly, collections from standing trees should begin when cones are ripe and just cracking. Collections from closed-cone pines can be safely delayed, and such delay is often desirable. Although the seeds may be mature, closed cones are difficult to open and added maturation on the tree facilitates both cone opening and seed extraction (Boskok 1970; Krugman and Jenkinson 1974).

To avoid extensive collections of immature or empty seeds, it is wise to check seed ripeness in small samples of cones from a number of typical individual trees. Mature seeds have a firm, white to yellow or cream-colored "endosperm," or female gametophyte tissue, and a white to yellow embryo that nearly fills the endosperm cavity (figure 3). This simple visual check is useful for most pines, and critical for some.

Cone ripeness in some pines can be usefully estimated by change in cone color (table 4). In Pacific ponderosa pine, for example, cones are mature when their color changes from green or yellow-green to brownish green, yellow-brown, or russet brown. In red pine, cones are mature when they turn from green to purplish with reddish brown on the

Table 5—*Pinus*, pine: specific gravity of ripe cones and flotation liquids used to assess cone ripeness*

Species	Specific gravity of ripe cones	Flotation liquid †
P. aristata	0.59–.80	Kerosene
P. arizonica	.88–.97	—
P. contorta var. *latifolia*	.43–.89	—
P. densiflora	1.10	—
P. echinata	.88	SAE 20 oil ‡
P. edulis	.80–.86	Kerosene
P. elliottii		
var. *densa*	<.89	SAE 20 oil
var. *elliottii*	<.95	SAE 20 oil
P. glabra	.88	SAE 20 oil
P. jeffreyi	.81–.86	SAE 30 oil
P. lambertiana	.70–.80	Kerosene
P. merkusii	1.00	—
P. palustris	.80–.89	SAE 20 oil
P. ponderosa		
var. *ponderosa*	.80–.89	Kerosene
	.84–.86	SAE 30 oil
var. *scopulorum*	<.85–.86	Kerosene
P. radiata	<1.00	Water
P. resinosa	.80–.94	Kerosene §
P. serotina	.88	—
P. strobiformis	.85–.95	95% ethanol
P. strobus	.90–.97	Linseed oil
P. sylvestris	.88–1.00	—
P. taeda	.88–.90	SAE 20 oil‡
P. virginiana	<1.00	—

Sources: Barnett (1976), Barnett and McLemore (1967b), Bonner (1986a&b), Bonner and others (1994), Eliason and Hill (1954), Fenton and Sucoff (1965), Fowells (1965), Krugman and Jenkinson (1974), Lindquist (1962), Schubert (1955), Schubert and Adams (1971), Stoeckeler and Slabaugh (1965), Wakeley (1954), Yanagisawa (1965).

* Test sample cones promptly after picking to avoid excessive drying. Five or more cones should float before the crop is considered ripe.
† Specific gravity of kerosene is 0.80; 95% ethanol, 0.82; SAE 20 motor oil, 0.88; and linseed oil, 0.93.
‡ Alternatively, use a 1:4 kerosene–linseed oil mix.
§ Cones that float in a 1:1 kerosene–linseed oil mix should be ripe within 10 days

scale tips, and in eastern white pine, when they turn from green to yellow-green with brown on the scale tips, or to light brown. In certain other pines, however, cone color changes too late to be a useful index to ripeness. In longleaf pine, for example, ripe cones are still green in color and may have already started to open before turning brown (Wakeley 1954).

In species for which cone color changes may not be useful, seed maturity may be assessed by flotation tests of the cone's specific gravity (table 5). Although the crucial factor in cone ripening is moisture content, not specific gravity, measuring specific gravity is the quickest and easiest way to estimate cone moisture content (Bonner 1991). To determine whether cones have reached a desired specific gravity, samples of newly picked cones are floated in liquids of known specific gravity. Thus, seeds of ponderosa pine are mature if the cones float in kerosene; seeds of eastern white pine, if the cones just float in linseed oil; and seeds of spruce pine, if the cones just float in SAE 20 motor oil. A very simple, workable method uses water displacement in a graduated cylinder (Barnett 1979). Cone weight equals the volume displaced when the cone is floated, cone volume equals the displacement of the fully immersed cone, and the cone's specific gravity is its weight divided by its volume. Sampled cones should be assessed immediately, as drying results in false conclusions about seed ripeness.

Oils and other organic liquids are seldom used on cones of the southern pines anymore; if measurements of specific gravity are required, the water flotation and volume method is used. In large-scale collections of loblolly pine in seed orchards, cones are typically picked when sample cones float in water, indicating a specific gravity of <1.0. The scale of the operations is so large that every tree cannot be harvested at the ideal time. Proper storage of the cones, however, ensures complete ripening of the seeds without damage. Good orchard managers keep records of the ripening sequence and dates for all families to aid in scheduling of collections.

To avoid risks of harvesting immature seeds, cones should not be collected from felled trees until the seeds are mature. Nearly mature cones ripen in the crowns of felled trees of some pines, such as loblolly and shortleaf pines, but not in others (Wakeley 1954). Slightly immature seeds can be ripened successfully in harvested cones of some pines, including after picking for slash pine (Bevege 1965; Wakeley 1954); in moist cold storage for sugar pine (Krugman 1966); and in dry cold storage in closed containers for Virginia pine (Church and Sucoff 1960). Ripening by such methods should be attempted only if mature seeds cannot be collected.

Cones usually are hand-picked from ladders and hydraulic lifts or by climbing the trees. In a typical loblolly pine seed orchard, it has been estimated that 9 bucket trucks and 14 workers can harvest 40 ha (100 ac) of trees with a "good" cone crop in 20 days (Edwards 1986). Less often, helicopters may be used where the trees are difficult to reach (Tanaka 1984). For some pines, hand-cutters or a cutting hook must be used to detach the cones, and hooks may be needed to pull the cone-laden branches to the picker. Mechanical tree shakers are used to harvest cones rapidly from species such as slash and longleaf pines (Kmecza 1970). Good shaker operation should remove 80% or more of the cones (Edwards 1986).

Table 6—*Pinus*, pine: cone processing schedules and safe times to cold- or freeze-store dry, mature seeds

Species	Cone processing schedule*				
	Boiling water dip (sec)	Air-drying (day)	Kiln-drying (hr)	Kiln temp (°C)	Seed storage (yr)†
P. albicaulis‡	0	15–30	0	—	8
P. aristata	0	2–8	0	—	9
P. arizonica	0	—	60	43	—
P. armandii	0	15	0	—	—
P. attenuata	15–30	1–3	48	49	16
P. balfouriana	0	2–8	0	—	16
P. banksiana	0	—	2–4	66	17–18
	10–30	3–10	0	—	—
P. brutia	0	3–20	0	—	3
	0	—	10	54	—
P. canariensis	0	2–10	0	—	18
P. caribaea	—	—	—	—	3
P. cembra‡	—	—	—	—	>1
P. cembroides§	0	2–8	0	—	—
P. clausa	10–30	1	2–4	63	5
P. contorta					
var. contorta	0	2–20	0	—	17
	0	—	96	49	—
var. latifolia II	30–60	2–30	0	—	20
	0	—	6–8	60	—
var. murrayana	0	2–20	0	—	17
P. coulteri	0–120	3–15	0	—	5
	0	—	72	49	—
P. densiflora	0–30	3–4	0	—	2–5
P. echinata	0	—	48	41	35
P. edulis §	0	2	0	—	—
P. elliottii					
var. densa	0	—	8–10	49	—
	0	4	0	—	
var. elliottii	0	—	8–10	49	50
	0	42	0	—	—
P. engelmannii	0	—	60	43	—
P. flexilis	0	15–30	0	—	5
P. gerardiana	0	15	0	—	—
P. glabra	0	—	48	38	>1
P. halepensis	0	—	10	54	10
	0	3–10	0	—	—
P. heldreichii	0	5–20	0	—	—
P. kesiya	0	5–20	0	—	—
P. jeffreyi	0	—	24	49	18
	0	5–7	0	—	—
P. lambertiana	0	—	24	49	21
	0	5–7	0	—	—
P. merkusii	0	5–7	0	—	7
P. monophylla §	0	2–3	0	—	—
P. monticola	0	—	4	43	20
	0	5–7	0	—	—
P. mugo	0	—	48	49	5
P. muricata	0	—	48	49	—
P. nigra	0	—	24	46	>10
	0	3–10	0	—	—
P. palustris	0	—	48	38	5–10
P. parviflora	0	5–15	0	—	—
P. patula	15–30	1–2	48	46	21
P. pinaster	0	—	—	46	11
	0	4–10	0	—	—

Table 6—*Pinus*, pine: cone processing schedules and safe times to cold- or freeze-store dry, mature seeds (continued)

Species	Cone processing schedule*				
	Boiling water dip (sec)	Air-drying (day)	Kiln-drying (hr)	Kiln temp (°C)	Seed storage (yr)†
P. pinea	—	—	—	—	18
P. ponderosa					
var. ponderosa	0	—	3	49	18
	0	4–12	0	—	—
var. scopulorum	0	—	2	74	>15
	0	4–12	0	—	—
P. pumila‡	—	—	—	—	—
P. pungens	0	—	72	49	9
	0	30	0	—	—
P. quadrifolia§	0	2–8	0	—	—
P. radiata	60–120	0	48–72	49	21
	60–120	3–7	0	—	—
P. resinosa	0	—	13–20	54	30
P. rigida¶	—	—	—	—	11
P. roxburghii	0	—	—	—	>4
P. sabiniana	0	—	48	49	5
P. serotina	0	—	48	41	—
P. sibirica‡	—	—	—	—	>2
P. strobiformis	0	14	0	—	—
P. strobus	0	—	15–20	54	10
P. sylvestris	0	—	10–16	49	15
	0	3–7	0	—	—
P. taeda	0	—	48	41	>9
P. thunbergiana	0–30	5–20	0	—	11
P. torreyana	0	5–20	0	—	6
P. virginiana	0	—	2	77	>5
P. washoensis	0	4–12	0	—	8

Sources: Barnett (1969, 1970), Barnett and McLemore (1967a&b), Bonner (1990), Church and Sucoff (1960), Dent (1947), FAO (1993), Goor and Barney (1968), Heit (1967b), Jones (1962, 1966), Kamra (1967), Karschon (1961), Krugman and Jenkinson (1974), LeBarron and Roe (1945), Little and Dorman (1952a), Lizardo (1950), Luckhoff (1964), McLemore (1961b), Mirov (1946), Nather (1958), NBV (1946), Nyman (1963), Ohmasa (1956), Schubert (1952), Schubert and Adams (1971), Simak and others (1961), Steinhoff (1964), Stoeckeler and Jones (1957), Swingle (1939), Troup (1921), Wakeley (1954), Wakeley and Barnett (1968).

* Air drying temperatures are 15.6 to 32.2 °C. Kiln drying, if used, should follow air drying. Recommended air drying time is 3 to 7 days, where none is listed.
† Seed germination was at least 50% after storage. Seeds of most pines were stored at 0.5 to 5 °C or –15.6 to –18.8 °C. Freezing is preferred. Seed moisture contents were between 5 and 10%.
‡ Cones of *P. albicaulis*, *P. cembra*, *P. pumila*, and *P. sibirica* must be broken up to free and extract the seeds.
§ An alternate extraction method for *P. cembroides*, *P. edulis*, *P. monophylla*, and *P. quadrifolia* is to shake the trees mechanically and collect shed seeds from cloths spread on the ground.
‖ Time needed in boiling water is estimated. Reported treatment was 5 to 10 minutes in water at 64 °C or higher.
¶ Cones were soaked in water overnight and dried in a warm room.

Large numbers of seeds of certain other pines, such as piñyon and singleleaf and Parry piñyons, are harvested by shaking or beating the tree crowns and gathering extracted seeds from the ground (Krugman and Jenkinson 1974). This technique has been expanded with the net retrieval system that is used in many seed orchards of loblolly, Virginia, and eastern white pines (Bonner 1991). The system, originated in the early 1970s by the Georgia Forestry Commission (Wynens and Brooks 1979), employs large rolls of polypropylene netting (carpet backing) spread out beneath the trees. As the cones open naturally on the trees, seeds fall onto the netting, usually aided by light mechanical shaking. When most of the crop is on the netting, it is rolled up and the seeds recovered. The recovered seeds are usually very moist and trashy, so they must be carefully dried and cleaned. If this is properly done, the seed quality is not damaged (Bonner and Vozzo 1986a). The net retrieval system can be used only where an orchard mix of families is desired for seedling production. If families are to be kept separate for site-specific planting, as is becoming increasingly common for loblolly pine, cones must be collected by hand from each tree.

Cone processing and seed extraction. In general, cones should be dried quickly after collection to avoid inter-

nal heating, mold development, and rapid seed deterioration (table 6). Cones may be dried in 2 to 60 days by immediately spreading them in thin layers on dry surfaces in the sun or on trays in well-ventilated buildings, or by hanging them in sacks from overhead racks protected against rain (Schubert and others 1970; Stoeckeler and Jones 1957; Stoeckeler and Slabaugh 1965; Wakeley 1954). Cones should be dried slowly to avoid "case hardening." After initial drying, cones can be stored temporarily in well-ventilated bags or trays. Ripe cones of many pines open quickly under such conditions, but those of others may require additional drying in either a heated shed or a cone-drying kiln.

In large-scale collections of cones of the southern pines, cones are frequently stored in burlap bags or 704-liter (20-bu) wire-bound boxes for as long as several months before going into heated kilns to complete drying. During this storage period, significant amounts of cone moisture are lost (thereby reducing fuel costs in later drying) and seeds in cones that were picked a little early complete the maturation process (Bonner 1991). There are species with "sensitive" seeds, such as longleaf and eastern white pines, that are more easily damaged during cone storage, and a maximum of 1 week is suggested for bulk storage of these cones. For loblolly, slash, shortleaf, and Virginia pines, cone storage in bags or boxes for 3 to 5 weeks appears to benefit seed yield and quality (Bonner 1991).

Properly air-dried cones may open amply after just a few hours in a kiln, or they may take several days, depending on species. With the exception of the white pines and perhaps others, cones must reach moisture contents of 10% for maximum seed release (Belcher and Lowman 1982). Seeds of most trees are killed at temperatures around 66 °C. Many kilns operate at temperatures of 32 to 60 °C. Maximums of 43 °C and lower have been recommended for most species (Tanaka 1984), but such temperatures are not always effective. Cones of most pines open at a kiln temperature of 54 °C or lower and relative humidity near 20% (table 6). Cones of a few pine species, including jack, sand, and Rocky Mountain ponderosa pines, need temperatures higher than 54 °C to open (Schubert and others 1970; Stoeckeler and Jones 1957; Stoeckeler and Slabaugh 1965). For all species, however, kiln temperatures will depend on initial cone moisture content, relative humidity, kiln load, and the type of kiln in use. The common types of cone kilns are rotating tumbler driers, progressive kilns, and tray kilns (Bonner 1991). For additional information on kilns, see chapter 3.

Cones that have been stored in containers long enough to dry without opening and cones that have been dried under cool conditions may not open properly during kiln drying. Such cones first should be soaked in water for 12 to 24 hours and then kiln-dried to open satisfactorily (Stoeckeler and Slabaugh 1965). In the South, most producers place their storage containers in the open, where the alternating wetting and drying in natural weather patterns facilitates cone opening (Bonner 1991).

Serotinous cones normally can be opened by dipping them in boiling water for 10 seconds to 2 minutes (table 6). Immersion times of up to 10 minutes in boiling water have been needed to open some lots of serotinous cones (Krugman and Jenkinson 1974). This procedure melts the resins bonding the cone scales, fully wets the woody cone, and causes maximum scale reflexing (LeBarron and Roe 1945; Little and Dorman 1952a). If serotinous cones are partially open, dipping them in boiling water may damage the seeds (Belcher 1984). To avoid this, the cones should be sprayed with water to close the scales, then dipped. Cones of sand pine are sometimes opened by quick exposure to live steam, a process that may be safer than dipping in boiling water (Bonner 1997).

Once opened, cones are shaken to extract the seeds. Most seeds are extracted by placing the opened cones in a large mechanical tumbler or shaker for large lots, or in a small manual shaker for small lots. Seeds from the extractor still must be separated from cone fragments, dirt, and other debris. Seeds are cleaned by rapid air movement, vibration, or screening or by a combination of these methods (Tanaka 1984). Extracted seeds are de-winged by using machines of various types, by flailing them in a sack, or by rubbing.

Table 7—*Pinus,* pine: flotation liquids used to separate empty seeds from full seeds

Species	Flotation liquid for empty seeds
P. brutia	Water
P. coulteri	Water
P. echinata	95% ethanol
P. echinata	Water
P. elliottii var. *elliottii*	Water
P. glabra	95% ethanol
P. halepensis	95% ethanol
P. nigra	95% ethanol
P. palustris	Pentane
P. pinaster	95% ethanol
P. pinea	Water
P. sabiniana	Water
P. strobus	100% ethanol
P. sylvestris	Petroleum ether
P. taeda	Water

Sources: Barnett (1970), Goor (1955), Karschon (1961), Krugman and Jenkinson (1974), Lebrun (1967), McLemore (1965), NBV (1946), Stoeckeler and Jones (1957), Wakeley (1954).

Table 8—*Pinus*, pine: cone and seed yields

Species	Place collected	Seed weight /cone wt g/kg	Seed weight /cone wt oz/lb	Seed weight /cone vol kg/hl	Seed weight /cone vol lb/bu	Clean seeds (x1,000)/wt Range /kg	Clean seeds (x1,000)/wt Range /lb	Clean seeds (x1,000)/wt Avg /kg	Clean seeds (x1,000)/wt Avg /lb	Lot
P. albicaulis	Idaho	—	—	—	—	4.8–6.6	2.2–3.0	5.7	2.6	3
P. aristata	Arizona	40	0.6	1.42	1.1	39–42	17–19	40	18	4
P. arizonica	Arizona	9–23	.14–.35	.90–1.3	.7–1.0	24–26	11–19	25	11	10
P. armandii	France	—	—	—	—	2.6–4.1	1.2–1.9	3.5	1.6	2
P. attenuata	California & Oregon	—	—	0.13	.1	33–71	15–32	56	25.4	6
P. balfouriana	California	—	—	—	—	31–49	14–22	37	17	3
P. banksiana	Great Lakes	10	.15	.26–.9	.2–.7	156–551	71–250	289	131	423
P. brutia	Europe	—	—	—	—	17–26	7.6–11.6	20.1	9.1	5
P. canariensis	South Africa	—	—	—	8.8–9.9	4.0–4.5	9.3	4.2	10	
P. caribaea	—	—	—	—	—	52–81	24–37	68.3	31	>10
P. cembra	Germany	—	—	—	—	3.5–5.1	1.6–2.3	4.4	2.0	>10
P. cembroides	—	—	—	—	—	1.4–4.6	0.6–2.1	2.4	1.1	5
P. clausa	Florida	35	.52	.77–1.2	.6–.9	143–187	65–85	165	75	>10
P. contorta										
var. *contorta*	California	—	—	.64–1.5	.5–1.2	245–364	111–165	298	135	28
var. *latifolia*	Montana to Colorado	8–10	.1–.15	.26–1.0	.2–.8	174–251	79–114	207	94	39
var. *murrayana*	California	5.5	.1	.26	.2	256–262	116–119	258	117	4
P. coulteri	California	22	.33	1.03	.8	2.6–3.5	1.2–1.6	3.1	1.4	8
P. densiflora	Japan	20	.3	.64–1.0	.5–.8	79–141	36–64	115	52	26
P. echinata	—	20–30	.3–.45	.52–1.4	.4–11.1	71–161	32–73	102	46	144
P. edulis	Arizona	28	.4	3.3	4.25	3.3–5.5	1.5–2.5	4.2	1.9	9
P. elliottii										
var. *densa*	S Florida	—	—	.64–1.3	.5–1.0	31–37	14–17	34	15	30
var. *elliottii*	—	10–20	.15–.3	.77–1.0	.6–.8	21–43	10–19	30	13	404
P. engelmanni	Arizona	11	.16	.52	.4	—	—	22	10	1
P. flexilis	—	—	—	—	—	7.1–15.0	3.2–6.8	10.8	10.0	44
P. gerardiana	India	—	—	—	—	2.4–2.9	1.1–1.3	2.4	4.9	10
P. glabra	Louisiana	—	—	.13–1.3	.1–1.3	88–115	40–52	101	1.1	8
P. halepensis	Italy	—	—	—	—	48–88	22–40	62	46	>10
P. heldreichii	—	—	—	—	—	35–71	16–32	46	28	18
P. jeffreyi	California	35	.52	1.2–2.6	.9–2.0	5.8–11.7	2.6–5.3	8.2	3.7	26
P. keisya	SE Asia	—	—	—	—	44–76	20–34	59.5	27	>5
P. koraiensis	Korea	—	—	—	—	1.6–2.0	0.7–0.9	1.8	3.7	3
P. lambertiana	California	37	.56	1.9–2.6	1.5–2.0	3.3–6.0	1.5–2.7	4.6	2.1	27
P. leiophylla var. *chihuahuana*	—	—	—	.90–1.2	.7–.9	—	—	88	40	>1
P. merkussi	—	—	—	—	—	28–59	13–27	40	18.2	11
P. monophylla	Nevada	—	—	2.2–6.0	1.7–4.7	2.3–2.6	1.0–1.2	2.4	1.1	2
P. monticola	Utah	10	.15	.4–1.03	.3–.8	31–71	14–32	59	27	>99
P. mugo	Germany	—	—	1.03	.8	126–201	57–91	152	69	10
P. muricata	California	4		.26	.2	86–112	40–50	103	46.8	3
P. nigra	—	20–40	.3–.6	.52–1.5	.4–1.2	31–86	14–39	57	26	>159
P. palustris	Louisiana	21	.32	1.03	.8	6.6–15.4	3–7	10.8	4.9	220
P. parviflora	—	—	—	—	—	6.8–10.1	3.1–4.6	8.6	3.9	>3
P. patula	South Africa & Mexico	—	—	—	—	88–132	40–60	116	53	>3
P. peuce	—	—	—	—	—	22–31	10–14	24	11	6
P. pinaster	—	35–55	.53–.82	—	—	15–29	7–13	22	10	16
P. pinea	Europe	—	—	—	—	1.1–1.6	0.5–0.7	1.3	0.6	4

Southern species, except for longleaf pine, are de-winged in mechanical de-wingers that spray a fine mist of water on the seeds as they slowly tumble; capacities are about 90 kg/hr. The seeds and wing fragments must be dried for separation, and if seed moisture goes above 10% during the process, additional drying may be necessary (Bonner 1991).

Longleaf pine must be de-winged dry. In a few pines, de-winging can be simplified by first wetting the seeds and then drying them. Proper redrying precludes loss in seed quality (Wang 1973). The loose seedwings can be fanned out (Stoeckeler and Slabaugh 1965; Wakeley 1954). Mechanical

Table 8—*Pinus*, pine: cone and seed yields (continued)

Species	Place collected	Seed weight /cone wt g/kg	Seed weight /cone wt oz/lb	Seed weight /cone vol kg/hl	Seed weight /cone vol lb/bu	Clean seeds (x1,000)/wt Range /kg	Clean seeds (x1,000)/wt Range /lb	Clean seeds (x1,000)/wt Avg /kg	Clean seeds (x1,000)/wt Avg /lb	Lot
P. ponderosa										
var. *ponderosa*	—	20–70	.3–1.0	.8–2.6	.6–2.0	15–51	7–23	26	12	185
var. *scopulorum*	Black Hills	39	.6	1.93	1.5	22–34	10–15	29	13	74
P. pumila	—	—	—	—	—	—	—	24	11	11
P. pungens	West Virginia	30	.45	.52	.4	68–84	31–38	75	34	3
P. quadrifolia	California	—	—	—	—	1.8–2.6	0.8–1.2	2.1	1.0	3
P. radiata	California	9	.14	.39	.3	23–35	10–16	29	13	7
P. resinosa	Lake States	10–20	1.5–.3	.64–1.0	.5–.8	66–166	30–76	115	52	529
P. rigida	Pennsylvania/ New York	20–30	.3–.45	1.03	.8	94–181	42–82	136	62	10
P. roxburghii	India	—	—	—	—	6.8–25	3–11	12	25	36
P. sabiniana	California	—	—	—	—	1.2–1.4	0.5–0.6	1.3	0.6	3
P. serotina	SE US	—	—	.52	.4	104–139	47–63	119	54	4
P. sibirica	Siberia	—	—	—	—	3.5–4.6	1.6–2.1	4.0	1.8	>10
P. strobiformis	Arizona	80	11.2	3.5	2.7	5.5–6.4	2.5–2.9	6.0	2.7	10
P. strobus	—	20–30	.3–.45	.4–2.2	.3–1.7	39–117	17.5–53	58	26	300
P. sylvestris	Europe, E US	20	.3	.5–0.8	.4–.6	74–245	33.8–111	165	75	>346
P. taeda	—	20–30	.3–.45	.8–1.7	.6–.63	27–58	12–26	40	18	652
P. thunbergiana	Japan, Korea, NE US	—	—	.26–1.0	.2–.8	57–110	26–50	75.0	34	50
P. torreyana	California	—	—	—	—	8.8–17.6	.4–.8	11.0	0.5	7
P. virginiana	—	30	.45	.64–1.2	.5–.9	101–201	46–91	122	55	30
P. wallichiana	India	—	—	—	—	16–23	7–10	20	9	163

Sources: Barnett and McLemore (1967b), Cooling (1968), Curtis (1955), Debazac (1964), Delevoy (1935), Eliason (1942), Heit (1963, 1969), Karschon (1961), Krugman and Jenkinson (1974), Letourneux (1957), Luckhoff (1964), Magini and Tulstrup (1955), Miller and Lemmon (1943), Mirov (1936), Nather (1958), NBV (1946), Ohmasa (1956), Poynton (1961), Pravdin (1963), Rafn (1915), Read (1932), Sen Gupta (1936), Steinhoff (1964), Stoeckeler and Jones (1957), Sudworth (1908), Swingle (1939), Takayama (1966), Troup (1921), Wappes (1932).

de-wingers can cause severe damage to seeds if they are not used properly. Seeds of 3 pines—bristlecone (Krugman and Jenkinson 1974), longleaf (Wakeley 1954), and Scots pine (Kamra 1967)—are highly susceptible to such damage and demand careful de-winging. De-winged seeds are cleaned by using air-screen cleaners, aspirators, or fanning mills to remove the broken wings, pieces of cone scale, and other impurities. The increasing use of family lots of known genetic identity has increased the use of small tumblers, de-wingers, and cleaners and decreased the use of large equipment for many species.

After de-winging and cleaning are completed, empty seeds of many pines can be separated from the filled ones with gravity tables or aspirators (see chapter 3). This separation can also be done by simple flotation in water for many species, such as loblolly, Coulter, and Italian stone pines. It is also possible to use organic liquids of suitable specific gravity on small lots of other species (table 7), but immersing seeds in an organic liquid like ethanol, pentane, or petroleum ether may reduce seed viability. Such reduction can be minimized by using a short immersion time and evaporating all traces of the organic liquid from the seeds retained before use (Barnett 1970). Seeds sorted in organic solvents should be used right away and not stored, as the potential for damage increases in storage (Bonner 1997). If plain water is used to float off empty seeds, the retained seeds should be dried to moisture contents between 5 and 10% before they are stored. Seedlots of some pines, notably lodgepole pine, can be upgraded with the IDS (incubation-drying-separation) method developed in Sweden (Simak 1984) (see chapter 3). Cleaned seeds per weight are known for 65 species and varieties, and cone and seed yields are available for many of them (table 8).

Seed storage. Pine seeds are orthodox in storage behavior, and seeds of most species can be stored easily for extended periods of time without serious losses in viability (table 6). Seeds of red pine that had been stored for 30 years still produced vigorous seedlings in the nursery, as did seeds of shortleaf and slash pines that were stored for 35 years (Krugman and Jenkinson 1974; Wakeley and Barnett 1968). Lots of slash and shortleaf pine seeds stored for 50 years still germinated at 66 and 25%, respectively (Barnett and Vozzo 1985). Seeds of many pines are now routinely stored for 5 to 10 years and more. They should be dried to a moisture content between 5 and 10% and stored in containers that prevent absorption of ambient moisture. For long-term storage of most pine seeds, temperatures of –18 to –15 °C or

Table 9—*Pinus,* pine: recommended moist seed chilling times, stratification at 0.5 to 5 °C

Species	Seed chilling (days)	
	Fresh	Stored
P. muricata	0	20–30
P. nigra	0	0–60
P. palustris	0	0–30
P. parviflora †	90	90
P. patula	60	60
P. peuce §	0–60	60–180
P. pinaster ‡	0	60
P. pinea ‡	0	0
P. ponderosa		
var. *ponderosa*	0	30–60
var. *scopulorum*	0	0–60
P. pumila	120–150	120–150
P. pungens	0	0
P. quadrifolia	0	0–30
P. radiata	0–7	7–20
P. resinosa	0	60
P. rigida	0	0–30
P. roxburghii	0	0
P. sabiniana ll	60–120	60–120
P. serotina	0	0–30
P. sibirica †	60–90	60–90
P. strobiformis	60–120	60–120
P. strobus	30–60	60
P. sylvestris	0	15–90
P. taeda	30–60	30–60
P. thunbergiana	0	30–60
P. torreyana	30–90	30–90
P. virginiana	0–30	30
P. wallichiana	0–15	15–90
P. washoensis	60	60

Sources: Andresen (1965), Asakawa (1957), Barnett (1970), Barton (1930), Bonner (1991), Dent (1947), Goor and Barney (1968), Hartmann and Hester (1968), Heit (1963, 1967a, 1968b, 1969), Hopkins (1960), ISTA (1966), Jones (1962), Krugman and Jenkinson (1974), Luckhoff (1964), Magini and Tulstrup (1955), Malac (1960), McLemore and Barnett (1967), McLemore and Czabator (1961), Mirov (1936), Rohmeder and Loebel (1940), Shafiq and Omer (1969), Swingle (1939), Swofford (1958), Wakeley (1954).

* Chilling time can be held to 90 days if seeds first are scarified mechanically or soaked for 3 to 5 hours in sulfuric acid. Acid soaks are not advised.
† Seeds of *P. cembra*, *P. koraiensis*, *P. parviflora*, and *P. sibirica* with immature embryos may need a warm, moist treatment, 60 days at 21 to 26 °C, before the cold one.
‡ Good germination of *P. edulis*, *P. pinaster*, and *P. pinea* can be obtained by soaking the seeds in cold water for 24 hours at 5 °C.
§ A 60-day moist chilling treatment was sufficient when the seeds first were soaked 30 minutes in sulfuric acid. Acid soaks are not advised.
ll Seed germination is faster if the seedcoats are cracked before the moist chilling treatment.

–6 to –5 °C are preferred (Krugman and Jenkinson 1974; Wakeley and Barnett 1968), but those of 0.5 to 5 °C are sufficient for 2 to 3 years (Bonner 1991). Seeds of Khasi and blue pines have remained viable at ordinary room temperatures for several years (Claveria 1953; Dent 1947), but such ambient storage is risky and not recommended. Seeds deteriorate rapidly if they are held long at room temperature after cold storage. Seeds in cold storage should be pulled within days of cold, moist stratification, sowing, or testing (Wakeley 1954).

Liquid nitrogen at –196 °C has been used to store seeds of several pines in research studies with no loss of viability for short periods, including shortleaf pine seeds for 4 months and ponderosa seeds for 6 months (Bonner 1990). This method is under study for germplasm conservation purposes, however, and not for routine storage.

Pregermination treatments. Seeds of most pines in temperate climates are shed in the autumn and germinate promptly the next spring. Seeds of certain others, such as Swiss stone and Balkan pines, may not germinate until the second or even third year after seed dispersal. Pine seeds display highly variable germination behavior when sown after extraction or after storage. Seed dormancy varies in type and degree among species, among geographic sources within species, and among seedlots of the same source. Secondary dormancy may result from prolonged extraction at too-high temperatures and may increase with extended time in cold storage (Heit 1967a; Krugman and Jenkinson 1974). Seeds of many pines germinate without pretreatment, but germination rates and amounts are greatly increased by pretreating the seeds, and especially stored seeds, using moist, cold stratification. Recommended moist chilling times for fresh and stored seeds are available for 65 species and varieties (table 9).

Air-dried and stored seeds of most pines are effectively readied for rapid, complete germination by first soaking them in clean, constantly aerated water at temperatures of 20 to 25 °C for 36 to 40 hours, or until they sink (Jenkinson and McCain 1993; Jenkinson and others 1993). The soaked seeds are promptly drained of free water, placed naked in polybags, and chilled at 0 to 1 °C for the times shown (table 9). Both the development of molds on and visible germination of seeds in the polybags are prevented by surface drying the seeds after their first 4 weeks of chilling.

Seeds of some pines show strong dormancy, that is, they require 60 to 90 days or more of moist chilling to attain rapid and complete germination (table 9). Such dormancy may be caused by physiological or physical factors. Pretreatment may be needed to overcome a physiological block in the embryo, as in sugar pine (Krugman 1966), or to effect a physical change in the seedcoat to make it more permeable to water, as in Digger pine (Griffin 1962; Krugman 1966). Seed dormancy can be even more complex. An anatomically immature embryo with a physiological block may be coupled with an impermeable seedcoat, as in Swiss stone pine. Acid scarification of seedcoats has been used for a few pines, including Swiss stone, Balkan, and Digger

Table 10—*Pinus*, pine: seed germination test conditions and results

Species	Seeds treated	Germination test condition: Daily light (hr)	Seed medium	Temp (°C)*: Light	Temp (°C)*: Dark	Days	Germinative energy: Rate amt (%)	Germinative energy: Time (days)	Germinative energy: Total (mean %)	Samples
P. albicaulis	+	8	A, P	30	20	28	—	—	—	—
	+	0	pe, s	21	10	365	—	—	30	2
P. aristata		0	A, P	30	20	14	—	—	—	—
		24	P	32	21	22	75	7	91	74
		0	pe, s	35	20	30	—	—	86	>7
P. arizonica		0	P, pl	—	24	20	52	10	75	8
P. attenuata	+	24	A, P	22	26	30	79	5	92	1
		8	s	30	20	120	69	10	85	4
P. banksiana		8	A, P	30	20	14	86	10	87	14
	+ †	8	s	30	20	8	54	5	69	29
		8	s	30	20	23	72	9	75	6
P. canariensis	+	0	A	—	20	28	58	20	74	9
		8	A	20	20	21	63	7	76	4
P. caribaea		>8	P	30	20	21	—	—	72	3
P. cembra	+	0	P, s	30	20	28	—	—	—	—
	+	0	A	30	20	90	21–42	17–37	37	8
	+	0	s	22	20	60	55	28	62	1
P. cembroides		0	B, P	—	20	28	—	—	—	—
P. clausa		8	K	20	20	21	86	14	90	19
		8	s + v	21	16–18	30	85	20	90	—
P. contorta										
var. contorta	+	>8	A, P, v	30	20	28	—	—	60	3
		0	pe, s	30	20	50	—	—	80	29
var. latifolia	+	8	A, P	30	20	21	73	10	80	10
	+	0	s	28	14	62	—	—	73	9
	– †	0	s	28	14	62	—	—	65	12
var. murrayana		10	s	26	26	30	—	—	75	3
P. coulteri	+	0	P, s	30	20	28	—	—	—	—
	+	8	s, v	30	20	28	—	—	37	7
P. densiflora		8	A, P	30	20	21	—	—	—	—
		0	s	30	20	30	75	15	87	3
	+	0	s	30	20	24–60	54	15	83	4
		0	A	—	24	30	—	—	74	20
P. echinata		>8	A, P	30	20	28	—	—	—	—
		8	s + v	22	22	28	88	14	90	139
	+	8	pl + s	22	22	27	81	10	90	148
P. edulis	+	0	A	30	20	28	—	—	—	—
	+	0	P	32	21	16	80	7	96	4
P. elliottii										
var. densa		>8	s + v	22	22	32	30–79	7–11	32–82	30
		16	K	22	22	28	86	7	87	28
var. elliotti		>8	A, P	30	20	28	—	—	—	—
		16	K	22	22	26	80	10	89	392
	+	16	K	22	22	26	75	9	84	83
P. engelmannii		0	P	32	21	16	70	4	88	4
P. flexilis	+	0	B, P	30	20	21	—	—	—	—
	+	8	A	30	20	21	—	—	—	—
		8	s + v	22	22	27	—	—	42	1
	+	8	A	30	20	30	69	14	82	1
P. gerardiana		0	A	—	21	30–60	—	—	47	2
P. glabra	+	8	A, P	30	20	21	—	—	—	—
	+	16	s + v	22	22	30	85	13	98	25
		16	s + v	22	22	30	46	30	98	30
P. halepensis		0	A, P	—	20	28	—	—	—	—
		0	A	—	20–22	30	50–66	20	79	5
		0	A	—	18–19	30	65–80	16–20	89	12

Table 10—*Pinus*, pine: seed germination test conditions and results (continued)

Species	Seeds treated	Germination test condition: Daily light (hr)	Seed medium	Temp (°C)* Light	Temp (°C)* Dark	Days	Germinative energy: Rate amt (%)	Time (days)	Total (mean %)	Samples
P. heldreichii	+	8	A, P	30	20	28	—	—	—	—
	+	8	A	30	20	40	—	—	72	14
		—	A	—	21	40	—	—	69	1
P. jeffreyi	+	8	A, P, s	30	20	28	—	—	—	—
	+	24	P	22	26	30	95	5	99	1
		0	v	30	20	21	—	—	79	5
P. kesiya		8	A	30	20	28	82	14	86	1
P. koraiensis	+	0	s	30	20	60	14	25	18	1
	+	>8	P	30	20	28	—	—	85–95	4
P. lambertiana	+	0	P, s	30	20	28	—	—	—	—
	+	—	v	30	20	28	—	—	59	5
	+	24	P, s	22	26	30	49	21	55	1
P. leiophylla var. *chihuahuana*		0	pl	—	24	22	60	6	70	3
P. merkusii		8	A	30	20	21	—	—	59	1
		8	A	20	20	21	—	—	67	1
P. monophylla		24	pl	75	21	35	39–50	7	86–90	2
P. monticola	+	0	P, s	30	20	28	—	—	—	—
	+	8	pl + s	22	22	71	39	11	44	11
P. mugo		8	A, P	30	20	14–21	—	—	—	—
		0	A	—	20	30	25	10	45	30
		8	A	30	20	20	76	10	80	30
P. muricata		0	A	30	20	35	—	—	—	—
	+	0	v	30	20	21	—	—	38	5
	+	24	P	22–26	—	30	70	7	85	1
P. nigra		8	A, P	30	20	14	91	10	92	49
		0	A	30	20	30	54	10	86	49
P. palustris		16	P	20	20	21	—	—	—	—
		16	s + v	22	22	30	90	10	95	100
P. parviflora		0	P	22	18	10–14	—	—	—	—
	+	8	s	30	20	28	71	35	—	—
	+	>8	A	25	25	28	—	—	80	1
P. peuce	+	0	s	30	20	28	—	—	—	—
		0	A	20	22	30	—	—	69	4
P. pinaster		8	A	20	20	35	—	—	—	—
	+	8	A, P	20	20	28	41	7	79	8
	+	0	A	—	20	30	70	20	83	5
P. pinea	+	0	s	—	20	21	—	—	—	—
	+	8	A	20	20	21	30	7	81	4
		0	A	—	18	22	88	14	98	3
P. ponderosa var. *ponderosa*	+	8	A	30	20	21	—	—	—	—
	+	>8	A	30	20	21	—	—	67	100
		0	pe, s	29	18	30–60	14–87	7–29	59	186
var. *scopulorum*		16	K	22	22	30	84	11	86	4
		0	s	20	30	30–60	50	19	64	40
P. pumila	+	>8	A	30	20	21	—	—	77	9
P. pungens		0	pe + s	—	21–29	45–60	—	—	55	3
		0	pe, s	—	24	40	—	—	65	9
P. quadrifolia	+	24	A	22–26	—	30	46	9	69	1
P. radiata	+	8	A	30	20	28	—	—	—	—
		>8	P	20	20	25	16	7	81	9
		>8	v	30	20	28	—	—	67	15
P. resinosa		0	A, P	30	20	14	69	10	83	23
		0	s	30	20	30	25–75	7–25	75	551
P. rigida		8	A, P	30	20	14	77	10	86	6
	+	0	A	30	20	30	24	10	47	6
		8	A	30	20	45	60	18	70	19

Table 10—*Pinus*, pine: seed germination test conditions and results (continued)

Species	Seeds treated	Germination test condition: Daily light (hr)	Seed medium	Temp (°C)* Light	Temp (°C)* Dark	Days	Germinative energy: Rate amt (%)	Time (days)	Total (mean %)	Samples
P. roxburghii		0	A	—	20–22	30	—	—	83	5
		0	s	—	—	30	79	10	81	135
P. sabiniana	+	0	s	—	22	30	—	—	76	3
	+	24	A	22–26	—	30	—	—	13	1
P. serotina		8	pl + s	22	22	21	90	10	73	1
P. sibirica	+	0	s	20	30	60	—	—	7	1
		0	A	20	22	>60	—	—	40	4
P. strobiformis		0	A	30	20	35	—	—	94	8
		0	pl	—	24	46	—	—	39	31
P. strobus	+	>8	A, P	30	20	21	—	—	—	—
	+	>8	K	30	20	40	33	8	100	20
	+	>8	K	22	22	40	—	—	93	28
P. sylvestris		8	A, P	30	20	14	78	10	81	99
		8	A	30	20	30	46	10	59	99
		24	s	22–25	—	50	—	—	89–99	36
		8	A	20	20	30	18–99	14	21–99	18
P. taeda		>8	A, P	30	20	28	—	—	—	—
		16	pl + s	22	22	30	90	17	90	481
P. thunbergiana		>8	A, P	30	20	21	50	10	75	4
		>8	A	24	24	30	69	10	76	19
	+	0	A	25	21	28	—	—	85	100
P. torreyana	+	0	pe, s	27	18	60	—	—	81	21
P. virginiana		>8	A	30	20	21	—	—	—	—
		>8	K	22	22	28	87	10	90	29
		0	pe, s	30	20	30	—	—	65	5
P. wallichiana		>8	A, P	30	20	28	—	—	—	—
		0	A	24	21	60	44	20	64	12

Sources: Andresen (1965), Asakawa (1957), AOSA (1965, 1996), Graber (1965), Heit (1958, 1963), Heit and Eliason (1940), ISTA (1966), Kamra (1969), Krugman and Jenkinson (1974), Luckhoff (1964), Magini (1955), McIntyre (1929), McLemore (1961a), Nather (1958), Ohmasa (1956), Rafn (1915), Rohmeder and Loebel (1940), Rossi (1929), Sen Gupta (1936), Simak and others (1961).

Note: The + symbol shows that the seeds were pretreated, usually by moist chilling. Letters show the seed germination media that were used, as follows: A = absorbent paper (filter, blotter), B = blotters supporting and covering seeds, K = Kimpak, P = absorbent medium in covered petri dish, pe = peat, pl = perlite, s = sand or soil, v = vermiculite.

* Alternating periods of high and low temperatures typically were 8 and 16 hours (8/16). The light period normally coincided with the warmer temperature. Temperatures of 10, 15, 20, 25, 30, and 35 °C equal 50, 59, 68, 77, 86, and 95 °F, respectively.

† Seeds were extracted from old cones.

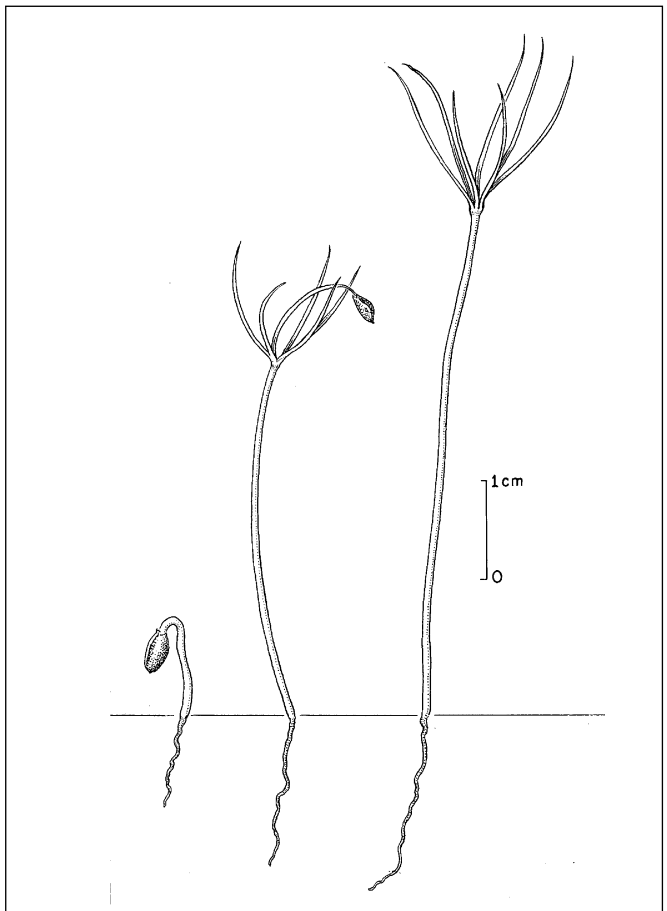
pines, but extended cold stratification, 6 to 9 months of moist chilling, is much more effective (Heit 1968b; Krugman 1966). In any case, acid scarification is not recommended for pine seeds (Krugman and Jenkinson 1974).

Seeds of some pines, including Swiss stone pine, Korean, Japanese white, and Siberian pine, may have immature embryos at the time of cone collection. Seed germination has been increased by placing seeds first in moist, warm stratification for several months and then in cold stratification for several more months (Asakawa 1957; Krugman and Jenkinson 1974).

Germination tests. For reliable tests of seed viability, seeds are germinated in near-optimum conditions of aeration, moisture, temperature, and light. Standardized tests for many of the pines have been established by the Association of Official Seed Analysts (AOSA 1996), International Seed Testing Association (ISTA 1996), and regional organizations such as the Western Forest Tree Seed Council (WFTSC 1966). Extensive research and abundant practical experience have developed reliable test conditions and germination data for seeds of 61 species and varieties (table 10).

Seed germination can be effectively tested in any medium or container that provides adequate aeration and moisture. Seeds of a few pine species need light for reliable tests. Light, when used, usually is supplied by cool white fluorescent lamps operated for 8 or 16 hours in each 24-hour period. Several different temperature regimes are employed, but the commonest are a constant 20 °C and an alternating 30/20 °C. Alternating regimes typically maintain the higher temperature for 8 hours and the lower one for 16 hours.

Figure 4—*Pinus resinosa*, red pine: seedling development at 1, 7, and 30 days after emergence.



Most tests of viable seeds are clear within 2 weeks and ended within 3 to 4 weeks. Sample sizes of 400 seeds per lot (4 replications of 100) are ample for most pines, but in some cases, up to 1,000 per lot may be used. Germination is epigeal (figure 4).

Cutting methods are often used to obtain fast, rough assessments of seed quality. Cutting seeds provides a visible check of seed soundness, and serves to guide fall-sowings of fresh seeds that have embryo dormancy. It is a surprisingly accurate method with fresh seeds. X-radiography can also provide visible estimates of seed soundness without destroying the seeds. Another rapid estimate of viability is the leachate conductivity test (Bonner and Vozzo 1986b). Because no seeds are actually germinated, cutting, x-ray, and conductivity tests provide only estimates of viability and are somewhat prone to error (Stoeckeler and Jones 1957; Stoeckeler and Slabaugh 1965; Wakeley 1954).

Biochemical methods, such as staining with tetrazolium chloride to indicate viability, are recommended in official testing for the very dormant stone pines (ISTA 1996), but they are used on other species for rapid tests only. Tetrazolium test estimates are highly dependent on the analyst's experience and seed age, and too often exceed the percentages attained in standard germination tests (Stoeckeler and Slabaugh 1965; Tanaka 1984).

Nursery and field practices. Pines are grown successfully in diverse soil types in most regions of the United States. Various regional handbooks, manuals, and reports on forest tree nursery and reforestation practices describe bareroot seedling production, illustrate typical nursery equipment and facilities, and provide critical guides on soil management, bed preparation, seed treatment, seed sowing, seedling cultural regimes and pest control, undercutting, wrenching, lifting, packing, transplanting, cold and freeze storage, shipping, field handling, and safe planting times (Cleary and others 1978; Duryea and Landis 1984; Heit 1964; ICIA 1963; Jenkinson 1980; Jenkinson and others 1993; Lowman and others 1992; Schubert and Adams 1971; Schubert and others 1970; Stoeckeler and Jones 1957; Stoeckeler and Slabaugh 1965; Wakeley 1954). Together, these references and work cited therein capture the bulk of knowledge and practical experience gained on pine seedling production and planting in the United States.

Productive nursery soils are invariably deep, arable, fertile, and drain rapidly to ensure root aeration. Most of the large mechanized nurseries fumigate their soils (in late summer–early fall) to control soil-borne diseases, insects, nematodes, and weeds before the scheduled sowing in fall or spring (Thompson 1984). Nursery climates, soils, seed sources, and their interactions have resulted in a wide range of cultural regimes and practices. Recommended practices for 35 different species and varieties show the wide ranges encountered in seed chilling time, in sowing time, density, and depth, in bed mulches, and in yields and types of planting stock produced (table 11).

In temperate regions, seeds can be sown in fall or spring. Seeds with embryo dormancy can be sown in fall without pretreatment. Normally, both dormant seeds and nondormant seeds are sown in spring more often than in fall. Dormant seeds in spring-sowings must be pretreated to enable rapid and complete germination. Applying the same treatment to the dormant seeds of all pines is inadvisable. Success of the treatment applied depends on species and seed source, and the one applied should be the one that achieves the highest germination and seedling emergence for the particular seedlot. Seedlings produced in fall-sowings after 1 growing season are often larger and better developed than those produced in spring-sowings. But fall-sowings are inherently risky. They typically incur excessive overwinter

Table 11—*Pinus,* pine: nursery practices

Species	Seed chill (days)	Seed sowing: Season	Seed sowing: Density† (/ft²)	Seedbed mulch: Depth‡ (mm)	Seedbed mulch: Material	Planting stock: Depth (mm)	Planting stock: Yield (%)	Type§
P. attenuata	60	Spring	25	10	None	—	80	1+0
P. banksiana	0	Fall or spring	30	6	None	—	50–60	1+0, 2+0, 1/2+1 1/2, 1+1, 1+2
P. canariensis	0	Spring	—	6	Sponge Rok®	6–13	35–50	1+0, 2+0, 1/2+1 1/2
P. clausa	0	Spring	—	6–13	None	—	70	1+0
P. contorta								
var. *contorta*	28	Spring	30	3	None	—	48	1+0
var. *latifolia*	28–35	Spring	48	3	Sawdust	13	60	2+0
var. *murrayana*	30–60	Spring	25–60	10	Peat mossII	6–13	70–75	1+0, 2+0
P. coulteri	60	Spring	25	13	None	—	80	1+0
P. densiflora	0	Spring	50	3–6	Sand	—	—	2+0, 3+0, 1+1
P. echinata	15–60	Spring	40	Press	Pine straw	—	60	1+0
P. edulis	60	Spring	30	6	Sawdust	13	80	2+0
P. elliottii								
var. *densa*	0	Spring	35	Press	Pine straw	13	80	1+0
var. *elliotti*	0	Spring	30–35	Press	Sawdust or pine straw	—	58–74	1+0
P. jeffreyi	28–60	Spring	25–30	6–10	None	—	58–80	1+0, 2+0, 1+1
P. kesiya	0	Spring	30	10	None	—	50	1+0
P. lambertiana	90	Spring	30–35	10–13	None	—	21–80	1+0, 2+0, 1+1
P. monophylla	90	Spring	25–30	13	Sawdust	6–13	33	2+0
P. monticola	42–90	Spring	35–120	6–10	Sawdust II	6–13	32–90	2+0, 3+0
P. mugo	40–50	Spring	50	10	Peat moss	6–13	55	3+0
P. muricata	28–40	Spring	30–75	3–19	Peat moss II	6–13	37–60	1+0
P. nigra	0	Fall	50–60	13–19	Peat moss	6–13	60–65	2+0, 2+1, 2+2
	35–45	Spring	—	—	—	—	—	—
P. palustris	0	Spring	15	Press	Pine straw	—	75	1+0
P. pinaster	0	Spring	30	6–13	—	—	—	1+0
P. ponderosa								
var. *ponderosa*	28–60	Spring	25–46	6–10	None	—	48–80	1+0, 2+0, 3+0, 1+1, 1+2
var. *scopulorum*	20–30	Spring	35–40	3–6	None	—	70	1+0, 2+0
	0	Fall or spring	50–65	13	None	—	70	1+2, 2+1, 2+2
P. pungens	0	Fall or spring	20–33	6–13	Straw	—	19–28	1+0, 2+0
P. radiata	35–45	Spring	25–75	3–19	Peat moss II	6–13	34–70	1+0
P. resinosa	0	Fall or spring	30–50	6–10	None	—	65–80	2+0, 3+0, 2+1, 2+2
P. rigida	0	Spring	30–35	Press	Sand	3	—	2+0
P. roxburghii	0	Spring	—	3–13	—	—	30–35	1+1, 2+1
P. strobus	0	Fall	20–50	16, or	Sawdust, or	3–6	55–85	2+0, 3+0, 2+1,
	30	Spring	—	Press	wood fiber	—	—	2+2
P. sylvestris	0	Fall	30–60	3–13	Peat moss II	6–13	25–70	1+0, 2+0, 2+1,
	2–60	Spring	—	—	—	—	—	2+2
P. taeda	30–60	Spring	40	Press	Pine straw	—	60	1+0
P. thunbergiana	0	Fall or spring	50–100	3	Burlap or straw in winter	—	31	2+0, 1+1
P. virginiana	0	Fall	30–35	6 or	Sand, pine	6–13	63–90	1+0, 2+0
	14	Spring		press	Needles or sawdust	—	—	—
P. wallichiana	0	Fall	cast	13	None	—	46	1+1, 1+1+1
	15–20	Spring	—	—	—	—	—	—
P. washoensis	60	Spring	25–30	6–10	None	—	50–80	1+0, 2+0

Sources: Claveria (1953), Derr (1955), Goor (1955), Heit (1968a), Krugman and Jenkinson (1974), Letourneux (1957), Magini and Tulstrup (1955), NBV (1946), Schubert and Adams (1971), Shoulders (1961), Stoeckeler and Jones (1957), Stoeckeler and Rudolf (1956), Stoeckeler and Slabaugh (1965), Troup (1921), Veracion (1964, 1966).

* Seeds were chilled in a moist medium at 0.5 to 5 °C.
† Multiply number per square foot by 10.758 to convert to number per square meter.
‡ The word "press" indicates that seeds were pressed flush to the soil surface.
§ Type of planting stock codes the number of growing seasons and transplant operations for seedlings in the nursery: 1+0 stock is lifted and shipped to the field for outplanting after 1 nursery growing season, and 2+0 stock, after 2 seasons; 1+1 stock is transplanted after its first growing season and shipped to the field after its second season.
II Mulch was not always used.

losses to birds and rodents, and they must be delayed until the soils are cold enough to prevent germination in fall and avoid winter freeze damage and mortality of germinants.

Seeds can be drill-sown or broadcast by hand or machine, but mechanized nurseries drill-sow in prepared seedbeds because it is most efficient and economical (Thompson 1984). Quantity of seeds sown per unit area of nursery bed varies with species, seed size, expected germination and emergence percentages, and the target seedling density, that is, stems per unit bed area. Sowing density controls seedling density, which markedly affects both the size and vigor of seedlings and transplants. Target density depends on species and stock type, on when seedlings are to be lifted and on whether they are to be transplanted.

Seeds are sown at rates that are selected to produce from 160 to 800 seedlings/m^2 (15 to 75/ft^2). Higher seedling survivals are obtained when medium and lower densities are used. Most nurseries sow seeds at slightly higher densities if the seedlings are to be grown in transplant beds for 1 or 2 additional years, and higher sowing densities are used for 1+0 than for 2+0 seedlings. Sowing densities range from 61 to 610 g of seeds/10 m^2 (2 to 20 oz/100 ft^2) of bed, depending on species, nursery, and seedlot. To produce 2+0 planting stock of western white pine, for example (Krugman and Jenkinson 1974), one western nursery drill-sows 115 seeds/m (35/ft) in rows spaced 9 cm (3 $^1/_4$ in) apart to get 1,290 seedlings/m^2 (120/ft^2), whereas another drill-sows 60 seeds/m (18/ft) in rows spaced 15 cm (6 in) apart to get 375 seedlings/m^2 (35/ft^2). Experience is the ultimate guide to sowing density for a given species and seed source in a particular nursery situation. Seed germination in the nursery has varied from just 20 to 85% of that obtained in laboratory tests. On average, 55% of the seeds germinated in nursery beds, with a range of 19 to 90%, have yielded acceptable seedlings.

At sowing time, seeds are drilled or pressed firmly into the soil and then uniformly covered with 3 to 19 mm ($^1/_8$ to $^3/_4$ inch) of soil, sand, or other mulch, with depth depending on seed size and the nursery (table 11). Fall-sown seeds are set slightly deeper than spring-sown seeds to protect them against frost heaving and wind erosion. For large-seeded pines such as whitebark and sugar pines and singleleaf piñyon, seeds may be covered to a depth of 13 mm ($^1/_2$ inch). Seeds of small-seeded pines require the least covering. Seeds of the southern pines—such as shortleaf, slash, longleaf, loblolly, and Virginia pines—are pressed into the soil surface and covered with burlap or chopped pine straw. Mulching protects seeds against rain displacement, helps protect against predations by birds, and slows evaporative loss of soil moisture. Seeds of shore, Rocky Mountain lodgepole, Japanese red, and Japanese black pines are typically sown 3 mm ($^1/_8$ in) deep, and seeds of jack, Canary Island, and western white pines as well piñyon, 6 mm ($^1/_4$ in) deep. Sowing seeds deeper than advised is to be avoided, because deep sowing at best delays and often disables seedling emergence.

Germination of most pines is completed 10 to 50 days after spring-sowing. Pretreated dormant seeds of certain lots of whitebark, Swiss stone, Balkan, and southwestern white pines, however, have taken from several months to a year to germinate after sowing (Krugman and Jenkinson 1974).

Fungicides are often needed during and after seedling emergence to limit damping-off in most nurseries, and both insecticide and fungicide sprays are needed during the growing season to control insects and foliar diseases. Repeated nursery applications of fungicides are needed to control fusiform rust (*Cronartium quercuum* (Bark.) Miy. ex Shirai f. sp. *fusiforme* Bards. et Snow) on slash and loblolly pines and brown spot (*Scirrhia acicola* (Dearn.) Sigg.) on longleaf pines in southern United States, and to control sweetfern blister rust (*Cronartium comptoniae* Arth.) on jack, ponderosa, and Scots pines in the Great Lakes region (Krugman and Jenkinson 1974).

Transplants and older planting stock types are generally recommended for more difficult planting sites (table 11). In the Great Lakes regions and the prairie-plains, stock types used for jack pine are 1+0 or 1+$^1/_2$ for usual sites; 1+1 or 2+0 for tough sites; and 1+2, 2+1, or 2+2 for windbreaks. Stock types used for most white pines are 2+0 and 3+0, or 2+1 and 2+2 transplants.

Pines are also routinely grown in specialized container nurseries. In general, seeds are sown or new germinants are transplanted in containers filled with a standard rooting medium or soil mix, partial shade is provided during seed germination and seedling establishment phases, and seedlings are cultured for 1 growing season before planting. Care must be taken not to grow pines in too small containers for prolonged times, as they become rootbound and grow poorly after planting. Container-grown longleaf pine has performed exceptionally well in the South (Brissette and others 1991), and this species is now widely regenerated with container stock. A vast literature details every aspect of container stock production which is fully captured in the 6 current volumes in the Container Tree Nursery Manual (Agric. Handbk. 674) (Landis and others 1989, 1990a&b, 1992, 1994, 1999). An updated directory of forest tree nurseries in the United States indicates their ownership (private, industry, state, federal, and other), location by state, stock offered (bareroot, container, rooted cuttings), and amount shipped in fall 1992–spring 1993 (Okholm and Abriel 1994).

All pines can be vegetatively propagated by rooting or grafting (Krugman and Jenkinson 1974; O'Rourke 1961; Ticknor 1969). Rooting success for most pines, however, decreases rapidly when scions are taken from trees older than 5 years. A few, such as Monterey, knobcone, Japanese red, and Japanese black pines, are relatively easy to root, but only Monterey pine is widely propagated by rooting cuttings under nursery and greenhouse conditions (Thulin and Faulds 1968). Considerable progress has been made in the last 20 years, but for many species, production costs for vegetative propagules still cannot compete with seedling production (Greenwood and others 1991). Selected trees of many pines are cloned by rooting cuttings. Grafting is routinely used to propagate rare materials and to clone selected superior forest trees, particularly in orchards designed to supply genetically improved seeds for intensive forest management programs (Krugman and Jenkinson 1974).

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Fabaceae—Pea family

Pithecellobium dulce (Roxb.) Benth.

guamúchil

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Nomenclature. *Pithecellobium* is a genus of about 110 species, mostly native to Asia and tropical America. The taxonomy of this genus has been changed in recent years, and the names of some species are still in debate. *Pithecellobium saman* (Jacq.) Benth., which was included in the 1974 edition of this work (Walters and others 1974), became *Albizia saman* (Jacq.) F. Muell., then *Samanea saman* (Jacq.) Merr. In the current book, it is included in *Albizia*. Texas ebony (*P. flexicaule* (Benth.) Coult.) is now *Ebenopsis ebano* (Berl.) Barneby & Grimes and appears under that name in this book.

Growth habit, occurrence, and use. *Guamúchil*, also known as Madras thorn and monkeypod, is valued primarily for its fuelwood, fodder, and ornamental properties (Parrotta 1991). It is found on the Pacific slopes of Mexico and southern California, south to Colombia and Venezuela. Guamúchil has been planted in Florida, Puerto Rico, and Hawaii (Little and Wadsworth 1964) and has been introduced to India and Pakistan as a hedge plant (Khatra and others 1994). The species has become naturalized where planted and is now considered a pest in Florida (Morton 1976). It is a medium-sized tree that reaches heights of 22 m.

Flowering and fruiting. Guamúchil's white flowers are umbels, about 3 cm in length, that are borne in paniculate clusters on branch ends (figure 1). The species flowers primarily from December to May but is known to fruit throughout the year in Puerto Rico (Parrotta 1991). Fruits are linear, curved legumes (pods) that range in length from 10 to 13 cm (figure 1). They turn from green to brown or black when they ripen in February to August. The legumes may contain 5 to 12 seeds each, and they are dehiscent (Parrotta 1991). The seeds are reddish brown to black, elliptical, beanlike, and about 1 cm in length. As the legumes split open, the seeds often hang down partially enclosed in a pulpy aril that may be 2 cm long (figure 2). Seeds vary widely in size, ranging from 6,000 to 26,000/kg (2,720 to 11,800/lb) (Little and Skolmen 1989; Parrotta 1991).

Collection, extraction, and storage. Legumes may be picked from the trees or from the ground, and air-dried in the sun. Seeds can be removed by hand-flailing or by use of a macerator, and pod fragments can be removed with screens. There are no long-term seed storage data for guamúchil, but these are typical hardseeded legumes with orthodox storage behavior. The seeds should be easy to store at low moisture contents (<10%) and low temperatures (any refrigeration) for a number of years.

Germination. Official seed testing organizations do not include guamúchil in their prescriptions for testing, but tests with a single seedlot in Costa Rica found that germina-

Figure 1—*Pithecellobium dulce*, guamúchil: flowering twig, leafy twig, legumes, and seeds (from Little and Wadsworth 1964).

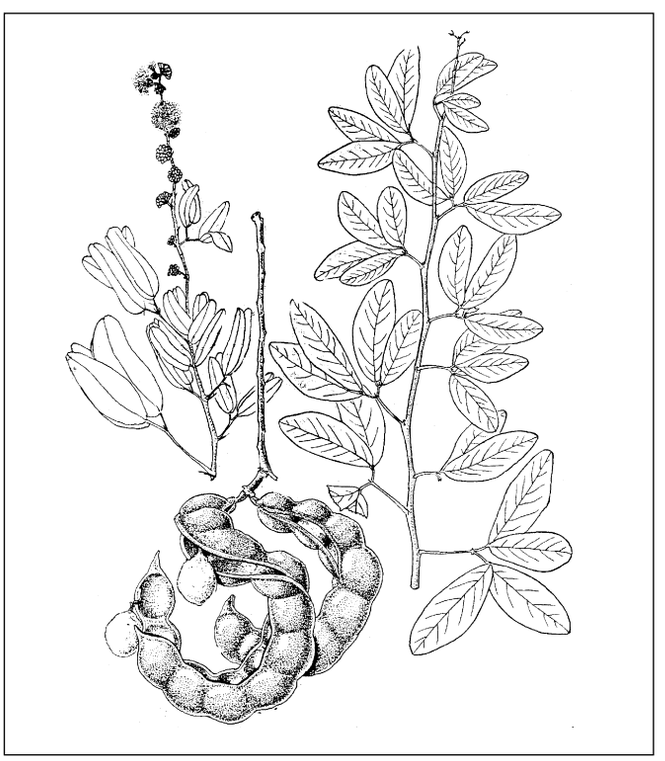
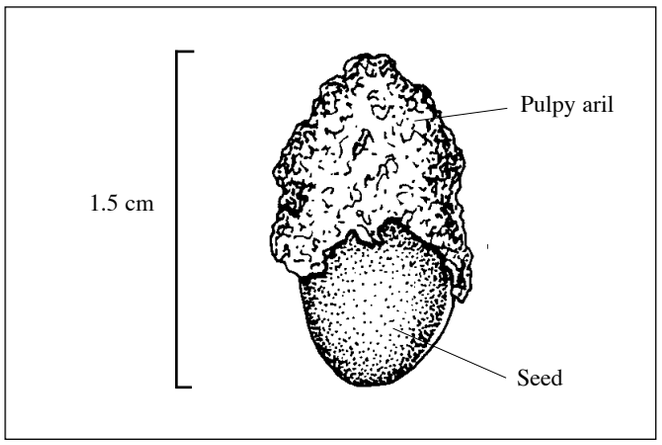


Figure 2—*Pithecellobium dulce*, guamúchil: seed partially enclosed in the pulpy aril (from Gunn 1984).



tion averaged 93% over a wide range of conditions (Castro 2000). Temperatures of 24, 27, 30, and 32 °C were equally good, and light from 0 to 24 hours made no difference either. Scarification with sulfuric acid or by clipping the seedcoats gave germination above 90%, but hot water treatments and long soaks at room temperature were not as successful. Good germination of this species without pretreatment has also been reported (Parrotta 1991).

Nursery practice. Guamúchil seeds germinate 1 to 2 days after sowing without treatment in Puerto Rico. Seedlings reach a good outplanting height of 40 cm about 3 months after sowing. This species can also be grown from cuttings (Parrotta 1991).

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Platanaceae—Planetree family

Platanus L.

sycamore

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Growth habit, occurrence, and uses. Sycamores—genus *Platanus*—are deciduous trees that range from 24 to 43 m in height at maturity. Two native and 1 introduced species are included in this manual (table 1). American sycamore is a large and valuable timber species in the eastern United States and has been widely planted in the Southeast for fiber production, wetlands restoration, and mine spoil reclamation (Haynes and others 1988; Wells and Schmidtling 1990). California sycamore is valued for watershed protection and wildlife food, whereas oriental planetree is primarily planted for ornamental purposes. London plane—*P.* × *aceriolia* (Ait.) Willd.—a hybrid between sycamore and oriental planetree, is also widely planted as an ornamental in the United States because of its tolerance of air pollution and alkali (Little 1961; Dirr and Heuser 1987). No geographic races of these species are recognized, but there is sufficient variation within American sycamore for growth (Ferguson and others 1977) and disease resistance (Cooper and others 1977) to justify tree improvement programs.

Flowering and fruiting. The minute monoecious flowers of sycamores appear in the spring (table 2). The dark red staminate flower clusters are borne on branchlets of the previous year's growth, and the light green pistillate flowers are found on older branchlets (Vines 1960; Wells and Schmidtling 1990). Sycamore fruiting heads are usually solitary, but California sycamore may have 2 to 7 heads grouped on a single stem (Bonner 1974) (figure 1).

Fruit heads are greenish brown to brown at maturity in the autumn (table 2). Those of sycamore are 25 to 40 mm in diameter, and those of the other species are closer to 25 mm. The true fruits are elongated, chestnut-brown, single-seeded achenes with a hairy tuft at the base (figure 2). They are closely packed, with their bases anchored in a hard central

Table 1—*Platanus,* sycamore: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. occidentalis* L.** *P. occidentalis* var. Sarg. *glabrata* (Fern.)	**American sycamore,** American planetree, buttonwood, planetree, buttonball-tree	Maine to Iowa, S to central Texas & NW Florida; also in NW Mexico; planted in South Dakota, Colorado, Nebraska, & Kansas
***P. orientalis* L.**	**oriental planetree**	SE Europe, W Asia to India; planted in US as an ornamental
***P. racemosa* Nutt.**	**California sycamore,** California planetree, western sycamore, *aliso*	Central to S California & into NW Mexico; below 1,200 m elevation

Sources: Little (1961, 1979).

Table 2—*Platanus,* sycamore: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
P. occidentalis	E US	Mar–May	Sept–Nov	Jan–Apr
P. orientalis	NE US	May	Sept–Oct	—
P. racemosa	—	—	June–Aug	June–Dec

Sources: Bonner (1974), Wells and Schmidtling (1990).

core. The elongated embryo is surrounded by a thin endosperm (figure 3). Sycamore usually bears good seed-crops every 1 to 2 years and light crops in the intervening years. Open-grown trees of this species as young as 6 years have produced seeds, but trees in dense natural stands are usually much older (25 years) before large crops are evident (Briscoe 1969; Wells and Schmidtling 1990). Fruit heads persist on the trees through the winter and break up the following spring. The hairy tufts at the base of the fruits act as parachutes for dissemination by wind. Sycamore fruits float easily and are therefore widely distributed by moving water (Wells and Schmidtling 1990).

Collection of fruits. Fruit heads of sycamore can be collected any time after they turn brown, but the job is easiest if done after leaf-fall. Because the heads are persistent, collections can be made into the next spring, usually making sycamore the last fall-maturing species to be collected in the East. This additional time on the tree after full maturity apparently does not harm seed quality (Briscoe 1969). Picking fruit heads by hand from the tree is the most common method of collection. At the northern and western limits of the range of sycamore, intact heads can sometimes be collected from the ground late in the season. As fruit heads begin to fall apart in the early spring, the seeds may sometimes be shaken loose by tapping the branches (Briscoe 1969). Once collected, fruit heads should be spread in single layers and dried in well-ventilated trays until they can be broken apart, no matter how dry they look at collection. This step is essential with fruit heads collected early in the season, as their moisture contents can be as high as 70% (Bonner 1972b).

Figure 1—*Platanus*, sycamore: fruiting heads of *P. occidentalis*, American sycamore (**top**) and *P. racemosa*, California sycamore (**bottom**).

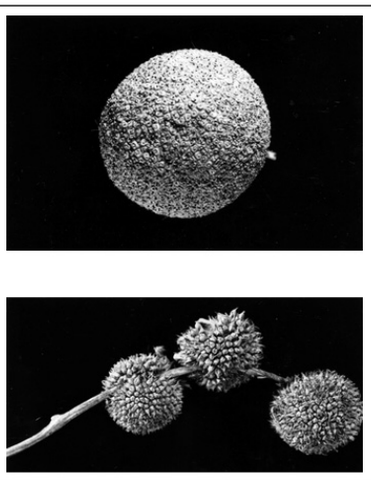


Figure 2—*Platanus*, sycamore: single achenes of *P. occidentalis*, American sycamore (**top**) and *P. racemosa*, California sycamore (**bottom**).

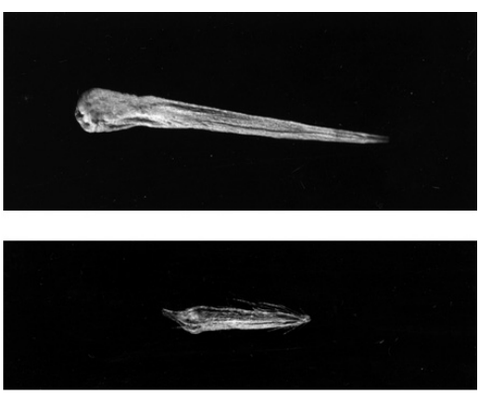
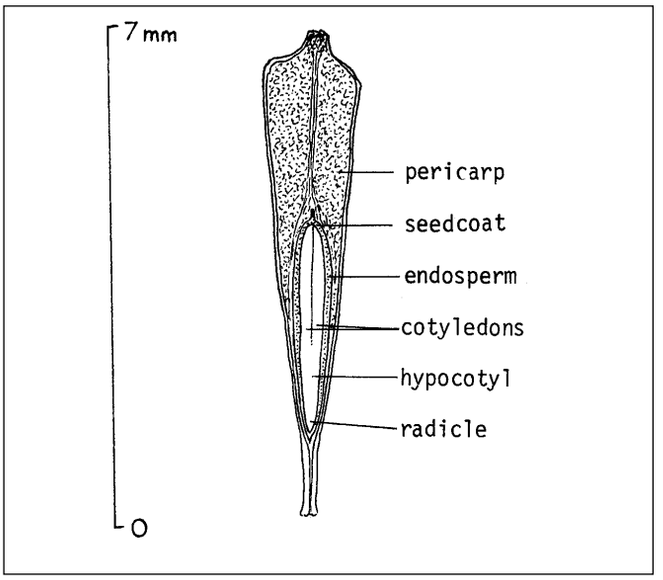


Figure 3—*Platanus occidentalis*, American sycamore: longitudinal section through a seed.



Extraction and cleaning of seeds. Seeds should be extracted by crushing the dried fruit heads and removing the dust and fine hairs that are attached to the individual achenes. Small lots can be broken up in small mechanical scarifiers or by hand-rubbing through hardware cloth (2 to 4 wires/cm) (Briscoe 1969). Medium-sized lots of up to 2 hl can be quickly broken up in mechanical macerators. Larger lots can be broken up in fertilizer distributors, hammermills, or centrifugal disks (Briscoe 1969; Bonner 1979). No matter which method is used, some method of dust removal should be provided and dust masks should be worn by workers! The fine hairs that are dislodged during extraction and cleaning are a danger to respiratory systems. The fertilizer distributor method is widely used, and the dust problem is

lessened when the operation is carried out in the open. The distributor can be loaded with fruits and pulled along with ejection gates closed, or a powered belt can be attached to a jacked-up wheel. With the jacked-up wheel arrangement, clean seeds will work out through the gates, while fruit cores and fluffs of the hairs will collect at the top.

Dust, fine hairs, and large trash can also be removed from seedlots with air-screen cleaners or aspirators. Studies with sycamore have shown that a 3 × 19 mm ($^{7}/_{64} \times {}^{3}/_{4}$ in) oblong-hole screen will remove twigs, leaves, and fruit cores, while dust, hairs, and small trash can be removed with 1.2 mm (1/21) round-hole screens (Bonner 1979). If the seedlot is especially trashy, 2 runs through the air-screen cleaner may be needed. The smaller cleaners can clean 5 to 7 kg of seeds/hour, and purities of greater than 99% are possible. Electrostatic seed cleaners can also do a good job cleaning sycamore. In a test by Karrfalt and Helmuth (1984), purity was increased from 88 to 99%. Louisiana and Mississippi collections of sycamore yielded 9 to 14 kg of seed/hl of fruitheads, and 55 to 66 kg of seeds/100 kg of fruitheads (Briscoe 1969). Some representative seed weight data for sycamore are listed in table 3.

Sycamore is noted for its low proportion of filled seeds, a condition due to poor cross-pollination and self-incompatibility in isolated trees (Beland and Jones 1967). Effective control of bed density in nurseries can be severely hampered by this condition, so upgrading of seedlots by mechanical means is highly desirable. Such operations are possible with gravity separators, aspirators, and electrostatic separators (Bonner 1979; Karrfalt and Helmuth 1984). For exmaple, a single pass on a gravity separator upgraded a sycamore seedlot from 27% filled seeds to 56% (Bonner and Switzer 1974).

Storage of seeds. Seeds of all sycamore species are orthodox in storage behavior and can be easily stored for long periods in cold, dry conditions. Storage tests with sycamore have shown that seed moisture contents of 5 to 10% and temperatures of 0 to 5 °C are suitable for short-term storage of up to 5 years. For longer storage periods, sub-freezing temperatures (–18 °C) at the same moisture content are recommended (Bonner 1979). The upper limit of storage potential for sycamore is not yet known, but current research suggests that it will be far beyond 10 years under optimum conditions (Bonner 1994). To maintain low seed moisture in moist surroundings, the dried seeds must be stored in moisture-proof containers, such as polyethylene bags or fiber drums with plastic liners (Bonner 1979). Several species of *Aspergillus* fungi have been identified as pathogens that harm viability of sycamore seeds in storage (Fakir and others 1971), but they have never been a major problem.

Pregermination treatments. Moist stratification for 60 to 90 days at 5 °C in sand, peat, or sandy loam has been reported as beneficial for germination of California sycamore (Bonner 1974). The other sycamores have no dormancy, and pregermination treatments are usually not required for prompt germination (Bonner 1972a; Webb and Farmer 1968). Germination rate of sycamore can be increased by treating with gibberellin (GA_3) at 100 to 1,000 mg/liter, but this increase seems to be simple growth stimulation that is not involved in seed dormancy (Bonner 1976).

Germination tests. Germination can be easily tested on wet paper or sand or even in shallow dishes of water (table 4). Official testing prescriptions call for alternating day/night temperatures of 30/20 °C on the top of moist blotters for 14 days (AOSA 1993). A large percentage of the sound seeds will usually germinate, but the great variation in number of sound seeds among lots will result in varied germination percentages. Surface sterilization of the seeds with a 30-second dip in a 1% commercial bleach solution is often beneficial to laboratory germination (Mullins 1976). Rapid viability tests can also be made on sycamore with tetrazolium staining and x-radiography (Bonner 1974).

Table 3—*Platanus,* sycamore: seed data

Species	Place of collection	Cleaned seeds/weight: Range /kg	Range /lb	Average /kg	Average /lb	Samples
P. occidentalis	Louisiana–Mississippi*	294,370–589,620	133,500–267,400	426,160	193,270	100+
	SE US	192,340–500,100	87,2330–226,800	330,530	149,900	28
P. orientalis	Denmark	178,600–357,200	81,000–162,000	282,240	128,000	8
	United States	249,160–370,440	113,000–168,000	308,700	140,000	2+

Sources: Bonner (1974), Briscoe (1969), Swingle (1939).

* Seedlots from these sources averaged 1,765 seeds/fruit (range from 804 to 3,050).

Nursery practice. Sycamores are usually sown in the spring by broadcasting or by mechanically drilling. For drilling, seeds should be placed no deeper than 3 mm ($^1/_8$ in) in rows 15 to 20 cm (6 to 8 in) apart. If sown on the surface of the beds, they should be covered with no more than 6 mm ($^1/_4$ in) of light mulch (Williams and Hanks 1976). Seedling density will depend on the intended use of the stock. For those wanting small seedlings, 110 seedlings/m^2 (10/ft^2) is recommended; for larger stock, 55/m^2 (5/ft^2) (Vande Linde 1960; Williams and Hanks 1976).

Bed surfaces must be kept moist through germination, and shading, while not necessary, can be helpful for the first month (Briscoe 1969; Engstrom and Stoeckler 1941). On neutral to slightly alkaline soils, damping-off may be a problem. Root pruning in midsummer is recommended to promote growth of smaller roots, and some nurseries prune seedling tops in late July or August to reduce size. Seedlings should not be both root- and top-pruned during the growing season (Briscoe 1969). Sycamore is usually outplanted as 1+0 stock, and oriental planetree is often planted as 1+1 or 2+0 seedlings in Europe (Bonner 1974). The sycamores are easy to propagate vegetatively by dormant or greenwood cuttings (Dirr and Heuser 1987), and many plantations of sycamore have been established in the South by these techniques. Some tests show no difference in growth after 1 year between seedlings and cuttings (Garrett 1975).

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Cupressaceae—Cypress family

Platycladus orientalis (L.) Franco

oriental arborvitae

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Synonym. *Thuja orientalis* L., *T. acuta* Moench., *Platycladus stricta* Spach., *Biota orientalis* (L.) Endl.

Other common names. Chinese arborvitae, biota.

Growth habit, occurrence, and use. Oriental arborvitae is native to northern and western China and Korea (Vidakovic 1991). This species was previously included in the genus *Thuja* (Schopmeyer 1974), but it has now been placed in *Platycladus,* a monotypic genus. It is a medium-sized tree (approximately 12 m tall) that is widely cultivated as an ornamental in the United States. Many ornamental cultivars have been developed (Dirr and Heuser 1987; LHBH 1976). The foliage of oriental arborvitae is not as aromatic as that of *Thuja* species, and its cones are rather fleshy (Rushforth 1987). It can be planted in many different soils and will tolerate drier soils than northern white-cedar—*Thuja occidentalis* L. Oriental arborvitae should be restricted to regions where the minimum temperature is above –24 °C (Rushforth 1987).

Flowering and fruiting. Flowering occurs in the spring, and the cones mature in the fall of the same year. The cones range from 1.5 to 2.5 cm in length and typically have 4 fertile scales. The seeds are dark reddish purple and wingless (figures 1 and 2) (Schopmeyer 1974).

Extraction, cleaning, and storage of seeds. Cones are usually collected by hand from the branches after they turn yellow or brown but before they open. Cones will open partially with only air-drying in the sun or inside at room temperature, but auxiliary heating is needed for complete extraction. Most cones should open in 24 to 36 hours when heated at 30 °C (Dirr and Heuser 1987). Seeds can be shaken from the cones with small cone tumblers or similar devices, then scales and trash can be removed with screens or seed blowers. If large numbers of empty seeds are present, seedlots can be upgraded with the careful use of seed blowers. Oriental arborvitae seeds range from 44,100 to 55,125/kg (20,000 to 25,000/lb) (Schopmeyer 1974).

Figure 1—*Platycladus* orientalis, oriental arborvitae: seeds.

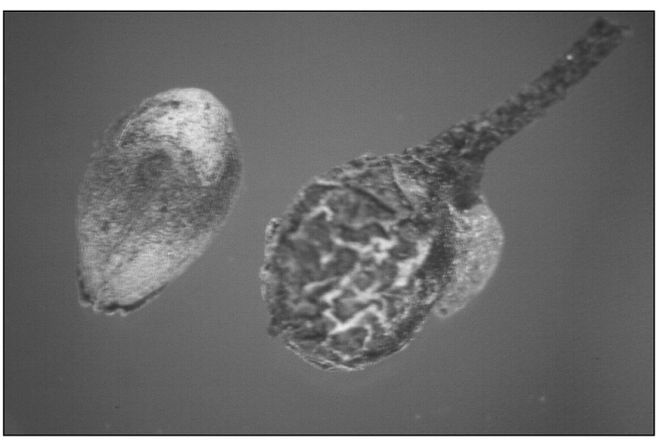
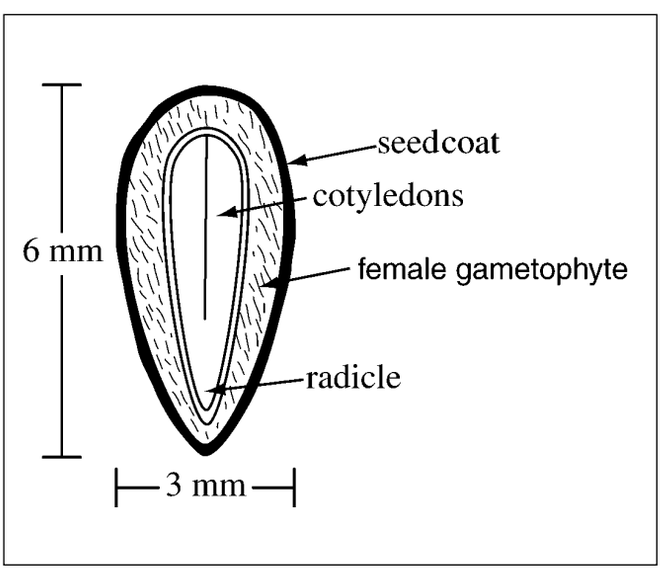


Figure 2—*Platycladus orientalis*, oriental arborvitae: longitudinal section through a seed.



Seeds of this species are orthodox in storage behavior. If dried to moisture contents of 5 to 10% and stored at near-freezing (0 to 5 °C) temperatures, viability should be main-

tained for at least 5 years. For longer storage periods, subfreezing temperatures of about –18 °C are recommended (Bonner 1991).

Germination tests. For most seedlots, pretreatments are not needed for germination tests, although beneficial effects have been reported for cold stratification for 1 to 1 $^1/_2$ months and for short soaks in weak solutions of gibberellic acid (Dirr and Heuser 1987; Schopmeyer 1974). Both AOSA (1993) and ISTA (1993) recommend testing oriental arborvitae on the top of moist paper media at a constant 20 °C for 21 days; no pretreatments are prescribed. Germination is epigeal.

Nursery practice. Sowing outdoor nursery beds should take place in the spring at a depth of 6 to 9 mm ($^1/_4$ to $^3/_8$ in) and no mulch. A bed density of 375 to 430/m^2 (35 to 40/ft^2) has been recommended (Schopmeyer 1974). Under most conditions, seedlings are grown for 2 years before outplanting, although this may vary according to individual nursery practices. Container production in greenhouses is also possible, using techniques that are successful with the closely related *Thuja* species.

Vegetative reproduction, while more difficult than it is with *Thuja* species, is possible with oriental arborvitae and is widely used for ornamental cultivars. Dirr and Heuser (1987) recommend taking cuttings from June to August, treating with indole-butyric acid (IBA) in talc and Benlate®, then rooting with mist and bottom heat in a peat and perlite mixture (2:1, v/v).

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Salicaceae—Willow family

Populus L.

poplar, cottonwood, aspen

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Growth habit, occurrence, and use. The Salicaceae, the family that includes poplars, cottonwoods, and aspens (*Populus* spp.) and willows (*Salix* spp.), is the most widespread group of woody plants in North America. The poplar genus—*Populus*—is subdivided into 5 sections (Aigeros, Leucoides, Leuce, Tacamahaca, and Turanga) and comprises 30 species, under the common names of poplar, cottonwood, and aspen. The taxonomy of the genus is complex because natural variation and hybridization are common among some sympatric species. In addition, species have been introduced from Europe, and both planned and natural hybrids have been produced for use in forestry and horticulture (Barnes 1961; Brayshaw 1966; Ceulemans 1990; Dickmann and Stuart 1983; Eckenwalder 1977, 1980; Einspahr and Benson 1964; Little and others 1957; Pregitzer and Barnes 1980; Rehder 1940; Schreiner and Stout 1934; Spies and Barnes 1982; Stettler and others 1996; Viereck and Foote 1970). The nomenclature and occurrence of the North American species and some of the exotic species and cultivars are presented in table 1. A thorough coverage of the nomenclature, distribution, genetics, evolution, hybridization, biology, and ecology of the genus can be found in Burns and Honkala (1990), Ceulemans (1990), Dickmann and Stuart (1983), Dickmann and others (2001), Einspahr and Winton (1977), FAO (1980), Hyun and others (1984), Schreiner (1971), Smith (1943), Stettler and others (1996), and Stout and Schreiner (1933).

The genus is wide ranging in North America (Burns and Honkala 1990). There are some unique aspects to the distribution of the poplar genus. Balsam poplar has the northernmost (and westernmost) range of any tree in North America, as it grows in the foothills transition from the Brooks Range to the Arctic coastal plain in northern Alaska and in the Mackenzie River delta in the Yukon (Viereck and Little 1972). These northernmost stands are associated with riparian areas. The distribution of poplar species within their natural ranges varies considerably. Quaking aspen, which has the most widespread range of any North American tree species, can form large monospecific stands of 40 to 50 ha consisting of only one clone. In fact, an aspen clone in Colorado is reputed to be the largest living organism known (Mitton and Grant 1996). Quaking aspen clones in the Great Lakes region, Alaska, and adjacent Canadian provinces, however, are generally small, seldom greater than .03 to 1.5 ha (Barnes 1966, 1969; Kemperman 1976; Kemperman and Barnes 1976; Parkerson 1977; Steneker 1973). Aspen in pure and mixed stands covers thousands of hectares in north temperate and boreal forests. Although some poplar species may have fairly large geographic ranges, they are restricted in occurrence and often exhibit their best development in (or are restricted to) riparian areas. Plains cottonwood, for example, occurs primarily in riparian areas in the Great Plains and occupies little of the dry upland area (Burns and Honkala 1990; Friedman and others 1997; Rood and others 1995; Stromberg 1993).

Species of the poplar genus occur mainly in early successional plant communities. They can quickly colonize after natural or human disturbances and grow rapidly where light, exposed mineral soil, and moisture are readily available. Depending on the species and site, they are usually replaced by more shade-tolerant species in 60 to 100 years. However, stands of some species have remained intact for more than 200 years in boreal forest environments in the Rocky Mountains. In areas with fire return intervals of 50 to 100 years, single clones of a species like aspen may persist for many centuries or, as some theorize, thousands of years (Barnes 1966; Burns and Honkala 1990; Mitton and Grant 1996). Although poplars are often viewed as being replaced by more tolerant trees, stands in the western Great Plains are replaced by grassland communities if they are not disturbed by periodic flooding (Friedman and others 1997).

Utilization and value of the genus can be considered in relation to their use in intensive culture and agroforestry plantations and in naturally occurring forests. Natural stands

Table 1—*Populus,* poplar, cottonwood, aspen: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. x acuminata* Rydb. (pro sp.)** *P. accuminata* var. *rehderi* (Sarg.)	**lanceleaf cottonwood,** lanceleaf poplar, smooth-bark cottonwood, & Andrews poplar	S Alberta, Montana, W North Dakota, Wyoming, W Nebraska, E Colorado, & New Mexico
***P. alba* L.**	**white poplar**, abele	Central & S Europe to W Siberia & Central Asia
***P. angustifolia* James**	**narrowleaf cottonwood,** narrowleaf poplar, black cottonwood, mountain cottonwood, *álamo*	S Saskatchewan & Alberta S to Arizona, W Nebraska, & trans-Pecos Texas; also in N Mexico (Chihuahua)
***P. balsamifera* L.**	**balsam poplar,** tacamahac poplar, cottonwood, hackmatack, tacamahac	Alaska to Labrador, S to New York & Oregon
***P. balsamifera* L. spp. *trichocarpa* (Torr. & Gray ex Hook.) Brayshaw** *P. trichocarpa* Torr. & Gray	**black cottonwood**, California poplar, cottonwood, balsam cottonwood, western balsam poplar	S Alaska & S Yukon to S California & W Nevada; local in Wyoming, SW North Dakota, & Lower California
***P.* x *canescens* (Ait.) Sm. (pro sp.)**	**gray poplar**	Europe & W Asia
***P. deltoides* Bartr. ex Marsh.**	**eastern cottonwood**, eastern poplar	Quebec to North Dakota, S to Texas & Florida
***P. deltoides* Bartr. ex Marsh. ssp. *monilifera* (Ait.)** *P. deltoides* var. *occidentalis* Ryb.	**plains cottonwood,** plains poplar, cottonwood, Texas cottonwood	SW Utah, Nevada, to N California, S to Arizona & New Mexico, NW Mexico
***P. deltoides* Bartr. ex Marsh. ssp. *wislizeni* S. Wats.** *P. fremontii* var. *wislizeni* S. Wats.	**Rio Grande cottonwood**, Rio Grande poplar, cottonwood, valley cottonwood, Wislizenus cottonwood, álamo	S Colorado, S Utah, New Mexico, W Texas, & N Mexico
***P. euphratica* Olivier**	**Euphrates poplar**, bahan, Gharab-Palk-Saf-Saf	Spain & W Morocco to Kenya, E to Central Asia
***P. fremontii* S. Wats.**	**Fremont cottonwood**, Fremont poplar, cottonwood, Arizona cottonwood, Macdougal cottonwood, *álamo*	SW Utah, Nevada, to N California, S to Arizona & New Mexico, NW Mexico
***P. grandidentata* Michx.**	**bigtooth aspen**, largetooth aspen, aspen, poplar, popple	Nova Scotia to NE North Dakota, S to Iowa & Pennsylvania, & along Appalachian Mtns to North Carolina
***P. heterophylla* L.**	**swamp cottonwood,** swamp poplar, cottonwood, black cottonwood, river cottonwood, downy poplar	Coastal plain from Connecticut & SE New York to Georgia & NW Florida, W to Louisiana, N in Mississippi Valley to Indiana, Ohio, & S Michigan
***P. laurifolia* Lebed.**	**laurel poplar**	Siberia
***P. maximowiczii* A. Henry**	**Japanese poplar**	NE Asia & Japan
***P. nigra* L.**	**black poplar**, European black poplar	Europe & W Asia
***P.* x *petrowskiana* R.I. Schrod. ex Regel**	**Petrowsky poplar,** Russian poplar	Europe
***P. sieboldii* Miq.**	**Siebold aspen,** Japanese aspen	Japan
***P. simonii* Carriere**	**Simon poplar**	NW China to Korea
***P. tremula* L.**	**European aspen**, tremble, Zitterpappel	Europe, North Africa, & NE Asia
***P. tremuloides* Michx.**	**quaking aspen**, quaking asp, aspen, golden aspen, mountain aspen, trembling aspen, Vancouver aspen poplar, popple, *alamo blanco*	Labrador to Alaska, S to Pennsylvania, Missouri, N Mexico, & Lower California

Source: Schreiner (1974).

of aspen, in particular, but other species too, are the basis for the pulp and paper industry in the north central United States and western Canada (Einspahr and Wyckoff 1990). Their ability to rapidly reoccupy a site by root suckering following harvest makes management of the species relatively easy. There is essentially no regeneration cost provided that care is taken to protect the root system of the harvested stand. Poplars have provided lumber for various uses and are important in the manufacture of reconstituted board products. Throughout human association with these species, virtually every part of the tree has been used for purposes that range from medicines to livestock feed to providing bark for carving art objects. Pure and mixed forests are important wildlife habitat. In the Great Plains areas of the

western United States and Canada, where they are the only tree cover, cottonwoods provide critical habitat for some species (Friedman and others 1997; Rood and others 1995; Stromberg 1993). They provide bark and male flowerbuds for specialist species such as beaver (*Castor canadensis*) and ruffed grouse (*Bonasa umbellus*) as well as forage for generalist browsers such as moose (*Alcea alcea*), elk (*Cervus elaphus*), and deer (*Odocoileus* spp.) (Burns and Honkala 1990; Dickmann and Stuart 1983; Dickmann and others 2001; Graham and others 1963; MacKinnon and others 1992; Peterson and Peterson 1995; Viereck 1987).

Poplars have long been important as ornamentals and in horticulture (tables 1 and 2). They were commonly used for amenity plantings in urban areas as ornamentals and landscaping. In rural areas, they have been used in shelterbelts and as ornamentals. The most rapidly increasing use of the species today is in intensive culture for wood fiber and biomass for energy in such diverse climates as the lower Mississippi Valley, western and eastern Washington, and western Minnesota. Shortages of fiber due to regulation of harvesting to protect critical wildlife habitat and old-growth forests, declining traditional forest land base, and concerns about effects of carbon dioxide (CO_2) from combustion of fossil fuels have renewed interest in intensive culture.

Poplars are ideal for short-rotation, intensive-culture management systems because (a) species and hybrids can be produced easily and propagated vegetatively, (b) juvenile growth is rapid, (c) response to cultural treatments is rapid, and (d) coppicing following harvest is prolific (Mitchell and others 1992; Stettler and others 1996). Poplar species are also readily propagated from tissue culture (Ostry and Ward 1991). Indeed, the first tree derived from tissue culture with both a shoot and attached root was a quaking aspen clone (Winton 1968a). Tree growth models are available for examining and predicting growth of poplar clones under different cultural regimes (Isebrands and others 1990; Stettler and others 1996).

In addition to classic tree breeding, advances have occurred due to the development of new genotypes using molecular genetics techniques (FAO 1980; Mitchell and others 1992; Stettler and others 1996).

Despite the large geographic range of the Salicaceae and the huge variation in growth form, there is remarkable uniformity in many aspects of the seed biology, dispersal, and germination. Thus information for willows, *Salix* spp. (Zasada and others 2005)—particularly those dispersing seeds during the summer—is relevant to poplar, *Populus* spp.

Table 2—*Populus,* poplar, cottonwood, aspen: height at maturity, first cultivation, minimum seed-bearing age, and seed crop frequency

Species	Height at maturity* (m)	Year first cultivated†	Minimum seed-bearing age (yr)	Years between large seedcrops
P. x acuminata	10.7–15.4 (18.5)	1898	5–10	1
P. alba	15.4–42.1	LC	10–15	—
P. angustifolia	10.7–15.4 (18.5)	1893	—	1
P. balsamifera	18.5–36.3	Before 1689	8–10	—
P. balsamifera spp. *trichocarpa*	15.4–61.5	1892	10	1
P. x canescens	29.2–30.8 (40)	LC	8–15	—
P. deltoides	24.6–58.5	Before 1750	10	1
spp. *monilifera*	12.3–30.8	1908	10	1
spp. *wislizeni*	2.3–30.8 (40)	1894	5	1
P. fremontii	15.4–30.8	1904	5–10	1
P. grandidentata	9.2–27.7 (30.8)	1772	10–20	4–5
P. heterophylla	24.6–27.3 (30.8)	1656	10	1
P. laurifolia	to 15.4	1830	8–10	—
P. maximowiczii	to 30.2	Before 1890	10	1
P. nigra	18.5–30.8	LC	8–12	1
P. simonii	to 12.3+	1862	10	—
P. tremula	21.5–38.5	LC	8–10	4.5
P. tremuloides	15.4–27.7 (30.8)	1812	10–20	4–5

Source: Schreiner (1974).

* Figures in parentheses indicate occasional heights on favorable sites.

† LC=long cultivated.

Flowering and fruiting. Poplars are mostly dioecious (Rehder 1940); but *P. lasiocarpa* Oliver (from China) has been described as a monoecious, self-fertilizing species (FAO 1980). Deviations from strict dioecism have been found in individual trees and catkins (Einspahr 1960a; Lester 1961, 1963; Maini and Coupland 1964; Pauley 1950; Pauley and Mennel 1957; Santamour 1956; Stettler 1971; Spies 1978). In addition, Santamour (1956), Pauley and Mennel (1957), and Lester (1963) reported that quaking aspen had bisexual frequencies of 7, 8.7 and 38%, respectively, and that hermaphroditism was higher among females (10.7, 20.6, and 32.3%) than among males (5.1, 4, and 27.4%). Stettler (1971) reported variation in sex expression among females of black cottonwood but not among males. Year-to-year variation in the frequency of abnormal flowers among individual trees was also reported.

Sex ratios in natural populations are not well-documented in the genus but appear to be male-dominated or equal, at least for quaking aspen (Einspahr 1960b; Einspahr and Benson 1971; Farmer 1964b; Grant and Mitton 1979; Lester 1963; Mitton and Grant 1996 ;Valentine 1975). Grant and Mitton (1979) and Comtois and others (1986) reported that sex ratios in quaking aspen and balsam poplar, respectively, were 1:1 on a regional or landscape basis, but the sexes seemed to be segregated to some extent within the regions studied. Grant and Mitton (1979) found that male quaking aspen trees were more common at higher elevations than females and that male balsam poplar trees tended to be more common on relatively drier and less fertile sites (Comtois and others 1986). Sex ratio reports have been criticized because of the biased sampling technique used in many of the studies. Generally, only flowering trees were sampled. Einspahr (1960b) attempted to eliminate this bias by girdling non-flowering trees within the sample population and returning to record sex the following year. Einspahr and Benson (1971) and Valentine (1975) also recorded the sex of individual trees within test plantings of quaking aspen over a period of years and thus observed flowering over enough years to determine the sex of all individuals in a population.

Aspen ramet growth rate and density, clone size, and rate of clone expansion appear to differ among male and female clones, with female clones surpassing males in the characteristics studied (Mitton and Grant 1996). Farmer (1964b) did not find differences among male and female trees in eastern cottonwood.

Age of first flowering shows considerable inter- and intraspecific variation (table 2). Cottonwoods and balsam poplars generally reach flowering age at 10 to 15 years. Usually, few seeds can be collected from plains and eastern cottonwood trees that are less than 10 inches in diameter or less than 10 years old (Maisenhelder 1951). Precocious flowering of seedlings a few months after germination has been observed in the poplar genus, but it is difficult to keep young seedlings alive to produce mature seeds (Riemenschneider 1996). Genetically engineered aspen that flower within months after germination have been developed (Weigel and Nilsson 1995).

Flowering and seed maturation differ within and among individual species (table 3). For example, aspen in the north temperate and boreal forests flowers in April or early May and seeds begin to disperse 4 to 6 weeks after flowering and finish in a few weeks. Winton (1968b) examined quaking aspen and eastern cottonwood fertilization under greenhouse and growth chamber conditions. Quaking aspen pollen germinated 6.5 hours after pollination and fertilization occurred after 8 to 72 hours, depending upon temperature. At 25 °C, aspen seeds mature in about 2 weeks in a controlled environment (Fechner 1972) and in 3 to 4 weeks in an environment with more variable temperatures (Brown 1989; Wyckoff 1975). By contrast, cottonwood in the lower Mississippi Valley flowers from March to early April; maximum dispersal of seeds occurs 8 to 10 weeks after flowering, with some dispersal occurring after 16 weeks (Farmer 1964a, 1966). In a controlled environment, viable cottonwood seeds are obtained in May to June following pollination in late February to early March (Farmer and Nance 1968). Cottonwood fertilization occurred between 24 to 72 hours after pollination.

Within these general flowering and dispersal patterns, there is significant variation among trees in local populations for most of the species studied. There are also observations of very early flowering and seed dispersal that are well outside the general ranges (table 3) attesting to the temperature controls over flowering. For example, Shafroth (1996) observed flowering in Fremont cottonwood in January and seed dispersal by mid-late February. Quaking aspen flowers have broken bud during warm spells in mid-February in interior Alaska; subsequent temperatures of –30 to –40 °C arrested development, but it resumed with the onset of higher temperatures in April (Barnes 1961; Farmer 1966; Pregitzer and Barnes 1980; Spies and Barnes 1982). Flowering in hybrids may be intermediate between or similar to one of the parents (Pregitzer and Barnes 1980; Spies and Barnes 1982).

Interspecific crossing between desired species or intraspecific crossing of selected individuals of the same species in a controlled environment is a common practice in breeding poplars. The general steps in this process are sum-

Table 3—*Populus*, poplar, cottonwood, aspen: phenology of flowering and fruiting

Species	Location	Flowering	Seed ripening & dispersal
P. x *acuminata*	Nebraska	May	July
P. alba	Nebraska	Apr–May	Early June
	NE US	Apr–May	May–June
	S Michigan	Mar–Apr	May–June
P. balsamifera	Alberta	Late Apr	Early June–early July
	Lake States	Apr–May	May–June
	Interior Alaska	May–June	July
P. balsamifera spp. *trichocarpa*	Vancouver Island, British Columbia	Apr–June	Late May–mid-July
P. x *canescens*	Great Lakes region	Late Apr	Late May
P. deltoides	Lower Mississippi Valley	Early Mar–early Apr	Mid-May–late Aug
	NE US	Apr–early May	May–mid-June
spp. monilifera	Alberta	—	late June–early Aug
	Lincoln, Nebraska	Apr–May	June
spp. *wislizeni*	Albuquerque, New Mexico	Apr–May	June–July
P. fremontii	Central Arizona	mid-Feb–mid-Mar	Mar–Apr
P. grandidentata	Syracuse, New York	Mid-Mar–mid-Apr	Mid-May–late May
	S Michigan	Late Mar–min-May	early May–late June
	New England	Mid-Mar–Apr	May–early June
	N Great Lakes region	Late Apr–early May	Late May–early June
P. heterophylla	Mississippi	Mar–May	Apr–July
P. maximowiczii	Rochester, New York	Late Apr	Aug
P. nigra	Rochester. New York	Apr	Late May
P. tremula	N Great Lakes region	Mid-Apr	Mid-May
P. tremuloides	Great Lakes region	Late Mar–early May	Mid-May–mid-June
	Alberta, Canada	Early Apr–early May	Mid-May–mid-June
	New England	Mid-Mar–Apr	May–early June
	Interior Alaska	Apr–May	Late May–early June
P. tremula	N Great Lakes region	Mid-Apr	Mid-May

Sources: Johnson (1990); Schreiner (1974).

marized below, but for more detail refer to Einspahr and Benson (1964), Farmer and Nance (1968), Gladysz (1983), Johnson (1945), Larsson (1975), Stanton and Villar (1996), Stettler and others (1980, 1996), Wettstein (1933), and Wyckoff (1975).

- Branches with flower buds are collected from male clones in late winter after cold requirements for dormancy have been satisfied. The branches are incubated in a controlled environment in water-filled containers. (Water should be changed 2 to 3 times per week. Before branches are placed in water and each time the water is changed, their ends should be recut. This removes 1 to 2 cm of wood and exposes fresh xylem to maintain water uptake.) Pollen is usually produced in 1 to 2 weeks, depending on species and temperature conditions. Pollen can be collected and stored in a desiccator for 1 to 2 months at about 0 to 1 °C and low humidity. For longer storage, the pollen should be kept under vacuum at –20 °C according to the procedure described by Hermann (1969).
- Branches or grafted material from female clones are brought into a controlled environment after cold requirements have been satisfied. This is usually timed to be several days after male branches are collected or after pollen has been extracted. The best length for cut branches is about 1 m. The cut stems are treated as described above for male branches. Alternatively, grafted or rooted cuttings have been recommended for species with large catkins or with longer flowering and seed maturation periods such as occur in eastern cottonwood.
- As the female flowers begin to elongate, pollen is applied with a brush or atomizer. Pollen is sometimes applied to flowers over several days to ensure good pollination and seed yield. Small quantities of viable, select pollen are often mixed with heat-killed pollen to extend the amount available. To make crosses between individuals with poor compatibility, irradiated or otherwise sterile pollen (mentor pollen) from a compatible source is mixed with the desired viable pollen (Stettler and Guries 1976). It may be necessary to remove a sig-

nificant number of flowers from the branches in order to ensure enough water, nutrition, and carbohydrate for full development of a limited number of catkins. Cooler greenhouse temperatures (15 to 21 °C) are better than warmer temperatures. Seeds are collected as the ripened capsules open. *In vitro* embryo culture has also been used in hybrid breeding programs where seed yield is low or non-existant.

An individual eastern cottonwood tree, measured to be 12.3 m in height with a stem diameter of 0.6 m and a crown spread of 13.8 m, bore about 32,400 catkins. These produced about 27 capsules per catkin and about 32 seeds per capsule. The average weight of 100 seeds (with cotton) was 0.065 g. On this basis, it was estimated that this tree produced nearly 28 million seeds, weighing about 18.2 kg (Bessey 1904). Aspen species also produce seeds in large quantities. Reim (1929) reported the following estimates of seed production for sample trees of European aspen in Estonia and Finland:

Age of tree (yr)	Catkins (no.)	Seeds (no.)
8	9	8,700
25	1,200	1,275,000
25	500	205,000
45	10,000	3,300,000
100	40,000	54,000,000

Although poplar seeds seem to be available each year, there have been few studies thoroughly documenting annual periodicity (Burns and Honkala 1990). Cottonwoods and balsam poplar (Figure 1) produce large seedcrops almost every year; aspens produce some seeds almost every year, and bumper crops are produced at intervals of 3 to 5 years. Six-year records for seed shedding by balsam and Petrowsky poplars in Alberta indicated an abundance of seeds in all years; aspen produced heavy seedcrops about 3 of every 7 years and comparatively little or no seeds in the other years (Moss 1938). During a 3-year period in interior Alaska, there was 1 excellent and 2 poor seedcrops (Zasada 1996).

Annual flowering records of 25- to 33-year-old quaking aspen clones (17 female and 16 male) established as grafts in a Wisconsin breeding arboretum indicated that the females flowered in 70% of the years of a 20- to 26-year period; males in 80% of the years and 2 bisexual clones in 78% of the years. (Note: these clones were randomly selected based on superior phenotypic characteristics, with no prior knowledge of tree gender. The male to female ratio for this collection covering a wide geographic area was basically 1:1 and substantiates studies cited above.) Individual female clones flowered in as few as 41% and as high as 100% of the years; individual male clones flowered in as few as 55% and as high as 100% of the years. Males tended to flower more frequently than females, with 38% of the male clones flowering in at least 95% of the years compared to 18% of the female clones flowering in at least 95% of the years. Eleven grafted clones established in the arboretum flowered 1 year after planting. Years when widespread flowering occurred in a Wisconsin arboretum appeared to be related to below normal rainfall in May of the previous years (Wyckoff 1996).

One clone of quaking aspen was established in the same year as both grafts and rooted root sprouts. The grafted ramets flowered in 70% of the years in a 23-year period; the rooted ramets flowered in 4% of the those years (Wyckoff 1996).

Figure 1—*Populus balsamifera*, balsam poplar: tree at peak stage of seed dispersal.

Flowering of 24- to 36-year-old grafted clones of bigtooth aspen (3 female and 7 male) was also followed in the above-mentioned Wisconsin arboretum. The female clones flowered in 35% of the years in a 20- to 25-year observation period and the males in 18% of the years. Flowering of individual female clones occurred in from 29 to 40% of the years; male clones flowered in 0 to 50% of the years (Wyckoff 1996).

Mature catkins are made up of many capsules, each developed from an individual flower (figures 1 and 2). The number of viable seeds per capsule has been reported to vary from 2 to 7 for quaking aspen (Brown 1989; Henry and Barnes 1977; Nagaraj 1952; Spies 1978); 2 to 10 for bigtooth aspen (Henry and Barnes 1977); 2 to 4 for bigtooth–quaking aspen hybrids (Henry and Barnes 1977); about 1 for white poplar (Spies 1978); 1 to 2 for white poplar hybrids with bigtooth aspen (Spies 1978); and 8 to 15 (Nagaraj 1952), 32 (Bessey 1904), and 40 to 60 for eastern cottonwood (Farmer and Nance 1968). Estimates of seed production per catkin for quaking aspen have varied considerably among studies and locations: 500 in central Alberta (Brown 1989), 77 in northern Wisconsin (Rudolph 1978) 280 to 290 in southern Michigan, (Henry and Barnes 1977; Spies 1978), and 150 to 300 in central Wisconsin (Einspahr and Benson 1964). Henry and Barnes (1977) reported 500 seeds per catkin for bigtooth aspen. Spies (1978) reported about 11 seeds per catkin for white poplar, 281 for quaking aspen, and 102 for the hybrid P. × *rouleauiana* Boivin.

Figure 2—*Populus*, poplar: catkins consisting of mature but unopened capsules.—*P.deltoides* ssp. *monilifera*, plains cottonwood (**top**); *P. fremontii*, freemont cottonwood (**middle**); *P. freemontii* ssp. *wislizeni*, Rio Grande cottonwood (**bottom**).

The distance traveled by poplar seeds during primary dispersal equals or exceeds that for any tree species in North America. If seeds should land in a river, the distance of

secondary dispersal can also be great. Aspen seed rain and seedling establishment have been observed in significant quantities at distances of 5 to 10 km from the nearest seed source (Dyrness and others 1988; Zasada 1996; Zasada and Densmore 1979). Large quantities of seeds are deposited in the parent stand too. The dispersal unit—seed plus hairs, also referred to as "cotton" and "coma" (Fechner 1972; Fechner and others 1981; Roe and McCain 1962)—is very buoyant and ideally suited for both vertical and horizontal long distance movement by wind and air turbulence. The hairs are an outgrowth of epidermal cells of the ovule and are attached to the seed near the radicle (Fechner 1972). The deployment of these hairs has been described by Lautenschlager (1984) and Lautenschlager and Lautenschlager (1994) for Willow and briefly summarized by Zasada and others (2005).

Estimating seed rain in the Salicaceae is more difficult than in other trees because of the small size and short life of seeds and the type of dispersal unit. Water-filled seed traps and germination seed traps have proved useful (Walker and others 1986; Zasada 1996; Zasada and Densmore 1979), as have traps that use sticky substances. Water is a particularly good medium in which to catch seeds because once the dispersal unit lands on water it remains and because Salicaceae seeds germinate in water, allowing an assessment of viability.

A seed consists of an embryo surrounded by a thin transparent seedcoat. Seeds are very small, measuring but a few millimeters in length and width (figures 3, 4, and 5). There may be a rudimentary endosperm, but it apparently contributes nothing to the vigor of seeds during germination (Simak 1980). Nagaraj (1952) reports that the endosperm is completely consumed by the developing embryo in both quaking aspen and eastern cottonwood. The dry seeds tend to be tan to straw-colored in some species and green in others. Seed weights can vary substantially within a species and among sympatric species. For example, quaking aspen seeds were reported to weigh 0.127 g/1,000 seeds (223,200/oz) (Spies 1978), 0.133 g/1,000 seeds (212,000/oz) (Benson 1972), and 0.035 g/1,000 seeds (818,000/oz) (Henry and Barnes 1977) and bigtooth aspen, 0.091 g/1,000 seeds (312,000/oz), 0.093 g/1,000 seeds (306,000/oz), and 0.021 g/1,000 seeds (1,350,000/oz), respectively, for seeds of the 2 species collected in different years. The seed size of hybrids may be intermediate or smaller than that of their parents (Henry and Barnes 1977; Spies 1978). Tables 4 and

Figure 3—*Populus balsamifera*, balsam poplar: catkins in different stages of capsule opening. Capsules on the catkin in the foreground are unopened whereas those on the catkin in the background, and on the same branch as catkin in foreground, are fully opened and their cotton is fully expanded. The small dark dots in the cotton mass are individual seeds.

Figure 4—*Populus*, poplar: cleaned seeds of quaking aspen, *P. tremuloides* (**left**); cottonwood, *P. deltoides* (**center**); and bigtooth aspen, *P. grandidentata* (**right**); units on the scale at right are millimeters.

5 provide seed weight information for several poplar species and their hybrids (Wyckoff and Harder 1996). These seed weights are in agreement with other published information (Schreiner 1974) and support the reports of intermediate seed weight of hybrids. Section Leuce poplars tend to have smaller and lighter weight seeds than do species of other sections.

Collection, extraction, and cleaning of seeds. Seeds can be safely collected when a small percentage of capsules begin to open (Brown 1989; Fung and Hamel 1993; Johnson 1946; Maisenhelder 1951; Moss 1938; Wyckoff 1975). For aspen, it has been suggested that catkins should be picked from the trees when the seeds are a light straw color; those collected before reaching this stage do not ripen completely, reducing the yield of viable seeds (Brown 1989; Faust 1936). Branches with attached, immature catkins can be collected, placed in water, and ripened in a greenhouse. Seeds are collected as open capsules.

Care must be taken in handling catkins after they have been removed from the tree. They should be transported in a container, for example a large paper bag, that allows some air circulation and from which water can evaporate; this is particularly true if the catkins are to be kept in the container for several days during transport. For rapid drying, catkins should be spread out in thin layers in pans or on screens at room temperatures as soon as possible. Seeds will be shed in 1 to 5 days, depending on the ripeness of the catkin. Eastern cottonwood seeds also have been extracted by putting the ripe catkins through a standard seed macerator with the cylinder teeth 1.3 cm ($^1/_2$ inch) apart and running the macerated catkins over a clipper fanning mill (Engstrom 1948).

If the catkins are permitted to mature on cut branches in water culture, the seeds can be collected with a shop vacuum cleaner using a clean cloth bag substituted for the dust bag (Harder 1970; Roe and McCain 1962). Seeds from detached catkins spread out to dry in a thin layer can also be collected with this machine.

The most efficient method for freeing poplar seeds from the cotton is by tumbling them in a rotating drum or stream of relatively high pressure air. For small quantities of seeds, separation can be done by placing the seeds with cotton in a container over a nest of soil sieves or between 2 soil sieves and applying a stream of air at high velocity to tumble the seeds in the container. The seeds fall through to the lower screen of smaller sieve openings (Einspahr and Schlafke 1957; Fung and Hamel 1993; Roe and McCain 1962). Compressed air from any source or air from a vacuum cleaner exhaust can be used. Screen mesh size (openings per inch) will depend on seed size (table 4); a larger-seeded

Table 4—*Populus,* poplar, cottonwood, aspen: seed weights by soil sieve size (20 to 50 mesh)*

Species	Seeds (millions)/weight							
	20-mesh		28-mesh		40-mesh		50-mesh	
	/g	/oz	/g	/oz	/g	/oz	/g	/oz
P. alba	5.09	2.31	8.89	4.03	19.71	8.94	—	—
P. balsamifera	—	—	7.90	3.58	8.69	3.94	—	—
spp. *trichocarpa*	2.71	1.23	4.54	2.06	—	—	—	—
P. x *canescens*	—	—	7.50	3.40	13.87	6.29	—	—
P. deltoides	2.93	1.33	4.92	2.23	—	—	—	—
P. grandidentata	—	—	—	—	21.52	9.76	39.58	17.95
P. tremula	—	—	—	—	17.46	7.92	—	—
P. tremuloides	—	—	13.19	5.98	18.46	8.37	23.62	10.70
Some hybrid crosses†								
P tremuloides x P. tremula	—	—	10.61	4.81	17.68	8.02	38.68	17.54
P. tremula x P. tremuloides	—	—	18.43	8.36	44.10	20.00	—	—
P. tremuloides x P. canescens	—	—	—	—	16.27	7.38	—	—
P. canescens x P. tremuloides	—	—	7.74	3.51	13.38	6.07	35.57	16.13
P. grandidentata x P. alba	—	—	—	—	23.09	10.47	47.83	21.69
P. alba x P. grandidentata	4.81	2.18	10.52	4.77	15.79	7.16	35.10	15.92
P. grandidentata x P. canescens	—	—	—	—	19.45	8.82	30.96	14.04
P. canescens x P. grandidentata	—	—	7.08	3.21	10.36	4.70	31.00	14.06
P. deltoides x P. balsamifera	4.34	1.97	5.18	2.35	—	—	—	—
P. deltoides x P. nigra	4.43	2.01	6.90	3.13	60.86	27.60	—	—
P. deltoides x P. trichocarpa	3.00	1.36	4.54	2.06	—	—	—	—
P. trichocarpax P. balsamifera	3.20	1.45	4.83	2.19	—	—	—	—

Source: Wyckoff (1999).

* Sieve=standard soil screen sieve openings per square inch.

† In hybrid crosses, the female parent is listed first.

species, for example cottonwood, requires larger mesh screens (Einspahr and Schlafke 1957). Nests of sieves recommended for aspen are 20-, 28-, 40-, and 50-mesh soil screens from top to bottom (Harder 1970). Seeds were collected on the 40- and 50-mesh screens, with the best seeds on the 28- and 40-mesh screens for aspen and 20- to 28 mesh screens for cottonwood (Fung and Hamel 1993; Harder 1970; Rudolph 1978). Larger quantities of seeds may be cleaned efficiently in a rotating drum with or without a fan to blow the seeds through the wire seed screen; the cotton will remain in the drum. Small quantities of seeds can be separated from the cotton by rubbing them over a wire soil screen with suitably small mesh, by hand, or with a heavy brush (Faust 1936; Maisenhelder 1951). However, only about 20% of the seedlot can be extracted by this method (Maisenhelder 1951). Simak (1980) stresses that dried seeds can be brittle and damaged with rough handling during the extraction process.

Debris can be partially removed from poplar seedlots by carefully applying low-pressure air to seeds placed in a 500-ml Erlenmeyer flask held at a 30 to 45% angle. A highly efficient technique used routinely by the University of

Figure 5—*Populus*, poplar: longitudinal section through the embryo of a seed.

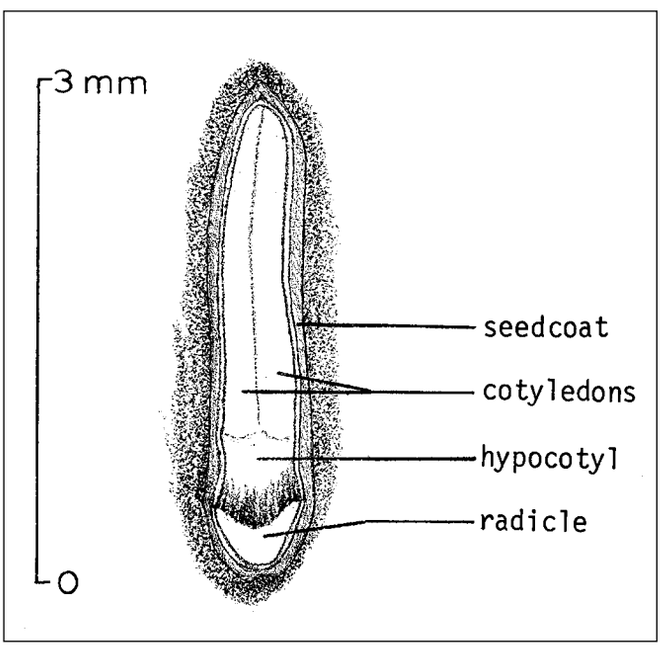


Table 5—*Populus*, poplar, cottonwood, aspen: seed weights of non-screened samples

Species	Seeds (x million)/weight				Samples
	Range		Average		
	/kg	/lb	kg	/lb	
P. deltoides	0.44–3.31	0.20–1.50	0.77	0.425	6+
P. deltoides spp. *monilifera*	0.55–1.06	0.25–0.48	—	—	4+
P. grandidentata	—	—	6.62	3.00	1
P. heterophylla	0.31–0.36	0.14–0.16	0.34	0.15	4
P. tremula	5.89–16.65	2.66–7.55	8.09	3.67	30
P. tremuloides	5.51–6.62	2.5–3.0	6.00	2.75	—

Source: adapted from Schreiner (1974).

Minnesota's Aspen and Larch Genetics Cooperative employs a vacuum seed sorter built after the one described by Edwards (1979). Seedlots cleaned by this technique are virtually free of contamination, an important consideration when seeds are to be sown mechanically in containers.

Storage of seeds. Under natural conditions, poplar seeds have been reported to maintain viability from 2 weeks to a month, varying with species, season, and microenvironment. There is some evidence that poplar seeds may have a longer lifespan under apparently adverse conditions such as in colder soils (Graham and others 1963; McDonough 1979; Moss 1938; Trappe 1964; Zasada and Densmore 1977).

Poplar seeds are one of the best examples of seeds with a short life-span (microbiotic seeds) among tree species. However, with proper drying and storage at subfreezing temperatures in sealed containers, the viability of seeds of eastern cottonwood (Tauer 1979, 1995; Wang 1982), and quaking and bigtooth aspen (Benson and Harder 1972, 1996; Wang 1982) have been maintained at fairly high levels for 10 to 12 years. Loss in viability during these relatively long storage periods varies among species and trees within species (Asakawa 1980; Benson and Harder unpublished data; Fechner and others 1981; Simak 1980; Tauer 1979, 1995; Wang 1982; Zasada and Densmore 1977, 1980). For example, Tauer (1995) found that percentage germination varied from 3 to 53% among individual trees after 12 years of storage, whereas initial germination ranged from 47 to 100%.

There is no single method of storage found to be generally acceptable for all species (Simak 1980). There are several elements that are important for maintaining long-term viability. Prestorage drying during capsule opening and immediately after extraction is essential for successful storage (Simak 1980). The desired moisture content for several species seems to lie between 6 and 10% (dry weight basis) (Simak 1980; Tauer 1979; Zasada and Densmore 1977, 1980), although Wang (1982) reported good long-term storage at 11 to 15% moisture content (dry-weight basis). Seed viability is maintained at lower moisture contents, but there is an indication that seedling vigor is reduced under these conditions (Simak 1980). Recommendations for drying time to achieve these approximate moisture contents have varied: for example, 2 to 3 days at 21 °C (Moss 1938); 3 to 8 days at 24 °C (Faust 1936); air-drying for 7 days (Tauer 1979); 1 day at 35 to 40 °C, and 1 day of drying over calcium chloride ($CaCl_2$) (Simak 1980). If achieving a specified moisture content is important, a method should be used that attains the desired content as quickly as possible while not affecting seed viability.

A number of research trials have compared storage under vacuum and with various desiccants to storage in sealed containers; unfortunately, the results are not definitive. In some cases, they work and in others they seem to be of no benefit or may even have a negative effect on viability.

Benson and Harder (1972) compared 4-year germination results from 40-mesh aspen and aspen hybrid seeds stored over calcium chloride in a desiccator at 4.4 °C and –24 °C. Freezer storage maintained higher levels of viability in each of the 4 years with the exception of 2 hybrids of bigtooth aspen during the first year. By year 4, all seedlots stored at 4.4 °C were either nonviable or had considerably reduced germination. Freezer-stored seeds maintained a high level of germinative ability at the end of 4 years, with the exception of gray poplar hybrids. Benson and Harder's study (1977, 1996) indicates that germination of freezer-stored seed of quaking aspen dropped from an average of 98% to 65% over a 10-year period. Hybrid seeds and 50-mesh seeds generally had lower germination than quaking aspen and 40-mesh seeds after 10 years of freezer storage. Seed viability of 3 of 4 open-pollinated cottonwood seedlots stored at –24 °C over calcium chloride did not decrease during 8 years of storage.

Hellum (1973) found that balsam poplar seedlots stored in sealed containers without desiccant at 7 °C and 21 to 24 °C rapidly lost viability after 130 days at both temperatures. Cold-stored seedlots retained viability longer (40 vs 5% at 200 days) but viability dropped to 5% at 245 days.

Simak (1980) reported that storage of European aspen seeds with a desiccant reduced viability because it dried seeds to a sub-optimal moisture content. Simak (1980) concluded that, when using desiccants, the desired moisture content of the seeds should be known and the type and quantity of desiccant should be selected to achieve the desired conditions. For example, seeds will equilibrate at the desired moisture content in an atmosphere of 10 to 30% relative humidity, and thus the desiccant should be selected that provides these conditions (Simak 1980). The optimum rate of drying is not known. Tauer (1979, 1995) reported that there was no difference in viability between cottonwood seeds stored with and without a vacuum at –22 °C after about 6 years. However, after 12 years, seeds from different families stored in a vacuum germinated at 10 to 99%, whereas those without vacuum germinated at 3 to 53%.

The one aspect of storage about which there seems to be no question is temperature conditions for long-term storage. Seeds should be extracted and placed in subfreezing storage as soon as possible. Seeds from boreal and Arctic species and those from warm climate species all seem to have the same general requirements. Temperatures from –5 to –24 °C seem acceptable and easy to achieve and maintain (Benson and Harder 1972; Fechner and others 1981; Moss 1938; Simak 1980; Tauer 1979; Wang 1982; Zasada and Densmore 1977, 1980). Seeds can be stored at 0 to 5 °C, but longevity is shorter and high levels of abnormal germination may occur sooner than at sub-freezing temperatures.

Germination tests. The criteria used to define germination are important when evaluating germination in the Salicaceae. The standards proposed by Simak (1980) for *Salix* and *Populus* germination provide a basis for assessing germination (figure 6). The work of Simak (1980) illustrates convincingly that use of criteria that do not include all of the stages leading up to appearance of a "normal" seedling may be suspect. Development of the hypocotyl hairs—or "coronet" as described by Fechner and others (1981)—and attachment of these hairs to the substrate is a departure from the usual pattern of epigeal germination (other species do not have these specialized hairs) and should be an assessment criteria for germination. The average time elapsed to achieve the various stages of development under greenhouse conditions are shown in figure 6; they will, however, vary depending on temperature and water availability (McDonough 1979; Schreiner 1974; Simak 1980).

Poplar seeds do not exhibit dormancy; they germinate at temperatures ranging from 2 to 40 °C (figure 7). Simak (1980) provides a thorough description of abnormal germination in Salicaceae. Average time required for aspen seeds to achieve various stages of germination under greenhouse conditions are indicated in hours and days (Wyckoff 1996). Optimum temperatures for germination may vary with species and possibly within widely distributed species like quaking aspen, but they appear to be in the range of 20 to 30 °C. Germination rate increases with temperature but appears to be fairly uniform above 15 to 20 °C and may decline slightly above 30 to 35 °C (figure 7). Temperatures above 35 °C caused a large decline in germination in aspen but had little effect on eastern cottonwood (Farmer and Bonner 1967; Faust 1936; Moss 1938; McDonough 1979; Zasada and Densmore 1980; Zasada and Viereck 1975). Seeds germinate fully in complete darkness, but rate of germination may be less than in light (Asakawa 1980; McDonough 1979).

Germination occurs on a wide variety of substrates. Some *Populus* species appear to have fairly exacting requirements for germination whereas others are less affected. Substrates with a steady supply of water during germination and early seedling development and a neutral or slightly acidic to slightly basic pH provide conditions for maximum germination (Dickmann and Stuart 1983; Farmer and Bonner 1967; Faust 1936; Fechner and others 1981; McDonough 1979; Segelquist and others 1993). Seeds germinate while floating in water or when fully submerged (Hosner 1957; Krasny and others 1988). Substrates with high salt concentrations appear to reduce germination potential (Faust 1936; Krasny and others 1988; McDonough 1979; Shafroth and others 1995).

At the University of Minnesota's Aspen and Larch Genetics Cooperative, seeds are germinated on damp filter paper in petri dishes for viability checks. However, for estimates of germination and vigor of seedlots to be used in nursery beds and containers, seeds are sown in clay saucers filled with commercial soil-less mix. This technique is more important for seedlots with germination less than 70 to 80% because it gives a more accurate prediction of cell occupancy in containers and seedlings per area in seedbeds (Wyckoff 1996).

Aspects of germination outlined above apply to newly collected seeds. Results may vary for the following reasons:

- Seeds stored for varying lengths of time may germinate slowly and exhibit poorer germination than would be

Figure 6—*Populus*, poplar: stages in the normal germination of a seed (adapted from Simak (1980) and McDonough (1979).

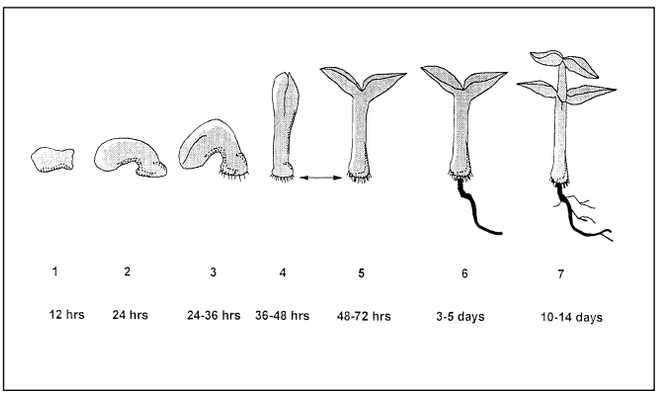
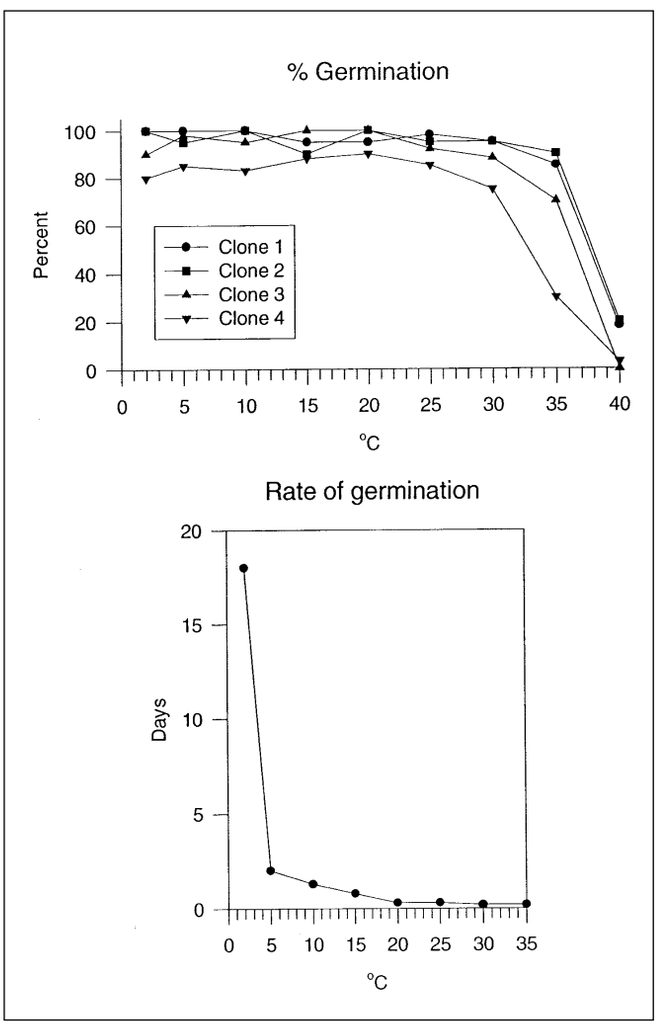


Figure 7—*Populus tremuloides*, quaking aspen: effects of temperature on percentage germination and germination rate in seeds (from McDonough 1979); rate is expressed as time for 10% of seeds to germinate.



expected for fresh seeds; this may be particularly true when germinating outside the optimum temperature range (Farmer and Bonner 1967; McDonough 1979).

- Small seeds may not germinate as well as large seeds. For example, Faust (1936) found that seeds graded to a 40-mesh soil screen showed a germination percentage of less than half that of seeds graded to a 30-mesh soil screen. The same relation holds true for seeds from 40- and 50-mesh soil screens (Rudolph 1978).
- Germination of stored seeds of white poplar was reduced due to too rapid imbibition of water (Polya 1961).

Seed testing rules (ISTA 1993) recommend that germination tests consist of four 100-seed replications and that tests be conducted at temperatures between 20 and 30 °C, with initial counts after 3 days. The results of the research summarized above suggest that using temperatures of 20 to 25 °C might be best for all seeds, including those tested following storage. Because of the rapid rate of germination and germinant development, there will be instances where evaluation would be desirable after 1 or 2 days, particularly when comparing germination rates of stored vs. newly collected seeds. Earlier versions of seed testing rules (ISTA 1966) called for using 0.25 g of seeds per replicate. Because of the small size of poplar seeds (table 4), this is an unmanageable number of seeds for most species.

Nursery practice. Poplar, aspen, and cottonwood seedlings can be produced in containers or as bareroot stock. High-quality seedlings can be grown under either system or a combination of the two (for example, plug+1 stock). The choice of a seedling production system will be determined by climate, economics, the method/system of planting, available facilities and equipment, and the type of seedling (diameter and root system characteristics) that will best meet management objectives. Containerized production seems to be more common, particularly in northern areas where greenhouse production can provide a longer and warmer growing season.

Early nursery techniques for direct-sowing cottonwood seeds into seedbeds have been described by Bull and Muntz (1943), Einspahr (1959), Engstrom (1948), Gammage and Maisenhelder (1962), Maisenhelder (1951), Peterson and Peterson (1992), Schreiner (1974), and Wycoff (1960). Currently, both bareroot and container-grown aspen and aspen hybrid seedlings are being produced on a commercial scale. Bareroot seedlings are grown by direct-sowing cleaned seedlots onto seedbeds that are formed with sideboards and watered prior to sowing. Seeds are sown at a

density of 265 viable seeds/m² (25/ft²) to produce 42 to 63 plantable seedlings/m² (4 to 6/ft²) at lifting. The beds are lightly watering again after sowing, then covered with 1.3-cm ($^1/_2$-in) mesh hardware cloth and 50% shadecloth (Wyckoff 1996). Sowing is often done by hand: enough seeds to cover a given area of bed space are weighed out and sprinkled from vials with small holes drilled in the caps. Mechanical sowing is used where seeders capable of handling such small seeds are available.

Seedbeds are watered from an overhead irrigation system as needed during the first 3 weeks to maintain a moist surface without runoff or standing water; the seedbed covers are left in place during irrigation. The shadecloth is removed at 3 weeks, having served primarily to reduce surface drying and allowing irrigation without removal of seedbed covers. The hardware cloth is left in place until seedlings begin to reach it, for it can serve as protection against hail. Seedlings are lifted in the fall after leaf drop, then graded and placed in polyethylene lined boxes for storage at –2 to –4 °C. Packing material such as sphagnum moss, shredded wet newsprint, and hydromulch have been used to keep roots from desiccating during storage. The same technique has also been used successfully with cottonwood, balsam poplar, and poplar hybrids (Wyckoff 1996).

Containers of different sizes and shapes have been used to produce aspen seedlings. However, plug-type containers with cavity volumes of 350 to 450 cm³ (21 to 27 in³) provide sufficient growing space to produce a large seedling with 5 to 7 mm (0.2 to 0.3 in) root collar diameters and 60 cm (2 ft) heights in 1 growing season (Burr 1985; Wyckoff and others 1995). The containers are typically sown by hand or with precision mechanical seeders, germinated in a greenhouse, then moved outside for the remainder of the growing season. Seedlings are planted in the same year that they are grown or stored for planting the following year. The time of planting will determine the sowing schedule, provided greenhouses can be heated (Carlson and Fung 1996).

A third technique, using both greenhouse and nursery beds to produce plug+1 bareroot aspen seedlings, combines the advantage of seed-use efficiency of greenhouse containers with the production of a high number of large-diameter seedlings from seedbeds (Wyckoff 1996). Typically, seeds are mechanically sown into horticulture bedding flats with cavity volumes of 15 to 25 cm³ (0.9 to 1.5 in³) and 1,280 cavities/m² (119/ft²). These are kept under greenhouse conditions for 8 to 9 weeks. At the end of this time, 8- to 10-cm (3- to 4-inch) tall seedlings are transplanted into seedbeds at densities of 43 to 54 seedlings/m² (4 to 5 seedlings/ft²) and grown for one season. On average, it requires 1.5 to 2 viable seeds to produce 1 container seedling with a minimum 5-mm (0.2-in) root collar diameter; 5 to 6 viable seeds to produce a bareroot seedling with a minimum 7-mm (0.3-in) root collar diameter; and 2.7 seeds to produce a plug+1 bareroot seedling with a minimum 7-mm (0.3-in) root collar diameter. Seedlings grown in the plug +1 regime attain heights of 1 m (3.2 ft) in a single growing season (Wyckoff 1996).

The following features are common to all growing systems:

- Sowing is most efficient when seeds are separated from the hair, which makes it easier to control seeding density and distribution in nursery beds and containers.
- It is necessary to determine seedlot viability prior to sowing; this is particularly important for seeds that have been stored for several or more years.
- Covering seeds with more than a few millimeters of soil may significantly reduce germination (Maisenhelder 1951; McDonough 1979; Richter 1936).
- Maintaining adequate water content of the seedbed surface is critical for germination and establishment. Application of a fine spray of water causes less flooding of the seedbed and less seed movement, resulting in more rapid seedling establishment and more efficient use of seeds.
- Shading may be beneficial during germination, but seedlings will grow most rapidly in full light (Burns and Honkala 1990).
- Use of a fungicide may be necessary because of the continuous high moisture levels during early development (Shea and Kuntz 1956). This may be more critical in greenhouse production where temperature and relative humidity are more conducive to development of damping-off fungi.

Seedling production is important in breeding and clone development, but once desirable clones have been identified for use in intensively managed biomass and energy plantations they are propagated exclusively by vegetative reproduction. For a discussion of various aspects of vegetative reproduction see Dickmann and Stuart (1983), FAO (1980), Stettler and others (1996), and Dickmann and others (2001).

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Fabaceae—Pea family

Prosopis L.

mesquite

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Growth habit, occurrence, and use. Mesquites—the genus *Prosopis*—are deciduous, thorny shrubs or small trees native to the tropical or subtropical regions of the Western Hemisphere, Africa, the Middle East, and India (Sargent 1965). Three native and 1 naturalized species are considered here (table 1); all are small trees, rarely exceeding heights of 15 m. Mesquite wood is an excellent source of fuel and charcoal and enjoys heavy local use for fenceposts, crossties, and furniture. Mesquite legumes make high-quality forage for livestock and wildlife, and the seeds were widely used by native American peoples in the Southwest (Davis and others 1975; Martin and Alexander 1974; Vines 1960). The crude protein contents of honey and velvet mesquite seeds are 31 and 24%, respectively (Becker and Grosjean 1980), and the legumes of honey mesquite are high in carbohydrates (Harden and Zolfaghari 1988). Mesquite flowers are a source of excellent honey, especially in Hawaii (Skolmen 1990). The tree is a hardy nitrogen-fixer and has been planted for erosion control in Hawaii, as well as for highway landscaping and mine spoil reclamation in the Southwest (Day and Ludeke 1980).

Flowering and fruiting. Mesquite's tiny, perfect flowers are greenish white or greenish yellow in color. They are 2 to 3 mm in diameter and are borne in spike-like axillary racemes some 3 to 10 cm long. Flowering of the mesquites occurs generally from late March to September in the Southwest (Sargent 1965; Vines 1960). In Hawaii, mesquite begins to flower at ages of 3 to 4, and although flowering can occur throughout the year, it is most frequent in January to March (Skolmen 1990). The fruit is an indehiscent legume (pod) that ripens from August to September (figure 1) (Martin and Alexander 1974). Ripe legumes are typically yellowish in color, although legumes of velvet mesquite may also be a mottled red and black at maturity (Ffolliott and Thames 1983). Legumes of mesquite, honey mesquite, and velvet mesquite are flat in shape and vary from 10 to 30 cm in length. Those of screwbean mesquite are coiled and may be as long as 70 cm. The flat, tan or brown seeds range from 1.5 to 7 mm in length (Ffolliott and Thames 1983; Sargent 1965) (figure 2).

Figure 1—*Prosopis juliflora*, mesquite: legume.

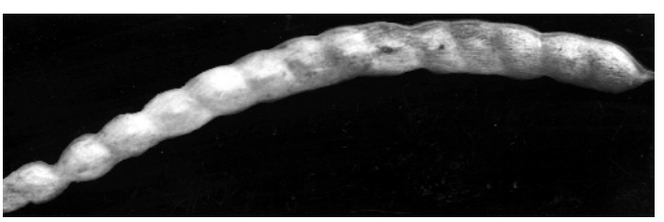
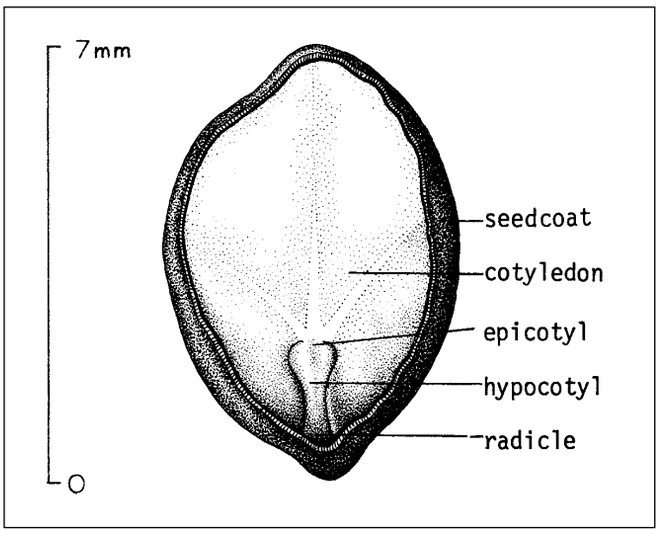


Table 1—*Prosopis*, mesquite: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. glandulosa* Torr.** *P. chilensis* var. *glandulosa* (Torr.) Standl. *P. juliflora* var. *glandulosa* (Torr.) Cockerell	**honey mesquite**	E Texas & Oklahoma to Utah, S California, & N Mexico
***P. juliflora* (Sw.) DC.**	**mesquite,** *kiawe* (Hawaii)	Mexico, S to Brazil & Peru
***P. pubescens* Benth.**	**screwbean mesquite,** screwbean, *tornillo*	Trans-Pecos Texas to Utah & S California
***P. velutina* Woot.** *P. juliflora* var. *velutina* (Woot.) Sarg.	**velvet mesquite,** mesquite	SW New Mexico, central Arizona, NW Mexico

Figure 2—*Prosopis juliflora*, mesquite: longitudinal section through a seed (**left**) and seeds (**right**).



Good seed production data are lacking, but there is a record from southern California of an average of 7.2 kg (16 lb) of fruits per tree from velvet mesquite (Felker and others 1984). In the same record, other yield averages were 2.2 kg/tree (5 lb) for honey mesquite, and less than 1 kg/tree (2 $^{1}/_{4}$ lb) for screwbean mesquite. There are numerous species of insects that feed on seeds of the mesquites; seed beetles (Bruchidae) are the most important group (Johnson 1983; Solbrig and Cantino 1975).

Collection, extraction, and storage. Ripe legumes may be stripped from trees by hand or picked up from the ground. Seed extraction and cleaning are not easy. One suggested method is to dry the legumes thoroughly (which may require oven-drying in humid climates) then running them through mechanical scarifiers or hammermills, and then screening out or blowing away the trash (Brown and Belcher 1979; Martin and Alexander 1974). Another method is to soak the legumes to soften them, then force the pulpy legumes and seeds through a sausage grinder with holes large enough for the seeds to pass. Hand grinders will suffice for small lots and commercial meat grinders have been successful for large lots (Skolmen 1990). Filled seeds may be separated from insect-damaged or immature seeds with aspirators or other blowers. If the seeds are dry, water flotation can also be used to separate good from damaged seeds. There are few seed yield and weight data for these 4 mesquite species: 1 kg of mesquite legumes may yield from 19,900 to 35,300 seeds (1 pound yields 9,025 to 16,000 seeds) (Goor and Barney 1968). Mesquite and honey mesquite average 8,000 to 30,000 seeds/kg (3,625 to 13,600/lb) (Glendening and Paulsen 1955; Von Carlowitz 1986), while as many as 38,300/kg (17,400/lb) have been reported for mesquite (Martin and Alexander 1974). Detailed studies of seed longevity are not available, but mesquite seeds, like those of most leguminous species, are orthodox in storage behavior. This means that seeds with low moisture contents may be stored at low temperatures for long periods without loss of viability. Air-dried seeds can be stored at ambient room temperature for at least 9 months with little loss in viability (Skolmen 1990). Martin (1948) reported that herbarium samples of velvet mesquite germinated after 44 years. Furthermore, mesquite seeds have been stored in liquid nitrogen (–196 °C) for 30 days without loss of viability (González-Benito and others 1994).

Pregermination treatments. Like most Fabaceae, mesquites have very hard seedcoats (that is, hardseededness) that require scarification as a pretreatment for timely germination. Small samples, such as those used in germination tests, can be scarified effectively by nicking each seed with a knife (Martin and Alexander 1974) or rubbing it on rough sandpaper, or by treating a small seedlot with a mechanical scarifier. For seedlots of any size, water soaks are often effective. For mesquite and honey mesquite, 48 hours in cold or tepid water or 1 hour in boiling water has been recommended (Von Carlowitz 1986). Seedcoat hardness may vary by year or seed source, however, and acid scarification may be required on some seedlots. For mesquite, 10 minutes in sulfuric acid increased the germination of a seedlot from 64 to 88% (Skolmen 1990). The safest procedure to use with hot water or acid treatments is to treat a few small samples to determine the best treatment period.

Germination. Some increases in germination capacity of mesquite seeds that resulted from scarification are shown in table 2. Germination of scarified seeds was complete 10 days after exposure to the test conditions. When velvet

Table 2—*Prosopis*, mesquite: germination test conditions and results

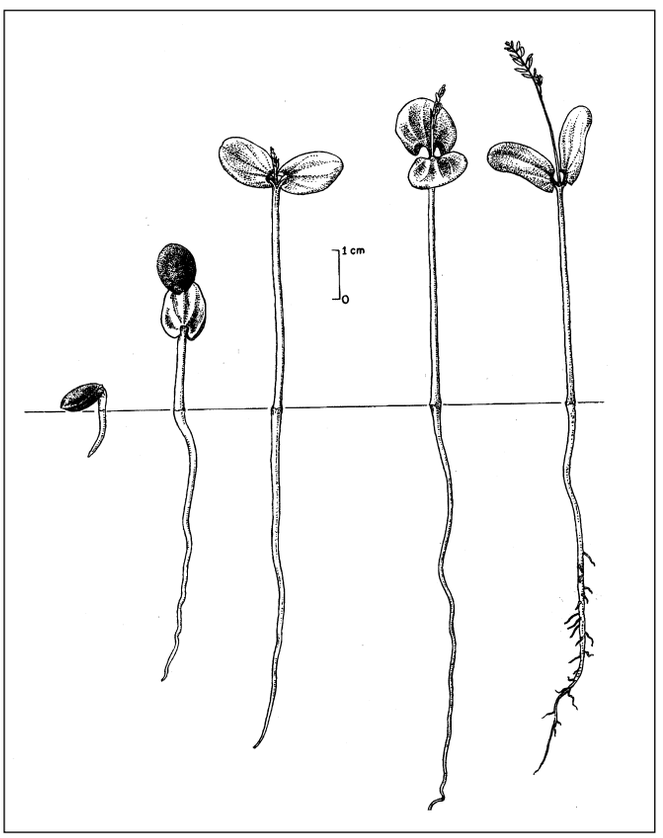
Seed age (yr)	Scarification treatment	Germination medium	Temp (°C) Day	Temp (°C) Night	Avg % germination
11	Nicking	Wet paper	27	27	98
50	Nicking	Wet paper	27	27	60
—	None	Wet paper	27	27	18
—	H_2SO_4	Wet sand	30	20	88

Source: Martin and Alexander (1974).

mesquite seeds were scarified with a knife, 94 to 100% of the seedlot germinated when kept at a constant 27 °C in the dark (Glendening and Paulsen 1955). Germination is epigeal (figure 3).

Nursery practices. There are few published guidelines for nursery practices, but growing mesquite seedlings should not be too difficult. Cox and others (1993) recommended a sowing depth of 1 to 2 cm ($^2/_5$ to $^4/_5$ in) for velvet mesquite. Greenwood cuttings from young plants of mesquite, honey mesquite, and velvet mesquite can be rooted in mist chambers (Felker and Clark 1981).

Figure 3—*Prosopis juliflora*, mesquite: seedling development at 1, 2, 5, 10, and 25 days after germination.



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Rosaceae—Rose family

Prunus L.

cherry, peach, and plum

Ted J. Grisez, Jill R. Barbour, and Robert P. Karrfalt

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Growth habit, occurrence, and use. The genus *Prunus*—often called the stone fruits—is one of the most important genera of woody plants. Its 5 well-marked subgenera include the plums and apricots *(Prunophora)*, the almonds and peaches *(Amygdalus)*, the umbellate cherries *(Cerasus)*, the deciduous racemose cherries (*Padus*), and the evergreen racemose or laurel cherries *(Laurocerasus)*. Plums can be distinguished from peaches and almonds by lack of a terminal bud, multiple flowers from a bud, and an elongated pedicel (Janick and Moore 1996). Plums can be distinguished from cherries by the lack of a terminal bud, the presence of a suture, a waxy bloom on the fruit, and a flatter pit.

Nearly 200 species—ranging from prostrate shrubs to trees over 30 m tall—are found in the Northern Temperate Zone, with a few in Central and South America (Harlow and Harrar 1958; LHBH 1978; Rehder 1940). By far the greatest number of species of cherries occur in eastern Asia (Hedrick 1915), but most of the long-cultivated food-producing species originated in Europe and western Asia (table 1). Over 100 species have been brought under cultivation, mostly as food crops or ornamentals (Rehder 1940), and 32 of the more important species for planting in the United States are described in table 1.

Many of the stone fruits have been cultivated since ancient times for their edible fruits and a few for edible seeds (almonds). Wild species have also been a source of food for Native Americans and early European settlers in this country and are still used to some extent. Many selections of wild plums have been propagated for fruit production. Several species are useful as ornamentals because of their showy flowers, variety of growth habits, relatively fast growth and ease of cultivation, and adaptability to a wide variety of soils and climates (Hedrick 1915; Olson and Nagle 1965; Rehder 1940; Strausbaugh and Core 1964).

Trees for fruit production and many ornamentals are propagated by budding or grafting, but seed production is necessary to grow the rootstocks and in breeding programs. The most important rootstock species and their scion combinations include almond rootstock for almonds and plums; apricot for apricots; mazzard cherry for sweet cherries; mahaleb cherry for sweet and sour cherries; peach for peaches, almonds, apricots, and plums; American plum for plums in cold climates; Bessey cherry for dwarf peaches; bullace plum (St. Julien types) for plums; myrobalan plum (mariana types) for almonds and plums; and myrobalan plum (myrobalan types) for plums (Cochran and others 1961; Sudworth 1908). Certain strains of peach, mahaleb cherry, and myrobalan plum are preferred for use as rootstocks because of their resistance to pests or for other qualities (Cochran and others 1961; Hedrick 1915).

Black cherry is the most important timber-producing species in the genus, but several others that attain sufficient size, such as mazzard cherry and mahaleb cherry in Europe and Japanese flowering cherry (*P. serrulata* Lindl.) in Japan, are used for wood products. Minor products include drugs, cordials, flavorings, honey, and perfume oil (Edlin 1967; Hedrick 1915). Probably all wild species are useful to wildlife as food. Birds and mammals eat the fruit, rodents eat the seeds, and deer (*Odocoileus* spp.) and beaver (*Castor canadensis*) use the leaves, twigs, and bark (Grisez 1974; Martin and others 1951; Van Dersal 1938). Several thicket-forming species of plums and cherries provide cover. Livestock feed on several species but others can be poisonous (Van Dersal 1938). Several species are used for erosion control and in shelterbelts (Engstrom and Stoeckeler 1941; Grisez 1974). In addition to those indicated in table 1, sour cherry, European bird cherry, and sloe are used for erosion control in Russia; and the same species plus mazzard cherry, apricot, myrobalan plum, garden plum, and pin cherry are used in shelterbelts (Al'benskii and Nikitin 1956; Koreisho and Morozov 1955).

Geographic races and cultivars. Very few racial differences affecting seed characteristics have been recognized.

Table 1—*Prunus,* cherry, peach, and plum: nomenclature, growth habit, and occurrence

Scientific name synonym(s)	Common name(s)	Growth habit	Occurrence
***P. alleghaniensis* Porter**	**Allegheny plum,** sloe, Allegheny sloe, Porter plum	Tree or shrub	Connecticut to Pennsylvania & S in mtns to Georgia; also in Michigan
***P. americana* Marsh.**	**American plum,** wild yellow plum, red plum, goose plum, hog plum	Tree or shrub	Massachusetts to Manitoba, New Mexico, central Texas & NW Florida
***P. angustifolia* Marsh.**	**Chickasaw plum,** sand plum	Tree or shrub	Missouri, S Nebraska to NW Texas & Louisiana; naturalized E to central Florida, New Jersey, & Illinois
***P. armeniaca* L.** *Armeniaca vulgaris* Lam.	**apricot**	Tree	W Asia; occasional escape from cultivation
***P. avium* (L.) L.** *P. cerasus avium* L. *Cerasus avium* Moench	**mazzard cherry,** sweet cherry, gean,* bird cherry*	Tree	Europe & W Asia; naturalized locally in SE Canada & E US
***P. caroliniana* (P. Mill.) Ait.**	**Carolina laurel cherry,** wild orange	Tree (evergreen)	North Carolina to Texas
***P. cerasifera* Ehrh.** *P. domestica* var. *myrobalan* L. *P. myrobalana* Loisel. *P. korolkowi* Vilm.	**myrobalan plum,*** cherry plum, marianna plum, flowering plum	Tree	W Asia; spread from cultivation from Washington to California, also in Michigan to Vermont, S to Ohio, New Jersey, & in Tennessee
***P. cerasus* L.** *Cerasus vulgaris* Mill.	**sour cherry,** pie cherry	Tree	W Asia & SE Europe; naturalized locally from Nova Scotia & Michigan to N Florida & W-ward
***P. domestica* L.** *P. damascena* Dierb. *P. communis* Huds.	**garden plum,** plum, European plum	Tree	W Asia & Europe; naturalized locally in SE Canada, NE US & Oregon
***P. domestica* var. *insititia* (L.) Fiori & Paoletti** *P. domestica insititia* Fiori & Paoletti	**bullace plum,** damson, damson plum	Tree or shrub	W Asia & Europe; naturalized locally from Nova Scotia & Maine to New York SW-ward
***P. dulcis* (P. Mill) D.A. Webber** *Prunus amygdalus* Batsch *Amygdalus dulcis* P. Mill. *P. communis* (L.) Arcang. *Amygdalus communis* L.	**almond**	Tree	W Asia & possibly North Africa; occasional escape from cultivation
***P. emarginata* (Dougl. ex Hook.) D. Dietr.** *P. mollis* Walpers *Cerasus prunifolia* Greene	**bitter cherry,** wild cherry, narrowleaf cherry	Shrub or tree	British Columbia to S California, Arizona, & Montana
***P. fasciculata* (Torr.) Gray**	**desert almond**	Shrub	California to Utah
***P. fremontii* S. Wats**	**desert apricot**	Shrub	S California
***P. gracilis* Engelm. & Gray**	**Oklahoma plum**	Shrub	Arkansas to Texas
***P. hortulana* Bailey**	**hortulan plum**	Tree	S Indiana to Iowa, Oklahoma, Arkansas, Alabama & W Tennessee
***P. ilicifolia* (Nutt. ex Hook & Arn.) D. Dietr.**	**hollyleaf cherry,** islay, evergreen cherry	Tree or shrub (evergreen)	Pacific Coast region, central to S California & in N Lower California, & Mexico

Differences in seed size, germination percentages, and other characteristics have been recognized, but these are likely to be treatment differences or simply random variations. For example, the moisture content of seeds (which is seldom reported) and tree-to-tree variation can have more effect than place of origin on numbers of seeds per weight (Grisez 1974). According to Hedrick (1915), "Cherries of any variety grown on poor soils or in uncongenial climates tend to have large stones and little flesh, while the pits are smaller and there is more flesh with the opposite extremes in environment." The weights of black cherry seeds increase with latitude (Pitcher 1984), ranging from 7 g in Florida to 14 g in northern Michigan. There is a significant negative correlation ($r = -0.35$) between seed size and germination in that smaller seeds have better germination (Pitcher 1984).

Table 1—*Prunus,* cherry, peach, and plum: nomenclature, growth habit, and occurrence (continued)

Scientific name synonym(s)	Common name(s)	Growth habit	Occurrence
***P. laurocerasus* L.**	**laurel cherry,** cherry-laurel	Tree (evergreen)	SE Europe, SW Asia
***P. mahaleb* L.** *Cerasus mahaleb* Mill.	**mahaleb cherry,** mahaleb, St. Lucie cherry, perfumed cherry	Tree	W Asia & Europe; naturalized locally in SW Canada & NE US
***P. maritima* Marsh.**	**beach plum**	Shrub	Maine to Delaware
***P. munsoniana* W. Wight & Hedrick**	**wildgoose plum,** Munson plum	Tree or shrub	Kansas, Kentucky, Texas & N Mississippi; naturalized E to S Ohio & Georgia
***P. padus* L.** *P. racemosa* Lam. *Padus racemosa* (Lam.) Schneid. *Cerasus padus* (L.) DC.	**European bird cherry,** mayday tree	Tree	Europe & N Asia to Korea & Japan; spread from cultivation in Canada & NE US
***P. pensylvanica* L. f.** *P. persicifolia* Desf. *P. montana* Marsh. *P. lanceolata* Willd.	**pin cherry,** fire cherry, wild red cherry, bird cherry	Tree or shrub	Newfoundland to British Columbia S to Colorado, South Dakota, Pennsylvania, & in mtns to Georgia
***P. persica* (L.) Batsch** *Amygdalus persica* L. *Persica vulgaris* Mill.	**peach,** common peach	Tree	China; naturalized locally, New England, S Ontario & Michigan to E Texas & Florida
***P. pumila* L.** *P. depressa* Pursh	**sand cherry**	Shrub	New Brunswick to Manitoba, Illinois, & New Jersey
***P. pumila* var. *besseyi* Bailey (Gleason)** *P. prunella* Daniels *P. pumila besseyi* (Bailey) Waugh. *P. susquehanae* Willd. *Cerasus canadensis* Mill.	**Bessey cherry,** western sand cherry, Rocky Mountain cherry	Shrub	Manitoba to Wyoming S to Kansas & Colorado
***P. serotina* Ehrh.** *P. virginiana* L. *Padus virginiana* (L.) Mill. *Padus serotina* Borkh.	**black cherry,** rum cherry, wild cherry wild black cherry,	Tree	Nova Scotia, S Ontario & Minnesota to E Nebraska, E Texas, & central Florida; also in Mexico & Guatemala
***P. spinosa* L.**	**sloe,** blackthorn	Shrub or tree	Europe, N Africa, & W Asia; naturalized locally in SE Canada & NE US
***P. subcordata* Benth.**	**Klamath plum,** Pacific plum, Sierra plum, western plum	Tree or shrub	W & S Oregon to central California
***P. tomentosa* Thunb.** *P. trichocarpa* Bge. *Cerasus tomentosa* Wall.	**Manchu cherry,** Nanking cherry downy cherry	Shrub	China, Japan, & Himalayas; central & N Great Plains
***P. umbellata* Ell.**	**hog plum**	Tree	North Carolina to Florida, Alabama, & Mississippi
***P. virginiana* L.** *P. nana* DuRoi *P. demissa* (Nutt.) D. Dietr. *Padus nana* (DuRoi) Borkh.	**common choke cherry**	Tree or shrub	Newfoundland to British Columbia, S to S California, New Mexico, Kansas, Illinois, Maryland, & S in mtns to Georgia

Sources: Grisez (1974), Wasson (2001).

* Names commonly used for the wild form.

There often are great differences among cultivars or groups within each of the domesticated fruit species, particularly in the percentage of viable seeds. In mazzard and sour cherries, the late-ripening cultivars, which require 80 days from flowering to fruit ripening, produce seedcrops with nearly 100% sound seeds. On the other hand, early cultivars, which require 60 days or less to ripen, produce almost no sound seeds. Those ripening in 60 to 75 days are intermediate (Tukey 1927). The final stage of fruit development is the rapid growth of the pericarp, and in early ripening cultivars of these species and peach, this stage begins before the embryo reaches full size (Tukey 1936). Garden plum also shows wide variation in germination capacity among cultivars tested under identical conditions (Suszka 1967). Immature embryos have been brought to a germinable stage by (1) growing excised embryos in artificial

culture, (2) storing whole fruit (Hesse and Kester 1955), and (3) not picking until the fruit is over-mature (Zielinski 1958). Current technology allows the successful culture of ovules as small as 0.6 mm (Janick and Moore 1996). Only 32% of embryos <10 mm long produce plants, compared to 78% for larger embryos (Ramming 1990).

Non-viability of apparently normal seeds derived from crossbreeding cherries or plums has been a problem (Cochran and others 1961). The Duke cherries—hybrids of mazzard cherry and sour cherry—often have empty seeds (Hedrick 1911).

Flowering and fruit-ripening dates vary among cultivars of a species grown in the same location (Hedrick 1911, 1915; Kester 1969). Individual trees of black cherry vary in a similar manner (Grisez 1974), and the same variation can be expected in other wild species. The food quality of fruit varies greatly among wild plants of Bessey cherry and the plums. Selections of 15 species of plums have been grown under cultivation for their fruit (Hedrick 1911, 1915).

American plum seeds from northern Minnesota germinate much better at a temperature of 10 °C than at higher temperatures, whereas those from Nebraska germinated as well and more rapidly at 21 °C (night) to 27 °C (day) (Grisez 1974).

In apricots, the variety called Russian apricot is hardier than the typical form (Grisez 1974). Mazzard cherry cultivars require 5 to 6 days longer to begin germination in stratification than wild mazzard cherry (Suszka 1967).

In a provenance study of black cherry, Cech and Kitzmiller (1968) found that the pattern of variation for seed traits is random throughout most of its range. However, seeds from the southern and southwestern parts of the range in the United States were characteristically lighter in weight and smaller in diameter as well as having thinner endocarps than seeds from other areas. Geographic locations and mother trees contributed about equally to the variability in total germination.

Flowering and fruiting. The flowers of nearly all species are bisexual. They normally have 5 white or pink petals and 15 to 20 or more stamens. In general, the pistil matures 3 or 4 days before the stamens (Hedrick 1915). The flowers are solitary, in umbel-like clusters or racemes, and usually appear before or with the leaves. The flowers are insect-pollinated. Except for plums and sweet cherries, most species are self-fertile and thus a tree will set fruit without a cross-pollinator (Janick and Moore 1996).

Of the 2 ovules, only 1 normally develops, resulting in a 1-seeded drupe. The drupe is thick and fleshy (except in the almonds) and has a hard, bony endocarp surrounding the seed itself (figures 1–3) (Fernald 1950; LHBH 1976; Kester 1969; Knuth 1906–09; Rehder 1940). The developed endocarp and seed are commonly called the stone or pit. Dates of flowering and fruiting are listed in table 2. Seeds are distributed mainly by birds and mammals (Grisez 1974). Fruit diameters of most species are between 5 and 25 mm, but

Figure 1—*Prunus*, cherry, peach, plum: seeds of *P. americana,* American plum (**upper left**), *P. angustifolia*, Chickasaw plum (**upper middle**); *P. armenica*, apricot (**upper right**); and *P. persica*, peach (**bottom**).

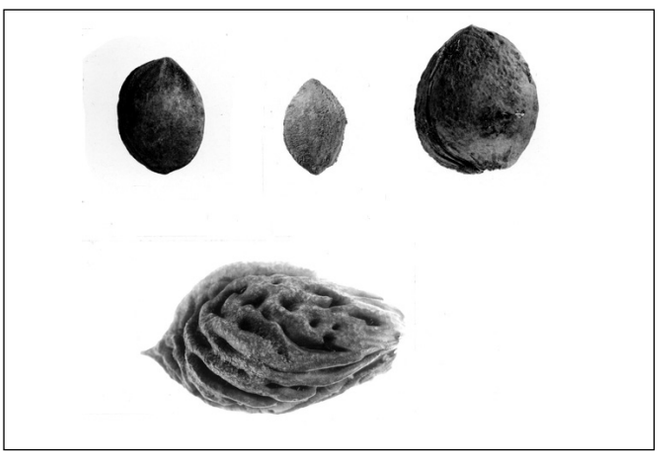


Figure 2—*Prunus*, cherry, peach, plum: seeds of *P. avium*, mazzard cherry (**top left**); *P. padus*, European bird cherry (**top right**); *P. pumila* var. *besseyi*, Bessey cherry (**second row left**); *P. pensylvanica*, pin cherry (**second row right**); *P. cerasus*, sour cherry (**third row left**); *P. pumila*, sand cherry (**third row right**); *P. marginata*, bitter cherry (**fourth row left**); *P. serotina*, black cherry (**fourth row right**); *P. mahaleb*, mahaleb cherry (**fifth row left**); *P. virginiana*, common choke cherry (**fifth row right**); *P. subcordata*, Klamath plum (**bottom left**); and *P. umbellata*, hog plum (**bottom right**).

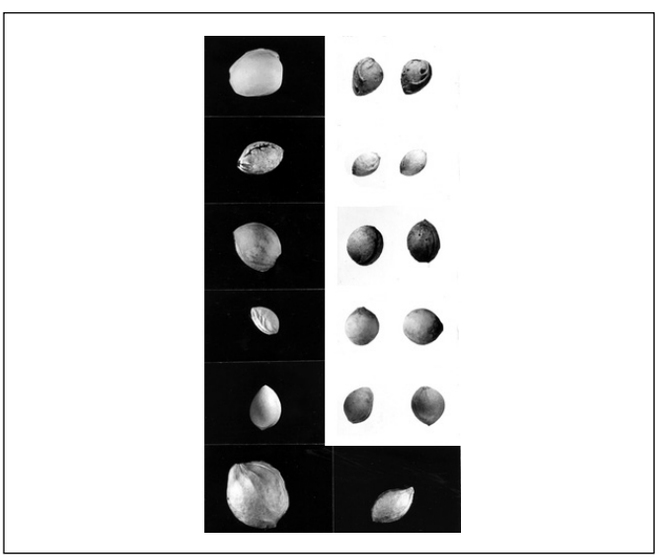


Table 2—*Prunus*, cherry, peach, and plum: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
P. alleghaniensis	Scattered	Late Apr–May	Aug–Sept	—
P. americana	—	Mar–May	June–Oct.	June–Oct
P. angustifolia	—	Mar–Apr	May–July	May–July
P. armeniaca	California	Feb–Mar	May–June	—
	USSR	Mar–Apr	July	July–Aug*
P. avium	NE US	Apr–May	June–July	—
P. caroliniana	SE US	Mar–Apr	Sept–Oct	—
P. cerasifera	Geneva, New York	May 12†	July 15–Aug 10	—
	USSR	Apr–May	Aug	—
P. cerasus	—	Apr–May	June–July	—
	Geneva, New York	May 8–18†	June–July	—
P. domestica	Geneva, New York	May 12–21†	July 15–Oct 1	—
	USSR	May	Aug	—
P. d. var. *insititia*	US & Canada	Late Apr–May	Aug–Sept	—
	Geneva, New York	May 16–21†	Aug 20–Oct 1	—
P. dulcis	California	Mid Feb–Mar	Late Aug–Oct*	—
P. emarginata	—	Apr–June	July–Sept	Aug–Sept*
P. hortulana	SE US	Mar–May	Aug–Oct	—
P. ilicifolia	—	Mar–May	Sept–Oct*	Oct–Dec
P. laurocerasus	SE Europe & Asia Minor	Apr–May	July–Aug	—
P. mahaleb	NE US & SE Canada	Apr–May	July	—
P. maritima	Maine to Delaware	Apr–June	Sept–Oct	—
P. munsoniana	—	Mar–May	July–Sept*	—
	Geneva, New York	May 20–24†	July 15–Sept 10	—
P. padus	Philadelphia & vicinity	End Apr–early May	Late June–July	—
	USSR	May–early June	June–Aug	Aug*
P. pensylvanica	—	Late Mar–early July	July–Sept	—
	Warren Co., Pennsylvania	May 1–15	Late July–early Aug	—
P. persica	NE US	Apr–May	July–Sept	—
	SE US	Feb–Apr	May–Aug	—
P. pumila	—	May–July	July–Sept	—
P. pumila. var. *besseyi*	Nebraska	Apr–May	July–Sept	July–Sept
P. serotina	Central Mississippi	Early Apr	June–July	July
	N Pennsylvania	Late May–early June	Late Aug–Sept	Aug 20–Sept; rarely Nov
	—	Late Apr–June 10	June–Sept.	July 1–Sept
P. spinosa	USSR	Apr–May	Aug–Sept	Sept
P. subcordata	—	Mar–May	Aug–Sept	—
P. tomentosa	Cheyenne, Wyoming	Early May	Late July	Early Aug
	Bismarck, N Dakota	May 10–15	July 10–15	July 15–Sept 1
P. umbellata	SE United States	Mar–Apr	Aug–Sept	—
P. virginiana	E US	Late Apr–early June	July–Oct	—
	Warren Co., Pennsylvania	May 10–20	Early Aug	—
	California	—	Aug–Sept*	—

Sources: Altman and Dittmer (1962), Bailey (1976), Bonner (1975), Fernald (1950), Grisez (1974), Hedrick (1911), Hedrick (1915), Hitchcock and others (1961), Kester (1969), Koreisho and Morozov (1955), Long (1923), McMinn (1959), Mirov and Kraebel (1937, 1939), Munz and Keck (1959), Pane (1966), Petrides (1958), Radford and others (1964), Rehder (1940), Sudworth (1908), Van Dersal (1938).

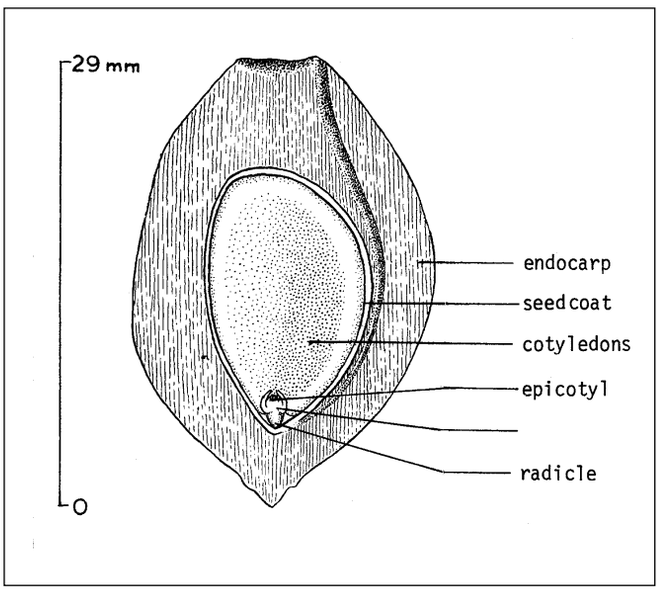
* Collecting dates.

† Average dates of height of bloom for one to several cultivars.

those of almonds, apricots, plums, and peaches are larger (table 3).

Collection of fruits. *Prunus* fruits should be collected when fully mature (Al'benskii and Nikitin 1956; Swingle 1925; Zielinski 1958); doing so facilitates cleaning and is more likely to result in good germination (Grisez 1974; Huntzinger 1968). It is especially important in certain cultivars when the seeds are in a critical stage at the time the fruits are ripe and may not develop to a sound condition if the fruits are picked prematurely (Tukey 1927). Height, seed-bearing age, seedcrop frequency, and fruit descriptions of 24 species are listed in table 3. Color and condition of the fruits indicate maturity. For those species in which the ripe fruit color is nearly black, the preripe color is red. In red-fruited species, the preripe color may be yellowish or partly green and red (Grisez 1974). Almonds are ready to harvest when the husks (mesocarps) of fruits in the inner parts of the tree crown have split (Kester 1969).

Figure 3—*Prunus persica*, peach: longitudinal section through a seed showing no endosperm. Seven species of *Prunus* have seeds without endosperm and 20 species have seeds with endosperm.



Fruits are collected by hand-stripping or by spreading sheets of suitable material under trees to catch the natural fall or fruits that are shaken or beaten off the tree (Grisez 1974; Huntzinger 1968; Stoeckeler and Jones 1957). Small quantities can be picked from the ground (Huntzinger 1971). Black cherry fruits may be collected from trees felled in logging, but when fruits have reached the dead-ripe stage, a high proportion of them will be knocked off during felling (Huntzinger 1968). Mechanical tree shakers are used in many commercial fruit orchards (Kester 1969; Miller 1960). There is even a machine to pick prunes (certain cultivars of garden plum) from the ground (Miller 1960).

Fruits may be carried in bags in small quantities—or in large quantities if they are to be processed immediately (Huntzinger 1971)—but boxes or baskets provide better protection against bruising and spoilage (Al'benskii and Nikitin 1956). Commercial cherries are often transported in water (Tennes and others 1968). Although this method was designed to protect the fruit, it could also be used to prevent spoilage and fermentation until the seeds are cleaned.

Extraction of seeds. Although satisfactory results have been obtained in a few cases by handling and sowing whole fruits (Engstrom and Stoeckeler 1941; Huntzinger 1968), it is generally desirable to clean the seeds of all pulp and juice (Heit 1945; Huntzinger 1968; Marcet 1951; Nyholm 1951; Robertson 1948–49; Shumilina 1949). Cleaning is done by macerators or hammermills with water to float off or screen out the pulp (Defler 1937; Dorn and Flick 1969; Grisez 1974; Hartman and Kester 1959; Huntzinger 1968; Steavenson 1940; Stoeckeler and Jones 1957). Hammermills should have worn or rounded hammers and be run at low speed (Mugford 1969). Small quantities may be cleaned by soaking and rubbing the fruits over a screen (Haut 1938; Jones 1963; Paton 1936) or by use of a household food blender (Huntzinger 1968).

Fermentation has been used to soften fruit to facilitate cleaning (Engstrom and Stoeckeler 1941; Grisez 1974; Rudolf 1961), but it is risky because the germination capacity of seeds may be severely reduced if seeds are allowed to become too warm or ferment too long (Cochran and others 1961; Engstrom and Stoeckeler 1941; Fogle 1958; Heit 1967). Fruits that are badly infested with brown rot should be discarded because this disease can spread through the seedlot (Janick and Moore 1996).

There is little need to separate out sound seeds in most species because the percentage of sound seeds is usually 96 to 100%, but it may be desirable in certain cultivars of commercial fruits. Separation of sound seeds of sour cherry has been done with 95% ethyl alcohol, density 0.8114 (Tukey 1927). A 17% salt solution (density 1.176) has been used to separate the heavy seeds of mazzard cherry, mahaleb cherry, and pin cherry, but the method is not always reliable (Cummings and others 1933). Seeds that float in water can be removed in the cleaning process, but some seeds that sink are not viable (Swingle 1925; Tukey 1927). The same methods should not be used with dried seeds because included air spaces can cause good seeds to float.

Seed yields and weights are listed in table 4. Additional data include the following weights per volume of fruit: sour cherry nested in water, 77 kg/hl (60 lb/bu) (Tennes and others 1968); black cherry, 72 kg/hl (56 lb/bu) (Stoeckeler and Jones 1957); and Manchu cherry, 77 to 85 kg/hl (60 to 66 lb/bu) (Grisez 1974). A bushel of black cherry fruit yields 5 kg (11 lb) of seed (Stoeckeler and Jones 1957).

Storage. Early experiences suggested that excessive drying for storage was detrimental (Cochran and others 1961; Engstrom and Stoeckeler 1941; Fogle 1958; Grisez 1974; Huntzinger 1968; Olson and Nagle 1965; Stoeckeler and Jones 1957); however, what was excessive was not defined. Very early ripening female parents may not produce fruits with fully mature embryos and these fruits should not be allowed to dessicate (Janick and Moore 1996). Apricot seeds can be dried to 6% moisture, mazzard cherry to 9 to 11%, and mahaleb cherry to 8% for storage without impair-

Table 3—*Prunus,* cherry, peach, and plum: height, seed-bearing age, seedcrop frequency, fruit color, and fruit size

Species	Height at maturity (m)	Year first cultivated	Min seed-bearing age (yrs)	Years between large crops	Ripe fruit color	Fruit size (mm)	
						Diameter	Length
P. alleghaniensis	4.9	1889	4	1	Dark purple	10	—
P. americana	3–9	1768	4	1–2	Red or yellowish	20–30	—
P. angustifolia	4.3–7.6	~ 1874	2	—	Red or yellow	10–20	—
P. armeniaca	10.4	Early	5	2	Yellowish with red	30+	—
P. avium	9–30.5	Early	6–7*	1	Yellow to red or purplish black	20–25	—
P. caroliniana	5.5–12	—	—	—	Black	10–13	10–13
P. cerasifera	8.2	Early	3	2–3	Red	16–25	—
P. cerasus	9–15	Early	6-7*	1	Light to dark red	8–25	—
P. domestica	9–12	Early	5	—	Often blue-purple	30+	—
P. d. var. *insititia*	6–7.6	Early	—	—	Yellow to bluish black	25+	15–20
P. dulcis	3–9	Early	4†,6–7	1	Brownish	30+	30–60
P. emarginata	1–15	1918	—	—	Bright red	8–12	—
P. fasciculata	1–2.4	—	—	—	—	13	
P. fremontii	1.5–3.7	—	—	—	Yellowish	15–20	13
P. gracilis	4.6	—	—	—	Red	13	—
P. hortulana	9	—	3	—	Red to yellow	25	—
P. ilicifolia	7.6–9	Pre-1925	3	—	Purple or black	13–17	25
P. laurocerasus	5.5	—	—	—	Purple to black	10	8–13
P. mahaleb	6–10	Early	3	1–2	Black	8–10	6–10
P. maritima	3	—	3	—	Purple	13–25	20
P. munsoniana	6–9	Pre-1909	3	—	Red or yellow	20–30	15–25
P. padus	15	Early	—	2	Black in typical variety	6–8	—
P. pensylvanica	3–12	1773	2	—	Light red	5–7	—
P. persica	3–7.6	Early	3	1–2	Yellow to red	30–60	30–75
P. pumila	0.3–2.4	1756	—	—	Purple-black	10	10
*P.*var. *besseyi*	0.3–1.2	1892	2–3	—	Purple to black	15	—
P. serotina	15.3–33.5	1629	5	1–5	Black	7–10	6–10
P. spinosa	4	Early	—	1–2	Blue-black	10–15	15
P. subcordata	3–7.6	~ 1850	—	2	Red or yellow	20–30	15–30
P. tomentosa	1.8–3	1870	2–3	1–2	Red	10–31	15
P. umbellata	—	—	3	—	Black, red, yellow	10–15	10–13
P. virginiana	1.8–9	1724	—	—	Red-purple to dark purple	8	—

Sources: Bailey (1976), Everett (1957), Fernald (1950), Giersbach and Crocker (1932), Grisez (1974), Gysel and Lemien (1964), Hedrick (1911, 1915), Huntzinger (1971), Kester (1969), Koreisho and Morozov (1955), Munz and Keck (1959), Peck (1961), Petrides (1958), Rehder (1940), Strausbaugh and Core (1964), Van Dersal (1938).

* Minimum commercial seed-bearing age.

† Ages are for seedling stock; grafted or budded stocks bear seeds 1 or 2 years younger (Wright 1966).

ing their germination (Suszka 1964). Seeds to be sown or stratified immediately need not be dried at all. Seeds to be used within a few weeks or months should only be surface-dried; apparently, excessive drying of seeds to be used within a year of collection is often harmful (Grisez 1974; Huntzinger 1968). For storage of 1 year or more, it is desirable to reduce the moisture content of seeds below the surface-dry condition. For mazzard cherry, the optimum moisture content is 9 to 11%, with optimum temperatures of –1 to 3 °C for storage up to 3 years and –10 °C for longer storage (Suszka and others 1996). The results of several storage studies are reported in table 5. In most cases, drying is done at room temperatures or lower. Surface drying usually requires only a few hours (Huntzinger 1968). The moisture content of black cherry seeds has been reduced from about 14% to 5% by drying at 32 °C for 3 hours (Huntzinger 1971).

Sealed containers are preferred for Prunus seeds if the moisture content is to be closely controlled. Seeds of mazzard cherry were dried to a moisture content of 11% and stored in sealed bottles at 1 °C for 4 $^{1}/_{2}$ years. During this period, viability decreased from 93% to 84% (Suszka 1970). Plastic bags have been satisfactory for storage of black cherry seeds for at least 3 years at cold temperatures (Huntzinger 1971). Cloth sacks may serve for short periods in cool temperatures (Suszka 1967). Maheleb cherry and

Table 4—*Prunus*, cherry, peach, and plum: seed data

Species	Seed weight/45 kg (100 lb) of fruit: Range kg	Range lb	Average kg	Average lb	Cleaned seeds/weight: Range /kg	Range /lb	Average /kg	Average /lb	Samples
P. alleghaniensis	—	—	—	—	—	—	2,950	338	1
P. americana	3–15	7–34	9	19	550–1,500	250–680	870	395	27+
P. angustifolia	4–14	8–30	7	16	770–1,530	350–694	1,030	467	14+
P. armeniaca									
USA	14–18	30–40	—	—	200–560	91–254	317	144	10+
USSR	5–7	10–15	—	—	270–495	123–225	382	173	—
P. avium									
USA	3–11	7–25	3	12	1,450–3,000	658–1,361	2,360	1,070	9+
USSR	7–8	15–18	—	—	1,640–2,770	3,616–6,108	4,740	2,150	—
P. cerasifera	—	5	10		782–1,330	355–603	994	451	7+
P. cerasus	—	—	9	20	1,510–4,000	685–1,815	2,910	1,320	6+
P. domestica	—	—	5	10	416–907	189–411	597	271	5+
P. d. var. *insititia*	—	—	3	7	625–1,920	284–871	1,380	626	3+
P. dulcis	—	—	—	—	126–225	57–102	181	82	3+
P. emarginata	—	—	11	25	4,120–8,790	1,869–3,987	7,020	3,184	6+
P. ilicifolia	—	—	—	—	200–240	91–109	220	100	2+
P. mahaleb	9–11	20–25	—	—	4,800–5,600	2,177–2,540	5,200	2,359	—
P. munsoniana	—	—	—	—	900–2,240	408–1,016	1,690	767	3+
P. padus	—	—	9	20	6,600–12,300	2,994–5,580	8,910	4,042	5+
P. pensylvanica	7–12	16–27	—	—	8,000–21,800	3,629–9,889	14,200	6,442	6+
P. persica	—	—	9	20	72–244	33–111	156	71	6+
P. pumila									
typical	—	—	—	—	2,460–4,000	1,116–1,815	2,920	1,325	4+
var. *besseyi*	7–13	15–28	10	21	1,500–4,000	681–1,815	2,400	1,090	10+
P. serotina									
fresh seeds	—	—	9	20	2,800–6,040	1,270–2,740	4,240	1,923	68
fresh & stored seeds	6–15	14–33	10	21	2,840–13,800	1,288–6,260	5,370	2,436	197
P. spinosa	—	—	5	10	1,970–2,670	894–1,211	2,240	1,016	—
P. subcordata	—	—	—	—	450–631	204–286	556	252	4+
P. tomentosa	3–5	7–12	5	10	1,730–6,400	785–2,903	4,740	2,150	9+
P. virginiana	8–11	18–25	9	20	3,010–8,400	1,315–3,810	4,790	2,173	19

Sources: Benjdl (1954), Cech and Kitzmiller (1968), Chittenden (1927), Cumming and others (1933), Defler (1937), Engstrom and Stoeckeler (1941), Everett (1957), Glazebrook (1941), Grisez (1974), Huntzinger (1971), King (1947), Koreisho and Morozov (1955), Krefting and Roe (1949), Krier (1948), Mirov and Kraebel (1937, 1939), Swingle (1939), USDA (1961), Van Dersal (1938).

myrobalan plum can be stored up to 2 winters at room temperature in jute sacks without loss of viability (Grzeskowiak and others 1983). Pin cherry seeds retained high viability after 10 years of storage at 1 to 3 °C under sealed conditions (Dirr and Heuser 1987).

Normally, storage temperatures should be within the range 0.6 to 5 °C, although American plum, mazzard cherry, and mahaleb cherry have been successfully stored at room temperatures for 2 to 5 years. American plum seeds can be stored at room temperature up to 30 months without loss of germinative capacity (Giersbach and Crocker 1932). Manchu cherry seeds stored for 21 months at room temperature did not lose viability (Dirr and Heuser 1987). Dried seeds of mazzard and mahaleb cherries and myrobalan plum can be stored up to 3 winters at –1 or –3 °C without significant loss of viability (Grzeskowiak and others 1983). Over 80% germination was obtained on black cherry seedlots containing 5% moisture after storage for 3 years in a freezer, but seedlots with about 15% moisture were completely spoiled when frozen (Huntzinger 1971).

Warm storage at a high moisture content for only a few months is harmful to seeds of mazzard cherry (Coe and Gerber 1934; Suszka 1967), black cherry (Huntzinger 1968), common choke cherry (Engstrom and Stoeckeler 1941), and probably other species as well. Black cherry seedlots should not be stored warm and moist more than 4 or 5 weeks, although about 2 weeks of such storage immediately after cleaning may be helpful for seeds about to be stratified (Huntzinger 1971).

Tables 5—*Prunus,* cherry, peach, and plum: germination of seeds after dry storage*

Species & storage period	Storage temp (°C)	Moisture content (%)	Germination (%)
P. americana			
18 months	7–10	Dry	70
53 months	7–10	Dry	45
18 months	Lab temp	Dry	72
53 months	Lab temp	Dry	16
18 months	30+	Dry	62
53 months	30+	Dry	0
P. avium			
7 years	–5	~10?	91–97
15 years	–5	~10?	98
55 months	1	11	84
55 months	1	11	88†
8-12 months	3	9–11	98–100
207 days	–3	8.6	100*
214 days	–3	9.0	99†
570 days	–3	8.6	100†
571 days	–3	9.5	94†
935 days	–1	8.3	99†
213 days	–3	9.0	99†
214 days	–3	8.9	98†
568 days	–3	8.6	100†
P. pensylvanica			
2 months	–18	Dry	95
6 years	1–3	Low	74
10 years	1–3	Low	76
P. serotina			
1 year	–18 to –14	4–6	52
2 years	–18 to –14	4–6	81
3 years	–18 to –14	4–6	81
5 years	–18 to –14	4–6	47
8 years	–18 to –14	4–6	66
1 year	–18 to –14	11–13	4
2 years	–18 to –14	11–13	7
3 years	–18 to –14	11–13	1
5 years	–18 to –14	11–13	4
8 years	–18 to –14	11–13	0
1 year	0.5–5	4–6	63
2 years	0.5–5	4–6	81
3 years	0.5–5	4–6	90
5 years	0.5–5	4–6	69
8 years	0.5–5	4–6	56
1 year	0.5–5	11–13	72
2 years	0.5–5	11–13	88
3 years	0.5–5	11–13	77
5 years	0.5–5	11–13	0
8 years	0.5–5	11–13	0

Sources: Ellis and Hong (1986), Giersbach and Crocker (1932), Grisez (1976), Heit (1967), Huntzinger (1971), Laidlaw (1983), Michalska and Suszka (1980c&d), Solovieva (1966, 1978), Suszka (1970).

† Viability determined by indigo carmine embryo-staining test (2 hours in 0.05% solution at 20 °C).

Pregermination treatments and germination tests. *Prunus* seeds have embryo dormancy and require a period of after-ripening in the presence of moisture and oxygen to overcome it. Because of their stony endocarps, *Prunus* seeds are often been thought to have seedcoat dormancy. The endocarp may offer some resistance to germination, but it is permeable to water and *Prunus* is not truly hard-seeded (Hartman and Kester 1959; Heit 1967; Tukey 1924).

Several mechanical and chemical methods have been used in attempts to crack, remove, or soften the endocarp, including freezing, mechanical scarification, boiling water, sulphuric acid, citric acid, lye, or hydrogen peroxide. In most cases, no advantage could be shown, and in many cases the treatments were detrimental. Peach seeds can be removed from the endocarp by applying pressure in the dorsal–ventral axis with a vise or special hand-clippers with a 2-sided blade (Janick and Moore 1996).

Removal of the endocarp by hand hastened or increased germination in American plum (Giersbach and Crocker 1932), almond (Gaudio and Pedone 1963), mazzard cherry (Zielinski 1958), sour cherry (Havis and Gilkeson 1949), peach (Crocker 1927, 1931), and sloe (Shumilina 1949). There was no advantage for bullace plum (Grisez 1974). Soaking for 48 hours in 0.1% citric acid resulted in 89% germination of black cherry; untreated seeds in this study germinated 57% (Jones 1963). In other studies, no advantage could be shown for citric acid treatments (Huntzinger 1968). Notching the endocarp and notching plus a hydrogen peroxide soak increased germination of an early-ripening mazzard cherry cultivar but had no effect on a late-ripening cultivar (Zielinski 1958). Gibberellin treatments apparently can substitute for a portion of the stratification period in apricot (Chao and Walker 1966), mazzard cherry (Fogle and McCrory 1960; Pillay 1962), garden plum (Janick and Moore 1996), and peach (Chao and Walker 1966), but it was effective only when the endocarp had been removed. Germination of mahaleb cherry seeds that were stored dry for several months was improved by 3 days of water-soaking prior to stratification (Swingle 1925).

Because good germination has been attained on stratified seeds of nearly all species of *Prunus* (table 6), it is evident that other pregermination treatments are not necessary if a seedlot is handled properly.

Although sand has often been used as a stratification medium, peat or sand–peat mixtures are preferred (Crocker 1930; Fogle and McCrory 1960; Huntzinger 1968; Shumilina 1949). Vermiculite was as good as peat in a test with black cherry seeds (Huntzinger 1971). Peat provides a larger and more constant supply of both air and water than sand (Crocker 1930; Shumilina 1949). The seeds are thoroughly mixed with the moist stratification medium. When peat is used, it should be soaked, then squeezed to remove all free water. The seeds should be mixed with about 1 to 3 times their volume of the medium (Crocker 1930; Grisez 1974; Huntzinger 1971). Seeds that had been dried for storage or those requiring a long period of after-ripening are sometimes stratified underground, in basements, or in shade prior to cold stratification or fall-sowing (Koreisho and Morozov 1955; Shumilina 1949).

Published results of experimental comparisons among various stratification temperatures for several species show that constant temperatures from 2 to 5 °C are more favorable than those below 1.7 °C or above 8 °C (Coe and Gerber 1934; Crocker 1931; Haut 1938). Seeley and Damavandy (1985) found that the optimum chilling temperature was between 4 and 6 °C for apricot, mazzard cherry, mahaleb cherry, and peach. The most suitable temperature for stratification of almond (cv. 'Truioto') with endocarp was 10 °C for 26 days (Therios 1982). A regularly alternating temperature range of 2 to 4 °C was better than constant 3 °C for 2 cultivars of mazzard cherry (Zielinski 1958).

Stratification periods necessary for after-ripening vary by species (table 6). In general, species and cultivars from warm climates require less chilling than those from cold climates. Satisfactory germination of the many cultivated species not included here can probably be attained by following general recommendations and the stratification requirements for closely related species of the same climatic zones.

Lockley (1980) stratified 13 open-pollinated families of common choke cherry for 10, 16, and 24 weeks at 3 °C and germinated the seeds at 3 alternating temperature regimes of 10 to 16 °C, 16 to 21 °C, and 21 to 27 °C. All germinating seeds were provided with 14 hours of light during the high-temperature portion of the cycle. Stratification for 10 weeks was inadequate. The best results, 77% germination on the average, were found with 16 weeks of stratification and germination at 21 to 27 °C. After 24 weeks of cold stratification, over 50% of the common choke cherry seeds germinated in stratification. There was a significant correlation ($r = 0.67$) between field emergence and laboratory germination at 16 to 21 °C and 21 to 27 °C when the seeds received 16 weeks of stratification. Common choke cherry families with low germination at 21 to 27 °C after 10 weeks of stratification were also low germinators in the nursery ($r = 0.68$).

In a comprehensive study on stones of 7 widely planted species of *Prunus* including several cultivars and seed sources, germination was much higher after warm plus cold stratification than after cold stratification only. The schedule was 14 days at 20 °C followed by 189 days at 3 °C (Suszka 1967). Seedlots of sloe given 2 weeks of warm stratification treatment followed by 18 weeks of chilling yielded 80% germination (Gordon and Rowe 1982). Myrobalan plum and garden plum germination was promoted by 2 weeks of warm stratification at 20 °C before chilling (Michalska and Suszka 1980b). Muller and others (1990) found that 3 cycles of warm and cold stratification at a moisture content of 30% improved the germination of mazzard cherry. Virtually full germination of Mazzard cherry seedlots was achieved with 2 weeks at 20 °C, 8 weeks at 3 °C, 2 weeks at 25 °C, then 3 °C for the remainder of the treatment (Michalska and Suszka 1980a).

Table 6—*Prunus*, cherry, peach, and plum: stratification periods, germination test conditions, and results

Species	Recommended stratification (days)		Germ. test conditions			Avg germination		Viability
			Temp (°C)					
	Warm*	Cold†	Day	Night	Days	(%)	Samples	(%)
P. alleghaniensis	0	150	10	10	60	25	7	—
P. americana	0	90–150	10	10	60	60	21	74
P. angustifolia	0	60–120	—	—	60	55	—	90
P. armeniaca								
endocarp removed	0	0	—	7	7	14	90	3
endocarp intact	14	189	3	3	‡	95	—	4
endocarp intact	0	80–90	5	5	‡	95	—	—
P. avium								
endocarp removed	0	90–125	21	21	—	91	—	69
endocarp intact	0	120–180	21	21	—	76	10+	—
endocarp intact	14	189	3	3	‡	88	—	—
P. caroliana	0	30–60	—	—	—	—	—	—
P. cerasifera	—	196	å1	å7	28	65	2	—
P. cerasus	0	90–150	—	—	—	—	82	—
P. domestica	14	189	3	3	‡	56	15	—
	0	120–150	—	—	—	—	85	—
	0	90	2	2	—	—	91	—
P. domestica var. *insititia*	0	84–112	18	18	—	89	7	—
P. dulcis	0	65	2	2	‡	—	90	—
P. emarginata	0	90–126	24	24	60	4	3+	—
P. ilicifolia								
fresh seed	0	0	—	—	—	—	—	—
stored seed	0	90	—	—	—	—	24	—
P. laurocerasus	0	60–90	—	—	—	—	—	—
P. mahaleb	0	80–100	—	—	—	89	5	—
	14	189	3	3	‡	55	3	—
P. maritima	0	90	—	—	—	—	39	—
P. munsoniana	0	80–100	—	—	—	100	10	—
P. padus								
fresh seeds	0	100–120	—	—	—	85	—	—
stored seeds	14	210	3	3	‡	50	3	—
P. pensylvanica	60	90	25	10	60	62	2	91
P. persica								
endocarp intact	0	98–105	5(§41)	5(§41)	‡	32	8	—
endocarp removed	0	70–105	5(§41)	5(§41)	‡	82	8	92
P. pumila var. *besseyi*	0	120	—	—	—	60	72	—
P. serotina	0	120	26	10	40–60	86	32	80
	14	189	3	3	‡	90	3	—
P. spinosa	0	170	—	—	—	—	90	—
P. subcordata	0	90	—	—	100	1	—	—
P. tomentosa	0	60–90	—	—	—	11	—	86
P. virginiana	0	120–160	25	10	40	77	3	62

Sources: Afanasiev (1940, 1942), Al'benshkii and Nikitin (1956), Chadwick (1935), Chao and Walker (1966), Coe and Gerber (934) Crocker (1927, 1931), Defler (1937), Dirr and Heuser (1987), Emery (1964), Engstrom and Stoeckeler (1941), Everett (1957), Fogle (1958), Fogle and McCrory (1960), Glazebrook (1941), Giersbach and Crocker (1932), Grisez (1974), Haut (1932, 1938), Havis and Gilkeson (1949), Hesse and Kester (1955), Heit (1938), Kester (1969), Koreisho and Morozov (1955), Krefting and Roe (1949), Morov and Kraebel (1937), Pollock (1959), Probocskal (1963), Roe (1941), Suszka (1964, 1967), Swingle (1939), Tukey (1924), USDA (1961).

* Seeds were in a moist medium at a constant temperature of 20 °C or at a temperature alternating diurnally from 30 °C (8 hours) to 20 °C (16 hours).
† Seeds were in a moist medium at a temperature between 0.6 °C and 5 °C; 2.8 to 5 °C was better.
‡ Germination occurred during the stratification period.
§ Results were similar at 10 °C.
ll Adequate germination was reported at unspecified temperatures.

To achieve germination greater than 90%, Seeley and Damavandy (1985) found that apricot seeds need 50 days of chilling; mazzard cherry seeds, 120 days; mahaleb cherry seeds, 100 days; and peach seeds, 90 days of chilling before germination. Zigas and Coombe (1977) reported that 10 weeks of stratification at 3 °C was enough time to remove any inhibitory properties of the testa of peach seeds. The best treatment reported for mazzard cherry seeds in Europe is alternating cold and warm stratification without medium, with seeds at 28 to 30% moisture: 2 weeks at 20 °C, 6 weeks at 3 °C, 2 weeks at 25 °C, 4 weeks at 3 °C, 2 weeks at 25 °C, then 11+ weeks at 3 °C, with the treatment ending when 40 to 50% of the seeds readily germinate at 3 °C (Suszka and others 1996).

Seeds usually are held in cold stratification until incipient germination occurs (Giersbach and Crocker 1932; Huntzinger 1968; Suszka 1967). Visible signs of incipient germination are split endocarps or emerging radicles. When the cold period was interrupted with warmer temperatures before these stages were reached, secondary dormancy was induced (Huntzinger 1971; Suszka 1967). Michalska (1982) reported a 10-week delay in root growth of mazzard cherry when a thermal induction treatment was interjected into a 3 °C chilling period. Root growth was activated only after 12 to 16 weeks of chilling at 3 °C. In a test by Suszka (1967), seedlots of mazzard cherry were stratified for 154 days at 3 °C and then separated into 3 fractions: intact seeds, cracked seeds, and those with emerging radicles. A sample of each fraction was sown separately at a depth of 1 cm ($^3/_8$ in) and subjected to a temperature of 20 °C. Epicotyls emerged from only 8% of the intact stones, but from 90% of the cracked seeds and from 95% of those with emerging radicles. The optimum temperature for epicotyl emergence from cracked seeds of European bird cherry, however, was between 5 and 10 °C (Suszka 1967). Seedlings have developed from up to 100% of cracked seeds of black cherry after sowing (Defler 1937; Huntzinger 1971).

Maximum germination, as judged by the presence of radicles at least 3 mm long, was obtained at 3 or 5 °C on seeds of apricot, mazzard cherry, myrobalan plum, garden plum, mahaleb cherry, European bird cherry, and black cherry (Suszka 1967). For many other species in table 6, temperatures somewhat higher than 5 °C were used for germination. Information is not available, however, on the proportion of seeds that had started to germinate during the cold stratification period before the temperature was raised. The diurnally alternating temperatures of 30 and 20 °C specified for *Prunus* in the International Rules for Seed Testing (ISTA 1996) apparently are much too high. The Association of Official Seed Analysts (AOSA 1996) specify a germination temperature of 18 to 22 °C for mazzard cherry and peach. ISTA (1996) rules specify 90 to 120 days of chilling for mazzard cherry, European bird cherry, and black cherry. Germination is hypogeal in many species as (figure 4), but epigeal in common choke cherry (figure 5).

Viability tests are usually preferred over germination tests because of the long stratification time required to break

Figure 4—*Prunus americanum*, American plum: seedling development at 1, 3, 5, and 9 days after hypogeal germination.

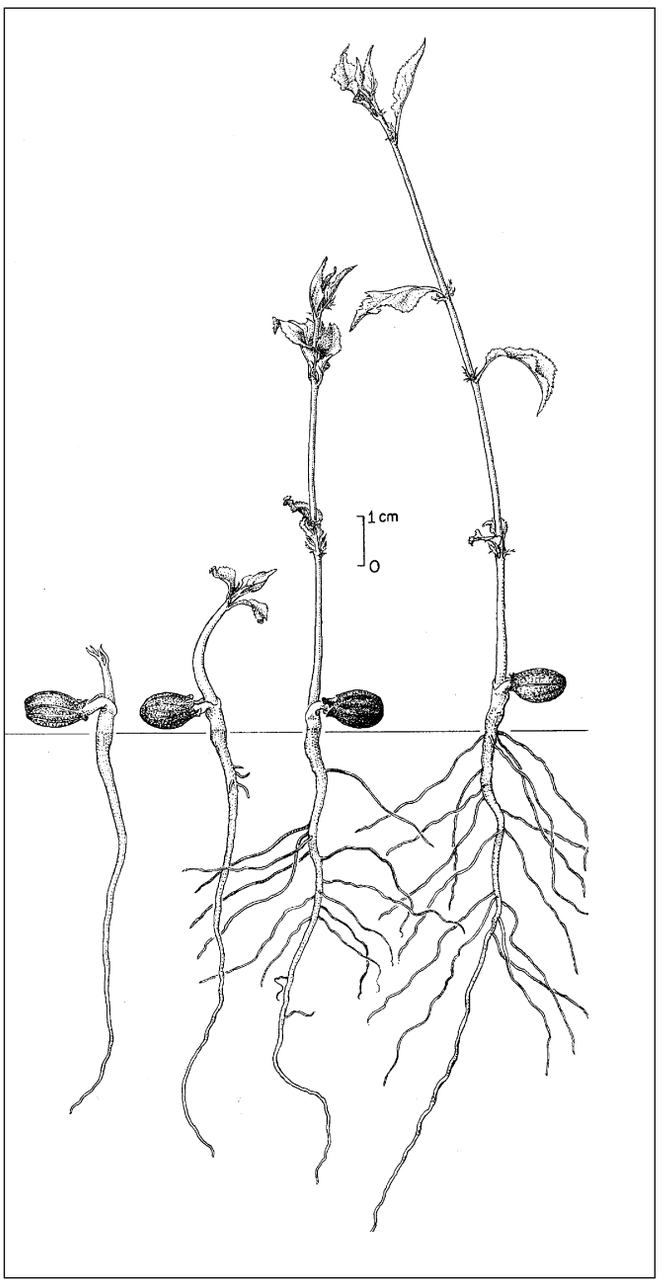
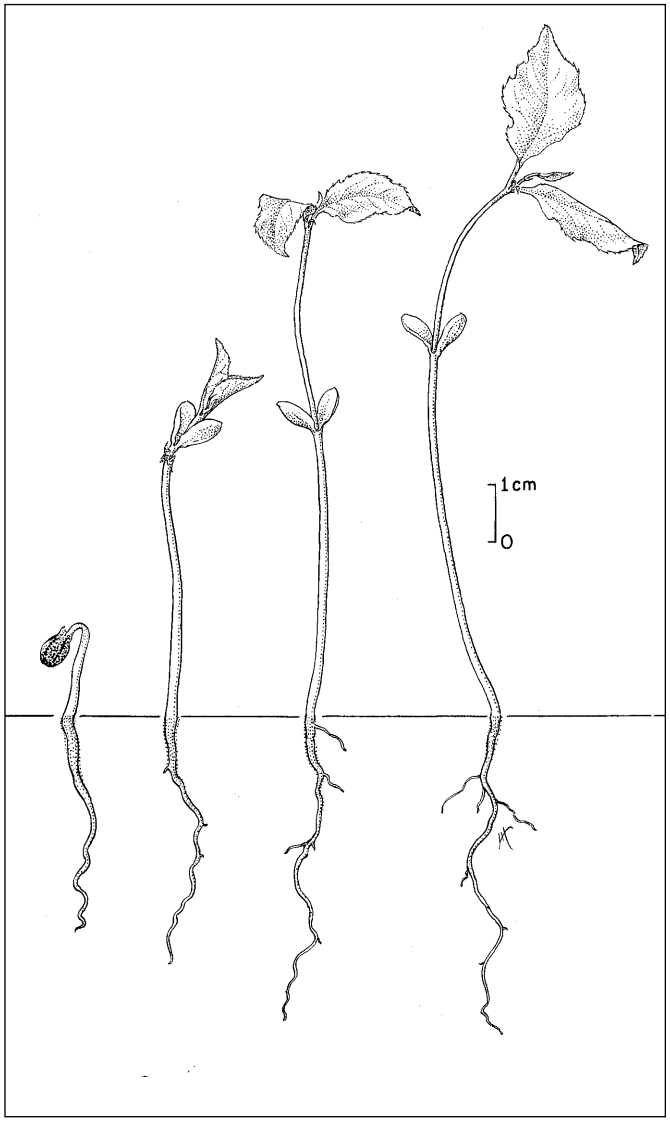


Figure 5—*Prunus virginianna,* common chokecherry; seedling development at 1, 3, 7, and 11 days after epigeal germination.



dormancy of most species. The excised embryo procedure is recommended by both AOSA (1996) and ISTA (1996) for all species, and it has been commonly used on American plum, almond, apricot, peach, sloe, and both wild and cultivated cherries (Chao and Walker 1966; Heit 1955; Shumilina 1949; Tukey 1944). Once the seedcoats are removed, the seeds are placed on dampened blotter paper in a 20 °C germinator for 10 days. The embryos are viable when the radicles begin to grow or the cotyledons turn green or open up.

The seeds of *Prunus* species also are easily stained with tetrazolium chloride, and they usually have high viability (table 6). The viability percentage is highly correlated with field emergence. Tetrazolium staining is recommended as an alternative method for viability tests on all *Prunus* species (AOSA 1996; ISTA 1996). The seed should be cracked and a small piece of cotyledon removed at the distal end, then soaked for 18 hours at 20 °C. The seedcoat should then be removed before incubation in a 1.0% solution for 8 to 12 hours at 30 °C (or 12 to 18 hours in 0.5%). Large-seeded species may require longer staining times. To be considered viable, the radicle tip and $^1/_3$ of the distal area of the cotyledons should be stained (ISTA 1996).

Nursery practice. Untreated *Prunus* seeds may be sown in the fall or stratified seeds may be sown in spring. Some species that require long periods for after-ripening are stratified warm and cool even before fall-sowing, or they may be planted as soon as collected (Al'benskii and Nikitin 1956; Grisez 1974; Koreisho and Morozov 1955). American and Chickasaw plums and common choke cherry seeds benefit from 30 days of warm stratification followed by 45 days of cold stratification before sowing (Huffman 1996). In fall-sowing, it is important to sow early enough to allow seeds to after-ripen before the ground freezes (Swingle 1925). Secondary dormancy can be induced in partially after-ripened seeds by high soil temperatures (Grzeskowiak and others 1983). Suszka (1978) recommends covering the nurserybed with 10 cm (4 in) of straw mulch. Seeds should be sown in early September, or by mid-October at the latest, in the northern states (Grisez 1974; Heit 1938, 1967; Huntzinger 1971). Mulching and deeper sowing help overcome the effects of late sowing and dry climates.

Stratified seeds should be sown as early in spring as possible because high temperatures and drying can reduce germination (Haut 1932; Huntzinger 1971; Koreisho and Morozov 1955; Suszka 1967). It is best if a high proportion of the seeds in the seedlot are cracked but have not yet begun radicle elongation (Koreisho and Morozzov 1955; Suszka 1964, 1967). Long radicles are easily broken in handling and sowing. For this reason, seeds should be checked toward the end of the stratification period for emerging radicles (Huntzinger 1968, 1971). Transparent containers are ideal for this purpose. If radicle elongation starts when it is too early to sow, the temperature should be reduced to near-freezing (Afanasiev 1942).

Normal precautions may be taken against fungi during stratification and sowing, but they do not appear necessary if seedlots are properly cleaned and handled. Rodents must be kept out of the nursery, however (Grisez 1974; Huntzinger 1971).

Prunus seedlings reach suitable planting size in 1 or 2 years. Low seedbed densities help assure adequate size the first year and reduce the proportion of culls (Grisez 1974; Stoeckeler and Jones 1957).

Seedlings may be planted 1 m (3 ft) apart in rows 3 to 4 m (10 to 13 ft) apart to produce 3,000 seedlings/ha (7,400 seedlings/ac) (Janick and Moore 1996). Seedlings that set terminal buds may be forced by gibberellin sprays or can be cut back to stimulate growth (Janick and Moore 1996). It has been observed in the nursery that apricot trees with large leaves and unbranched shoots are more likely to produce medium or large sized fruits, but plants with much branching, very thin shoots, and small leaves are likely to have small fruit and fruit at an older age (Janick and Moore 1996). Nursery practices that have been successful are listed in table 7.

Table 7—*Prunus,* cherry, peach, and plum: nursery practice

Species	Stratification periods* (days)		Seeds sown/ft²	Sowing depth (in)	Tree %	Outplanting age (yr)
	Fall-sowing	Spring-sowing				
P. americana	0–90	120	4	1–2†	33–50	1
P. angustifolia	0	15–20	1	33	1	—
P. armeniaca	0	90	9	2	50	1
P. avium	60‡	120	13	1–2	—	1 or 2
P. cerasifera	0‡	—	10	2	64§	1
P. cerasus	90‡	90	21	—	—	1 or 2
P. domestica	0	—	13	2	—	1 or 2
P. mahaleb	0–60	60	—	1–2	45§	—
P. padus	60‡	120	50	1/2–1‖	—	1 or 2
P. persica	0	85	0.75	2	—	—
P. pumila var. *besseyi*	0	120	6–7	—	77	—
P. serotina	0	120	10–20	1 1/2–2‖	7–83	1
P. spinosa	0‡	170	17–28	1–2	70–75§	1 or 2
P. tomentosa	0	60	15–30	1‖	72	1
P. virginiana	0	120–160	25	_	3–34	1 or 2

Sources: Afanasijev (1962), Al'benskii and Nikitin (1956), Bailey (1969), Bejdl (1954), Engstrom and Stoeckeler (1941), Grisez (1974), Heit (1938, 1967), Huntzinger (1971), Koreisho and Morozov (1955), Nyholm (1951), Rudolf (1961), Schaaf (1938, 1940), Shoemaker and Teskey (1959), Shumilina (1940, 1949), Stoeckeler and Jones (1957), Swingle (1939), Talbert (1946).

* Stratified in a moist medium at a temperature between 2.8 and 5 °C.

† Add a 10 to 15 cm (4- to 6-in) soil ridge to the nurserybed.

‡ Or stratify from time of collection to time of sowing when fresh seeds are used.

§ Germination percent (not tree percent).

‖ On fall-sown beds, add ~8 cm (3 in) of straw or moss for a mulch.

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Pinaceae—Pine family

Pseudotsuga Carr.

Douglas-fir

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Growth habit, occurrence, and uses. Seven species are currently included in the genus *Pseudotsuga;* they are Douglas-fir (*P. menziesii* (Mirb.) Franco) and bigcone Douglas-fir (*P. macrocarpa* (Vasey) Mayr) in North America and *P. japonica* (Shirasawa) Beissner, *P. wilsoniana* Hayata, *P. sinensis* Dode, *P. forrestii* Craib, and *P. gausseni* Flous in eastern Asia (Hermann 1982; Little 1979). The generic name—*Pseudotsuga,* meaning "false hemlock"—reflects the difficulties taxonomists had in classifying the genus (Little 1952).

Fossil records indicate that *Pseudotsuga* has been present in western North America since the Early Tertiary Epoch, and later also in Japan and perhaps in Europe (Hermann 1985). Its limited early range in North America expanded during interglacial intervals to approximately its current range.

Only 1 species, Douglas-fir, is widely distributed; the other 6 species are relatively sparse and their natural distributions are narrow and restricted. The range of Douglas-fir extends from latitude 19°N in central Mexico to 55°N in central British Columbia, and from longitude 97°W in Mexico northwesterly to the Pacific Ocean and to 128°W in British Columbia (Little 1971; Silen 1978). Two varieties are recognized—coastal Douglas-fir (var. *menziesii*) and interior Douglas-fir (var. *glauca*) (table 1). The 2 varieties adjoin and introgress in British Columbia (Li and Adams 1989; Rudloff 1972) but occur in separate territories from southern British Columbia southward. Bigcone Douglas-fir occurs only in southwestern California and is separated by 34 km from the southernmost known locality for coastal Douglas-fir (Griffin 1964). Both North American species have been propagated successfully in Europe but only Douglas-fir has gained worldwide prominence. It is the most important exotic grown in western and central Europe and is also very important in Chile, New Zealand, and Australia (Kleinschmit and Bastien 1992), becoming naturalized in several countries (Jones 1946; Ledgard 1988).

In North America, Douglas-fir naturally occupies a wide span of elevations and climatic conditions. Coastal Douglas-fir is found on soils derived from marine, glacial, and vol-

Table 1—*Pseudotsuga,* Douglas-fir: nomenclature and occurrence

Scientific name & synonyms	Common name(s)	Occurrence
***P. macrocarpa* (Vasey) Mayr** *Abies douglasii* var. *macrocarpa* Torr. *A. macrocapa* Vasey	**bigcone Douglas-fir**, bigcone-spruce, desert-fir	Mtns of SW California
***P. menziesii* var. *glauca* (Beissn.) Franco** *P. douglasii* var. *glauca* Mayr *P. menziesii* var. *caesia* (Schwerin) Franco *P. taxifolia* var. *glauca* (Beissn.) Sudworth	**interior Douglas-fir,** blue Douglas-fir, Rocky Mountain Douglas-fir, Colorado Douglas-fir, inland Douglas-fir	Central British Columbia & SW Alberta, S in mtns to N & central Mexico, from E Washington, Oregon, Nevada, & W Arizona to E Montana, Wyoming, Colorado, New Mexico, & NW Texas
***P. menziesii* var. *menziesii* (Mirb.) Franco** *P. douglasii* var. *viridis* Schwerin *P. menziesii* var. *viridis* (Schwerin) Franco *P. mucronata* (Raf.) Sudworth *P. taxifolia* (Lamb.) Britton	**coastal Douglas-fir,** green Douglas-fir, Oregon Douglas-fir, Douglas-fir, Douglas-spruce	SW British Columbia through Washington & Oregon to central California, E into Cascade & Sierra Nevada ranges to W Nevada

Sources: Griffin and Critchfield (1976), Hermann (1982), Hermann and Lavender (1990), Little (1952, 1971, 1979), McDonald (1990), Minnich (1982).

canic origins at elevations from sea level to 1,250 m in the north to 2,300 m near its southern limits in the Sierra Nevada (Hermann and Lavender 1990). Interior Douglas-fir is found on soils derived from many parent materials at elevations from 550 to 2,440 m in the north and from 1,550 to 3,260 m in southern Arizona. Bigcone Douglas-fir is also found on a wide variety of soils at elevations from 275 to 2,400 m on gentle to steep slopes (McDonald 1990). The altitudinal distribution of these species shifts from southerly slopes at high elevations or in northern parts of their ranges to northerly slopes in the southern parts in response to the interacting limitations of temperature and moisture. The presence of large canyon live oaks—*Quercus chrysolepis* Liebm.—apparently modifies fire intensity and appears to be a third crucial influence on distribution of bigcone Douglas-fir (Minnich 1977, 1980).

Both species are found in pure and mixed stands, generally as dominants or codominants, and grow to large sizes that vary by elevation and site. On favorable sites, mature bigcone Douglas-fir trees average 24 to 30 m tall and 61 cm or more in dbh; the largest living individual is 44.2 m tall and 213 cm dbh (AFA 2000). Interior Douglas-fir trees average 30 to 37 m tall and 38 to 102 cm dbh; the largest individual now on record is 42.4 m tall and 255 cm dbh (AFA 2000). Coastal Douglas-fir grows much larger; heights of 76 m and diameters of 150 to 180 cm are common on favorable sites. The largest living tree is 85.6 m tall and 408 cm in diameter (AFA 2000). The lifespan of bigcone and interior Douglas-firs is up to 400 years and that for coastal Douglas-fir about 500 years (Hermann and Lavender 1990; McDonald 1990). The recorded maximums are 622 years for bigcone Douglas-fir and 1,400 years for coastal Douglas-fir (McArdle and others 1961; McDonald 1990).

Because of its wide distribution and many desirable characteristics, Douglas-fir is a major factor in timber production, watershed protection, wildlife habitat, and aesthetics whereas bigcone Douglas-fir's contribution is primarily local and limited. Douglas-fir is the premier species used where strength is needed in construction—laminated beams and arches, timbers, poles, piling, and structural plywood—and also for general construction, fiberboard, millwork, furniture, and specialty products. It is also the leading species used in the West for sulfate pulp (Panshin and Zeeuw 1970) and for Christmas trees.

To further its propagation within and beyond its native range, Douglas-fir's genetic and regeneration traits have been studied intensively. Clinal genetic variation has been demonstrated in both the coastal and interior varieties for many traits, including survival, growth, form, phenology, insect and disease resistance, cold hardiness, wood characteristics, and chemical composition (Campbell 1986; Campbell and Sorensen 1978; Campbell and Sugano 1993; Ching and Bever 1960; Griffin and Ching 1977; Joly and others 1989; Li and Adams 1989; Read and Sprackling 1976; Rehfeldt 1979, 1989; Schowalter 1988; Silen 1978; Sorensen 1983; St. Clair and Adams 1991; Strauss and Tsai 1988). Because the survival and growth of Douglas-fir at a given location varies by the genetic source used, much effort has been expended in defining guidelines and zones for informed use of seeds and stock beyond the local geographic and climatic area of origin (Campbell 1991; Kleinschmit and Bastien 1992; Randall 1996; Rehfeldt 1981, 1983a&b.) Inspection systems have been developed to ensure that Douglas-fir seedlots and stock are correctly labeled and their origins certified (Portlock 1992; Schrumpf and Pfeifer 1993.)

Efforts to genetically improve Douglas-fir began over 50 years ago (Isaac 1949) and have developed into large long-term cooperative programs in western North America and abroad. In the Pacific Northwest, most of the seeds used in reforestation of coastal Douglas-fir now come from seed orchards (Daniels 1995). The species' use in the breeding zone of origin and other breeding zones is guided by results of outplanting tests and general rules for seed transfer (Randall 1996). A 10% gain in juvenile height growth is predicted for selections representing 6 low-elevation breeding zones in western Oregon and Washington (Stonecypher and others 1996). An international program for genetic improvement of Douglas-fir was started in 1967 and is continuing under IUFRO agencies involving 59 institutions in 36 countries (Kleinschmit and Bastien 1992). Other genetic improvement efforts involve selection for Christmas trees (Douglass and TerBush 1975; Silen 1978) hybridization (Rehfeldt 1977), and clonal propagation (Silen 1978). Many cultivars of Douglas-fir have been propagated by horticulturists (Hermann 1982).

Flowering and fruiting. Male and female strobili burst bud during late winter and spring (table 2), about a year after their initiation as axillary bud primordia (Allen and Owens 1972). Male strobili are generally borne abundantly over much of the crown on the proximal half of year-old shoots; these strobili become somewhat pendant when mature and are about 2 cm long. Female strobili develop more distally on year-old shoots that are located primarily in the upper half of the crown. The female strobili are erect at the time of pollen shedding and measure about 3 cm long; their appearance is dominated by large trident bracts (Allen and Owens 1972). The color of female strobili (seed cones) ranges from deep green to deep red, and that of male strobili

Table 2—*Pseudotsuga,* Douglas-fir: phenology of flowering and fruiting

Species	Location	Flowering	Cone ripening	Seed dispersal
P. macrocarpa	S California	February–mid-Apr	Early Aug–early Oct	Late Aug–late Oct
P. menziesii var. *glauca*	Central Colorado (elev. 2,060–2,880 m)	Mid-Apr–early May	—	—
	Montana (elev. 700–1,700 m)	Late May–early June	Late July–early Aug	Late Aug–mid-Sept*
	Northern Idaho (elev. 820–1,000 m)	Early May–late June	Mid-Aug	Early Sept*
	Central Oregon	Mid-May–mid-June	—	Mid-Aug–mid-Sept*
P. menziesii var. *menziesii*	Coastal British Columbia	Late Mar–mid-May	Aug	Sept–late Mar
	W-central Oregon & W Washington	Mid-Mar–early June†	Aug	Late Aug–late Mar‡
	S Oregon	Early Apr–early May	—	Mid-Aug*
	N California	—	August	Sept–early winter§

Sources: Allen (1942), Allen and Owens (1972), Ching and Ching (1962), Gashwiler (1969), Gause (1966), Griffith (1968), Isaac (1943), McDonald (1990, 1992), Morris (1952), Owston and Stein (1974), Roeser (1942), Silen (1963), Sorensen and Campbell (1971), Sudworth (1908).
* Beginning dates only.
† Upslope progression in pollen shedding and female receptivity averaged 23.5 m of elevation per day on 4 transects in western Oregon and Washington (Silen 1963).
‡ About 70 to 90% of the seeds usually disperse in September and October; most of the remainder disperse between November and March (Allen 1942; Isaac 1943).
§ Seedfall usually greatest in October (McDonald 1992).

from yellow to deep red. Strobili of the same sex tend to be of uniform color on individual trees, but the color of the males and females may differ (Griffith 1968).

Seed cones become receptive to pollination when they have emerged by half to two-thirds from the bud scales, and they remain so for at least 6 to 10 days (Ho 1980; Owens and others 1991; Silen 1978). Pollen dispersal occurs for 20 to 30 days in a given locality (Silen 1963). Seed cones soon become pendant, and fertilization takes place about 10 weeks after pollination (Allen and Owens 1972). Seeds develop through late spring and summer, reaching maturity in August or early September. Cones generally begin to dry and turn brown in August or September, and most seeds are released in September and October (table 2).

Calendar dates for phenological events vary with latitude and elevation (Silen 1963), between individual trees in a locality (Orr-Ewing 1956), and by position within the crown (Orr-Ewing 1956; Roeser 1942). Timing also varies from year to year, depending on weather conditions. Because cones open by drying, time of seed dispersal is particularly influenced by low humidity and drying winds in late summer and fall.

The mature cones of Douglas-fir are readily identified by their 3-lobed bracts, which protrude beyond the cone scales (figure 1). On each scale are 2 seeds that have relatively large wings (figure 2). One side of the seed is variegated light brown; the other is more glossy and dark brown. Embryos are linear (figure 3). The number of filled seeds per cone varies widely and tends to be greater for large

Figure 1—*Pseudotsuga menziesii* var. *menziessii*, coast Douglas-fir: mature, closed cones have characteristic 3-lobed protruding bracts.

cones (Willis 1917). In interior Douglas-fir, filled-seed numbers ranged from 20 to 30 per cone in some collections (Owston and Stein 1974). For coastal Douglas-fir, filled-seed numbers ranged from 4 to 54 per cone in 309 collections from individual 35-year-old trees in northwestern Oregon (Olson and Silen 1975). Numbers averaged 16 per cone in collections from 127 individual trees in 10 westside areas located from north-central Washington to south-central Oregon (Willis and Hofmann 1915) and 19.4 per cone (range 2 to 35) in collections made between 1966 and 1978

Figure 2—*Pseudotsuga*, Douglas-fir: seeds of *P. macrocarpa*, bigcone Douglas-fir (**top**) and *P. menziesii*, Douglas-fir (**bottom**); the 2 varieties of the latter bear seeds similar in appearance and anatomy.

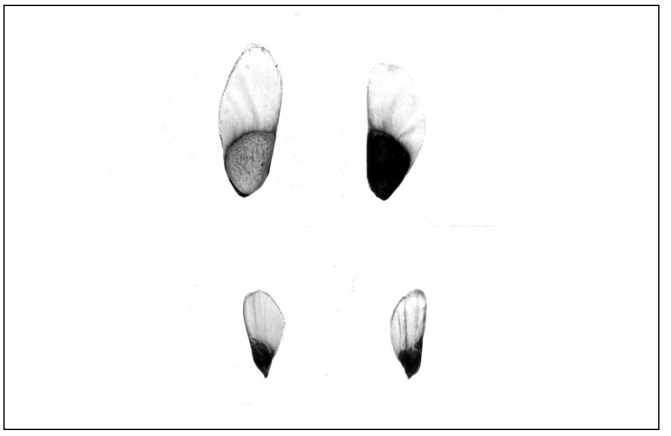
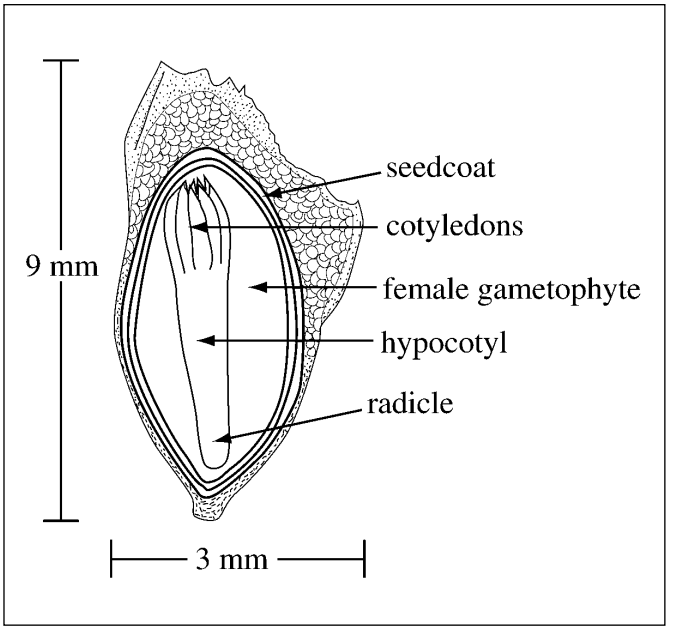


Figure 3—*Pseudotsuga menziesii*, Douglas-fir: longitudinal section through a seed showing fully developed embryo.



from 923 individual trees with sparse to good crops in 95 coastal and Cascade stands in Oregon and Washington (Sorensen 1997).

The seeds of Douglas-fir are disseminated by gravity and wind; their distribution varies widely—it is influenced by crop abundance, tree height and position, wind velocity, and other factors (Isaac 1930). Most seeds of bigcone Douglas-fir fall beneath the tree of origin; wider dissemination occurs primarily during high winds (McDonald 1990). Some Douglas-fir cones remain attached to the tree for a year or more after seed dispersal.

Seed production in Douglas-fir is highly variable from tree to tree. In a good seed year, an average mature, forest-grown coastal Douglas-fir produces about 0.45 kg (1 lb) of cleaned seeds (Isaac 1943), whereas widely spaced trees may produce 0.91 kg (2 lb) or more (Allen 1942; Isaac 1943). Because not all trees produce seeds, stand production averages considerably less than 0.45 kg (1 lb) of seeds per tree (Isaac 1943). Trees 100 to 200 years old are most prolific, but cones on younger trees are larger and contain more viable seeds (Willis 1917; Willis and Hofmann 1915). In young stands, seed production of coastal Douglas-fir begins at 7 to 10 years of age and somewhat later for interior Douglas-fir (table 3). When cultural and chemical techniques are used to stimulate precocious flowering, seeds have been produced on 2- to 5-year-old Douglas-firs, but pollen production is sparse (Silen 1978). Bigcone Douglas-firs may bear cones beginning about age 20, but they are rare on trees less than 40 years old (McDonald 1990).

Generally, some seeds are produced annually by coastal Douglas-fir except for about 1 year in any 4- to 5-year period (Isaac 1943; Reukema 1982); however, higher crop failure rates have been reported (McDonald 1992). Stand conditions as well as environmental and internal factors make the crop cycle erratic (Baron 1969; Eis 1973; Lowry 1966; Owens and others 1991). Abundant crops have occurred from 2 to 11 years apart (table 3). The seed production cycle for interior Douglas-fir is quite similar. Bigcone Douglas-fir usually has small cone crops; abundant crops occur infrequently and usually only in localized areas (USDA FS & CDF 1955–1971).

The existence of a cone crop cannot be confirmed until about 2 months before seedfall; poor pollination, frost, cone abortion, insects, and other factors may cause widespread failure after cones are visible (Owens and others 1991). Forecasts of crop potential are possible 12 months in advance of seedfall by counts of female buds (Allen 1941) or 17 months in advance by counts of male buds (Silen 1967). Bud counts are more accurate in predicting crop failures than in forecasting successful crops.

The high economic value of Douglas-fir seeds, especially genetically improved seeds, has prompted many studies, including those on the following topics: (1) factors affecting seed set (Owens and others 1991); (2) effects of inbreeding level on filled seed production (Woods and Heaman 1989); (3) influence of reproductive phenology on genetic diversity of seed crops (Copes and Sniezko 1991; El-Kassaby and Askew 1991); and (4) differences in fruitfulness between clonal and seedling orchards (El-Kassaby and others 1989). Cultural practices to stimulate seed production in natural

Table 3—*Pseudotsuga,* Douglas-fir: height, seed-bearing age, crop frequency, and cone length

Species	Mature height (m)	Minimum seed-bearing age (yr)	Years between large seedcrops	Cone length (cm)
P. macrocarpa	9–30	20*	—	11–17
P. menziesii				
var. *glauca*	23–49	20	3–10	4–7
var. *menziesii*	27–91	7–10†	2–11	6–10

Sources: Allen (1942), Boe (1954), Gause (1966), Hermann and Lavender (1990), Lowry (1966), McArdle and others (1961), McDonald (1990), Roeser (1942), Sudworth (1908).

* Occasionally earlier on good, open sites (Gause 1966).

† The minimum age for commercial collections has been considered 20 to 25 years (Allen 1942).

stands or seed orchards include thinning and spacing (Reukema 1982, Williamson 1983); fertilization (Edwards 1986); girdling (Wheeler and others 1985; Woods 1989); top pruning (Copes 1973); and use of growth regulators alone (Ross and others 1980) or in combination with girdling, root-pruning, top-pruning, and branch-thinning (Ross and Bower 1991; Ross and Currell 1989; Ross and others 1985). In 1990, Cress and Daniels reported that existing coastal Douglas-fir seed orchards had the production potential to reforest 11 million acres with genetically improved stock by the year 2000.

Hedlin and others (1980) have developed a key for the many insects that damage cones and seeds of Douglas-fir. The Douglas-fir cone moth (*Barbara colfaxiana Kearfott*) causes major damage throughout the range of Douglas-fir but is most persistent in dry areas (Miller and Ruth 1989). As few as 3 larvae can destroy all of the seeds in a cone. The Douglas-fir cone gall midge (*Contarinia oregonensis* Foote) is another major destroyer of seeds, particularly in wet areas; severe infestations can destroy an entire crop. The Douglas-fir seed chalcid (*Megastigmus spermotrophus* Wachtl.) is found on both Douglas-fir and bigcone Douglas-fir and frequently destroys 2 to 15% of the crop. Other insect pests include the western flower thrips (*Frankliniella occidentalis* Pergande), which feeds on Douglas-fir pollen in California; Douglas-fir cone scale midge (*Contarinia washingtonensis* Johnson); coneworms (*Dioryctria abietivorella* Groté, *D. pseudotsugella* Munroe, and *D. reniculelloides* Mutuura and Munroe); western conifer seed bug (*Leptoglossus occidentalis* Heidemann); and the fir cone looper (*Eupithecia spermaphaga* Dyar). The western spruce budworm (*Choristoneura occidentalis* Freeman) has also caused heavy damage to flower buds, flowers, and developing cones (Dewey 1970; Frank and Jenkins 1987).

A variety of efforts have been made to assess and curb insect damage to cones and seeds of Douglas-fir. The effects of cone and seed insects were evaluated in natural stands (Shearer 1984) and in Douglas-fir seed orchards (Schowalter and Haverty 1989; Schowalter and others 1985). Dombrosky and Schowalter (1988) suggested an inventory monitoring system to better identify causes of seed loss, and Miller (1986) described damage prediction systems to judge the need for protection from the Douglas-fir cone gall midge and other insects. Rappaport and Volney (1989) found that control of one pest resulted in increased damage from another. Insecticide treatments have been tested for protecting against all cone and seed insects (Stein and Koerber 1989; Stein and Tilden 1987; Summers and Miller 1986), and specifically from the cone gall midge and seed chalcid (Stein and Markin 1986) and the western spruce budworm (Stipe and Green 1981). The role of 2 recently identified pests, the Douglas-fir twig mining beetle (*Pityophthorus orarius* Bright) and a flightless weevil (*Lepesoma lecontei* (Casey), have also been investigated (Rappaport and Wood 1989; Sexton and Schowalter 1991).

Douglas-fir flowers, cones, and seeds are also affected by frost, small mammals, and birds. Buds, flowers, and conelets are periodically damaged by spring frosts (Roeser 1942; Silen and Keene 1969; Timmis 1977). Squirrels start clipping cones early, but they cut cones in large quantities mainly after seeds mature (Lavender and Engstrom 1956; Moore 1940; White and White 1985).

Collection of cones. Douglas-fir cones are collected from untended natural stands; from natural stands tended for seed production; from seed orchards; and even from trees growing in yards, playgrounds, and parks. The scope of collection ranges from a few cones for scientific or personal purposes to region-wide collections to achieve technical or commercial objectives. Thus, collection techniques range from simple hand methods to highly mechanized efforts with commensurate preharvest planning and organization

(Brown 1983; Maxwell and Aldhous 1967). Whatever the size of the collection, the same key considerations are involved—where, when, and how to collect and how to care for the cones afterward.

With 2 varieties to choose from and demonstrated genetic, geographic, and ecologic adaptation within each, choosing the right source from which to collect Douglas-fir cones is complex. Fortunately, the general axiom to collect seeds from sources ecologically similar to where they are to be used has been implemented by designation of seed zones (Rudolf 1974; Stein and others 1986) and development of seed transfer guidelines (Campbell 1986, 1991; Campbell and Sugano 1993; Randall 1996; Rehfeldt 1981, 1983a&b). Though much less is known about genetic variation in bigcone Douglas-fir, the same attention should be given to ecologically matching the seed source to the planting location.

Seeds are sufficiently ripe and ready for collection from 3 to 4 weeks before cones begin to open and shed seeds (Allen 1958a; Finnis 1950; Rediske 1969). This short collection period may start as early as August at low elevations and latitudes and as late as October at high elevations and latitudes (table 2), and it also varies with yearly weather conditions and from tree to tree (Allen 1958a; Brown 1983).

In general, cone color is not a good indicator of seed ripeness; browning of the external bracts is more diagnostic (Ching and Ching 1962). Ripeness is best determined by cutting cones open to reveal the seeds' color and appearance. The seedcoat should be golden brown to dark brown and the seed-wing light brown to tan; the endosperm should be full and firm; and the embryo should be yellowish green and fill most of its cavity (Brown 1983; Ching and Ching 1962; Finnis 1950; Willis 1917). Sample cones are cut longitudinally to check on seed ripeness and estimate seed yield. The count of filled seeds visible on one cut surface multiplied by 4.5 approximates the number of filled seeds per cone (Olson and Silen 1975). An average of 5 filled seeds per cut surface is generally needed for an economic large-scale harvest; lesser yields may be sufficient when supplies are scarce or only minor quantities are needed (Douglass and TerBush 1975; Portlock 1996; Schaefer and Miller 1985).

Douglas-fir cones are collected from standing trees, from felled trees or tops, and from squirrel caches. A whole array of spurs, ladders, cable methods, lifts, and axillary devices are used to assist climbers in getting into the crowns of tall trees and safely collecting cones (Matusz 1964; Portlock 1996). Vehicle-mounted lifts are often used in seed orchards. Shaking the cones from trees has been accomplished without serious crown damage (Copes 1985; Copes and Randall 1983; USDA FS 1972). Cost-effective methods have been devised to aerially rake crowns or clip tops by helicopter (Camenzind 1990; Wallinger 1985). Gathering squirrel-cut cones from the ground or from caches is still a key method of obtaining cones from tall trees in natural stands (Brown 1983; Maxwell and Aldhous 1967; White and White 1985). Squirrel caches provide a means of extending the harvest season, as the cones are usually cached in moist areas and remain closed. However, damage from molds may be greater than in cones harvested from trees. Silvicultural and practical advantages and disadvantages of each collecting method have been summarized by Edwards (1985).

Picked cones are bagged, then transported either first to a collection station or directly to a processing plant where they may be held before seeds are extracted, cleaned, and stored. Two concerns are paramount: keeping the collected cones adequately identified and ensuring good ventilation to prevent killing seeds from overheating or molding. A label on the inside and outside of each bag or container should at least indicate the species, geographic location, elevation, date, and signature of the collector (Stein and others 1986). Plastic mesh bags are preferred over burlap sacks because of better aeration and thus decreased likelihood of contamination by molds. To facilitate air circulation and cone expansion, bags are usually filled only half full, loosely tied, and kept in shade on racks at field sites, collection stations, and even during transport (Brown 1983).

Cones may be stored for 2 to 4 months under dry, well-ventilated conditions without impairing seed viability (Bloomberg 1969; Lavender 1958; Rediske 1961; Rediske and Shea 1965). In fact, under good cone storage conditions, seeds may benefit from after-ripening (Bloomberg 1969; Rediske 1961), whereas lengthy storage of green cones under warm moist conditions can result in severe seed losses from increased molding (Rediske and Shea 1965). Because of tree-to-tree variation in time of seed ripening, any broad-scale collection contains cones with immature seeds that need after-ripening (Allen 1958a; Olson and Silen 1975; Rediske 1961; Silen 1958). Currently, some processors after-ripen cones in well-ventilated, refrigerated vans at temperatures of 7 to 10 ºC (Lippitt 1996). Air-drying cones in protected, well-ventilated storage for several weeks or longer is more common, however (Brown 1983; Schaefer and Miller 1985).

Extraction, cleaning, and storage of seeds. At most extractories, Douglas-fir cones are at least partially air-dried during storage, then kiln-dried to fully open them. Where warm, low-humidity conditions prevail, air-drying may be sufficient, but in much of the West, some supplemental heat is necessary. Slow drying at moderate temperature is recom-

mended (table 4), as high heat applied to green cones and seeds of high moisture content can be very damaging (Allen 1958b; Hall 1984; Morris 1936; Willis 1917). Cones may be moistened just before kiln-drying to overcome any case-hardening and to facilitate a uniform rate of drying (Brown 1983). Cones of coastal Douglas-fir open fully with loss of 35 to 51% of their wet weight (Willis 1917).

Seeds are extracted from fully open cones in a variety of tumbling devices, ranging from a hand-turned, screen-covered wooden frames to large rotary combination dryer-tumblers (Stein and others 1974). Because both heat and sharp impacts can damage Douglas-fir seeds (Allen 1958b), loose seeds are often removed at several stages of processing—before kiln-drying, during drying, and during tumbling. A seed moisture content of 7.5% (wet weight basis) or less is sought during kiln-drying or by later supplemental conditioning (Brown 1983).

Post-extraction processing of seeds usually includes (1) screening to separate seeds from cone scales, dirt, and debris, (2) de-winging, and (3) fanning or blowing to remove hollow seeds, wings, and dust. Vibrating, air, or gravity separators; soaking and drying; and other methods may be used to get seedlots extra clean (Hergert and others 1971; Lowman 1975; Sweeney and others 1991). Elimination of small seeds by sizing is not recommended, however, as this reduces genetic diversity (Silen and Osterhaus 1979). In every stage of cleaning, sharp impacts need to be minimized to produce Douglas-fir seedlots of highest quality (Allen 1958b). An attainable processing standard for Douglas-fir is 98% for purity and 80% or higher for viability (Brown 1983; Lippitt 1996; Stein and others 1986).

Cone sizes and seed weights of Douglas-fir vary by variety, year, geographic location, elevation, aspect, stand age and density, tree and family, and time of collection (Hermann and Lavender 1968; Kozak and others 1963; Olson and Silen 1975; Silen and Osterhaus 1979; Sorensen 1967, 1980, 1983; St. Clair and Adams 1991; Willis and Hofmann 1915). Bigcone Douglas-fir has much larger cones and yields more seeds per weight of cones (table 4). Its smallest seeds average 5 times the weight of the largest seeds of interior and coastal Douglas-firs (table 5).

For coastal Douglas-fir, the number of cones per volume ranged from 977 to 5,067/hl (344 to 1,784/bu) in collections from 309 individual 35-year-old trees (Olson and Silen 1975); in collections from 127 individual 15- to 600-year-old trees, cones per volume ranged from 1,988 to 5,441/hl (700 to 1,916/bu) (Willis and Hofmann 1915). For both coastal and interior Douglas-fir, size of seeds tends to decrease from southern to northern latitudes, that is, to increase in number per weight (table 5). Douglas-fir seeds near the coast tend to be smaller than those from further inland, and seeds from lower elevations are sometimes smaller than those from higher elevations (Griffin and Ching 1977; Hermann and Lavender 1968; Lippitt 1996; Sorensen 1967, 1983; Sorensen and Miles 1978; Sweet 1965). Seeds produced in a seed orchard from trees of coastal Oregon origins were similar in weight to those produced by trees in untended stands (table 5).

Seeds of Douglas-fir are usually stored at or near –18 °C at moisture contents of 5 to 9% (wet weight basis) in sacks or plastic-lined fiberboard drums (Brown 1983; Stein and others 1986). Viability of good seedlots can be maintained for many years under these storage conditions; 85 to 87% germination of several coastal Douglas-fir seedlots has been maintained for 27 years (Lippitt 1996). Moderate to good seed viability has been maintained for varying lengths of storage around 0 to 5 °C, but viability declines rapidly in storage at room temperature and at high moisture content (Allen 1957, 1962a; Barton 1954; Schubert 1954).

Pregermination treatments and germination tests. Pregermination treatment of Douglas-fir seeds strongly influences their subsequent response to various germination conditions. Most seedlots benefit from stratification, but some do not require stratification, some are harmed by it,

Table 4— *Pseudotsuga,* Douglas-fir: cone drying schedules and seed yield data

Species	Cone drying schedule			Cone wt/cone vol		Seed yield		
		Kiln-drying				Seed wt/cone vol		Ratio seed wt/
	Air-drying (days)	Time (hr)	Temp (°C)	kg/hl	lb/bu	kg/hl	lb/bu	100 cone wt
P. marocarpa	8–10	—	—	32–39	25–30	1.03	0.8	2.8
P. menziesii								
var. *glauca*	4–60	2–10	38–43	32–77	25–60	0.65–1.03	0.5–0.8	1.0–1.3
var. *menziesii*	8–60	16–48	32–43	39–64	30–50	0.26–1.03	0.2–0.8	0.5–2.0

Sources: Brown (1983), Owston and Stein (1974), Radcliffe (1952), Swingle (1939).

Table 5—*Pseudotsuga,* Douglas-fir: cleaned seeds per weight

Species & location	Average /kg	Average /lb	Range /kg	Range /lb	Samples[a]
P. macrocarpa					
S California	7,145	3,241	6,137–8,115	2,800–3,681	2
S California	7,716	3,500	6,614–9,921	3,000–4,500	2
S California	11,001	4,990	9,259–13,927	3,460–6,317	3
S California	6,748	3,061	—	—	1
P. menziesii var. *glauca*					
Arizona	70,768	32,100	52,911–75,619	24,000–34,300	8
New Mexico	83,555	37,900	72,312–90,830	32,800–41,200	8
Colorado	85,539	38,800	73,414–96,122	33,300–43,600	33
Montana	88,405	40,100	79,807–99,869	36,200–45,300	14
E Washington	102,354	46,427	101,834–103,093	46,191–46,762	3
British Columbia	97,665	44,300	62,832–117,506	28,500–53,300	19
British Columbia	119,905	54,388	104,166–163,398	47,249–74,116	23
P. menziesii var. *menziesii*					
Coastal California					
Fog-belt	86,882	39,409	80,257–104,058	36,404–47,200	4[b]
Inland	70,028	31,764	55,618–78,493	25,228–35,604	5[c]
California	71,752	32,546	33,951–116,845	15,400–53,000	41
N California	67,250	30,504	40,858–109,171	18,409–49,519	20[d]
California					
Zones 090	72,305	32,797	63,268–93,268	28,698–42,605	62
Zones 300	65,538	30,181	54,780–81,359	24,848–36,904	29
Zones 500	56,906	25,812	48,028–69,867	21,785–31,691	37
W Oregon	76,278	34,599	58,343–99,109	26,464–44,955	8[d]
W Oregon	110,498	50,121	84,104–126,263	38,149–57,272	10
NW Oregon	99,503	45,134	69,589–182,150	31,565–82,622	309[e]
W-central Oregon	83,333	37,799	62,501–109,409	28,350–49,627	39
W Oregon	78,626	35,664	59,000–98,000	26,762–44,452	8[f]
Oregon & Washington	84,336	38,254	77,162–125,664	35,000–57,000	127[g]
Oregon & Washington	86,589	39,276	73,634–102,458	33,400–46,474	97
Coastal Oregon (seed orchard)	87,268	39,584	76,128–110,972	34,531–50,336	23
Washington Cascades	81,183	36,824	75,074–87,336	34,053–39,615	2[d]
W Washington	77,499	35,153	74,999–79,999	34, 019–36,287	2[f]
W Washington	116,822	52,990	82,576–153,845	37,456–69,783	46
British Columbia	86,999	39,462	65,001–99,999	29,484–45,359	4[f]
British Columbia	130,891	59,371	107,411–173,012	48,721–78,749	21
British Columbia	93,584	42,449	79,807–120,593	36,200–54,700	16

Sources: Allen (1942), Bialobok and Mejnartowicz (1970), Ching and Bever (1960), Griffin and Ching (1977), Heit (1968), Lippitt (1996), Olson and Silen (1975), Owston and Stein (1974), Rafn (1915), Randall (1997), St. Clair and Adams (1991), Sweet (1965), Willis and Hofmann (1915).

a Data represent seedlots of unknown size and number of trees unless otherwise noted.

b Four locations representing 41 elevation points (stands) totaling 87 trees.

c Five locations representing 44 elevations points (stands) totaling 94 trees.

d Each provenance (sample) represented by 10 trees under 50 years of age.

e Collected over the entire season (August 12 to September 15) from individual 35-year-old trees growing at 122 to 518 m of elevation.

f Each sample collected from 14 to 89 trees within a 40-km radius.

g From individual open-pollinated parent trees.

and some that need it are harmed by too lengthy stratification (Allen 1960; Allen and Bientjes 1954; Gosling 1988; Jensen and Noll 1959; Taylor and others 1993). Based on accumulated experience, seeds of coastal Douglas-fir generally require or benefit from stratification, those of interior Douglas-fir from northern sources may benefit, those from southern sources may not benefit, and the response to stratification by bigcone Douglas-fir is unknown (Allen 1960, 1962c; Heit 1968).

Stratification overcomes different degrees of seed dormancy that may be related to seed source and family, year of collection, cone and seed drying conditions, length and kind of storage, and other causes (Allen 1960; Allen and Bientjes 1954; El-Kassaby and others 1992; Jensen and Noll 1959; Sorensen 1991). Several pretreatments used with or in lieu of stratification also stimulate germination or reduce pathogen damage. These include a light rinse with cold or hot water, fungicide, bleach, hydrogen peroxide, ethanol, polyethylene glycol, or ethylene (Borno and Taylor 1975;

Ching 1959; Dumroese and others 1988; James and others 1988; Li and others 1994; Paci 1987; Shearer and Tackle 1960; Trappe 1961; Wenny and Dumroese 1987).

For seedlots that benefit, stratification speeds the rate of germination; for many, it also increases total germination (table 6). Although the increase in total germination was often not large, it occurred in 76.1% of samples submitted for standard service testing (Jensen and Noll 1959). The increase in germination may be substantial after lengthy stratification when seeds are tested at low temperatures or have been produced in seed orchards (Allen 1960, 1962c; Campbell and Sorensen 1984; Jones and Gosling 1994; Muller and others 1999; Sorensen 1991). Even small gains are important when using valuable improved seeds.

Douglas-fir seeds are usually stratified "naked," that is, without medium. For testing, dry seeds are often placed directly on the moistened substratum in a closed dish, or soaked in tap water for 24 hours, drained, and then placed in a closed container or bag to prechill at 2 to 5 °C for 3 weeks (AOSA 2001).

The official germination test procedures for both coastal and interior Douglas-firs require paired samples—one prechilled for 21 days at 2 to 5 °C and one not—then subjected to alternating day and night temperatures of 30 °C for 8 hours and 20 °C for 16 hours, with light at least during the high temperature period (AOSA 2001; ISTA 1996). Test duration is 21 days. A variety of absorbent blotters and other materials may be used as substratum—Sponge Rok®, vermiculite, Terralite®, and mixtures with sand. Alternating temperatures are prescribed because these yielded the highest and most consistent germination in comparison tests (Jensen and Noll 1959). But given appropriate prechilling and germinating periods, Douglas-fir will germinate with or without light in constant temperatures from 10 to 30 °C but higher temperatures cause damage (Allen 1960, 1962c; Gosling 1988; Jones and Gosling 1994; Sorensen 1991; Wright 1931). Seed position influences rate of germination; when the side of the seed that developed against the cone scale is on top, 50% germination on a moist surface is obtained in 4.6 days versus 6.3 days for those of opposite orientation, and response varies among seeds of different geographic origin (Sorensen and Campbell 1981). Rate of germination also varies among seedlots and is not directly linked with total viability (Thomson and El-Kassaby 1993). Average germination and germinative energy data from source-paired comparisons and other test experiences are listed in table 6.

Germination conditions for bigcone Douglas-fir are relatively untested (table 6). Techniques that work well for the other Douglas-fir species may prove satisfactory.

Several methods are used to quickly appraise the quality and vitality of Douglas-fir seeds when approximations are adequate or time is too short for germination tests. Determining viability by a tetrazolium (TZ) test is officially recognized and standard procedures have been designated (AOSA 2000). Seeds are soaked in water at room temperature (20 to 25 °C) overnight, then sliced longitudinally,

Table 6—*Pseudotsuga,* Douglas-fir: stratification periods, germination conditions, and results

Species	Stratification* (days)	Germination conditions: Moist medium	Temp (°C): Day	Temp (°C): Night†	Germination conditions: Days	Germinative energy: Amt (%)	Germinative energy: Time (days)	Germ. capacity (%): Avg	Germ. capacity (%): Range	Germ. capacity (%): Samples
P. macrocarpa	28	Vermiculite	30	20	28	—	—	31	—	3
	—	—	—	—	100	14	60	28	14–36	3
	—	Sand	27	21	20–90	—	—	30	15–57	5
P. menziesii	21	Sponge Rok®	30	20	14–21	60	9	68	24–83	8
var. *glauca*	0	Sponge Rok	30	20	21–35	40	12	60	27–75	8
	30	Paper	30	20	17	70	10	78	—	3‡
	0	Paper	30	20	29	76	9	84	—	3‡
	20–40	Vermiculite	25	25	30	—	—	95	86–100	6
	0	Vermiculite	25	25	50	—	—	93	88–98	6
P. menziesii	21	Sponge Rok	30	20	14–35	55	10	81	38–95	194
var. *menziesii*	0	Sponge Rok	30	20	28–35	54	17	75	29–93	194
	20–40	Vermiculite	25	25	30	—	—	87	34–100	20
	0	Vermiculite	25	25	50	—	—	84	42–100	20
	28	—	30	20	28	—	—	84	66–98	129

Sources: Allen (1962c), Lippitt (1996), Owston and Stein (1974), Rafn (1915).

* Seeds stratified "naked" (Allen and Bientjes 1954) or on moist Sponge Rok, vermiculite, or paper at 0 to 5 °C.

† Alternating temperatures included 8 hours of light during the high temperature period; light apparently was provided with constant temperature.

‡ Var. *glauca* from north-central Colorado seed sources.

soaked in a 1% TZ solution at 30 to 35 °C for 4 to 6 hours (or longer at lower temperatures), and evaluated. Healthy endosperm and embryo tissue stains uniformly pink to red. Vitality can also be determined by 2 other tests. In the one test, embryos are excised and placed in conditions favorable for growth for several days (Heit 1955); in the other test, radicle tips are cut and the seeds soaked in weak hydrogen peroxide solution under conditions that promote radicle elongation (Ching and Parker 1958). In a visual test, the oldest and simplest, seeds are cut open to determine if they are full or empty, insect damaged, or shriveled and their quality judged by the appearance and color of the endosperm and embryo; this test is still useful for a quick evaluation, particularly in the field. Seeds can be evaluated non-destructively from x-ray views, which can reveal full, empty, shriveled, and insect-filled contents, as well as any damage to the seedcoat and interior (Belcher and Vozzo 1979). Estimates of Douglas-fir seed viability are now similar if measured by x-radiography and by germination, TZ, or hydrogen peroxide testing (Hardin 1981).

Nursery practices. Millions of Douglas-fir seedlings are grown in both bareroot and container nurseries. Bareroot production predominates in the United States; container production predominates in Canada. Many sizes of seedlings are produced, ranging from small 1+0 to 3+0 bareroot stock; 1-year-old container (plug) stock; and 1+1, 1+2, 2+1, 2+2, or plug+1 transplants. Use of 1+1 transplants is now very common and plug+1s are gaining attention. Extra large stock is often used to combat animal damage or competing vegetation and for restoration plantings in riparian areas.

Technology for the production of Douglas-fir seedlings is detailed and varies by nursery and the type and size of stock to be produced. Careful management of growing-medium fertility and drainage in both bareroot and container nurseries is critical for growth and hardiness of Douglas-fir. The factors and specific techniques involved in producing bareroot Douglas-fir seedlings are presented in the Forest Nursery Manual (Duryea and Landis 1984); those for containers in the multiple-volume Container Tree Nursery Manual (Landis and others 1989, 1990a&b, 1992, 1995). The concept and practices for producing seedlings with morphological and physiological characteristics targeted for specific field conditions were brought together in a symposium (Rose and others 1990).

Production and grading practices have the potential of influencing the genetic composition as well as the physical characteristics of the seedling populations produced (Campbell and Sorensen 1984; El-Kassaby and Thomson 1996; Sorensen and Campbell 1993; St. Clair and Adams 1993). Thus, every nursery practice needs scrutiny to avoid severely altering the intrinsic characteristics for which each seedlot is valued.

Both bareroot and container nurseries usually sow stratified seeds as early in late winter or spring as possible to maximize growth and vigor of first-year seedlings (Sorensen 1996). Fall-sowings can produce even larger seedlings, but the risk of seed losses over winter from natural causes is usually too great (Duryea 1984). Before sowing outdoors or in containers, seeds are commonly soaked in tap water at 10 to 22 °C for 24 to 48 hours, drained of excess water, perhaps surface-dried, and then prechilled in 2-kg (5-lb) quantities per plastic bag in a cooler at 1 to 5 °C (Allen 1962b; Allen and Bienjes 1954; Johnson 1983; Tanaka 1984). A breather tube may be inserted in the neck of the bag and such intermediate tending as rinsing, addition of water, and turning may be done during 28 to 60 or even 90 days of stratification. Results from germination tests help guide the choice and length of pretreatments applied to individual seedlots. Germination is epigeal (figure 4).

When necessary, stratified Douglas-fir seeds can be stored for later use. Stratified seeds that were air-dried and stored at relatively high moisture content at 2 °C for 3 months or oven-dried to 7 to 15% moisture content and

Figure 4—*Pseudotsuga menziesii* var. *menziesii, coast* Douglas-fir: epigeal seedling development at 2, 5, 8, and 22 days after emergence from a peat moss–vermiculite potting mixture.

stored at –7 to 3 °C for 9 months or more retained the viability and stratification effect (Allen 1962b; Belcher 1982; Danielson and Tanaka 1978; Jones and Gosling 1994; Muller and others 1999). In other trials, viability was retained by partial drying of stratified seeds followed by low temperature storage, but the stratification effect was lost (Hedderwick 1970; Malavasi and others 1985). Seeds cannot be held in stratification indefinitely; seeds of some lots will deteriorate and those of others will germinate (Allen 1960; Danielson and Tanaka 1978; Sorensen 1980, 1991).

For bareroot production, most Douglas-fir seeds are drill-sown at a depth of 3 to 6 mm (0.1 to 0.2 in). The larger seeds of bigcone Douglas-fir are usually sown at a depth of 13 mm (0.5 in). Seedbed density varies depending on the stock size desired. For 2+0 Douglas-fir stock, seedling densities vary from 161 to 323/m^2 (15 to 30/ft^2); for 1+1s, bed densities of first-year seedlings range from 538 to 753/m^2 (50 to 70/ft^2) (Thompson 1984). Seedbed density has more effect on size of seedlings produced, and on their subsequent field survival and growth, than does irrigation frequency or undercutting and wrenching (Stein 1988).

Irrigation is used in bareroot nurseries to supply moisture to seeds and seedlings, prevent overheating or frost damage, promote growth, and augment other practices such as fertilizing and root wrenching (Duryea 1984). Carefully planned irrigation regimes are also used to control moisture stress, harden seedlings, and initiate dormancy. Specific irrigation regimes should be developed for each nursery and kind of stock—seedlings can be harmed by either too much or too little water.

The fertilizer mix and the timing and number of applications must also be developed for each bareroot nursery. Physical and chemical characteristics of the soil and irrigation water and the density of the seedling crop are critical influencing factors. A pH of 5.0 to 6.0 has been suggested for nurseries in the Pacific Northwest and 5.5 to 6.5 for nurseries in Intermountain region, as well as concomitant target levels for key mineral elements (Youngberg 1984). Most nurseries stop fertilizing in July or early August to promote seedling hardening (Duryea 1984).

Almost all bareroot nurseries undercut Douglas-fir seedlings to stimulate root growth in the upper soil layers (Duryea 1984). Timing, frequency, and depth vary by nursery and stock type. Eighty percent of nurseries in the Pacific Northwest also wrench the roots of Douglas-fir seedlings to promote fibrous root systems, stress and harden seedlings, control shoot height, and aerate the soil.

Many other cultural techniques including transplanting, weed and pest control, top pruning, and mycorrizhal inoculation are used to condition bareroot Douglas-fir seedlings for specific field conditions. Emphasis continues on fine tuning and evaluating seedling quality. Thus, an array of morphological and physiological tests have been developed to assess the quality of Douglas-fir seedlings (Duryea 1985; Jenkinson and others 1993; Rose and others 1993, 1997). Grading criteria and target sizes have been recognized for different types of stock (Iverson 1984), but more importantly, the trend is to specify seedlings by height and stem caliper as well as by stock type.

In containers, plantable stock can be produced in one season in greenhouses, outdoors under shade, or in the open. Douglas-fir grows well in the containers commonly used in forestry. High-quality, well-stratified seeds are particularly important in producing container-grown Douglas-fir. Other important considerations include keeping the pH of the potting mixture between 4.5 and 6.0; using growing practices that produce seedlings with tops and roots in balance; and hardening the seedlings to withstand direct sunlight and cold.

Fast growth of Douglas-fir is achieved in containers by providing greater control of the growth environment than possible in a bareroot nursery (Landis and others 1995). A precise growing regime must be developed suited to the capabilities at the individual container facility and the requirements of the stock to be produced. For example, Wenny and Dumroese (1992) describe a regime for producing interior Douglas-fir container stock at a facility in Idaho. Producing this variety in a single season requires use of artificial light to lengthen the photoperiod early in the growing season.

To produce extra hardy, compact stock, seedlings are grown in containers for the first year and in outdoor beds for a second year. The resulting plug+1 stock has a very fibrous root system and is usually larger and sturdier than 1+1 stock (Iverson 1984).

Douglas-fir is also propagated commercially by adventitious rooting of cuttings (Myers and Howe 1990; Ritchie 1991). Cuttings are rooted in 1 season, transplanted to a bareroot nursery in the fall to overwinter, and then grown for 1 year as bareroot stock. Over 5 years, stock from cuttings has performed similarly to 1+1 transplants. Cuttings from juvenile wood root better than those from older wood and have less plagiotropic tendencies (Copes 1992). Juvenile meristems are produced in quantity by accelerating first-year growth of stock plants (Ritchie 1994) or by maintaining juvenility on older trees by pruning (Copes 1992). Limited numbers of Douglas-fir emblings are produced by micropropagation techniques (Gupta and Grob 1995; Hutzell and

Durzan 1993; Tabor and others 1998). Rapid multiplication of superior genetic strains is made possible by practical vegetative propagation.

Seedling care. Whether bareroot or container-grown, Douglas-fir stock is best able to withstand the shock of lifting, storage, and outplanting when dormant, that is, after adapting to winter conditions. Midseason reductions in applying water and fertilizer, root wrenching, and other techniques are used to slow growth and enhance the normal climatic progression toward dormancy.

Because Douglas-fir seedlings are quite vulnerable, great care should be taken to minimize mechanical damage, desiccation, and molding during lifting, processing, storage, transportation, and planting. Protective practices include hydrating seedlings before lifting; minimizing exposure of lifted seedlings to direct sunlight, temperature extremes, and wind; preventing metabolic over-heating; misting during processing; storing and transporting them at low temperatures in bags or cartons with vapor barriers; and minimizing handling and exposure during field planting (Burdett and Simpson 1984).

Properly hardened Douglas-fir nursery stock can be stored for lengthy periods at temperatures just above or below freezing (Burdett and Simpson 1984; Hee 1986). Freezer storage prevents molding and some dormancy developments that would occur if seedlings were exposed outdoors (Ritchie 1987). Frozen bareroot and container seedlings should be thawed before they are planted (Hee 1986; Rose and Haase 1997).

Douglas-fir is usually outplanted any time from late fall through spring, depending on local climate. Winter and early spring plantings are usually best in areas with mild winters west of the Cascade Mountains. The planting season may extend into early summer in interior regions and at high elevations where snow lingers. Seedlings are extracted from most types of containers either before storage or before shipment to the field. Bigcone Douglas-fir was planted periodically from 1905 to 1975 in Los Angeles County, California, but results are unknown (McDonald 1990); in contrast, there is overwhelming evidence on successful plantings of coastal and interior Douglas-fir.

Nursery managers are dedicated to producing the size and vigor of Douglas-fir stock needed for an extremely wide range of field conditions. In many instances, the kind of stock required and the nursery practices needed to produce it are well defined; in some instances, however, either the stock or the field practices need improvement. Specific trials testing variations in a nursery's practices for producing stock of different sources may be needed, for example, "lifting windows" as investigated by Jenkinson and others (1993).

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Fabaceae—Pea family

Psorothamnus Rydb.

indigobush

Jane E. Rodgers and Carol Miller

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Other common names. dalea.

Growth habit, occurrence, and use. The indigobush genus—*Psorothamnus*—includes 9 species that are spread throughout the southwestern United States into Mexico (table 1). The majority of these shrubs are ornamental and many of them also contribute to the forage value of stock ranges. Branches of dyeweed have been used by Native Americans in southwestern Arizona and southern California for dye, medicine, and basket construction (Bean and Saubel 1972; Kearney and Peebles 1951).

Flowering and fruiting. Flowering occurs during the summer months (Benson and Darrow 1954). Calyx lobes are usually unequal, with the upper pair often largest. Petals emerge from the receptacle in violet, blue, or purple and white together (Jepson 1993). Fruits are indehiscent, included in or protruding from the calyx. The fruits are usually glandular and produce just 1 seed (figures 1 and 2) (Jepson 1993).

Seed collection can begin in July and continue through September for Schott dalea and smoketree as seeds get plump and change color (CALR 1993). Insect-infested seeds on the ground should be avoided. Seeds of this genus are orthodox in storage behavior and have been stored successfully under a variety of conditions (table 2).

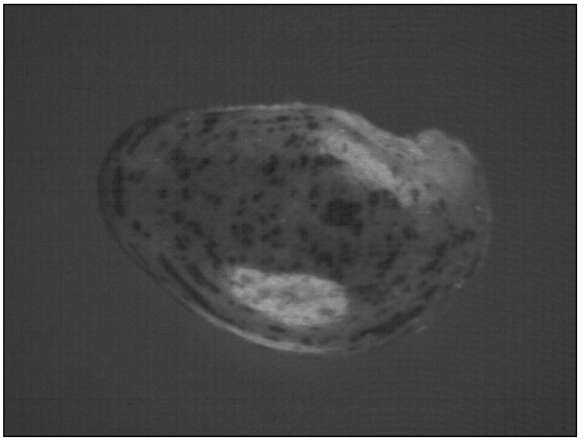
Table 1—*Psorothamnus,* indigobush: nomenclature and occurrence

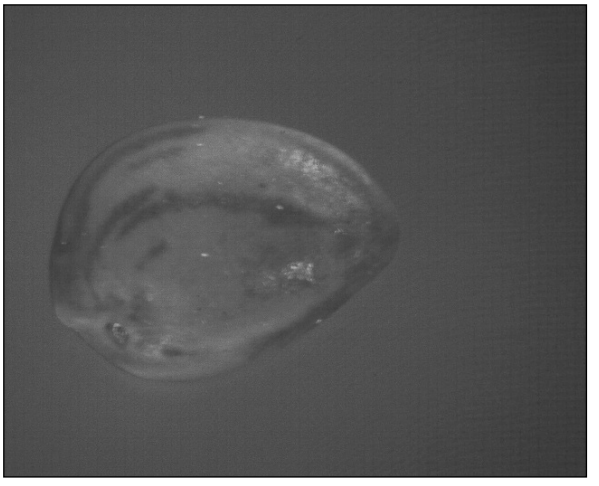
Scientific name & synonyms(s)	Common name(s)	Occurrence
***P. arborescens* (Torr. ex Gray) Barneby** *Dalea arborescens* Torr. ex. Gray. *Parosela arborescens* Heller *Parosela neglecta* Parish	**indigobush,*** Mojave dalea	San Bernadino Mtns, Mojave Desert, S Nevada, Mexico
***P. arborescens* var. *arborescens* (Torr. ex Gray) Barneby**	**Mojave indigobush,** Saunder dalea	SW Mojave Desert, Mexico
***P. arborescens* var. *minutifolius* (Parish) Barneby**	**Johnson dalea**	Mojave Desert, S Nevada
***P. arborescens* var. *simplifolius* (Parish) Barneby** *P. californica* *Dalea californica* S. Wats.	**California dalea**	Mojave Desert & San Bernadino Mtns.
***P. emoryi* (Gray) Rydb.** *Dalea emoryi* Gray	**dyeweed,*** dyebush	Mojave & Sonoran Deserts
***P. fremontii* (Torr. Ex Gray) Barneby** *Dalea fremontii* Torr.	**Fremont dalea**	Desert mtns to S Utah, Arizona
***P. polydenius* (Torr. ex S. Wats.) Rydb.**	**Nevada dalea,** Nevada smokebush	Mojave Desert
***P. schottii* (Torr.) Barneby** *Dalea schottii* Torr.; *Parosela schottii* Heller	**indigobush**, Schott dalea	Sonoran Desert of Arizona & Mexico
***P. spinosus* (Gray) Barneby** *Dalea spinosa* Gray; *Parosela spinosa* Heller	**smoketree,** smokebush	California deserts to Arizona & NW Mexico

Sources: Jepson (1993), Munz (1962, 1974).

* Despite the name, not a source of true indigo dye.

Figure 1—*Psorothamnus*, indigobush: seeds of *P. arborescens* var. *simplifolius,* California dalea (**top**); *P. schottii*, indigobush (**center**); *P. spinosa*, smoketree (**bottom**).





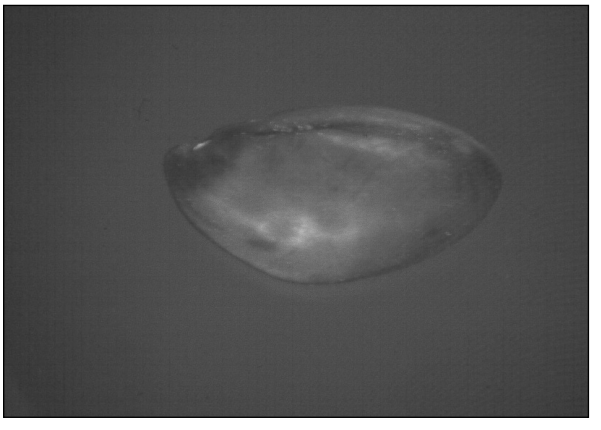
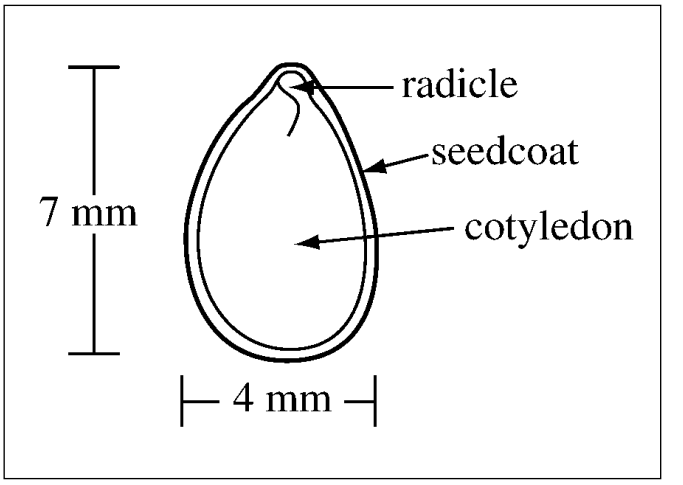


Figure 2—*Psorothamnus arborescens* var. *simplifolius,* California dalea: longitudinal section through a seed.



Pregermination treatments and germination tests. Various seed treatments have been used at the Native Plants Nursery of the U.S. Department of the Interior National Park Service's Joshua Tree National Park (JTNP); however, Emery (1988) does not suggest any pre-treatments. At JTNP, Schott dalea has been germinated by clipping and leaching seeds for 12 to 24 hours, with an average germination rate of 50%. Success with smoketree using a soak in 1:1 bleach–water solution for 30 minutes, followed by leaching for 3 to 4 hours, has resulted in an average germination rate of 40% (CALR 1993).

Other trials by Kay and others (1988) (table 2) refer to initial germination of seeds using 4 replications of 100 seeds each wrapped in damp paper toweling and stored in a growth chamber at 15 °C. Test conditions were maintained for 28 days, with germination percentages recorded every 7 days. Germination tests, conducted annually to test the effects of storage, were then averaged to a "best germination." These annual tests consisted of 4 replications of 50 seeds using the same initial testing methods.

Nursery practice. Seedlings can be successfully grown in a variety of containers. At JTNP, Schott dalea and smoketree have been successfully grown in tubes that are 76 in (30 in) long and 15 cm (6 in) in diameter and 36 cm (14 in) high and in 3.8-liter (1-gal) containers. Outplanting survival has been moderate, depending on rainfall and planting conditions (CALR 1993).

Seedling care. Seedlings can be very susceptible to damping-off. Keeping seedlings where air circulates freely and avoiding over-watering will help boost survival (CALR 1993).

Table 2—*Psorothamnus,* indigobush: seed weight, initial and best germination, and storability of seeds

Species	Seeds/weight /kg	Seeds/weight /lb	Percentage germination Initial	Percentage germination Best	Storability
P. emoryi	600	275	58	75	Stores well
P. fremontii	35	16	41	97	50% hard seed, stores well
P. polydenius	460	210	2	99	90% hard seed, stores well
P. schottii	22	10	90	88	Good storage
P. spinosus	50	23	22	58	17–47% hard seed, stores well

Source: Kay and others (1988).

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Rutaceae—Rue family

Ptelea trifoliata L.

common hoptree

Kenneth A. Brinkman, R. C. Schlesinger, and Jill R. Barbour

Drs. Brinkman and Schlesinger retired from the USDA Forest Service's North Central Forest Experiment Station; Ms. Barbour is a germination specialist at the USDA Forest Service's National Tree Seed Laboratory, Dry Branch, Georgia

Synonym. *P. trifoliata* var. *mollis* Torr. & Gray.

Other common names. wafer-ash, hoptree, woolly common hoptree.

Growth habit, occurrence, and use. Hoptree—*Ptelea trifolia* L.—is a shrub or small tree up to 7.5 m tall with some value for wildlife, shelterbelt, and environmental plantings. It occurs from Connecticut and New York to southern Ontario, central Michigan, and eastern Kansas; south to Texas; and east to northern Florida (Little 1953). The shrub is distributed primarily along waterways in moist forests and successfully colonized sand dunes along Lake Michigan (McLeod and Murphy 1977a). In Canada, common hoptree occurs primarily in sand on the windward side of beaches along Lake Erie (Ambrose and others 1985). Hoptree propagates sexually through seed germination on adverse beach sites because 93% of annual precipitation occurs during the growing season. The species has been cultivated since 1724 (Rehder 1940).

Flowering and fruiting. Common hoptree is an obligate entomophilous, polygamo-dioecious plant. Sex ratios are skewed toward maleness, with a 60 to 40 ratio in a population (Ambrose and others 1985).

The white flowers bloom from April in the Carolinas (Fernald 1950; Radford and others 1964) to July in the North (Fernald 1950). Flowers are formed on terminal cymes with 2 ovaries, 2 stigmas, and 3 to 5 stamens (McLeod and Murphy 1977a; Radford and others 1964). Male flowers produce copious amounts of pollen grains; whereas underdeveloped staminodes of females flowers produce no pollen (Ambrose and others 1985).

Male plants have 3.7 times the amount of floral tissue for reproduction as do female plants, as determined by floral area (Ambrose and others 1985). Despite that, there is a slight (but not significant) skewness toward female flower preference by insects (Ambrose and others 1985).

In southern Ontario, over 102 insects from nearly 40 families visited hoptree plants. Hoptree was found to be the primary host for the rare giant swallowtail— *Papthо creshontes* Cramer (Ambrose and others 1985). Insect pollinators show little preference between female and male plants.

Fruits are reddish brown, orbicular, 2-seeded samaras (figures 1 and 2) that ripen from June to November (Rehder 1940) and may persist until spring (Van Dersal 1938). The seedcoat is composed of a black, crisp outer layer with a thin, brown membranous inner layer (Ambrose and others 1985). The samara is 1.5 to 2.5 cm broad and weighs from 0.026 to 0.067 g (Radford and others 1964). Most fruits only contain 1 seed, but 10% of them may contain 2 seeds. Hoptree is an abundant seeder and the samaras are dispersed by wind. Annual fruit production is about 300,000 samaras per hectare. The reniform seeds are 6.4 mm long, 2.3 wide, and weigh from 0.007 to 0.012 g (McLeod and Murphy 1977a). The embryo is completely embedded in endosperm tissue.

Figure 1— *Ptelea trifoliata*, common hoptree: fruit (samara).

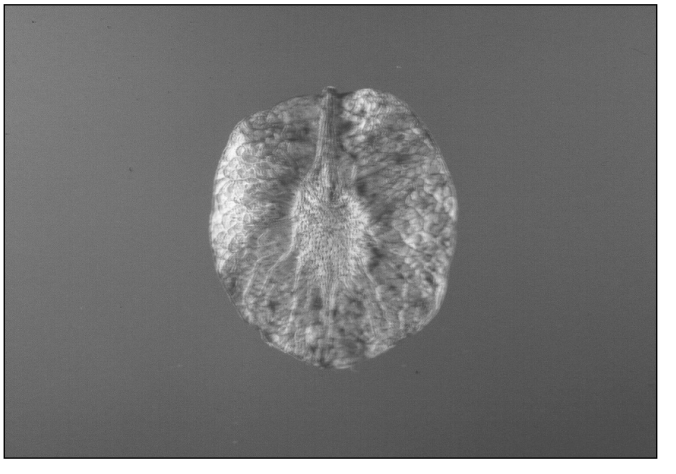
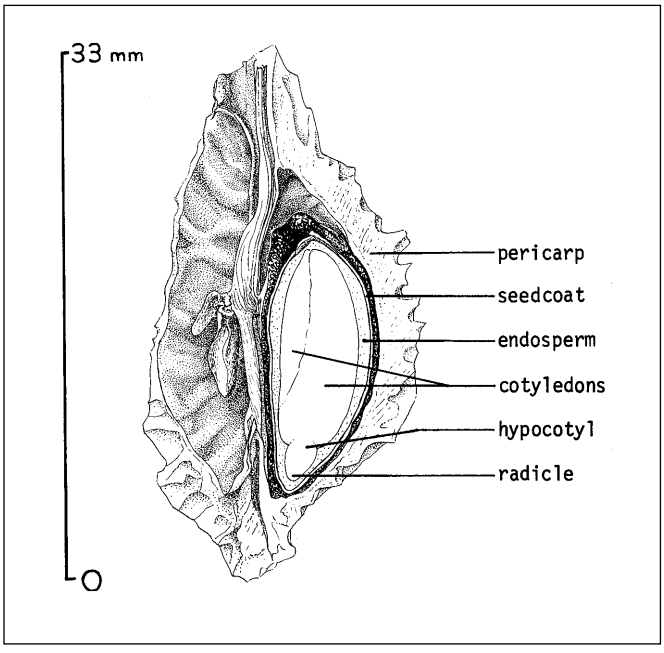


Figure 2— *Ptelea trifoliata*, common hoptree: longitudinal section through a samara.



Collection and storage of seeds. The ripe samaras may be picked from September to November. They may require a few days of drying if they are to be stored. Because samara tissue inhibits germination, removal is recommended (McLeod and Murphy 1977b). In 5 samples, the number of samaras ranged from 19,850 to 39,700/kg (9,000 to 18,000/lb) and averaged 26,500/kg (12,000/lb). About 97% of the fruits contain sound seeds.

The seeds are apparently orthodox in storage behavior—if stored in sealed containers at 5 °C, common hoptree seeds will retain most of their viability for at least 16 months. Seedlot viability determined by the 2,3,5-triphyenyl tetrazolium chloride test was over 90% after 220 days of storage at room temperature and remained over 95% during monthly checks while the seeds were being stratified (McLeod and Murphy 1977b). Viability remained at 90% when seeds were subjected to lower temperatures during germination; higher than optimum temperatures reduced viability to 45% (McLeod and Murphy 1977b).

Germination tests. Hoptree seeds have numerous barriers to germination. No germination resulted from whole fruits, punctured fruits, or whole seeds that were left unstratified (McLeod and Murphy 1977b). Unstratified embryos develop into physiological dwarfs with very short internodes and a low-vigor radicle, suggesting embryo dormancy. Excising the embryo yielded 39.5% germination; removing the seedcoat, 17%; and removing the endosperm covering the radicle, 25% (McLeod and Murphy 1977b). Endosperm tissue is a barrier to radicle elongation, not a dormancy mechanism.

Leachates of fruit parts, diluted 50, 20, 10, and 4%, applied to embryos inhibited development. Of embryos exposed to 5 ml of leachate, only 9% of those exposed to seedcoat leachate germinated; 33% to samara leachate; 45% to endosperm leachate; and 58% to no leachate (McLeod and Murphy 1977b). Stratification negated the effect of the samara leachate on embryo germination (92%) versus the control values (100%).

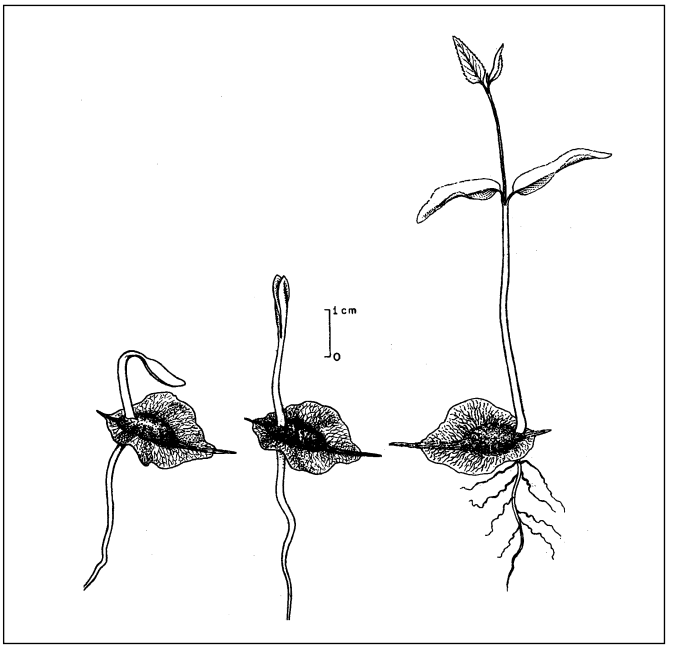
Seeds must be stratified to germinate. Artificial stratification (3 °C) is only successful when the samara is removed. Seed germination of intact fruit was 6% after 211 days of cold stratification; without the samara the germination jumped to 81% after 181 days of stratification (McLeod and Murphy 1977b). During natural stratification, decomposition of the samara is 3 times that resulting from cold-room stratification. Under natural stratification, the samaras were 71% half-decomposed in 150 days compared to the negligible degradation resulting from artificial stratification (McLeod and Murphy 1977b).

Maximum laboratory germination (72%) occurred when temperature fluctuated between 16 and 22 °C; germination of 60% was the best constant temperature (17 °C) value (McLeod and Murphy 1977b). Germination of imbibed seeds exposed to 4 hours daily of 40 °C temperatures was reduced from 45% after 1 week down to 0% after 4 weeks of exposure (McLeod and Murphy 1977b). Germination tests can be made in sand flats at temperatures alternated diurnally from 25 to 10 °C. Germinative capacity in 6 tests ranged from 10 to 91% but averaged only 28% (Brinkman and Schlesinger 1974).

Germination is epigeal (figure 3). In imbibed seeds, it takes 5 to 20 days for the hypocotyl to emerge in the field. Root extension occurred over the 10 weeks following radicle emergence, with 65% completed in 4 weeks and growth about 11 cm long (McLleod and Murphy 1977b).

Nursery practice. Seed should be either fall-sown or stratified over most of the winter and sown in the spring. Seedlots of cultivar 'Aurea' sown immediately after collection germinated 47%; those seeds subjected to 2 to 3 months of cold stratification and then sown germinated 100% (Dirr and Heuser 1987). If seeds are sown in the fall, the seedbeds should be mulched to reduce effects of freezing and thawing. When seeds were buried 4 cm (1 $^1/_2$ in) deep, over two-thirds never emerged from the ground after germination (McLeod and Murphy 1977b). Some of the seedlings have yellow foliage color (Dirr and Heuser 1987). Propagation also is possible by layering, grafting, or budding.

Figure 3—*Ptelea trifoliata*, common hoptree: seedling development at 1, 2, and 10 days after germination.



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Fabaceae—Pea family

Pterocarpus Linn.

padauk, narra

John K. Francis

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Growth habit, occurrence, and use. Although there are several *Pterocarpus* species scattered throughout the tropics, only Burma *padauk* (*P. macrocarpus* Kurz) and India *padauk* (*P. indicus* Willd.), also called *narra* or Burmese rosewood, are commonly planted. Both are large trees that produce reasonably long and straight boles in closed stands but develop short boles and spreading crowns when open-grown. Older trees have moderate buttresses and large roots that run along the surface of wet or clayey soil. Both have lush, green foliage and cast a moderately dense shade. Both have naturalized in Puerto Rico but spread very slowly.

Burma padauk is native to upland areas in Myanmar, Thailand, Kampuchea, and Vietnam (Francis 1989). Because of its annual yellow floral display and pleasing foliage and form, this species has become a very popular ornamental and shade tree in Puerto Rico, Florida, and the U.S. Virgin Islands (Francis 1989). It has naturalized in (at least) Puerto Rico (Francis and Liogier 1991). Burma padauk is quite at home in frost-free areas that receive from 1,000 to 2,000 mm of mean annual precipitation.

India padauk is native to the Andaman Islands (India), Malaysia, Indonesia, and the Philippines (Little and Wadsworth 1964). Although it has virtually the same form, foliage, and floral display as the Burma padauk, India padauk requires somewhat higher rainfall (above 1,500 mm/year) (Troup 1921). It has been planted for reforestation in Hawaii (Neal 1965) and in forestry trials in Puerto Rico.

Both species have good forestry potential. They tolerate a wide range of soil types and can be planted in cleared sites or small forest openings. The wood of both species varies from yellow to dark red; the rich colors and figures are highly prized for furniture and decorative uses (Chudnoff 1984). Even the lower grades of wood are useful for posts, ship timbers, and construction because of their resistance to termites and rot (Hundley 1956; Rendle 1970).

Flowering and fruiting. The sweet-scented flowers are produced copiously in panicles and racemes. Individual flowers are about 1.6 cm across. They are pollinated by honey bees (*Apis mellifera* L.) and other insects. Fruits mature about 6 months after flowering and fall off the tree gradually over several months. Padauk fruits are lenticular-shaped legumes with a flat wing that circles its edge (figure 1). The straw-colored to light brown legumes of India padauk are generally 3 to 4 cm across and the light brown legumes of Burma padauk measure 4.5 to 7.5 cm across (Little and Wadsworth 1964; Little and others 1974). However, considerable variation in size occurs between the legumes of individual trees and tress from various sources within both species. Legume production usually begins in open-grown trees between 5 and 10 years of age. Large trees produce about 35 liters (1 bu) or more of legumes annually.

Collection, cleaning, and storage. At maturity, the legumes dry and turn from greenish yellow to straw colored or light brown. Seed-bearing branches can be clipped with pruning poles if the need for legumes is urgent. Because the legumes and their seeds do not deteriorate for several months after falling, it is more efficient to wait until most of the crop has fallen and pick up the legumes from the ground. A sample of air-dried legumes of Burma padauk grown in Puerto Rico yielded 1,067 legumes/kg (485/lb) (Francis 1989). The legumes of India padauk (source unknown) were reported to yield 1,200 to 1,300 legumes/kg (545 to 590/lb) (MacDicken and Brewbaker 1984). The seeds of padauk are fragile (figure 2) and the legumes are tough, making extraction impossible mechanically and difficult by hand. A sample of legumes of Burma padauk from Puerto Rico yielded an average of 2.6 seeds/legume (Francis 1989); shelled seeds averaged 11,500/kg (5,200/lb) (Francis and Rodríguez 1993). Padauk seeds are normally stored and planted in the legumes. Air-dried seeds in their legumes will still germinate after 1 year of storage in plastic bags at room temperature. The effect of refrigeration is unknown but probably beneficial.

Figure 1—*Pterocarpus macrocarpus*, Burma padauk: legumes and seeds (**top right**).

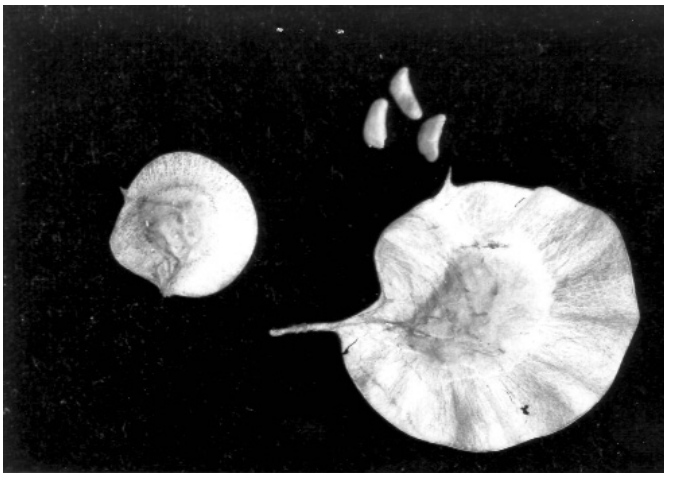


Figure 2—*Pterocarpus macrocarpus*, Burma padauk: longitudinal sections of seeds.

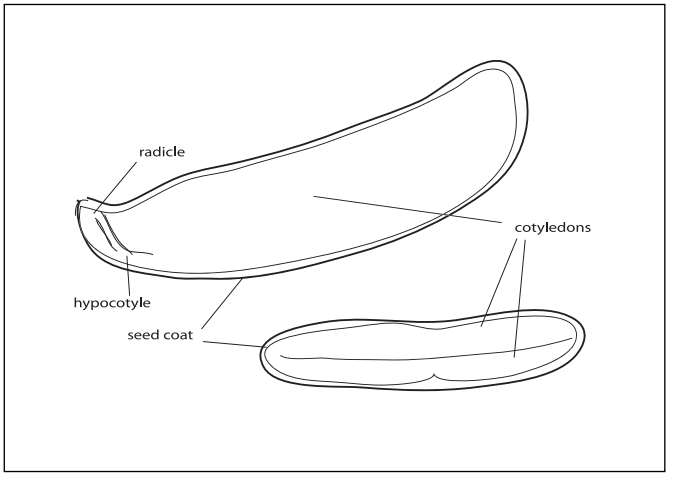
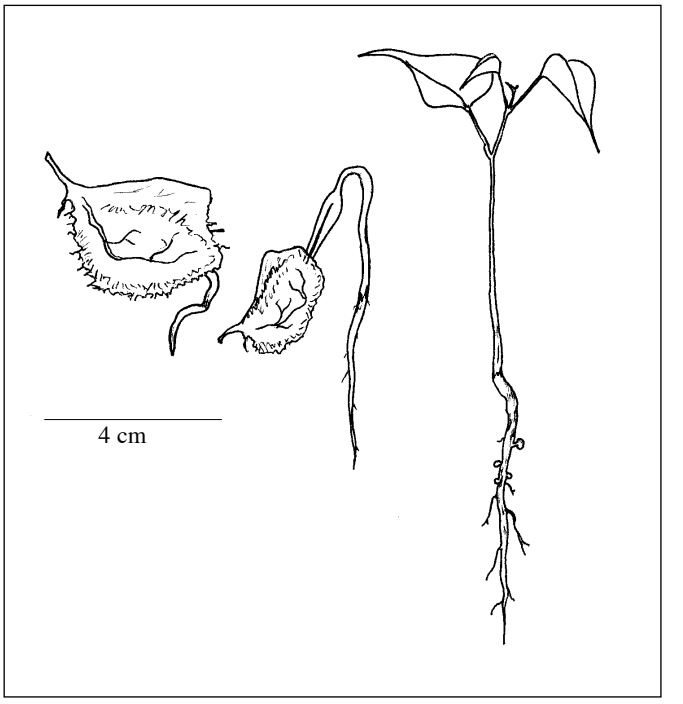


Figure 3—*Pterocarpus macrocarpus*, Burma padauk: germinating seed showing seedling development.



Germination. The first seeds germinate within and begin to grow through the legumes about 1 to 2 weeks after planting. The remaining seeds continue germinating for several weeks thereafter. Often 2 or 3 seedlings emerge from each legume. Germination is epigeal (figure 3). In a comparison of the germination of shelled seeds to seeds within legumes in Puerto Rico, shelled seeds germinated in 5 days and gave 70% germination within 2 weeks. Unshelled legumes did not begin germination for 11 days and only 64 seedlings/100 legumes emerged within 2 months. However, effective yield was only about two-thirds this amount because about half the seedlings occurred in multiples and only 1 germinant/legume can produce a plantable seedling. In Burma, shelled seeds gave 80 to 90% germination. Moreover, seeds from 1-year-old legumes collected from the ground germinated better than new seeds collected from the tree (Hundley 1956). Seeds from Burma padauk germinated well (around 80% over a wide temperature range; the best temperature regime seemed to be about 30 °C day and 25 °C night (Liengsiri and Hellum 1988).

Nursery practice. The use of shelled seeds would be recommended, except that they are so difficult to extract. The use of seeds in the legumes requires thinning the plants soon after germination to remove multiples. When true leaves have developed, seedlings are transplanted from the germination bed to bags filled with a potting mixture. After growing under light shade for a few months, the seedlings reach about 0.5 m (1.6 ft) in height and are ready for outplanting (Francis 1989). In Burma, seedlings in plantations grow to 0.6 to 1.2 m (2 to 4 ft) the first year and 1.2 to 2.1 m (4 to 7 ft) the second (Hundley 1956). Thirty planted trees in a small forest plantation in Puerto Rico (situated on clay soil over porous limestone) averaged 1.3 m tall at 14 months after outplanting (Francis 1989). Seedlings intended for ornamental use are often grown in 12- to 20-liter (3- to 5-gal-size) plastic pots until they reach 2 to 3 m (6.5 to 7.5 ft) in height before outplanting. In the Philippines, branch cuttings of India padauk about 8 cm (3 in) in diameter are rooted after hormone treatment to produce "instant trees" (Dalmacio and others 1978).

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Rosaceae—Rose family

Purshia DC. ex Poir.

bitterbrush, cliffrose

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Growth habit, occurrence, and use. The bitterbrush genus—*Purshia*—as presently circumscribed comprises 8 species of decumbent to arborescent shrubs of interior western North America. Three are common in the United States (table 1). The type species—antelope bitterbrush—has an essentially northern distribution, whereas cliffrose has an essentially southern distribution, and desert bitterbrush occurs in parts of the geographic area where the other 2 species have overlapping distributions. Cliffrose, along with the 5 Mexican species of the genus, has been traditionally referred to the genus *Cowania* D. Don. Cliffrose regularly forms hybrids with antelope bitterbrush, and desert bitterbrush could be interpreted as a stabilized hybrid between these species (Stutz and Thomas 1964). In fact, molecular genetics work by Jabbes (2000) indicates that *Purshia* was derived from *Cowania*. We follow Welsh and others (1987) in treating the group as congeneric under the name *Purshia*.

Members of the genus are erect, spreading or decumbent, freely branched shrubs up to 6 m in height. They have small, alternate, simple, apically lobed leaves that may be evergreen (cliffrose) to winter deciduous (antelope bitterbrush). Layering forms of bitterbrush (principally antelope bitterbrush) may resprout after fire, but erect forms are usually not fire tolerant. Because of their interesting habits, attractive foliage, and showy flowers, bitterbrush species have potential as ornamentals in low-maintenance landscapes.

Bitterbrush species are hardy and drought tolerant. Antelope bitterbrush occurs mainly on well-drained soils over a wide elevational range and is often a principal component of mixed shrub, pinyon–juniper, ponderosa pine, and sometimes lodgepole pine communities, where it is notable as a nurse plant for conifer seedlings (Geier-Hayes 1987; McArthur and others 1983; Nord 1965; Tew 1983). It is valued as a high-protein browse for domestic and wild ungulates, being especially important on winter ranges (Bishop and others 2001; Scholten 1983). It also supplies high-quality forage during spring and summer months (Austin and Urness 1983; Ngugi and others 1992). Cliffrose grows primarily on rocky sites in blackbrush–joshua tree woodland, sagebrush–grassland, piñyon–juniper woodland, mountain brush, and ponderosa pine communities, sometimes forming extensive stands on south-facing ridge slopes (McArthur and others 1983). It is also an important browse species, especially for mule deer (*Odocoileus hemionus*) (Plummer and others 1968). Desert bitterbrush is a component of blackbrush, chaparral, and piñyon–juniper communities.

The bitterbrush species form actinorhizal root nodules that fix nitrogen when soil water is adequate (Bond 1976;

Table 1—*Purshia,* bitterbrush, cliffrose: common names and geographic distributions

Scientific name & synonym(s)	Common name	Geographic distribution
***P. glandulosa* Curran** *P. tridentata* var. *glandulosa* (Curran) M.E. Jones	**desert bitterbrush**	SW Utah, S Nevada, & S California
***P. mexicana* (D. Don) Henrickson** *Cowania mexicana* D. Don	**cliffrose**	S Colorado W through Utah to S California & S to New Mexico, Arizona, Sonora, & Chihuahua
***P. tridentata* (Pursh) DC.**	**antelope bitterbrush**	British Columbia to W Montana, S to New Mexico, California, & N Arizona

Sources: Little (1979), Sargent (1965), Vines (1960).

Kyle and Righetti 1996; Nelson 1983; Righetti and others 1983). They readily function as pioneer species that colonize harsh, steep disturbances and have been used extensively in revegetation and disturbed-land reclamation. An ethanol extract of antelope bitterbrush aerial stems was found to inhibit reverse transcriptase of HIV-1 and to contain the cyanoglucosides pushianin and menisdaurin (Nakanishi and others 1994). Unfortunately, the cyanoglucosides lacked the inhibitory activity of the original extract. Cliffrose has also been examined for beneficial secondary products (Hideyuki and others 1995; Ito and others 1999). Specific populations of antelope bitterbrush with distinctive attributes are recognized and are commercially harvested and sold, although to date only two ('Lassen' and 'Maybell') have been formally named (Davis and others 2002; Shaw and Monsen 1995).

Flowering and fruiting. Most of the medium to large, perfect, cream to sulfur yellow flowers of this genus appear during the first flush of flowering in April, May, or June, depending on elevation. In areas where they co-occur, antelope bitterbrush usually flowers 2 to 3 weeks before cliffrose. The flowers are borne on lateral spurs of the previous year's wood (Shaw and Monsen 1983). In cliffrose, summer rains may induce later flowering on current-year leaders, but these flowers rarely set good seeds (Alexander and others 1974). The flowers have a sweet fragrance and are primarily insect-pollinated. Each has 5 sepals, 5 separate petals, numerous stamens, and 1 to 10 pistils borne within a hypanthium. Flowers of antelope and desert bitterbrushes usually contain a single pistil with a relatively short, non-plumose style, whereas those of cliffrose contain multiple pistils. The pistils develop into single-seeded achenes with papery pericarps. In cliffrose the achenes are tipped with persistent) plumose styles, 22 to 50 mm (1 to 2 in) in length, that give the plants a feathery appearance in fruit.

The main fruit crop ripens from June through August, depending on species and elevation. Plants begin to bear seeds as early as 5 years of age. At least some fruits are produced in most years, and abundant seedcrops are produced on average every 2 to 3 years (Alexander and others 1974; Deitschman and others 1974). Cliffrose seeds (figure 1) are apparently dispersed principally by wind (Alexander and others 1974). Scatter-hoarding rodents such as chipmunks (*Tamias* spp.), disperse bitterbrush seeds (figure 2) and seedlings from rodent caches appear to account for nearly all (99%) natural recruitment as survivors from seedling clumps containing 2 to >100 individuals (Evans and others 1983; Vander Wall 1994).

Seed collection, cleaning, and storage. Bitterbrush plants produce more leader growth in favorable water years,

Figure 1—*Purshia*, mexicana, cliffrose: achenes:

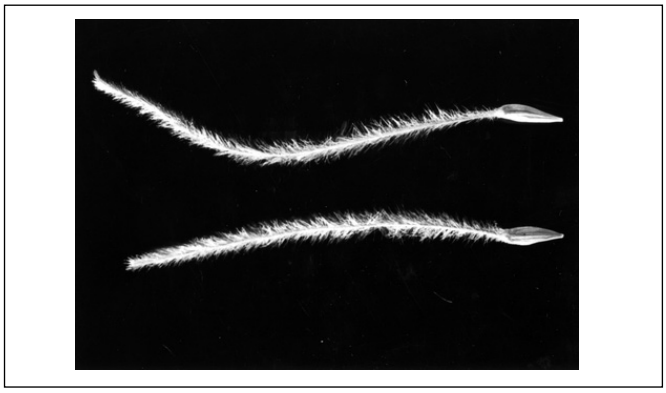
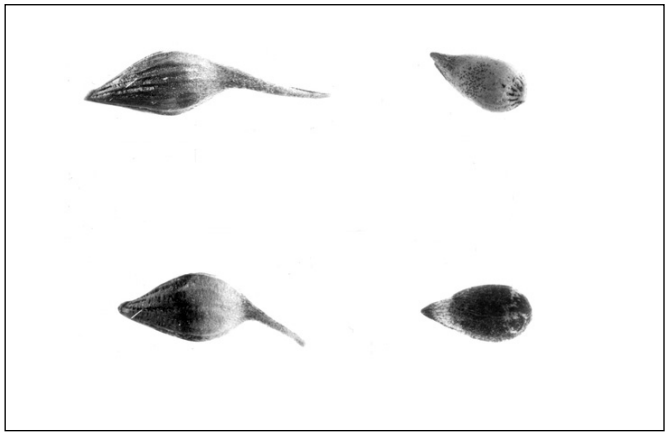


Figure 2—*Purshia*, bitterbrush: achenes (**left**) and cleaned seeds (**right**) of *P. glandulosa*, desert bitterbrush (**top**) and



and leader length is an indicator of the potential for seed production the following year (McCarty and Price 1942; Young and Young 1986). Fruits may be hand-stripped or beaten into hoppers or other containers when fully ripe; harvesters should take care to protect themselves from the fiberglass-like style hairs in the case of cliffrose. The window of opportunity is quite narrow, as ripe fruits are easily detached by wind and do not persist long on the plant, making close monitoring during ripening advisable. Plants in draws and other areas protected from wind may retain their seeds longer. Maturation dates for antelope bitterbrush have been predicted with reasonable accuracy using elevational and latitudinal predictors (Nord 1965). Well-timed harvests of antelope bitterbrush average 168 to 224 kg/ha (150 to 200 lb/acre) but may range up to 560 kg/ha (500 lb/acre) (Nord 1965). Fill percentages are usually high, although insects or drought stress during filling can damage the crop (Shaw and Monsen 1983). Krannitz (1997a) reported the variation in seed weight from 240 bitterbrush plants representing 10 sites in the southern Okanagan Valley of Canada varied from

5 to 46 mg/seed with the population being skewed toward the small seeds. The representative weights given in table 2 are of cleaned seeds (the smaller fraction is removed in cleaning). Krannitz also found that larger seeds had greater concentrations of nitrogen than smaller seeds and that shrubs that had been browsed most intensively the winter before seed-set had seeds with greater concentrations of magnesium (Krannitz 1997b).

A seed cleaner or barley de-bearder may be used to break the styles from cliffrose achenes and to remove the papery pericarps of bitterbrush species. The achenes (cliffrose) or seeds (bitterbrush species) may be separated from the inert material—which usually comprises from one-third (antelope bitterbrush) to two-thirds (cliffrose) of the total weight—using a fanning mill (Alexander and others 1974; Giunta and others 1978). In cliffrose, the achene is considered the seed unit, as the seed is held tightly within the pericarp and cannot be threshed out without damage. In bitterbrush species, the seeds are easily threshed free of their papery pericarps, and the seed unit is the seed itself. If properly dried (<10% moisture content), seeds of bitterbrush species can be warehouse-stored for 5 to 7 years (Belcher 1985) or even up to 15 years without losing viability (Stevens and others 1981).

Germination and seed testing. Bitterbrush and cliffrose seeds are mostly dormant but the inhibiting mechanism(s) is not understood (Booth 1999; Booth and Sowa 2001; Dreyer and Trousdale 1978; Meyer 1989; Meyer and Monsen 1989; Young and Evans 1976, 1981). Moist chilling is preferred for breaking dormancy (table 3). Although some collections are less dormant than others are—as indicated by germination percentages for untreated or partially treated seeds (table 3) (Booth 1999; Meyer and Monsen 1989)—there is no obvious relationship between collection site and chilling requirement (Meyer and Monsen 1989). Dormancy might be affected by high seed temperature (30 °C) while in the dry state (Meyer 1989) and is certainly affected by imbibition temperature (Booth 1999; Meyer 1989).

Young and Evans (1981) reported the required chilling period was shorter at 5 °C, than at 2 °C for all 3 species, and that adequately chilled seeds could germinate over a wide range of temperatures. A 28- to 30-day chill at 1 to 3 °C is highly recommended (AOSA 1993; Belcher 1985; Booth 1999; Meyer 1989) followed by post-chill incubation at 15 °C (10/20 °C for cliffrose). Desert bitterbrush needs only 14 days of chilling (Belcher 1985). Germination of antelope bitterbrush seeds can be facilitated by 24 hours of soaking in cold (2 °C) water prior to moist chilling, but soaking in

Table 2—*Purshia,* bitterbrush and cliffrose: seed yield data (seeds/weight) for mechanically cleaned seeds*

Species	Mean /kg	Mean /lb	Range /kg	Range /lb
P. glandulosa	50,850	26,540	45,000–90,000	20,300–40,900
P. mexicana	129,000	58,600	108,000–210,000	49,000–95,000
P. tridentata	35,000	15,750	29,000–51,000	13,400–23,200

Sources: Alexander and others (1974), Belcher (1985), Deitschman and others (1974), Meyer (2002), Meyer and others (1988).

Table 3—*Purshia,* bitterbrush and cliffrose: germination data

Species	Mean percentage of initially viable seeds: 0	2 wk	4 wk	6 wk	8 wk	10 wk	12 wk	Samples
P. glandulosa	—	—	—	93	—	—	100	1*
	10	56	81	100	65	—	32	1†
P. mexicana	6	33	83	94	100	—	—	6
	6	64	91	100	32	—	19	1†
P. tridentata	2	43	88	98	100	—	—	13
	13	60	100	100	36	—	37	1†

Sources: Deitschman and others (1974), Meyer (2002), Meyer and Monsen (1989), Young and Evans (1981).
Note: Values are expressed as percentage of initially viable seeds after moist chilling at to 2 °C for 0 to 12 weeks followed by incubation at 15 °C or 10/20 °C for 4 weeks.
* These seeds were chilled at 3 to 5 °C and germination was scored during chilling.
† Decrease in germination percentage after 6 weeks was due to seed mortality during the test.

warm water (>10 °C), or holding imbibed seeds at warm temperatures, decreases seedling vigor and increases pregermination seed-weight loss (Booth 1999; Booth and Sowa 2001). Longer, colder chilling periods (28 days, 2 °C vs 14 days, 5 °C) increases seedling vigor (Booth 1999; Booth and Morgan 1993). Recommended germination test periods are 28 days for antelope bitterbrush and cliffrose (AOSA 1993).

Soaking seeds in hydrogen peroxide (Everett and Meeuwig 1975) or a 1 to 3% solution of thiourea (Pearson 1957; Young and Evans 1981) will induce germination but these methods have not proven useful for field plantings. Booth (1999) found thiourea-treated seeds to have the lowest seedling vigor among 8 dormancy-breaking treatments and attributed the lower vigor to residual dormancy and to weight loss resulting from accelerated respiration (Booth 1999; Booth and Sowa 2001).

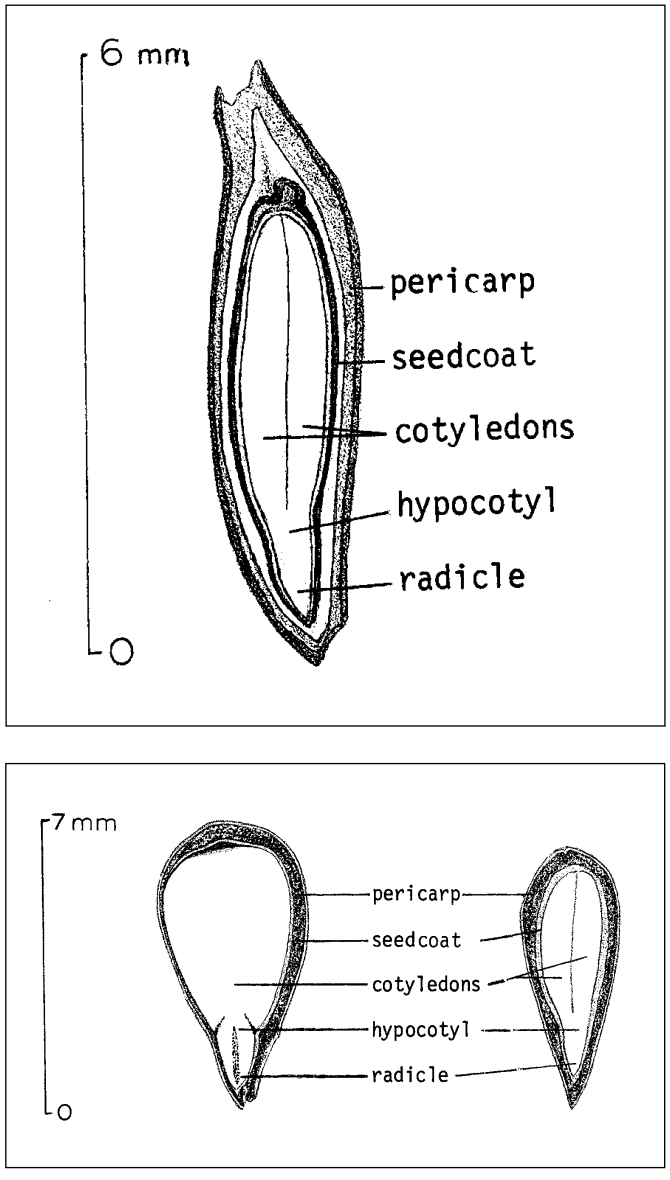
Tetrazolium (TZ) staining is acceptable for evaluating seed quality of bitterbrush (AOSA 1993; Weber and Weisner 1980). Meyer (2002) found no significant difference between TZ viability estimates and germination perentages after 8 weeks of chilling for either cliffrose or antelope bitterbrush. For TZ viability testing, seeds should be clipped at the cotyledon end (figure 3) and soaked in water for 6 to 24 hours. Then, the embryos can be popped-out of the cut end by gentle finger pressure and immersed in 1% TZ solution for 4 to 12 hours at room temperature before evaluation. Cliffrose must be soaked longer than bitterbrush before the embryos can be popped out.

Field seeding and nursery practice. Bitterbrush species are generally sown in fall or early winter in a mixture with other shrubs and forbs. They are used in upper sagebrush, piñyon-juniper woodlands, and mountain brush vegetation types to improve degraded wildlife habitat or revegetate bare roadcuts, gullies, south slopes, and other difficult sites (Alexander and others 1974). Because of the chilling requirement, spring-seeding should be avoided. Seeds may be drilled at a depth of 6 to 12 mm ($^1/_4$ to $^1/_2$ in) or deeper. Deeper seeding may provide some protection from rodent depredation, which can be a serious problem (Alexander and others 1974; Evans and others 1983; Vander Wall 1994). Seeding in late fall or early winter, when rodents are less active, may also alleviate this problem.

Broadcast-seeding is generally unsuccessful unless provision is made for covering the seeds. Aerial seeding is not recommended. The seedlings do not compete well with weedy annual grasses such as red brome (*Bromus rubens* L.) and cheatgrass (*B. tectorum* L.), or with heavy stands of perennial grasses. They are sensitive to frost and drought during establishment (Plummer and others 1968). Recommended (drill) seeding rates for cliffrose are 5 to 10% of the shrub mix at 8 to 10 kg/ha (7 to 9 lb/ac) (Alexander and others 1974; Plummer and others 1968) and 16 to 65 seeds/m (5 to 20 seeds/ft) for bitterbrush. The higher rates are advisable for both species when seeding in crust-forming soils. The most effective method of seeding large areas in conjunction with chaining is with a seed dribbler that drops seeds in front of the bulldozers pulling the chain.

Hand-planting into scalped sites with a tool such as a cased-hole punch planter can be very effective on a small scale (Booth 1995). The purpose of scalping is to control herbaceous competition within a half-meter ($1\ ^1/_2$-ft) radius of the planting spots. Treating seeds with fungicide, planting seeds in groups, and planting with vermiculite to aid in moisture retention have all improved emergence and establishment of antelope bitterbrush (Booth 1980; Evans and

Figure 3—*Purshia*: longitudinal section of *P. mexicana*, cliffrose (**top**) and *P. tridentata*, antelope bitterbrush (**bottom**).



others 1983; Ferguson and Basile 1967). Good emergence depends on adequate snowcover (Young and others 1993).

Bitterbrush species are readily grown as bareroot or container stock, and outplanting may succeed where direct seeding has failed (Alexander and others 1974). Care must be taken to lift or transplant stock only when the plants are hardened or dormant, as survival of actively growing plants is generally low (Landis and Simonich 1984; Shaw 1984). Plants are easier to handle and have higher survival rates if allowed to reach sufficient size before field transplanting. One-year-old bareroot stock or container seedlings 16 to 20 weeks of age are usually large enough (Alexander and others 1974; Shaw 1984). On more level terrain, a conventional tree-planter may be used (Alexander and others 1974). Transplanting should be carried out at a time and in such a way as to assure that the transplants will have adequate moisture for root development for 4 to 6 weeks after planting. This may be accomplished by planting in very early spring or by watering at the time of planting. Fall-planted seedlings may require supplemental watering. Controlling competition from weedy annual or perennial grasses before planting will enhance survival and first-season growth.

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Rosaceae—Rose family

Pyrus L.

pear

Kim E. Hummer and Joseph D. Postman

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Growth habit, occurrence, and use. The pear genus—*Pyrus*—probably originated in the mountain regions of what is now western and southwestern China and evolved and spread eastward and westward. Throughout the world, 24 primary species are presently recognized (table 1). Pear species are not native to North or South America (Rehder 1986), although some species have naturalized here.

The common pear (*P. communis*), which is cultivated for its fruit, probably originated from complex hybridization of wild progenitors, the wild European pear, *P. korschinskyi* (synonym = *P. pyraster*), and *P. communis* var. *caucasica* in the region of the Caucasus Mountains (Westwood 2002). Fruits of the common pear are pyriform, although the fruits of its progenitors tend to be round. The astringent fruits of the snow pear and hybrids between the common pear and the snow pear have been used in Western Europe to produce the fermented cider-like beverage called "perry."

Pears have been cultivated in Asia for at least 3,000 years (Kikuchi 1946). The fruits of many pears cultivated in Asia tend to be round. Lombard and Westwood (1987) consider that the (Japanese or Chinese) sand pear was the first pear species domesticated for its edible fruit. The Ussuri pear, the other predominant Asian species, has small, round astringent fruits. Natural hybridization between these 2 wild species occurred in central China and selection for large fruited, edible types has been occurring for several thousand years.

Most modern Japanese and Korean pear cultivars are derived from the sand pear. The principle commercial pears in China are derived from 3 species—sand and Ussuri pears and the hybrid species *P.* × *bretschneideri,* which is also known as the "Chinese white pear" (Lombard and Westwood 1987; Teng and others 2002). Recent analysis of pear species using DNA markers such as simple sequence repeats (SSR) suggest that the Chinese white pear is closely related to both sand and Ussuri pears (Yamamoto and others 2002) and might be considered as a subspecies of sand pear (Teng and others 2002).

Several Asian species have fruits with the size and shape of a pea. The Japanese and Korean pea pears and the evergreen pear are considered by some to be varieties or subspecies of Callery pear (Rehder 1986; Yu 1979). The birchleaf pear has the smallest sized fruit of the pea pears.

The common pear has naturalized in the United States (Gill and Pogge 1974). The Ussuri pear, introduced from Asia about 1855, has been grown on the northern Great Plains in shelterbelt and environmental plantings and in New England. It has contributed genes for cold-hardiness and resistance to fire blight in pear breeding programs (Stushnoff and Garley 1982). Other traits inherent in this species include vigor, dense growth, attractive glossy foliage, and scarlet autumn leaf color. Pear cultivars adapted to warm winter areas have been derived from the Pashia pear of central Asia. The pendulous form of the willow-leaf pear makes it a unique ornamental landscape plant. Flowering ornamental selections of the Callery pear and the evergreen pear are widely planted as street trees in the United States. The use of the evergreen pear is limited to warm-winter areas such as California and the more southerly states. These species are often referred to as "flowering pears" in the urban landscape. The Callery pear has become naturalized in the eastern United States and is now considered a weed in some areas such as the Maryland suburbs of Washington, DC.

Pears are deciduous, rarely evergreen, sometimes thorny trees or shrubs. Their leaves are serrate, crenate, or entire; rarely lobed. The petioles are stipulate and the buds are involute, with imbricate scales.

Flowering and fruiting. Pear species are cross-compatible sexual diploids (x = 17). Individual genotypes are generally self-incompatible. The perfect flowers bloom on 2-year or older spurs, between March and April in the Northern Hemisphere and appear before or with the new leaves (table 2). The inflorescence consists of 6 to 8 flowers occurring in umbel-like racemes. Petals are white, or rarely pinkish with reflexed or spreading sepals, 20 to 30 pink, red,

Table 1— *Pyrus,* pear: nomenclature, growth habit, and occurrence

Scientific name & synonym(s)	Common name(s)	Growth habit	Range & extensions
***P. amygdaliformis* Vill.** *P. sinaica* Dom.-Cours.	**almond-leaf pear**	Shrub to small tree, 1–2 m	Mediterranean Europe & Asia Minor
***P. betulifolia* Bunge**	**birch-leaf pear**	Large tree, 5–6 m	Central & N China
***P. calleryana* Decne.**	**Callery pear,** pea pear, Chinese pea pear	Medium tree, 3–5 m	Central & S China
***P. communis* L.** *P. asiae-mediae* Popov; *P. balansae* Decne *P. boissieriana* Buhse; *P. elata* Rubtzov *P. medvendevii* Rubtzov	**common pear,** European pear, cultivated pear	Large broad pyramidal tree, 5–6 m	W to SE Europe, Turkey; in world-wide cultivation
***P. communis* ssp. caucasica (Fed.) Browicz** *P. caucasica* Fed.	**Caucasus pear**	Large tree, 5–6 m	SE Europe, Greece
***P. cordata* Desv.**	**heart-leaf pear,** Plymouth pear	Shrub to small tree, 2–3 m	SW England, W France, Spain, & Portugal
***P. cossonii* Rehder** *P. longipes* Coss, S. Dur.	**Algerian pear**	Medium tree, 3–4 m	Algeria
***P. dimorphophylla* Makino** *P. calleryana* var. *dimorphophylla* (Makino) Koidz	**Japanese pea pear**	Medium tree, 3–4 m	Japan
***P. elaeagrifolia* Pall.** *P. kotschyana* Boiss ex Deone	**elaeagnus-leaf pear**	Medium tree, 3–4 m	SE Europe, Russia, & Turkey
***P. fauriei* C.K. Schneid.** *P. calleryana* var. *fauriei* (Schneid.) Rehd.	**Korean pea pear**	Shrub to small tree, 1–2 m	Korea
***P. gharbiana* Trab.**	—	Small tree, 1–2 m	Morocco & W Algeria
***P. glabra* Boiss.**	—	Medium tree, 3–4 m	Iran
***P. koehnii* C.K. Schneid**	**evergreen pear**	Small to medium tree, 1–3 m	Taiwan & SE China
***P. korshinskyi* Litv.** *P. pyraster* Burgsd. *P. communis* var. pyraster	**wild European pear**	Tree to 15 m	Afghanistan; W Russia; Central Asia
***P. mamorensis* Trab.**	**Mamor Mountain pear**	Small tree	Morocco
***P. nivalis* Jacq.**	**snow pear,** perry pear	Thornless medium tree, 3–4 m	W Central & S Europe
***P. pashia* Buch.-Ham. ex D.Don** *P. kumaoni* Decne *P. varoilosa* Wall ex G. Don. *P. wilhelmii* C. Schneid.	**Pashia pear,** India wild pear	Medium tree, 3–4 m	Pakistan, India, & Nepal
***P. pseudopashia* T.T. Yu**	**Kansu pear**	Tree	NW China (Yunnan & Guizhou)
***P. pyrifolia* (Burm.f.) Nakai** *P. serotina* Rehd.	**sand pear,** Japanese pear, Chinese pear	Medium to large tree, 3–5 m	China, Japan, Korea, & Taiwan
***P. regelii* Rehder** *P. heterophylla* Regel G.Schmalh	**Regel pear**	Shrub or tree to 1–2 m	S central Asia & Afghanistan
***P. salicifolia* Pall.**	**willow-leaf pear**	Small tree, 1–2 m	NW Iran, Armenia, Turkey, & S Russia
***P. syriaca* Boiss.**	**Syrian pear**	Small tree, 1–2 m	Middle East, SW Russia
***P. ussuriensis* Maxim.;** *P. lindleyi Rehd.* *P. ovoidea* Rehd. *P. sinensis* Lindley	**Ussuri[an] pear,** Harbin pear, Manchurian pear	Small to medium tree, 1–3 m	Siberia, N China, Korea, Mongolia
***P. xerophylla* T.T. Yu**	—	Tree	N China

Sources: LHBH (1976), Bell (1991), Hedrick (1921), Lombard and Westwood (1987), Rehder (1986).

Table 2—*Pyrus,* pear: flowering and fruiting dates*

Species	Bloom season†	Ripening season‡
P. amygdaliformis	M–ML	L
P. betulifolia	M–ML–L	L
P. calleryana	E–EM–M	L
P. communis (wild types)	EM–M–ML	EM–M–ML–L
P. communis (cultivars)	E–EM–M–ML–L	E–EM–M–ML–L
P. cordata	M–ML–L	ML–L
P. cossonii	M–ML–L	M–ML–L
P. dimorphophylla	E–M–ML	L
P. elaeagrifolia	EM–M–ML	ML
P. fauriei	EM–M–ML	ML–L
P. gharbiana	ML	ML
P. glabra	EM	M–ML
P. hondoensis	EM–M–ML	M–ML–L
P. koehnei	E–EM–M–ML	L
P. korshinskyi	EM–M–ML	EM–M–ML–L
P. mamorensis	ML	L
P. nivalis	ML	ML–L
P. pashia	E–EM–M–ML–L	L
P. pyrifolia (wild types)	EM–M	M–ML–L
P. pyrifolia (cultivars)	EM–M–ML	EM–M–ML–L
P. regelii	M–ML	ML
P. salicifolia	EM–M–ML	ML–L
P. syriaca	EM–M	ML–L
P. ussuriensis (wild types)	E–EM	EM–M–M– L
P. ussuriensis (cultivars)	E–EM–M	M–ML–L

* Observations made at the USDA ARS National Clonal Germplasm Repository in Corvallis, OR, 1988 through 1994.
† Average full bloom: E = March 13–March 23, EM = March 24–April 2, M = April 3–April 7, ML = April 8–April 17, L = April 18–April 26.
‡ Average fruit ripening: E = before July 6, EM = July 6–August 8, M = August 9–August 25, ML = August 26–September 28, L = after September 28.

or purple anthers, 2 to 5 free styles that are closely constricted at the base, and 2 ovules per locule.

The fruit is a globose or pyriform pome with persistent or deciduous calyx. Most Asian species, with the exception of the Ussuri pear, have deciduous calyxes. The fruit of different species ranges from about 0.5 to 20 cm in length and are quite diverse (figure 1). The extracarpellary tissue, which comprises the bulk of the fruit flesh, may contain sclerenchyma, that is, stone cells. The ground-color of the fruit skin may change from green to yellow or red during maturation, and russeted lenticels may be prominent on some species. Environmental conditions, such as humidity, may cause russetting or browning of the maturing skin. The ripening season for cultivated pears in the Northern Hemisphere ranges from June through December (table 2). Fruit from some species can be eaten directly from the tree, whereas others may require a period of cold storage to ripen or soften the fruit before it can be eaten. Common pears growing wild in Russia are reported to be biennial producers (Al'benskii and Nikitin 1956).

Collection of fruits; extraction and storage of seeds. The mature fruits can be picked from trees or some can be shaken to the ground. Seeds (figure 2) can be recovered by macerating the fruit, drying the pulp, and using a screen to extract the seeds. Small quantities of seeds can also be effectively removed by carefully transversely cutting fruit to expose the locules. Water can also be used to float immature seeds, flesh, and skin away from viable seeds, which sink. Each ripe fruit contains up to 10 smooth black (or nearly black) seeds, each with a thin layer of endosperm (Gill and Pogge 1974). The seeds can then be air-dried. Pear seed characteristics differ greatly by species (figure 3). The small-seeded species—*P. gharbiana,* from N. Africa, and the birch-leaf pear—contain more than 88,000 seeds/kg (40,000/lb). The largest seeded species—Regel, Syrian, and Mamor Mountain pears—contain 11,000 or fewer seeds/kg (5,000 or fewer/lb). The domesticated species contain about 22,000 to 26,000 seeds/kg (10,000 to 12,000/lb) (table 3). Pears are outcrossing species, so seedlings will not be identical to parental genotypes.

Figure 1—*Pyrus,* pear: fruit and seed of *P. ussuriensis*, Ussuri pear (**left**); seeds of *P. calleryana*, Callery pear (**right**).

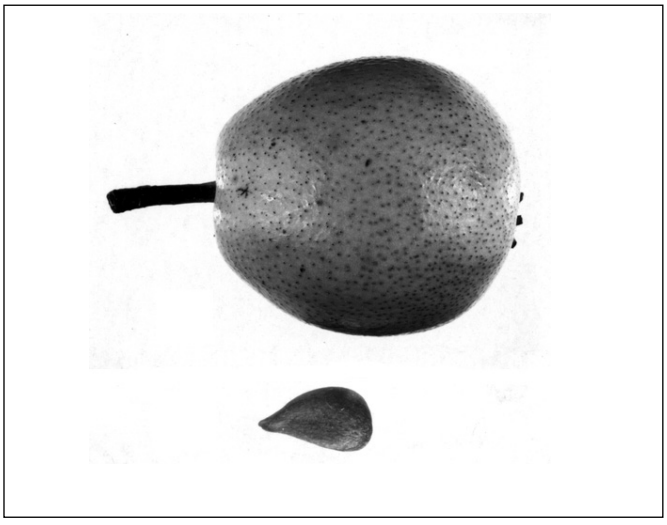
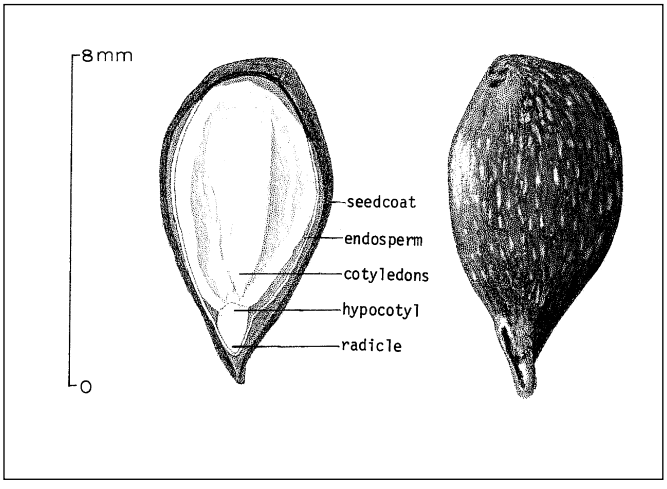


Figure 2—*Pyrus communis* L., common pear: longitudinal section through a seed.



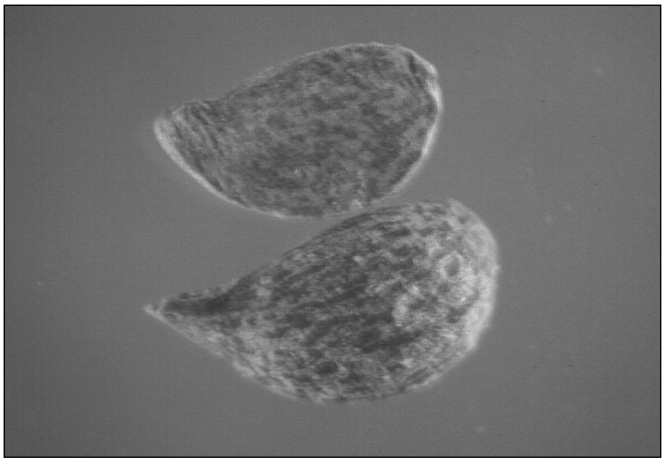
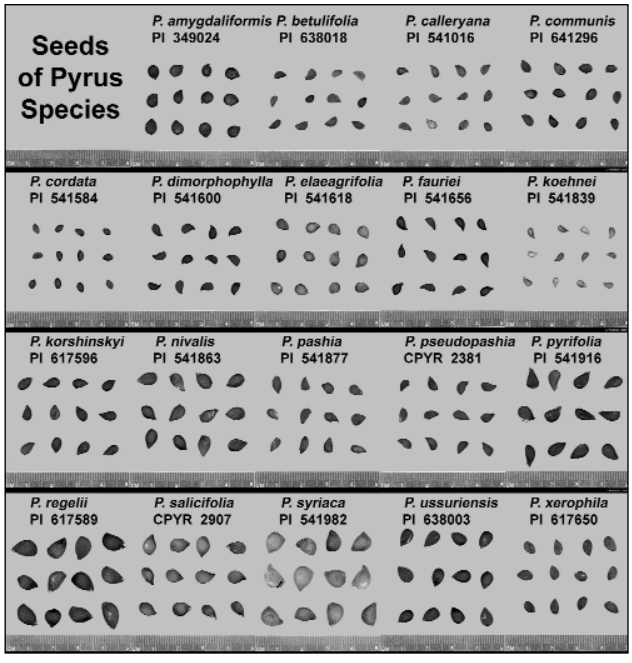


Figure 3—*Pyrus*, pear: seeds of *P. cossonii*, Algerian pear (X); *P. amygdaliformis*, almond-leaf pear (X); *P. betulifolia*, birch-leaf pear (X); *P. calleryana*, Callery pear (X); *P. communis*, common pear (X); *P. cordata,* heart-leaf pear (X); *P. dimorphophylla*, Japanese pea pear (X); *P. elaeagrifolia*, elaeagnus-leaf pear (X); *P. fauriei*, Korean pea pear (X); *P. gharbiana* (X); P. koehnii, evergreen pear (X); *P. korshinskyi* wild European pear (X); *P. mamorensis*, Mamor Mountain pear (X); *P. nivalis,* snow pear (X); *P. pashia*, Pashia pear (X); *P. pseudopashia*, Kansu pear (X); *P. pyrifolia*, sand pear (X); *P. regelii*, Regel pear (X); *P. salicifolia*, willow-leaf pear (X); *P. syriaca*, Syrian pear (X); *P. ussuriensis*, Ussuri pear (X); *P. xerophylla* (X).



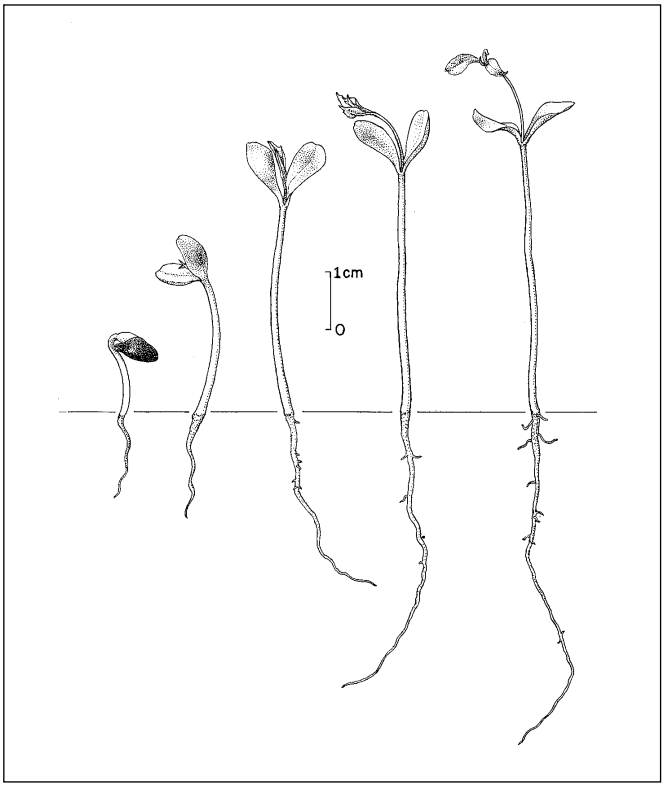
Germination. Seeds of pears extracted from fresh mature fruit in the fall or winter have dormant embryos that require stratification. Species differ in their stratification requirements (table 3). Seed preparation for germination includes a thorough washing and 1 day of water soaking prior to stratification. Seeds must be stratified for 60 to 100 days at about 4 °C. Germination is epigeal (figure 4) and may require from 5 to 30 days at 20 °C (Ellis and others 1985; Macdonald 1986). Because of the long stratification periods required for germination, official seed testing rules (AOSA 1993; ISTA 1993) recommend tetrazolium staining or the excised embryo test. For the excised embryo test,

Table 3—*Pyrus*, pear: seed properties

Species	Chilling requirement (days)	Best chilling temp (°C)	Seed size Length (mm)	Seed size Width (mm)	L/W ratio	Seeds/wt /kg	Seeds/wt /lb
P. amygdaliforms	25–27	7	6.7	4.2	1.60	24,000	11,000
P. betulifolia	55–86	4	4.0	2.3	1.74	90,000	41,000
P. calleryana	30–87	7	5.2	2.6	2.00	55,000	25,000
P. communis ssp. *caucasica*	130	4	7.7	4.2	1.83	40,000	18,000
P. communis (domestic)	90	4	8.4	4.8	1.77	22,000	10,000
P. cordata	—	4	4.6	2.6	1.77	86,000	39,000
P. dimorphophylla	65–88	7	5.2	2.8	1.86	77,000	35,000
P. elaeagrifolia	90–127	4	6.7	4.2	1.6	22,000	10,000
P. fauriei	38–88	7	4.7	2.9	1.62	57,000	26,000
P. gharbiana	60–78	7	4.6	2.4	1.92	99,000	45,000
P. koehnii	—	7	4.4	2.4	1.83	79,000	36,000
P. mamorensis	50–58	7	8.9	5.9	1.51	11,000	5,000
P. nivalis	110	4	10.0	4.3	2.32	18,000	8,000
P. pashia	15–43	10	6.5	3.1	2.10	55,000	25,000
P. pyrifolia	120–170	4	8.7	4.4	1.98	26,000	12,000
P. regelii	—	—	11.3	7.6	1.49	7,000	3,000
P. salicifolia	—	4	7.2	4.6	1.59	24,000	11,000
P. syriaca	—	7	9.3	6.2	1.50	9,000	4,000
P. ussuriensis	100	7	7.4	4.5	1.64	20,000	9,000

Sources: Gill and Pogge (1974), Lombard and Westwood (1987), Rudolph (1949), Swingle (1939), Westwood and Bjornstad (1968), Yerkes (1930), Young and Young (1992)

Figure 4—*Pyrus communis*, common pear: seedling development at 1, 2, 3, 6, and 12 days after germination.



embryos should be germinated for 10 to 14 days at alternating temperatures of 18/22 °C (AOSA 1993).

Nursery practice. Seeds are planted thickly, about 13 mm ($^1/_2$ in) deep in a seedbed, and allowed to grow for 1 season. The following spring, plants are dug, their roots and top are cut back, and they are transplanted to nursery rows. After a second season, the rootstock are of correct size for budding in the fall (Hartmann and others 1990). Seedlings of 1+0 nursery stock can be either field-planted or root-pruned at a depth of 15 to 20 cm (6 to 8 in) and transplanted for 1 year (Gill and Pogge 1974). Common pear seedlings may be subject to powdery mildew, which is caused by *Podosphaera leucotricha* (Ellis & Everh.) E.S. Salmon, and by root rots.

Cultivars are propagated by budding or grafting onto rootstocks. Bench-grafting dormant scions onto bareroot rootstocks is no longer common in large-scale nursery production. Nursery trees can be produced more efficiently by T-budding onto field-grown rootstocks in late summer when the bark is "slipping." Chip-budding is an alternative technique for seasons when the rootstock bark is not slipping (Frecon 1982). A whip-and-tongue graft or cleft-graft is commonly used when top-working growing trees in early spring. Scions can be grafted a few centimeters off the ground on a young rootstock, as in side-grafting, or multiple grafts can be placed higher up onto scaffold branches to convert an older tree over to a different cultivar, that is, top-working.

Seedlings of wild native species are used as rootstocks throughout the world (Lombard and Westwood 1987). In North America, seedlings of commercial cultivars of common pear such as 'Bartlett' or 'Winter Nelis' are grown for rootstocks. Seedlings of the Callery pear and birch-leaf pear are often used as rootstocks for Asian cultivars. Seedlings of the Ussuri pear may be used as rootstocks where extreme cold hardiness is needed. Pears are potentially graft-compatible with a number of other genera in the Maloideae subfamily, including serviceberry (*Amelanchier*), cotoneaster (*Cotoneaster*), hawthorn (*Crataegus*), apple (*Malus*), medlar (*Mespilus*), squaw-apple (*Peraphyllum*), mountain-ash (*Sorbus*), and others (Lombard and Westwood 1987; Postman 1992). The common quince (*Cydonia oblonga* Mill.) has traditionally been used as a dwarfing rootstock for edible European pears.

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Fagaceae—Beech family

Quercus L.

oak

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Growth habit, occurrence, and use. The oaks—members of the genus *Quercus*—include numerous species of deciduous and evergreen trees and shrubs and make up the single most economically important genus of hardwoods in North America. *Quercus* is also the largest genus of trees native to the United States (Little 1979) and has recently been designated as the "national tree" by the National Arbor Day Foundation. About 500 species are widely distributed throughout the temperate regions of the Northern Hemisphere in both the Eastern and Western Hemispheres as well as southward through Central America to the mountains of Colombia and through Turkey to Pakistan (Sargent 1965). There are about 58 tree and 10 shrub species native to the United States, 104 species in Mexico, and another 30 in Central America and Colombia. At least 70 hybrids have been described, and there are probably many more (Little 1979). Information on hybrids and genetic variation has been summarized for 25 species in Burns and Honkala (1990).

Oaks are divided into 2 subgenera: *Lepidobalanus* (white oaks) and *Erythrobalanus* (black oaks). These subgenera differ in several ways, but most importantly for seed considerations, they differ in time required for fruit maturation, chemical composition of their stored food reserves, and degree of dormancy. In this book, 48 taxa are considered (table 1). Oaks are valuable for a very wide range of products and uses: construction timber, furniture, interior trim, and flooring; watershed protection, wildlife habitat and food, and ornamental plantings; as well as tannins and other extractives and cork. Consequently, many oak species are widely planted for a variety of purposes. For additional information on growth habit, uses, ecology, and silviculture of individual oak species, consult Burns and Honkala (1990).

Flowering and fruiting. Flowering is monoecious. The staminate flowers are borne in clustered aments (catkins) and the pistillate flowers in solitary (or in 2- to many-flowered) spikes in the spring (February to May) before or coincident with emergence of the leaves. Staminate flowers develop primarily from leaf axils of the previous year and range in length from 3 to 35 cm, depending on the species. Pistillate flowers develop from axils of leaves of the current year. The fruit is a nut, commonly called an acorn (figure 1). Acorns of white oaks mature in the year of flowering, whereas acorns of black oaks mature at the end of the second year after flowering (Sargent 1965). Acorns are 1-seeded, or rarely 2-seeded, and occur singly or in clusters of 2 to 5. They are subglobose to oblong, short-pointed at the apex, and partially enclosed by a scaly cup (the modified involucre) at their base. Removal of the cup discloses a circular scar that is often useful in judging acorn maturity. Acorns range in size from 6 mm in length and diameter for willow oak to 50 mm in length and 38 mm in diameter for bur oak (Sargent 1965). Fruits ripen and seeds disperse in the autumn, from late August to early December (Olson 1974; Radford and others 1964; Sargent 1965). The embryo has 2 fleshy cotyledons, and there is no endosperm (figure 2). Acorns are generally green when immature and turn yellow, brown, or black when ripe.

The oaks vary widely in initiation of seed bearing and frequency of large crops (table 2). Acorn production by coppice shoots of chestnut oak only 3 and 7 years old indicates that seed production may start earlier on trees of sprout origin, although coppice sprouts of scarlet and black oaks of comparable ages did not bear seeds (Sharik and others 1983). Environmental factors—such as late spring freezes (Neilson and Wullstein 1980), high humidity during pollination (Wolgast and Stout 1977), or summer droughts (Johnson 1994)—will reduce the acorn crop, but some inherent periodicity seems to exist in many species. Most species produce good crops ("mast years") 1 year out of 3 or 4 (Beck 1977; Christisen and Kearby 1984; Downs and McQuilkin 1944; Goodrum and others 1971). Sork and others (1993) reported good acorn crops in Missouri every 2, 3, and 4 years for black, white, and northern red oaks, respectively. In central California, a study of acorn production in

Figure 1— *Quercus*, oak: acorns of **(top row, left to right)** *Q. alba*, white oak; *Q. falcata*, southern red oak; *Q. kelloggii*, California black oak; *Q. lyrata*, overcup oak. **(second row, left to right)** *Q. macrocarpa*, bur oak; *Q. marilandica*, blackjack oak; *Q. michauxii*, swamp chestnut oak. **(third row, left to right)** *Q. muehlenbergii*, chinkapin oak; *Q. nigra*, water oak; *Q. pagoda*, cherrybark oak; *Q. phellos*, willow oak. **(fourth row, left to right)**, *Q. rubra*, northern red oak; *Q. shumardii*, Shumard oak; *Q. sinuata*, Durand oak; *Q. stellata*, post oak. **(bottom row, left to right)**, *Q. texana*, Nuttall oak; *Q. velutina*, black oak; *Q. wislizeni*, interior live oak.

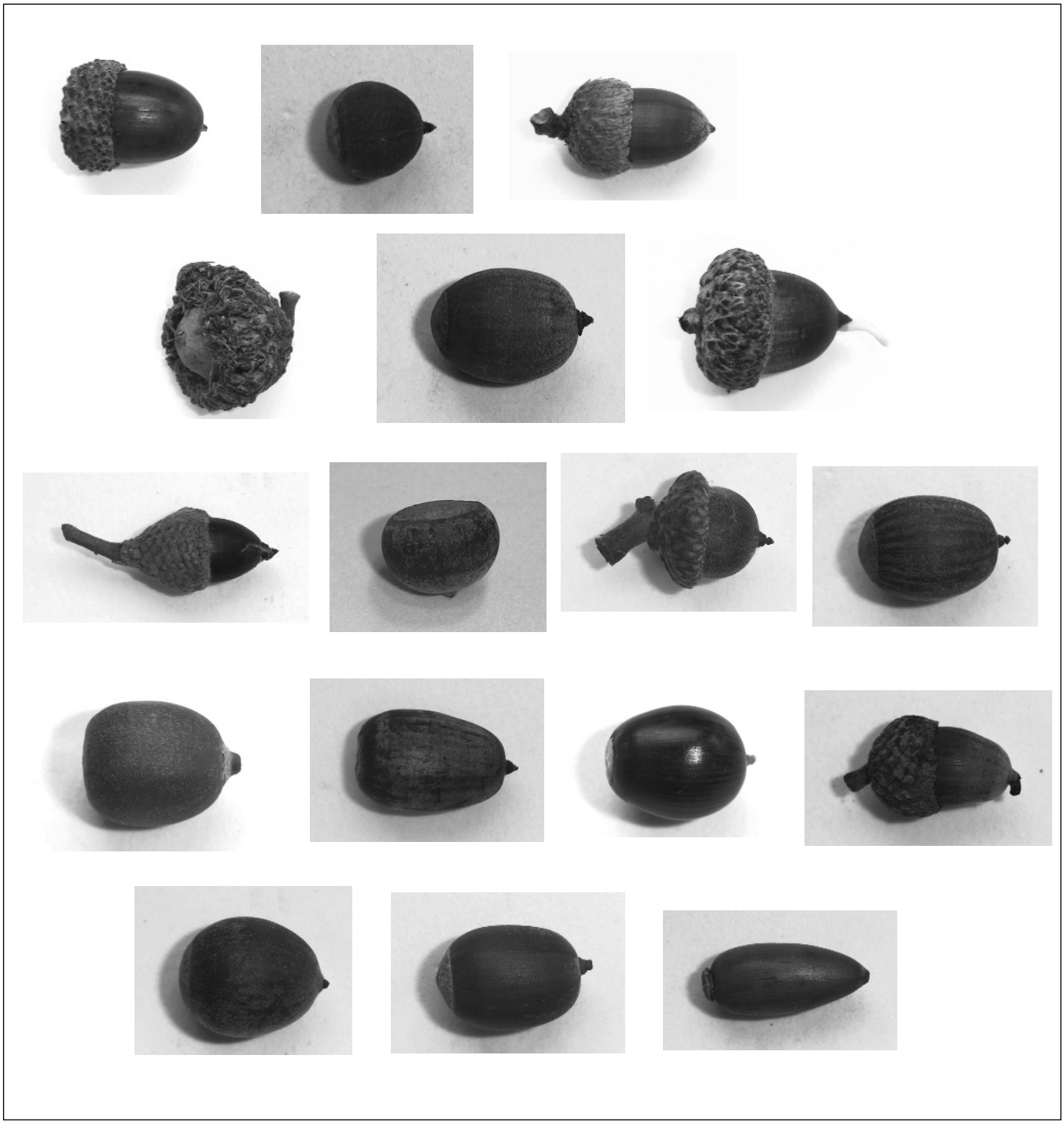


Table 1—*Quercus,* oak: nomenclature and occurrence

Scientific name & synonym(s)	Group*	Common names	Occurrence
Q. *acutissima* Carr.	white	**sawtooth oak**	E Asia & Japan; introduced to E US
Q. *agrifolia* Née	black	**California live oak,** coast live oak; *encina*	Coastal ranges from central to S California
Q. *alba* L.	white	**white oak,** fork-leaf white & stave oaks	SW Maine to N Wisconsin; S to N Florida & E Texas
Q. *arizonica* Sarg.	white	**Arizona white oak,** Arizona oak; *roble*	SW Texas to New Mexico, Arizona, & N Mexico at 1,500–3,000 m
Q. *bicolor* Willd.	white	**swamp white oak,** cow oak	SW Maine to N Wisconsin S to Tennessee & Missouri
Q. *cerris* L.	white	**European turkey oak,** turkey oak	S Europe to W Asia; introduced to central US
Q. *chrysolepis* Liebm.	white	**canyon live oak,** canyon, maul, goldcup, & live oaks	Mtns of SW Oregon, S to S California & N Mexico; local in mtns. of Nevada & Arizona
Q. *coccinea* Muenchh.	black	**scarlet oak,** black & Spanish oaks	SE Maine to Michigan; S to Georgia, & S Alabama & Missouri
Q. *douglasii* Hook. & Arn.	white	**blue oak,** California blue, iron, & mountain white oaks	Foothills of Sierra Nevada & coastal ranges of California
Q. *dumosa* Nutt.	white	**California scrub oak**, scrub oak	Coast Ranges & offshore islands of California & Baja California
Q. *ellipsoidalis* E. J. Hill	black	**northern pin oak,** black, jack, & Hill oaks	Michigan to SW North Dakota; S to Iowa & NW Ohio
Q. *emoryi* Torr.	black	**Emory oak,** black oak, *bellota, roble negro*	Mtns of Trans-Pecos Texas, SW New Mexico, SE & central Arizona, & N Mexico
Q. *falcata* Michx. *Q. triloba* Michx.	black	**southern red oak,** Spanish & red oaks	SE New York to S Missouri; S to N Florida & SE Texas
Q. *gambelii* Nutt. *Q. vreelandii* Rydb. *Q. utahensis* (A. DC.) Rydb.	white	**Gambel oak,** Rocky Mtn. white & Utah white oaks; *encino*	Colorado and Wyoming, W to Utah & S to Arizona, New Mexico, Texas, & NW Oklahoma
Q. *garryana* Dougl. ex Hook.	white	**Oregon white oak,** Garry, post, Oregon, Brewer, & shin oaks	British Columbia; S in mtns to central California
Q. *grisea* Liebm.	white	**gray oak**	SW Texas to New Mexico, Arizona, & N Mexico
Q. *ilicifolia* Wangenh.	black	**bear oak,** scrub oak	S Maine, W to New York; S to West Virginia, SW Virginia, & W North Carolina
Q. *imbricaria* Michx.	black	**shingle oak,** laurel oak	Pennsylvania, S to S Michigan; North Carolina & Arkansas; local in Louisiana & Alabama
Q. *incana* Bartr.	black	**bluejack oak,** sandjack, bluejack, shin, & turkey oaks	Coastal plain from Virginia to central Florida; W to Louisiana, E Texas, Oklahoma, & Arkansas
Q. *kelloggii* Newb.	black	**California black oak,** black & Kellogg oaks	SW Oregon; S through Coast Ranges & Sierra Nevada to S California
Q. *laevis* Walt. *Q. catesbaei* Michx.	black	**turkey oak,** scrub & Catesby oaks	Coastal plain from SE Virginia to central Florida, & W to Louisiana
Q. *laurifolia* Michx.	black	**laurel oak,** Darlington, water, swamp, laurel, & diamond-leaf oaks	Coastal plain from SE Virginia to S Florida; W to E Texas & S Arkansas
Q. *lobata* Née	white	**California white oak,** valley, valley white, weeping, & water oaks; *roble*	Valleys & foothills in California; also Santa Cruz & Santa Catalina Islands
Q. *lyrata* Walt.	white	**overcup oak,** swamp post, water white, & swamp white oaks	Coastal plain from Delaware to Florida; W to E Texas & SW Indiana
Q. *macrocarpa* Michx.	white	**bur oak,** mossycup, blue oak, mossy-overcup, & scrub oaks	S New Brunswick & Manitoba; S to Tennessee & SE Texas

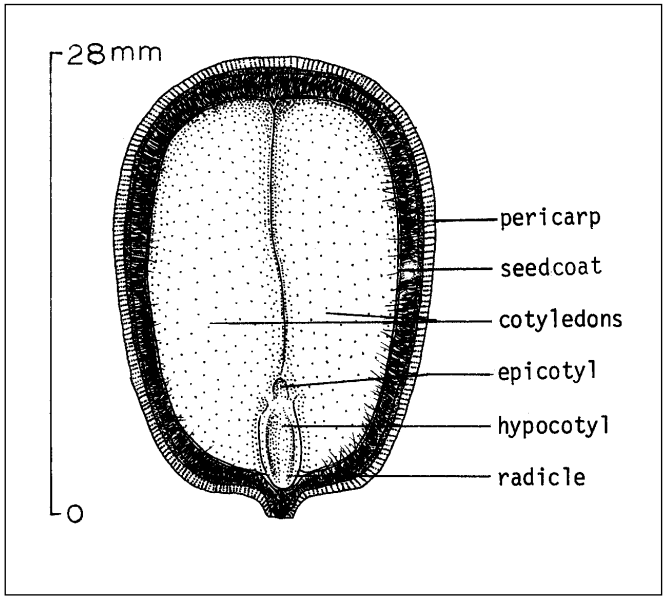
Table 1—*Quercus,* oak: nomenclature and occurrence (continued)

Scientific name & synonym(s)	Group*	Common names	Occurrence
Q. *marilandica* Muenchh.	black	**blackjack oak,** barren & jack oaks; blackjack	New York, W to Ohio, Iowa, & Oklahoma; S to Texas & NW Florida
Q. *michauxii* Nutt. *Q. prinus* L.	white	**swamp chestnut oak**, cow & basket oaks	Coastal plain from New Jersey to N Florida; W to E Texas; N in Mississippi Valley to S Illinois & Indiana
Q. *muehlenbergii* Engelm.	white	**chinkapin oak**, rock, yellow, chestnut, yellow chestnut, & rock chestnut oaks	W Vermont & New York to Minnesota & SE Nebraska; S to NW Florida & central Texas
Q. *nigra* L.	black	**water oak,** possum oak	Coastal plain from New Jersey to S Florida, W & spotted oaks to E Texas, & N in Mississippi Valley to SE Oklahoma
Q. *pagoda* Raf. *Q. falcata* var *pagodaefolia* Ell.	black	**cherrybark oak,** bottomland red, Elliott, & swamp red oaks	SE New Jersey to E Oklahoma; S to N Florida & E Texas
Q. *palustris* Muenchh.	black	**pin oak,** swamp, water, Spanish, & swamp Spanish oaks	Massachusetts & Vermont to S Michigan; S to NE Oklahoma, Tennessee, & central North Carolina
Q. *petraea* (Mattusch) Liebl. *Q. sessiliflora* Salisb.	white	**durmast oak**, sessile oak	Europe & W Asia; planted in central & NE US
Q. *phellos* L.	black	**willow oak**, pin, peach, & swamp willow oaks	Coastal plain from New Jersey to N Florida; W to E Texas & S Illinois
Q. *prinus* L. *Q. montana* Willd.	white	**chestnut oak,** rock chestnut, rock, & tanbark oaks	SW Maine & S Ontario; S to central Georgia & NW Mississippi
Q. *robur* L.	white	**English oak**, pedunculate oak	Europe, N Africa, & W Asia; naturalized in SE Canada & NE US
Q. *rubra* L. *Q. borealis* Michx.f.	black	**northern red oak**, red, common red, eastern red, & gray oaks	Cape Breton Island & Nova Scotia; W to Ontario & S to eastern Oklahoma & Georgia
Q. *shumardii* Buckl.	black	**Shumard oak,** spotted, Schneck, swamp red, & Shumard red oaks	Coastal plain, mostly, from North Carolina to N Florida; W to central Texas, Kansas, & S Illinois
Q. *sinuata* Walt. *Q. durandii* Buckl.	white	**Durand oak,** Durand white, bluff, & bastard oaks	Coastal Plain from North Carolina to N Florida & W to Texas, Oklahoma, & NE Mexico
Q. *stellata* Wangenh.	white	**post oak,** iron oak	SE Massachusetts to SE Iowa, & S to central Florida & Texas
Q. *suber* L.	white	**cork oak**	SW Europe & N Africa; planted in California
Q. *texana* Buckl. *Q. nuttallii* Palmer	black	**Nuttall oak**, red, Red River, & pin oak	Gulf coastal plain from Alabama to SE Texas; N in Mississippi Valley to SE Missouri
Q. *turbinella* Greene	white	**shrub live oak,** turbinella & scrub oaks; *encino*	SW Colorado & Utah; S to S California, Arizona, & northern Mexico
Q. *turbinella* var. *ajoensis* (C.H. Muller) Little	white	**shrub live oak,** Ajo oak	SW Arizona & N Mexico
Q. *vaccinifolia* Kellog	white	**huckleberry oak**	SW Oregon to central California
Q. *variabilis* Bl. *Q. chinensis* Bge.[not Abel] *Q. serrata* Carruth. [not Thunb.]	black	**oriental oak**	N China, Korea, & Japan; planted in central & NE US
Q. *velutina* Lam.	black	**black oak**, yellow, smooth-bark, quercitron, & yellow-bark oak; *quercitron*	SW Maine to SE Minnesota; S to N Florida & E Texas
Q. *virginiana* P. Mill.	white	**live oak**, Virginia live oak; *encino*	Coastal plain from SE Virginia to S Florida (including Florida Keys); W to S Texas
Q. *wislizenii* A. DC.	black	**interior live oak**, highland live & Sierra live oaks	Foothills of Sierra Nevada & Coast Ranges in California, S to Mexico

Sources: Little (1979), Olson (1974), Sargent (1965).

* White oaks belong to subgenus *Lepidobalanus;* black oaks belong to subgenus *Erythrobalanus.*

Figure 2—*Quercus rubra,* northern red oak: longitudinal section through a seed.



valley, blue, and California black oaks and canyon live and coast live oaks (Koenig and others 1994) found no mast production patterns at the population level. Crop failures did occur frequently but they were probably more related to lack of pollination and fertilization success than to inherent patterns. Cecich (1993) concluded that most of the potential seedcrop in oaks in Missouri is lost when pistillate flowers abort between the time of pollination and fertilization. Really good crops of California black oak acorns were found to occur only every 8 years or so (McDonald 1992). The following yield averages on an area basis have been reported: 3.2 to 1,620 kg/ha (2.9 to 1,448 lb/ac) for white oak in Illinois (Johnson 1975); 208 kg/ha (186 lb/ac) for southern Appalachian oaks (Beck 1977); and 560 kg/ha (500 lb/ac) for Oregon white oak in California (Stein 1990).

Collection and cleaning of acorns. Collecting acorns of high quality requires an awareness of the indices of acorn maturity. Natural dissemination from the tree is a sure sign of maturity, of course, but collections are often made before this time to reduce losses to deer, rodents, and other predators that quickly eat fallen acorns. Good indices of maturity for most species are (1) change in pericarp color from green to yellow, brown, or black; (2) a cup scar colored pink, lemon, orange, or white; and (3) cups that slip easily from the acorns without resistance (Bonner and Vozzo 1987; Lotti 1959). Ripe acorns may be collected from August to December from the ground or they can be shaken from trees onto canvas or plastic sheets after ripening. Mechanical tree shakers can be very effective with oaks where the terrain or stand conditions permit it. Collecting acorns from downed trees in logging operations also can be successful if the trees were cut after the acorns matured. Acorns should be collected from the ground within a few days after dispersal to avoid losses to predators, desiccation of the acorns, and early germination of the non-dormant species (primarily the white oaks). California black oak also requires prompt collection because mold often infects fallen acorns (McDonald 1990).

To avoid desiccation, which can quickly reduce acorn quality, acorns should be floated in water after collection, preferably at the end of each collection day. This action will maintain high moisture contents and permit removal of trash and unsound acorns. Sound acorns will sink and the other material will float. For acorns collected from the ground, moisture conditions at time of collection can affect the flotation process. If the ground is very dry, many good acorns may float initially, and the lot may have to stay in the water overnight to allow sound acorns enough time to take up moisture and sink. In contrast, when the ground is wet, many unsound acorns may be heavy enough to sink in water, and a few hours of drying at ambient temperature can help the separation. Water flotation is never 100% effective, but common sense and attention to detail will enable collectors to make dramatic improvements in the quality of their acorns. Another way to allow for different acorn moisture conditions may be to use salt solutions to change the density of the water. In a test with water oak and willow oak (Johnson 1983), 230 g of salt/liter of water for unsaturated acorns and 285 g/liter for saturated acorns, led to recovery of up to 11% more good acorns. The acorns were not in the salt solutions long enough to take up the chemical, and a quick rinse after recovery removed surface salt. In the dry climate of California, acorns of blue oak dry so quickly that collection directly from the tree may be the only way to ensure seed quality (McCreary and Koukoura 1990). A loss of only 10% acorn moisture resulted in almost 40% less germination for blue oak.

Data on acorn size and weight are summarized in table 3. For many years, nurseries did little sizing of acorns, but now that is changing, at least in the South. Numerous nurseries now size acorns with screens or other devices (Bonner and Vozzo 1987) to gain in uniformity of germination and bed density. Positive correlations between acorn size and leaf area have been reported for northern red, chestnut, white, and bear oaks (Farmer 1980) and also between acorn size and shoot growth for English and durmast oaks (Kleinschmit and Svolba 1979).

In years when light crops are produced, the percentage of acorns that are infested with insect larvae will be large,

Table 2—*Quercus,* oak: height, seed-bearing age, and seedcrop frequency

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yrs)	Years between large seedcrops
Q. acutissima	15	1862	5	—
Q. agrifolia	23	1849	15	—
Q. alba	30	1724	20	4–10
Q. arizonica	12	—	—	—
Q. bicolor	30	1800	20	3–5
Q. cerris	30	1735	—	—
Q. chrysolepis	30	1877	20	2–4
Q. coccinea	30	1691	20	3–5
Q. douglasii	18	—	—	2–3
Q. dumosa	6	—	—	—
Q. ellipsoidalis	21	1902	—	2–4
Q. emoryi	18	—	—	—
Q. falcata	27	1763	25	1–2
Q. gambelii	15	—	—	—
Q. garryana	21	1873	—	2–3
Q. grisea	20	—	—	—
Q. ilicifolia	6	1800	—	—
Q. imbricaria	21	1724	25	2–4
Q. incana	12	—	—	—
Q. kelloggii	26	1878	30	2–3
Q. laevis	9	1834	—	1–2
Q. laurifolia	27	1786	15	1
Q. lobata	30	1874	—	2–3
Q. lyrata	24	1786	25	3–4
Q. macrocarpa	30	1811	35	2–3
Q. marilandica	15	—	—	—
Q. michauxii	30	1737	20	3–5
Q. muehlenbergii	24	1822	—	—
Q. nigra	24	1723	20	1–2
Q. pagoda	34	1904	25	1–2
Q. palustris	24	1770	20	1–2
Q. petraea	30	Long	40	5–7
Q. phellos	30	1723	20	1
Q. prinus	24	1688	20	2–3
Q. robur	34	Long	20	2–4
Q. rubra	30	1724	25	3–5
Q. shumardii	34	1907	25	2–3
Q. sinuata	23	—	—	—
Q. stellata	18	1819	25	2–3
Q. suber	24	1699	12	2–4
Q. texana	30	1923	5	3–4
Q. turbinella	3	—	—	3–5
Q. vaccinifolia	1	1895	—	—
Q. variabilis	24	1861	—	2
Q. velutina	27	1905	20	2–3
Q. virginiana	18	1739	—	1
Q. wislizenii	18	1874	—	5–7

Sources: Burns and Honkala (1990), Olson (1974), Sargent (1965), Smith (1993), Sork and others (1993), Vines (1960).

and flotation offers a simple way to remove these damaged acorns. The major insect pests of acorns in the United States are the acorn weevils (*Curculio* spp.), filbertworms (*Melissopus latiferranus* Walsingham), and acorn moths (*Valentinia* spp.) (Baker 1972; Gibson 1972, 1982; Oliver and Chapin 1984; Vozzo 1984). A cynipid wasp that causes galls on acorns of European turkey oak and English oak is a major pest in Europe, causing 30 to 50% losses of the acorn crop each year in the United Kingdom (Collins and others 1983). Prevention of infestation is not possible, so infested acorns must be removed from the lots. Some collectors kill the larvae of acorn weevils by immersing the acorns in hot water (48 °C) for 40 minutes (Olson 1974). This temperature is dangerously close to conditions that will damage the

Table 3—*Quercus,* oak: seed yield data

Species	Seed weight/ fruit vol		Cleaned seeds/weight				Samples
			Range		Average		
	kg/hl	lb/bu	/kg	/lb	/kg	/lb	
Q. acutissima	—	—	210–245	95–110	85	187	2
Q. agrifolia	—	—	—	—	200	440	1
Q. alba	58–129	45–100	155–465	70–210	98	215	23
Q. bicolor	—	—	200–385	90–175	265	120	3
Q. cerris	—	—	130–320	60–145	240	110	4
Q. chrysolepis	—	—	110–310	50–150	—	—	—
Q. coccinea	39–77	30–60	230–890	105–405	520	235	4
Q. douglasii	—	—	120–330	55–180	220	100	4
Q. dumosa	—	—	—	—	220	100	1
Q. ellipsoidalis	—	—	450–640	205–290	540	245	11
Q. falcata	42–64	33–50	705–1,730	320–785	1,190	540	9
Q. garryana	50	39	165–220	75–100	185	85	3
Q. ilicifolia	—	—	—	—	1545	700	1
Q. imbricaria	—	—	695–1,750	315–795	915	415	11
Q. incana	—	—	500–1,500	225–680	—	—	—
Q. kelloggii	—	—	115–325	52–145	210	95	49
Q. laevis	—	—	—	—	870	395	1
Q. laurifolia	—	—	860–1,520	90–690	1,235	560	3
Q. lobata	—	—	165–525	75–237	285	130	4
Q. lyrata	—	—	285–340	130–154	265	120	6
Q. macrocarpa	39–45	30–35	90–300	40–135	165	75	8
Q. michauxii	51–80	40–62	75–430	35–195	125	55	35
Q. muehlenbergii	60–66	47–51	580–1,145	265–520	870	395	4
Q. nigra	57–72	44–56	510–1,545	230–700	640	290	226
Q. pagoda	—	—	925–1,640	420–745	690	312	41
Q. palustris	—	—	705–1,190	320–540	475	220	33
Q. petraea	—	—	130–650	60–295	375	170	9
Q. phellos	59–60	46–47	600–1,530	270–695	835	380	183
Q. prinus	—	—	120–430	55–195	220	100	5
Q. robur	—	—	200–495	90–225	285	130	10
Q. rubra	28–134	22–104	165–565	75–255	235	105	55
Q. shumardii	64	50	170–280	80–130	220	100	27
Q. sinuata	53	47	—	—	6,400	290	1
Q. stellata	69	54	440–1,400	200–635	840	380	9
Q. suber	—	—	110–220	50–100	165	75	13
Q. texana	67	52	125–315	55–145	220	100	83
Q. turbinella	—	—	660–770	300–350	715	325	2
Q. vaccinifolia	33	26	1630–2,910	740–1,320	2,270	1,030	2
Q. variabilis	—	—	165–275	75–125	230	105	12
Q. velutina	53–63	41–49	275–882	125–400	540	245	7
Q. virginiana	71	55	530–1,125	240–510	775	350	4
Q. wislizenii	36	28	100–152	100–150	275	125	3

Sources: Burns and Honkala (1990), Olson (1974), Toumey and Korstian (1942), Van Dersal (1938).

acorns, however, so caution must be used. In a study with live oak, germination and seedling growth dropped dramatically after hot water treatments of 7.5 to 60 minutes (Crocker and others 1988). Because none of these insects attacks other acorns during storage, the infestation cannot spread. Only in cases of exporting acorns to other countries where seed health regulations require treatment would this treatment be completely justified.

Storage. Acorns are recalcitrant seeds; they cannot tolerate desiccation below a rather high minimum moisture content and are therefore very difficult to store. Oaks are by far the most commercially important group of recalcitrant species in the temperate zone. The lethal moisture contents vary by species, but range from 15 to 20% in black oaks and 25 to 30% in white oaks. Most species of the black oak group can be stored for 3 years by maintaining high acorn moisture levels (above 30%) and storing just above freezing (1 to 3 °C) in containers that allow some gas exchange with the surrounding atmosphere (Bonner 1973; Bonner and Vozzo 1987; Suszka and Tylkowski 1982). Most species will germinate in storage under these conditions, but pre-sprout-

ing does not prevent sowing or production of plantable seedlings (Bonner 1982). White oak acorns can be stored in a similar fashion, but safe moisture levels are 45 to 50%. White oaks germinate in storage much more readily than black oaks, and do not survive as well. As a practical matter, storage of white oak acorns for more than 6 months is seldom attempted in this country. Acorns of English oak have been successfully stored for 3 years in Europe by lowering the moisture levels slightly and mixing them with dry sawdust or peat (Suszka and Tylkowski 1980). Acorns of the same species are routinely stored for 3 years in Denmark also by lowering the moisture content slightly and storing the acorns right at freezing in open containers with no medium. In the case of another white oak, partial drying of California scrub oak acorns significantly improved viability retention over 8 months (Plumb and McDonald 1981). The partial drying may be beneficial because it reduces the incidence of fungi on the surface of the acorns.

Acorns can be stored in plastic bags, drums, or even boxes as long as the containers are not completely sealed and the acorns do not get too dry. Some European species can be stored by immersion in water (Jones 1958), and Nuttall oak has been successfully stored overwinter submerged in water at 3 to 5 °C (Johnson 1979). If drums or boxes are used, it is wise to insert a plastic bag liner. Respiration is rapid in seeds with high moisture levels, and oxygen will be depleted and carbon dioxide increased dramatically in just a few weeks. Plastic bags at least 4 mils thick are useful for storage; tops should be loosely folded over, not sealed. There is some evidence that white oaks should be stored in thinner bags (1.75 mils) because of their greater requirement for oxygen (Rink and Williams 1984). Most species can actually tolerate temperatures a few degrees below freezing (Suszka and Tylkowski 1980), but storage below –5 °C is usually fatal.

Pregermination treatment. Acorns of the white oak group generally have little or no dormancy and will germinate almost immediately after falling. These species should usually be planted in the fall. They will quickly put down radicles, but epicotyl dormancy occurs in some species and prevents shoot growth until the following spring. Epicotyl dormancy has been noted in English oak (Wigston 1987) and in eastern and southern white and chestnut oaks (Farmer 1977). White oaks in the warmer climate of California—coast and canyon live oaks, and blue, California scrub, and valley oaks—apparently do not have epicotyl dormancy (Matsuda and McBride 1989). Acorns of bur oak from the northern portion of its range actually require 60 days of cold, moist stratification for prompt germination (Tinus 1980). Acorns of the black oak group exhibit variable dormancy that is apparently imposed by the pericarp, the embryo, or both (Hopper and others 1985; Jones and Brown 1966; Peterson 1983), and stratification is usually recommended before spring-sowing or certain types of germination tests. Epicotyl dormancy has been reported in at least 1 black oak species—bear oak (Allen and Farmer 1977). If proper procedures are followed for storage of black oak acorns, the storage conditions will also serve to complete the stratification requirement, and additional treatment is not necessary (Bonner and Vozzo 1987). If additional stratification is needed, imbibed acorns should be held for 4 to 12 weeks at temperatures of 2 to 5 °C. The acorns may be mixed with peat or other media, but this is not necessary. Most managers stratify in plastic bags without medium, turning the bags each week or so to prevent pooling of excess moisture in the bags (Bonner and Vozzo 1987). Acorns of the black oak group sown in the fall or early winter need not be stratified before to sowing.

Germination tests. In the standard official laboratory test procedure for all oaks, the acorns should be soaked in water for 48 hours; then a third of the acorn at the cup scar end should be cut off and the pericarp removed from the top half and placed on thick, moist blotters at alternating temperatures of 20 to 30 °C (ISTA 1993). No other pretreatments are necessary, and germination should be complete within 14 days. Germination can also be tested with intact acorns in sand, peat, or other media in greenhouse flats. In such tests, stratification may be necessary for black oak species (table 4). Germination is hypogeal (figure 3) and is generally complete in 3 to 5 weeks. Rapid estimates of viability can also be made with cutting tests, radiography, or tetrazolium staining (Belcher and Vozzo 1979; Bonner and Vozzo 1987). Cutting tests are reliable on freshly collected acorns, and radiography is very good for quick determination of insect infestation. Tetrazolium staining can also provide information on seed vigor, but acorn chemistry and morphology present some problems in this test (Bonner 1984).

Nursery practice. Numerous research studies have shown that success in planting oaks depends on production of vigorous seedlings through low sowing densities and undercutting in the beds (Schultz and Thompson 1990). Container production in greenhouses is also practiced for a few species (Tinus 1980). Fall-sowing acorns is preferable to spring-sowing in many instances if weather allows bed preparation in the fall. Fall-sowing eliminates the need for a large storage capacity for acorns and avoids the problems of fungi and early germination in storage. One disadvantage to

Table 4—*Quercus,* oak: germination test conditions and results

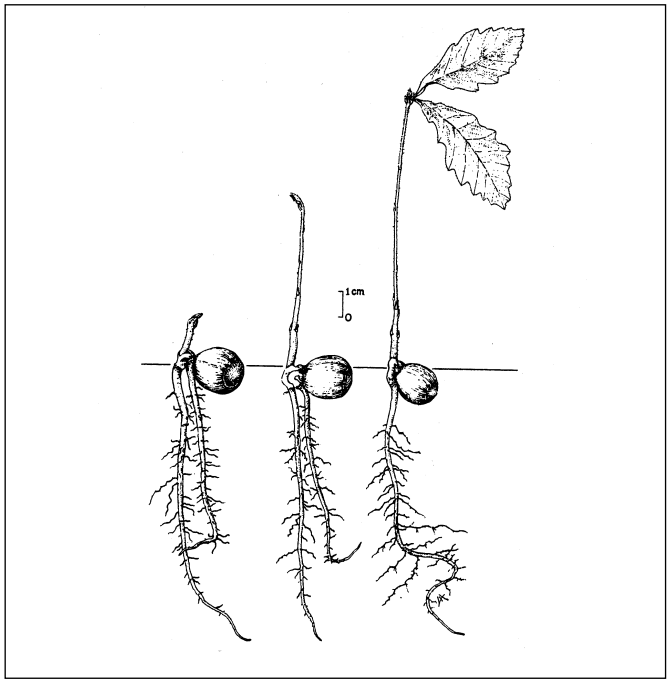
Species	Cold stratification (days)	Germination test conditions: Medium	Temp (°C): Day	Temp (°C): Night	Germinative rate: Day	Germinative rate: Avg (%)	Germinative rate: Days	Germination (%)	Samples
Q. acutissima	—	—	—	—	—	—	—	98	1
Q. agrifolia	0	—	—	—	15–40	—	—	73	1
Q. alba	0	Kimpac	30	20	30–98	39–93	10–41	50–99	21
Q. bicolor	0	Sand	21–35	10–16	60–240	65–95	80–120	78–98	3
Q. cerris	0	Germinator	22	20	30	—	—	33–76	3
Q. chrysolepis	0–60	Peat/loam	30	20	56–60	—	—	56–75	2
Q. coccinea	30–60	Kimpac	30	20	30–60	97	16	94–99	7
Q. douglasii	0	Sand	30	20	30	—	—	70–72	4
Q. durmosa	30–90	Sand	30	20	28	—	—	80–90	3
Q. ellipsoidalis	60–90	Sand	30	21	30–60	80–93	18–26	95	5
Q. falcata	30–90	Sand	23–27	23–27	30–57	62–74	22–36	75–100	8
Q. gambelii	14	—	—	—	—	92	15	92	1
Q. garryana	0	Loam	30	21	90	—	—	77–100	4
Q. ilicifolia	60–120	Sand/perlite	30	20	36–81	—	—	86–94	12
Q. imbricaria	30–60	Sand	24	16	30	—	—	28–66	2
Q. kelloggii	30–45	Sand	30	21	30–40	—	—	95	1
Q. laevis	60–90	Sand	27	23	7	—	—	82	2
Q. laurifolia	0	Soil			108	—	—	50	1
	14–90	Sand	27	23	30–90	—	—	45–92	6
Q. lyrata	0	Sand	21–35	10–16	160	82	100	84	1
	42	Sand	27	23	128	—	—	82	4
Q. macrocarpa	30–60	Sand	30	20	40	28-85	25-45	45	11
Q. marilandica	90	—	—	—	—	—	—	91	1
Q. michauxii	0	Soil	32	21	50–84	23–48	40–60	49	2
	30	Soil	32	21	50	86	22	98	1
Q. muehlenbergii	0	Kimpac	30	20	45	95	8	98	4
Q. nigra	30–60	Sand/peat, Kimpac	30–32	20–21	52–73	54–80	31–73	60–94	12
Q. pagoda	60–120	Sand/perlite	30	20	30–40	85–90	21–38	86–98	11
Q. petraea	0	Sand	30	20	30	—	—	65–74	7
Q. phellos	30–90	Soil, Kimpac	32	21	45–100	41	55	67	4
	0	Soil	32	21	90	83	47	89	1
Q. prinus	0	Sand	27	18	60	72–78	40	82	3
Q. robur	0	Sand	25	16	30–60	—	—	81	4
Q. rubra	30–45	Sand	30	20	40–60	39–85	13–42	58	11
	70	Sand/peat	20	20	20	80	10	100	1
Q. shumardii	60–120	Soil, Kimpac	32	21	29–50	53–66	21–28	72–82	3
Q. sinuata	0	Kimpac	30	20	30	81	21	87	4
Q. stellata	0	Sand, Kimpac	30	20	45–60	42–93	10–45	54–98	7
Q. suber	0	Sand	27	27	20–30	—	—	73-100	5
Q. texana	60–90	Soil	32	21	58–87	—	—	60–69	20
Q. turbinella		Sand	38	5	—	—	—	95	2
Q. vaccinifolia	0	Loam	23	19	180	38	30	43	1
Q. variabilis	0	Sand	25		28	55	28		2
Q. velutina	30–60	Sand	27	18	30–50	—	—	47	5
Q. virginiana	0	Kimpac	30	20	—	92	8	97	4
Q. wislizenii	30–60	Sand/peat	30	20	69	—	—	75	1

Sources: Dirr and Heuser (1987), Korstian (1927), Larsen (1963), Olson (1974), Swingle (1939).

fall-sowing in the southern part of the country is that mild winters may not completely satisfy the stratification requirement of dormant black oaks, and germination in the spring may be slow and erratic. Another disadvantage is prolonged exposure to predators, such as grackles (*Quiscaluis spp.*) and blue jays (*Cyanocitta cristata*), that dig up acorns from the beds. If spring-sowing is used (very common in the South), the acorns should be stratified.

Acorns should be drilled in rows 20 to 30 cm (8 to 12 in) apart and covered with 6 to 25 mm ($^1/_4$ to 1 in) of firmed soil. The planting depth should at least be equal to the average acorn diameter. Desirable seedbed densities are 100 to

Figure 3—*Quercus macrocarpa*, bur oak: seedling growth 1, 5, and 12 days after germination



160 seedlings/m^2 (10 to 15/ft^2) (Williams and Hanks 1976), or less. For cherrybark oak, a study of bed densities from 43 to 108/m^2 (4 to 10/ft^2) showed that the lowest density produced more plantable seedlings per weight of seed, even though nursery costs were approximately 20% higher (Barham 1980). Another study with this same species found that 86/m^2 (8/ft^2) produced the greatest number of plantable seedlings (Hodges 1996). Fall-sown beds should be mulched with sawdust, ground corncobs, burlap, straw, or similar materials. Where high winds may blow the mulch, some sort of anchoring device, such as bird netting, must be used. Mulches reduce erosion and frost heaving and provide some protection against rodents and birds. In the spring, after frost danger is past, the straw and hay mulches should be removed, but sawdust can remain on the beds. Partial shade has been found to improve germination of Nuttall (Johnson 1967) and cherrybark oaks (Hodges 1996) but is not commonly used for other oaks. The common planting stock for oaks is a 1+0 seedling.

Oaks can also be direct-seeded in the field but must be covered to control predation by animals. Spot-seeding at depths of 2 to 5 cm (1 to 2 in) have been successful for bur, chestnut, white and pin oaks in Kentucky (Cunningham and Wittwer 1984); white, northern red, and black oaks in Tennessee (Mignery 1975); and cherrybark, Nuttall, sawtooth, Shumard, and water oaks in Mississippi (Francis and Johnson 1985; Johnson 1984; Johnson and Krinard 1985). Rapid germination will also reduce losses to rodents and birds, so acorns direct-seeded in the spring should be stratified. In recent years, large areas have been seeded to oaks in the Mississippi River floodplain in Mississippi and Louisiana. Results have been mixed; some operations have been successful and others have not, but the reasons for failure have not always been understood. In these sites, control of competing vegetation is often necessary in the first few years.

Oaks in general are extremely difficult to propagate vegetatively on a commercial scale, although a few successes have been reported. Grafting and budding have been somewhat successful for ornamental selections (Dirr and Heuser 1987), and some advances have been made in tissue culture of certain oaks (Chalupa 1990; Gingas 1991).

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Rhamnaceae—Buckthorn family

Rhamnus L.

buckthorn

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Growth habit, occurrence, and use. Until recently, the buckthorn genus—*Rhamnus*—and the closely related genus *Frangula* have been treated as the single genus *Rhamnus* consisting of more than 125 species of evergreen or deciduous shrubs and trees with alternate branches and simple leaves with prominent pinnate veins (Hickman 1993). Kartesz and Gandhi (1994), however, used floral morphology and leaf venation, as well as anatomical features of xylem vessels to support segregation of *Frangula*. Under their treatment, *Rhamnus* spp. have winter buds protected with bud scales and arcuate leaf nerves. Both *Rhamnus* and *Frangula* are native to the temperate regions of North America, Europe, and Asia, and also occur in the Neotropics and southern Africa as shrubs and trees up to 1.5 m dbh and over 60 m tall (Johnston and Johnston 1978; Krüssmann 1985). The common name buckthorn, which is shared by both genera, may have arisen in Europe, where some of the species are thorny (Mozingo 1987; USDA 1937). *Rhamnus* is the Latinized form of the ancient Greek name for the genus. At least 14 species and subspecies are distributed within the United States (table 1) (USDA NRCS 2001).

European buckthorn, native to Europe and temperate Asia and widely naturalized in the northeastern United States, is a common old-field invader (Gill and Marks 1991) that grows to about 4 m in height with branches that may end in sharp thorns. The bark yields yellow and saffron-colored dyes. The black fruits have been collected for over a thousand years as the source of a strong cathartic and laxative that is so potent that its purgative properties may be retained in the flesh of animals that have consumed the fruit (Mozingo 1987).

Alder buckthorn has perhaps the broadest distribution of all the species native to North America. The specific epithet refers to its similarity to alder (*Alnus*) in leaf shape. The leaves are deciduous, and the wood has been used as a source of the finest charcoal for gunpowder (Everett 1982). It grows to a height of 1.5 m on moist mountain slopes and streambanks.

Spiny, hollyleaf, and island redberries are evergreen shrubs or small trees of California chaparral. The fruits of spiny and hollyleaf redberries may be preferred browse of deer (*Odocoileus* spp.) (Conrad 1987).

Alder buckthorn and European buckthorn are alternate hosts for crown rust—*Puccinia coronata* Corda.—which causes yellow leaf spot in the aecial stage. Economic damage by crown rust is confined to heavy damage in fields of oats grown in close proximity to hedges and fence-rows of buckthorns (Ziller 1974).

The dates of earliest known cultivation of species native to North America includes 1778 for alder buckthorn and the mid-1800's for spiny redberry (Krüssmann 1985).

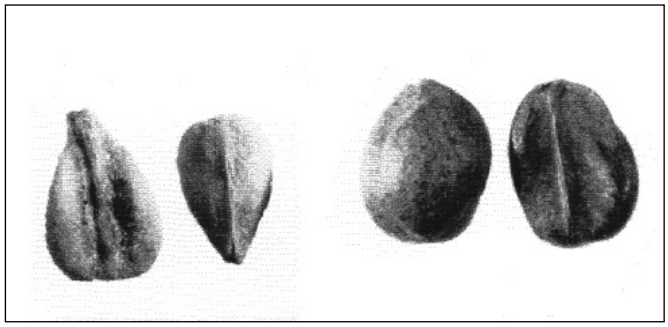
Flowering and fruiting. The inconspicuous flowers are either perfect or imperfect and are borne in small axillary racemes, fascicles, or occasionally reduced to single flowers in alder buckthorn and spiny, hollyleaf, and island redberries. The shallow to deeply campanulate hypanthium is rimmed with 4 deltoid, thin and spreading sepals, with the upper part of the hypanthium falling after maturity and the lower part remaining around the developing fruit (Hitchcock and others 1961; Kartesz and Gandhi 1994). White to greenish white petals are equal to the sepals in number and alternating, or lacking. There are 4 stamens, and the anthers are shorter than filaments. The ovary has 2 to 4 cells. Flowers are unisexual in spiny, hollyleaf, and island redberries; alder buckthorn and European buckthorn plants may be dioecious. Flowers appear in the spring and fruits ripen several weeks to months later (Hubbard 1974).

Fruits are drupaceous, the berrylike pulpy mesocarp embedding several free 1-seeded stones (figure 1) (Johnston and Johnston 1978). Fruits are 6 to 8 mm in diameter; they are generally black in alder buckthorn and red in spiny, hollyleaf, and island redberries. Spiny, hollyleaf, and island redberries have 2 stones per fruit; alder buckthorn has 3 stones per fruit; and European buckthorn has 3 or 4 stones per fruit (figure 2). Stones are grooved on the outside (Kartesz and Gandhi 1994). Dispersal is mostly by birds.

Table 1—*Rhamnus*, buckthorn: nomenclature and occurrence

Scientific names & synonym(s)	Common name(s)	Occurrence
***R. alnifolia* L'Hér.**	**alder buckthorn**	Transcontinental in S Canada, Maine to Virginia, Tennessee, W to Utah, California
***R. arguta* Maxim.**	—	Introduced in Indiana
***R. cathartica* L.**	**European buckthorn,** waythorn, common buckthorn	Europe & Asia; naturalized from Nova Scotia, Maine, S to Virginia, W to Montana, Wyoming, Utah, & California
***R. crocea* Nutt.** *R. pilosa* (Trel.) Abrams	**spiny redberry,** redberry buckthorn	California to Baja California Sur, Arizona, & New Mexico
***R. davurica* Pallas**	**Dahurian buckthorn**	Siberia to N China; introduced in Rhode Island, Pennsylvania, North Carolina, E to North Dakota, Nebraska
***R. davurica* Pallas ssp. *nipponica* (Makino) Kartesz & Gandhi**	**Dahurian buckthorn**	Introduced in Rhode Island
***R. ilicifolia* Kellogg** *R. crocea* Nutt. ssp. *ilicifolia* (Kellogg) C.B. Wolf *R. crocea* Nutt. var. *ilicifolia* (Kellogg) Greene	**hollyleaf redberry**	Oregon, California, Nevada, & Arizona
***R. japonica* Maxim.**	**Japanese buckthorn**	Japan: introduced in Illinois
***R. lanceolate* Pursh ssp. *glabrata* (Gleason) Kartesz & Gandhi** *R. lanceolata* Pursh var. *glabrata* Gleason	**lanceleaf buckthorn**	Virginia, Ohio, Tennessee, Alabama, W to South Dakota, Arkansas, Texas
R. lanceolate* Pursh ssp. *lanceolata	**lanceleaf buckthorn**	Pennsylvania, Virginiana, W to Wisconsin, Indiana, Missouri, Tennessee, Alabama
***R. pirifolia* Greene** *R. crocea* Nutt. var. *pirifolia* (Greene) Little *R. crocea* Nutt. ssp. *pirifolia* (Greene) C.B. Wolf	**island redberry**	S California to Mexico
***R. serrata* Humb. & Bonpl. ex J.A. Schultes** *R. fasciculata* Greene *R. smithii* Greene ssp. *fasciculata* (Greene) C.B. Wolf	**sawleaf buckthorn**	Arizona, New Mexico, Texas
***R. smithii* Greene** *R. smithii* Greene ssp. *typica* C.B. Wolf	**Smith buckthorn**	Colorado & New Mexico
***R. utilis* Dcne.**	**Chinese buckthorn**	E China; introduced in Michigan & Illinois

Figure 1—*Rhamnus*, buckthorn: cleaned seeds of *R. alnifolia*, alder buckthorn (**left**) and *R. davurica*, Dahurian buckthorn (**right**).



Good seedcrops for all species are likely to occur in most years. Regeneration of spiny and hollyleaf redberries is primarily by stump-sprouting after fire (Conrad 1987; Keeley 1981).

The reproductive biology of a few non-North American species has been investigated, including (1) the obligatory re-sprouting of *R. palaestina* Boiss. in Israel (Naveh 1974); (2) population sex ratio, flowering phenology, and between-sex differences in reproductive allocation in Italian buckthorn (*R. alaternus* L.), a dioecious shrub of the Mediterranean region (Guitián 1995a); (3) the population sex ratio, pollen-to-ovule ratio, and flowering and fruiting phenology in *R. legionensis* Rothm., a dioecious shrub restricted to limestone areas in the León Province of northwest Spain (Guitian 1995b); and (4) the partitioning of dry mass and nitrogen between flesh and stone in European buckthorn (Lee and others 1991).

Collection, extraction, and storage. Fruits can be collected from the shrubs and trees when ripe, although collection timed to occur about 2 weeks before the fruit is fully ripe may limit losses to birds (Hubbard 1974). Fruits can be

Figure 2—*Rhamnus cathartica*, European buckthorn: longitudinal section through a seed (**left**) and transverse section (**right**) through 4 seeds in a fruit.

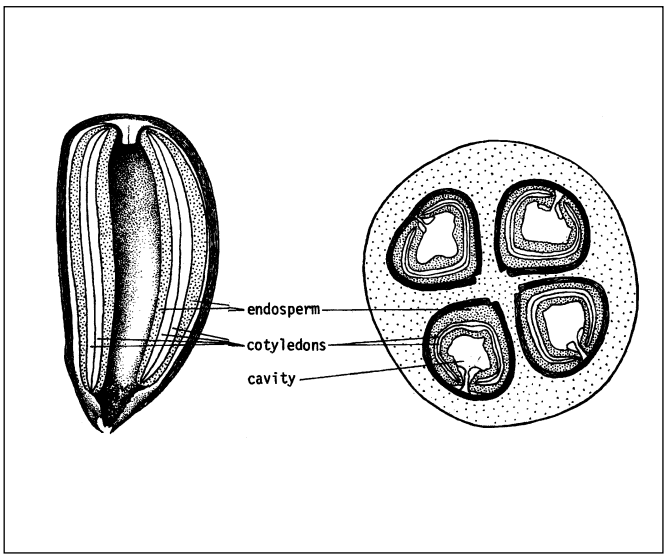
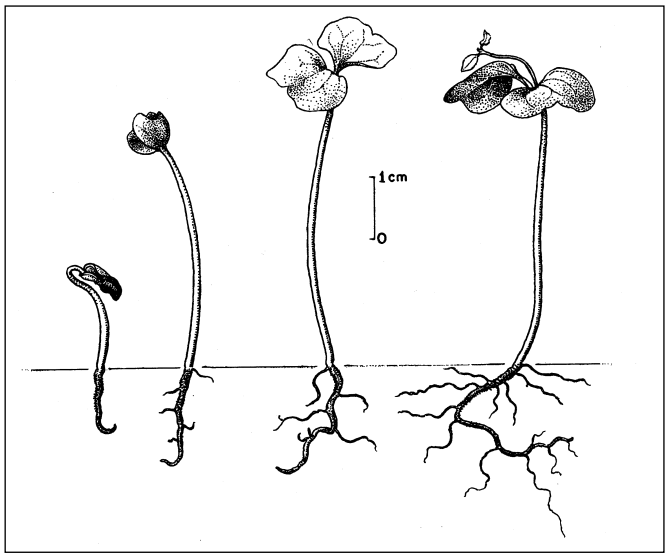


Figure 3—*Rhamnus cathartica*, European buckthorn: seedling development at 1, 4, 19, and 28 days after germination.



run through a macerator with water soon after collection; full seeds can then be cleaned of other material by repeated decantation. Data on yield of seeds are scant and based on limited samples; yields are about 105 seeds/g (2,975 seeds/oz) for spiny redberry (Keeley 1987) and 95 seeds/g (2,690 seeds/oz) for European buckthorn (Lee and others 1991).

Seed storage guidelines have not been developed for buckthorn species, but it appears that seeds can be stored adequately for several years if they are kept in sealed containers at low temperatures (Hubbard 1974).

Pregermination treatment. Considerable variability seems to exist in the need for pregermination treatments of buckthorn seed. Fresh seeds of alder buckthorn and spiny redberry apparently have no innate germination requirements (Hubbard 1974; Keeley 1987). During laboratory tests involving 1 month of stratification at 5 °C, however, more than 75% of the total germination occurred after 7 days of incubation at 23 °C in the dark. Germination increased to 90% when seeds were incubated with an initial heat treatment of 100 °C for 5 minutes and seeds were placed on soil containing 0.5 g powdered charred wood (charate) of the chaparral shrub chamise or greasewood—*Adenostoma fasciculatum* Hook. & Arn.—a treatment designed to simulate conditions after a chaparral fire (Keeley 1987). Seeds of spiny redberry germinated best after 1 month of cold stratification followed by an initial heating treatment of 100 °C for 5 minutes and incubation at 23 °C in charate-enriched soil under a 12-hour photoperiod of 350 μmol/m^2/sec. Seeds germinated slowly, with more than 75% of the total germination delayed until a second cycle of stratification and incubation (Keeley 1987). Seeds of European buckthorn have been stratified for 2 to 3 months in moist peat at 5 °C (Dirr 1990). Soaking European buckthorn seeds in concentrated sulfuric acid treatment for 20 minutes to break dormancy was found to be harmful (Hubbard 1974).

There are no officially prescribed germination tests procedures for buckthorns. Viability tests by tetrazolium staining have been suggested for European species (Enescu 1991). Seeds should be soaked in water for 24 hours, cracked open in a vise, then re-soaked overnight. Staining should take place in a 1% tetrazolium solution for 24 hours at 30 °C (Dirr 1990). To be considered viable, the embryos must be completely stained, with the exception of the extreme third of the distal ends of the radicle and cotyledons.

Nursery and field practice. Detailed nursery techniques have not been developed for most buckthorn species. The available information suggests that for most of the species, the seeds should be sown in the spring at a depth of 10 to 40 mm (0.4 to 1.6 in) after they have been treated to break dormancy (Hubbard 1974). Germination is epigeal with thin, usually curved cotyledons (figure 3) (Kartesz and Gandhi 1994). Some buckthorns also are propagated by layering and by cuttings or by grafting (Hubbard 1974).

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Ericaceae—Heath family

Rhododendron L.

rhododendron and azalea

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Occurrence. The genus rhododendron—*Rhododendron* L.—is indigenous mainly to the Northern Hemisphere, with large concentrations in the mountain ranges of China, Tibet, and upper Burma as well as in Japan and the eastern United States. Plants are found commonly in regions with highly organic soils, high rainfall, high humidity, and a temperate climate (Cox 1990). Species range from tiny, prostrate, alpine shrubs only 5 cm tall to trees with enormous leaves that reach heights of 24 m (Leach 1961). Species native to North America are listed in table 1.

Growth habit. There are over 900 species of rhododendrons and numerous cultivars (Davidian 1992). They include many of the most spectacular flowering trees and shrubs and are one of the most important and diverse groups of ornamental plants in cultivation (Dirr and Heuser 1987). The genus comprises both rhododendrons and azaleas. General characteristics are listed in table 2; however, these distinct characters are now known to be part of a continuum of gradation. Therefore, there are no clear delineations between azaleas and rhododendrons.

Uses. Besides their aesthetic appeal, rhododendrons in the wild provide erosion control for steep watersheds and protection for wildlife. In addition, some Himalayan species have been utilized for medicinal purposes, as a tea substitute, or for incense (Cox 1990). Under cultivation, the species are recognized as one of the most important plants available due to their attractive foliage and extremely showy flowers. For landscaping, rhododendrons are unsurpassed with their variations in form, flower color, texture, and leaf morphology. Those with larger leaves should be planted in a woodland or similar setting. Rosebay rhododendron is ideal as a woodland shrub or for tall evergreen backgrounds, but its texture is much too coarse and its stature entirely too large for home foundation plantings. Catawba rhododendron and its western relative, west coast rhododendron, are also well suited for woodland plantings, although in cooler climates Catawba rhododendron occurs often in full sun. Catawba rhododendron also has been used as a parent in many breeding programs to provide cold-hardy cultivars for the northeastern United States (LHBH 1976). Piedmont rhododendron can endure temperatures to –32 °C and flowers later in the year, when there is not much floral color from other shrubs (Leach 1961). It is also among the most heat tolerant of all rhododendrons. Piedmont rhododendron grows too tall for foundation plantings but is useful as a robust, evergreen background shrub that tolerates shade. Carolina rhododendron is one of most useful and adaptable of all rhododendrons, thriving on a wide variety of sites and exposures (Leach 1961). It is well suited as a foundation planting due to its moderate size and growth habit. Chapmans' rhododendron is suited for lowland southern gardens, probably the only evergreen rhododendron that is truly heat resistant and easy to grow in the Deep South (Leach 1961). Deciduous, dwarf, small-flowering species of azaleas should be mass planted, as no other shrubs can provide such intense color in a mass planting (Hillier Nurseries 1994).

Geographic races and hybrids. Rhododendrons in the wild are quite variable. A single species may have numerous varieties and forms, and some of the deviations are extreme (Leach 1961). In addition, natural introgression among species is common, so species tend to merge with one another. Within a species, the environmental conditions present in northern locations or at high elevations can dwarf species normally attaining much larger proportions when grown in the more favorable environmental conditions present in more-southern or lower-elevation sites. At higher altitudes, leaves of various species diminish in size, which helps them to resist the drying effects of strong winds (Leach 1961).

Cultivated rhododendrons and azaleas may be species, but frequently they are cultivars of well-known hybrids. Hybrids usually result from controlled pollinations in attempts to produce plants possessing desirable characteristics of both parents. A selected hybrid is known as a clone,

Table 1—*Rhododendron*, rhododendron and azalea: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
EVERGREEN RHODODENDRONS		
***R. carolinianum* Rehd.**	**Carolina rhododendron,** Carolina azalea	Higher slopes of Blue Ridge Mtns
***R. catawbiense* Michx.**	**Catawba rhododendron,** Catawba rosebay, mountain rosebay, purple laurel,	Mtns of West Virginia & Virginia to Georgia & Alabama
***R. chapmannii* A. Gray** *R. minus* var. *chapmanii* (A. Gray) Duncan & Pullen	**Chapman's rhododendron**	Sandy coastal plain of NW Florida
***R. macrophyllum* D. Don ex G. Don** *R. californicum* Hook. *R. washintonianum* Hort. ex Zab.	**west coast rhododendron,** California rosebay, Pacific rhododendron	Pacific Coast from British Columbia to central California
***R. maximum* L.** *R. maximum* var. *roseum* Pursh *R. ashleyi* Coker	**rosebay rhododendron,** rosebay, great laurel rhododendron	Ontario & Nova Scotia S along Appalachian Mtns to Georgia & Alabama
***R. minus* Michx.** *R. cuthbertii* Small; *R. punctatum* Andr.	**piedmont rhododendron**	Piedmont & lower mtn elevations of Tennessee & North Carolina to Alabama
DECIDUOUS RHODODENDRONS		
***R. alabamense* Rehd.** *Azalea alabamensis* (Rehd.) Small	**Alabama azalea**	Alabama
***R. albiflorum* Hook.** *Azalea albiflora* (Hook.) O. Kuntze *Azaleastrum albiflorum* (Hook.) Rydb.	**Cascade azalea**	Rocky Mtns of British Columbia & Alberta to Oregon & Colorado
***R. arborescens* (Pursh) Torr.** *Azalea arborescens* Pursh	**smooth azalea,** sweet azalea	Pennsylvania to Georgia & Alabama
***R. atlanticum* (Ashe) Rehd.** *Azalea atlantica* Ashe.	**coast azalea,** dwarf azalea	Delaware to South Carolina
***R. austrinum* (Small) Rehd.** *Azalea austrina* Small	**Florida flame azalea,** orange azalea	Florida to SE Mississippi
***R. calendulaceum* (Michx.) Torr.** *Azalea calendulacea* Michx. *Azalea lutea* auct. non L.	**flame azalea,** yellow azalea	SW Pennsylvania & Ohio to Georgia
***R. camtschaticum* Pallas** *Therorhodion camtschaticum* (Pallas) Small	**Kamchatka rhododendron**	NE Asia, Alaska to British Columbia
***R. canadense* (L.) Torr.** *Azalea canadensis* (L.) O. Kuntze *Rhodora canadensis* L.	**rhodora**	Newfoundland to Pennsylvania
***R. canescens* (Michx.) Sweet** *Azalea canescens* Michx. *R. candidum* (Small) Rehd.	**Florida pinxter**, hoary azalea, mountain azalea	North Carolina to Florida & Texas
***R. cumberlandense* E.L. Braun** *R. bakeri* auct. non (Lemm. & McKay) Hume	**Cumberland rhododendron**	Kentucky & West Virginia to North Carolina, Georgia, & Alabama
***R. flammeum* (Michx.) Sarg.** *R. speciosum* (Willd.) Sweet *Azalea speciosa* Willd.	**Oconee azalea,** Piedmont azalea	South Carolina & Georgia
***R. lapponicum* (L.) Wahlenb.** *Azalea lapponica L.*	**Lapland rhododendron,** Lapland rosebay	Mtns of N Europe, N Asia, & N North America
***R. oblongifolium* (Small) Millais** *Azalea oblongifolia Small*	**Texas azalea**	Arkansas, SE Texas, & E Oklahoma
***R. occidentale* (Torr. & A. Gray ex Torr.) A. Gray**	**western azalea**	S Oregon to S California

or cultivar, and does not come true from seed. Thus, vegetative propagation is essential, as seed propagation results in inevitable variation among individuals. Generally, hybrids are more adaptable because they possess a combination of those genes required by their parents to withstand the environments where they originated. As a group, hybrids flower at an earlier age and more regularly year after year than their original parents (Leach 1961). However, every improvement in flower size or color is often accompanied by a loss in some other trait, such as foliage characteristics or disease resistance.

Table 1—*Rhododendron*, rhododendron and azalea: nomenclature and occurrence (continued)

Scientific name & synonym(s)	Common name(s)	Occurrence
***R. periclymenoides* (Michx.) Shinners** *R. nudiflorum* (L.) Torr. *Azalea nudiflora* L. *R. periclymenoides* var. *eglandulosum* Seymour *R. nudiflorum* var. *glandiferum* (Porter) Rehd.	**pinxterbloom,** pinxter flower, honeysuckle, pink azalea	Maine to South Carolina & Tennessee
***R. prinophyllum* (Small) Millais** *R. roseum* (Loisel.) Rehd. *R. nudiflorum* var. *roseum* (Loisel.) Wieg. *Azalea prinophylla* Small	**rose-shell azalea,** early azalea, piedmont azalea, mayflower azalea	S Quebec, through New England to Virginia & W as far as Missouri
***R. prunifolium* (Small) Millais** *Azalea prunifolia* Small	**plumleaf azalea,** plum-leaved azalea	Georgia & Alabama
***R. vaseyi* A. Gray** *Azalea vaseyi* (A. Gray) Rehd. *Biltia vaseyi* (A. Gray) Small	**pink-shell azalea**	North Carolina
***R. viscosum* (L.) Torr.** *Azalea viscosa* L. *R. serrulatum* (Small) Millias *Azalea serrulatum* Small *R. viscosum* var. *aemulans* Rehd. *R. viscosum* var. *glaucum* (Michx.) A. Gray *R. viscosum* var. *montanum* Rehd. *R. viscosum* var. *nitidum* (Pursh) A. Gray *R. viscosum* var. *serrulatum* (Small) Ahles *R. viscosum* var. *tomentosum* Rehd. *R. coryi* Shinners	**swamp azalea,** white swamp azalea, swamp honeysuckle, clammy azalea, hammock-sweet azalea	Swamps from Maine to Florida & Louisiana

Source: LHBH (1976).

Table 2—*Rhododendron*, rhododendron and azalea: general distinguishing characteristics

Plant part	Rhododendrons	Azaleas
Leaves		
Duration	Evergreen	Deciduous
Texture	Coriaceous	Membranous
Abaxial surface	Scaly or punctate	Pubescent
Margin	Entire	Ciliate or ciliolate
Flowers		
Corolla	Campanulate	Funnelform
Stamens	10 or more	5
Ovary	Scaly or tomentose	Setose

Source: LHBH (1976).

Hybrids began to appear about 1825, with most of the early ones derived from Catawba and rosebay rhododendrons, tree rhododendron (*R. arboreum* Sm.), Caucasian rhododendron (*R. caucasicum* Pall.), and *R. ponticum* L., indigenous to the United States, the Himalayas, Caucasus, and Turkey, respectively. Most of these early hybrids possessed ample foliage, firm and full flower trusses, and the ability to withstand exposure to freezing temperatures, and hence are often referred to as the "hardy hybrids." They are suited for landscape plantings in cold climates, and many are ideal as informal hedges or screens (Hillier Nurseries 1994). With the exploration of China and the eastern Himalayas during the first part of the 20th century, many new species were discovered and included in breeding programs. These newer hybrids show even greater variation in foliage, flower color, and growth habit (Hillier Nurseries 1994).

Two examples of hybrids that are planted widely throughout the southeastern United States are the Indian and Kurume azaleas. In fact, the Indian hybrid azaleas are likely the most popular of all flowering evergreen shrubs. They are derived primarily from Sims azalea (*R. simsii* Planch.) and macranthum azalea [*R. indicum* (L.) Sweet]—which, despite its specific epithet, is native to southern Japan not India. These hybrids are confused often with the parent species macranthum azalea, as they are sometimes sold as varieties or cultivars of *R. indicum* (LHBH 1976). Indian hybrids are broad mounding shrubs that are 2.5 to 3.0 m tall and usually grow dense in full sunlight and open and airy in the shade. They are utilized in the landscape as accent plants, for screening, and in mass groupings. The large showy flowers are 5 to 9 cm across, blooming in May with colors ranging

from white, to pink, magenta, and orange-red (Odenwald and Turner 1987). Indian azaleas are grown also as large-flowered greenhouse azaleas.

Kurume azaleas are derived primarily from Hiryu azalea—*R. obtusum* (Lindl.) Planch.—also indigenous to Japan. These low-mounding, fine-textured hybrids are slow growers with relatively small, single or "hose-in-hose" double flowers in a variety of colors (Odenwald and Turner 1987). Many selections are available and they are planted widely in the southern United States, even though they are very site-specific and temperamental shrubs.

Flowering and fruiting. The perfect, showy flowers appear from March to August (table 3). Flower colors vary widely, with white, pink, and purple predominating. Flowers are pollinated by bees (Gibson 1901) and to a lesser extent by birds (Cox 1990). Fruits are oblong, 5-valved, dehiscent capsules that generally ripen during autumn (figure 1). When mature, capsules turn from green to brown, at which time they split along the sides, releasing minute seeds (figures 2–4). Capsules of rosebay rhododendron contain about 400 viable seeds/capsule (Romancier 1970).

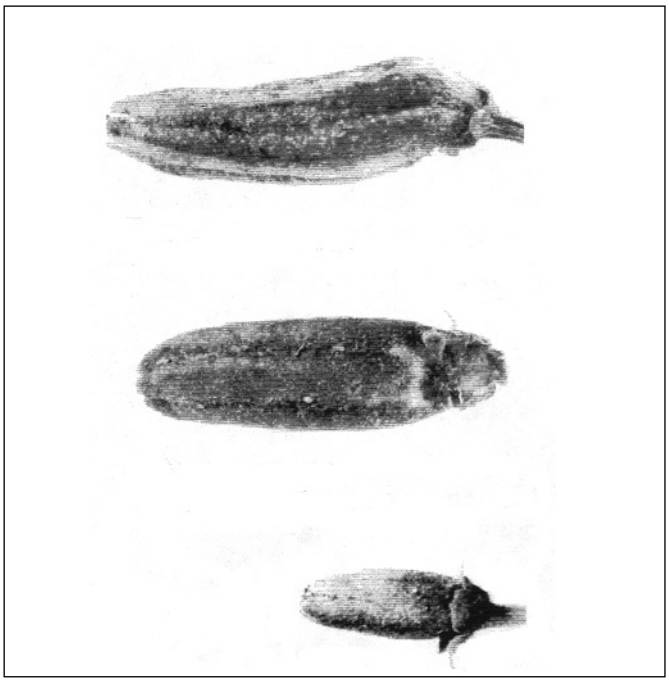
Collection of fruits, seed extraction, and cleaning. In general, capsules should be observed closely from mid-September onward and collected as they start to turn from green to brown (Bowers 1960). Fruits are dehiscent and if capsules are not collected before they open, most of the seeds will be lost. However, capsules can be picked green and then opened in gentle heat as long as their seeds are fully developed. Capsules may be air-dried at about 21 °C for 2 to 4 weeks (Blazich and others 1991; Malek and others 1989) or oven-dried for 12 to 24 hours at 35 °C (Dirr and Heuser 1987). Many capsules will split open during drying,

Table 3—*Rhododendron*, rhododendron and azalea: growth habit and flowering

Species	Growth habit & maximum height	Flowering	Flower color
EVERGREEN RHODODENDRONS			
R. carolinianum	Compact shrub; to 1.8 m	May	Pink, mauve, white
R. catawbiense	Spreading, rounded in the open; generally wider than tall to 3 m, sometimes small tree to 6 m	May–June	Magenta, pink, white, red
R. chapmanii	Shrub to 1.8 m	May	Rose
R. macrophyllum	Open tree-like shrub; often erect to 3–9 m	May–June	Purplish rose, white
R. maximum	Shrub in cultivation; to 4.6 m (sometimes to 12 m in the wild)	June–July	White, pink, purplish red
R. minus	2.8 m	June	Rose, white
DECIDUOUS RHODODENDRONS			
R. alabamense	Low stoloniferous shrub; to 0.6–2.4 m	Apr–May	White
R. albiflorum	Erect shrub; from 0.9–2.1 m	June–July	Creamy white, yellow
R. arborescens	From low spreading bushes in open to tall and leggy in shade; up to 6 m	June–July	White
R. atlanticum	Stoloniferous shrub, forms branching sprays when well established; 0.3–1.5 m	May	White, pink
R. austrinum	Stiff and upright; from 3.0–3.6 m	Apr	Yellow-orange
R. calendulaceum	Stiff and upright; to 3.6 m	May–June	Yellow, orange, scarlet, pink
R. camtschaticum	Very small shrub; to 0.2 m	May	Reddish purple
R. canadense	Much branched shrub; to 0.9 m	Apr	Rose-purple, white
R. canescens	Sparingly branched shrub; to 4.6 m	Apr–May	Pink, white
R. cumberlandense	Low and twiggy, often stoloniferous shrub; to 2.4 m but rarely over 1.8 m	June–July	Yellow, orange, scarlet
R. flammeum	Mounding form; to 2.5 m	May	Scarlet, orange, yellow
R. lapponicum	Dwarf, procumbent shrub; to 0.3 m	Apr	Purple
R. oblongifolium	Upright, somewhat stoloniferous shrub; to 1.8 m	June	White, pink
R. occidentale	Rounded, occasionally upright or low shrub; to 1.0–4.6 m	Apr–Aug	White, pink, pale yellow
R. periclymenoides	Usually tall, vigorous and much- branched shrub; to 2.7 m & up to 4.5 m in wild	May	Pale pink, rose, reddish, white
R. prinophyllum	Upright, well branched shrub; to 2.5 m	May	Pink, white, rosy red
R. prunifolium	Tall, rounded-topped; up to 3.6 or 5.5 m in wild	July–Aug	Yellow, orange, scarlet
R. vaseyi	Upright shrub to 3.6 m	Apr–May	White, pink, crimson
R. viscosum	Form various: large & upright to dwarf, small tree; from 3–6 m, rounded or straggly shrub, stoloniferous form to 4.6 m	July–Oct	White, pink

Sources: Davidian (1992), Leach (1961), LHBH (1976).

Figure 1—*Rhododendron*, rhododendron: capsules with styles removed of *R. catawbiense*, Catawba rhododendron (**top**); *R. macrophyllum*, west coast rhododendron (**center**); and *R. maximum*, rosebay rhododendron (**bottom**).



whereas others may require crushing. Seeds should be cleaned well to remove chaff and broken pieces of capsules by shaking through various sized sieves. Seeds should then be graded further by removal of abnormal, damaged, or undersized seeds.

Rhododendrons normally produce copious amounts of seeds (Cox 1990; Romancier 1970); however, viable seeds are not always available on a yearly basis. Seeds are extremely small and size can vary greatly among species (Arocha and others 1999; Blazich and others 1991, 1993; Glenn and others 1998; Olson 1974) and among provenances within a species (Rowe and others 1994a). However, small differences in moisture content can cause wide variability in estimates of the number of seeds per given weight (table 4).

Storage. There is little information on proper storage techniques for maintaining long-term viability in the rhododendrons, but the evidence available suggests that the seeds of this genus are orthodox in storage behavior.

Seeds of rhododendrons with a moisture content of 4 to 9% will remain viable about 2 years at room temperature (Bowers 1960; Olson 1974). However, at room temperature,

Figure 2—*Rhododendron*, rhododendron: seeds of *R. calendulaceum*, flame azalea (**upper left**); *R. carolinianum*, Carolina rhododendron (**upper right**); *R. catawbiense*, Catawba rhododendron (**center**); *R. chapmanii*, Chapman's rhododendron (**lower left**); and *R. maximum*, rosebay rhododendron (**lower right**).

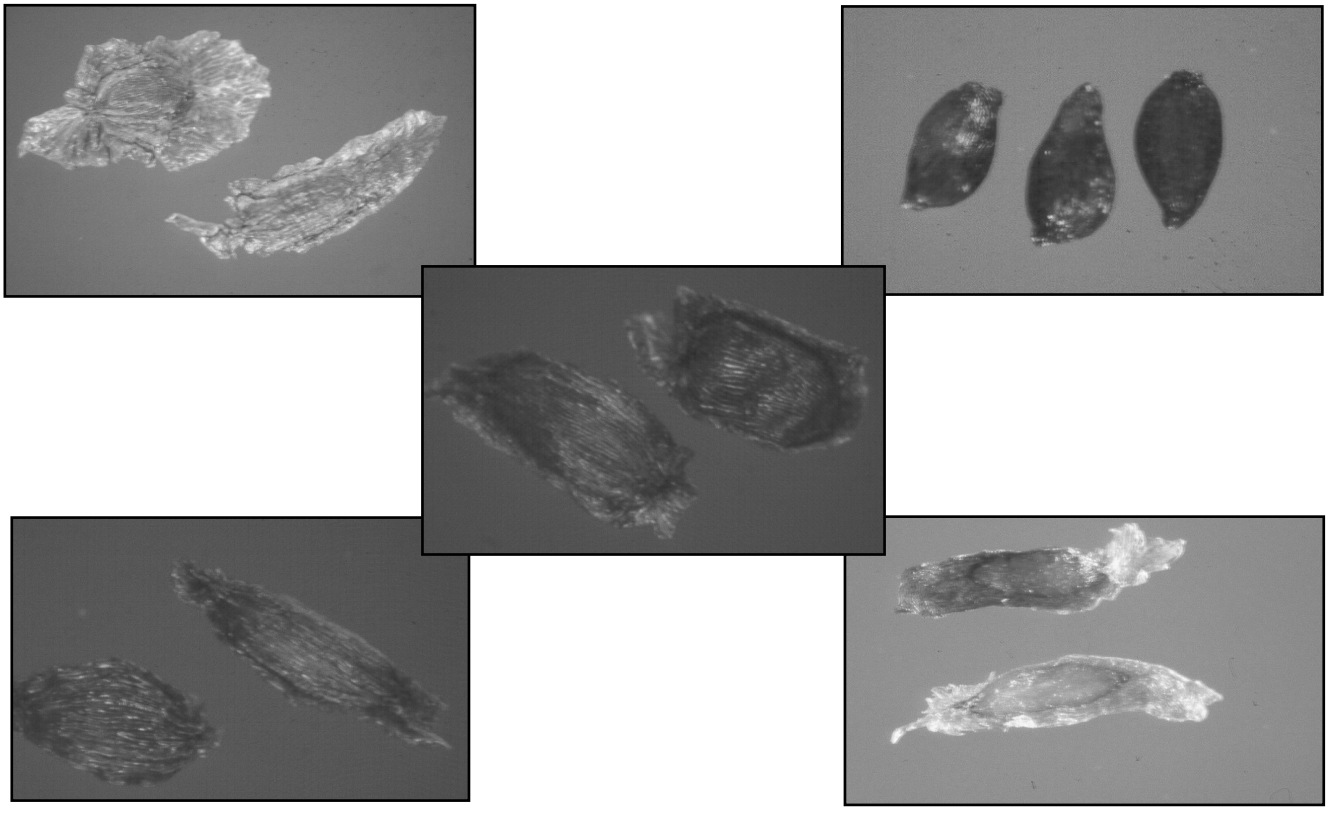


Figure 3—*Rhododendron macrophyllum*, west coast rhododendron: seeds in external view (**top left**), longitudinal section (**center**), and cross section (**bottom right**).

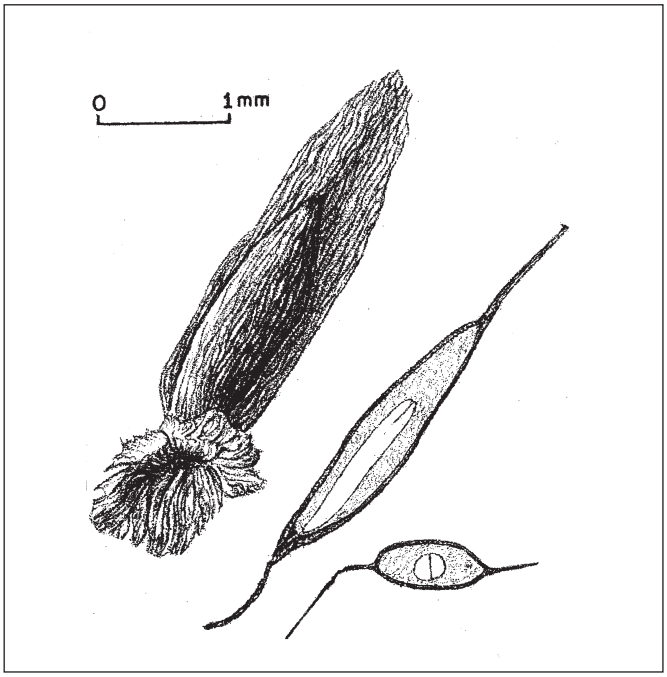
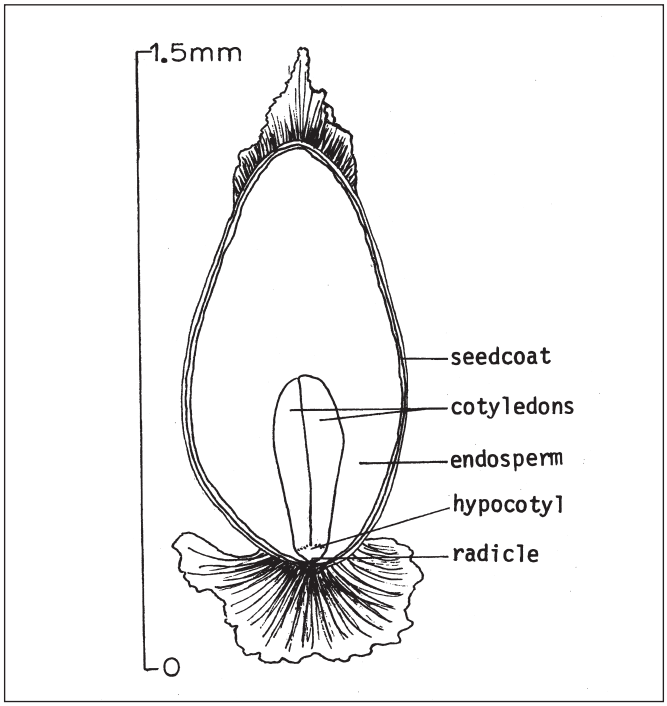


Figure 4—*Rhododendron maximum*, rosebay rhododendron: seed in longitudinal section.



seeds lose their viability at a rate of 50% a year, and those that retain their ability to germinate will sprout more slowly (Leach 1961). For Catawba and rosebay rhododendrons, Glenn and others (1998) compared seed germination under storage conditions analogous to storage in a home freezer at –18 °C, a refrigerator at 4 °C, and at room temperature (23 °C). Seed viability remained unchanged after 5 years of storage at –18 °C and 4 °C, which strongly suggests that viability for even longer periods is possible. Thus, long-term seed storage of Catawba and rosebay rhododendrons is possible, provided seeds are first dried to moisture contents of 5 to 7% and then stored in sealed containers at –18 or 4 °C. Room temperature storage (about 23 °C) should be avoided, as viability is lost rapidly (Glenn and others 1995). In the same study, Glenn and others (1998) also included seeds of Carolina rhododendron that were stored for only 4 years. After these 4 years at –18 or 4 °C, viability remained unchanged. Although viability decreased with storage at 23 °C, the decrease was not as dramatic as that observed for seedlots of Catawba and rosebay rhododendrons at the same temperature.

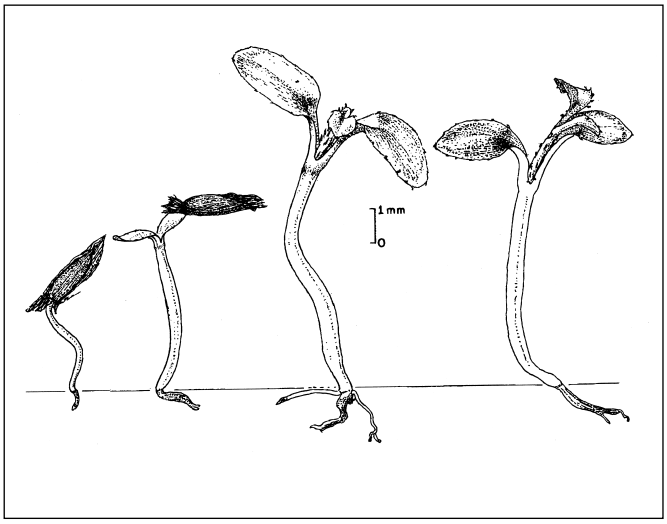
Pretreatment and germination tests. Mature seeds of rhododendrons possess no dormancy and will germinate shortly after sowing (Fordham 1960; Romancier 1970). Official testing rules prescribe a 21-day test on the top of moist blotter paper at 8 hours of daylight at 30° C and 16 hours of night at 20° C or a constant of 25° C with 8 hours of light daily (AOSA 1993). Germination is epigeal (figure 5). Several 30-day germination tests have been conducted for various species at a constant temperature of 25 °C or an alternating 8/16 hour thermoperiod of 25/15°C in combination with photoperiods ranging from total darkness to 24 hours. During these tests, light was provided by cool-white fluorescent lamps that provided an approximate photosynthetic photon flux (400 to 700 nm) of 28 µmol/m^2/sec (2.2 klux). Species tested included flame azalea (Malek and others 1989) and Carolina (Blazich and others 1993), rosebay (Blazich and others 1991), and Catawba rhododendrons (Blazich and others 1991; Rowe and others 1994a). In all species tested except one, seeds required light to germinate. In addition, an alternating thermoperiod enhanced germination when light was limiting. These results agree partially with the work of Cho and others (1981), who also reported that seeds of 5 species of rhododendron native to Korea—macranthum azalea, *R. indicum* (L.); Sweet; Japanese azalea, *R. japonicum* A. Gray Suring; *R. mucronulatum* Turcz*;* royal azalea, *R. schlippenbachii* Maxim.; and yodogawa azalea, *R. yedoense* Maxim. ex Regel—did not germinate in darkness at a constant temperature but did germinate in darkness when subjected to an alternating temperature. In addition, germination sometimes is inhibited by long photoperiods. For equivalent photoperiods, inhibition (when present) will be more pronounced at 25/15 °C than at 25 °C because an alternating temperature can substitute partially

Table 4—*Rhododendron*, rhododendron and azalea: variation in seed size among species and seed source

Species	Seed source	Elevation (m)	Seed moisture content (%)	Cleaned seeds/wt /g	Cleaned seeds/wt /oz
R. calendulaceum	Watauga Co., North Carolina	1,400	6	4,350	122,000
R. carolinianum	Henderson Co., North Carolina	720	6	29,460	825,000
	Burke Co., North Carolina	1,100	4	23,930	670,000
R. catawbiense	Buncombe Co., North Carolina	1,860	7	6,070	170,000
	Buncombe Co., North Carolina	1,860	6	6,070	170,000
	Yancey Co., North Carolina	1,954	10	6,780	190,000
	Johnston Co., North Carolina	67	9	5,700	160,000
	Cherokee Co., Georgia	320	7	5,000	140,000
R. chapmanii	Gadsden-Liberty Cos., Florida	—	5.5	29,100	815,000
R. macrophyllum	Oregon	—	—	4,460	125,000
R. maximum	Avery, Co., North Carolina	950	6	11,790	330,000
	Avery, Co., North Carolina	950	5	11,430	320,000

Sources: Arocha and others (1999), Blazich and others (1991, 1993), Glenn and others (1998), Malek and others (1989, 1990), Olson (1974), Rowe and others (1994a).

Figure 5—*Rhododendron macrophyllum*, west coast rhododendron: seedling development at 1, 9, 40, and 60 days after germination.



for the light requirement for some species (Toole and others 1955). However, this inhibition usually dissipates by the end of 30 days of germination (Blazich and others 1991, 1993; Rowe and others 1994a).

A test of seeds of flame azalea collected from the Blue Ridge Mountains of western North Carolina demonstrated that (at a constant temperature of 25 °C) increasing photoperiods increased germination, with maximum germination (85%) occurring by day 12 under continuous light (Malek and others 1989). An 8/16-hour thermoperiod of 25/15 °C enhanced germination when light was limiting. Maximum germination of 84 to 91% was reached by day 24 for all photoperiods ≥ $^1/_2$ hour, although at photoperiods ≥ 4 hours, comparable germination was noted at day 18 (Malek and others 1989). Similar results were reported for seeds of Carolina rhododendron collected in Henderson County, North Carolina, except that cumulative germination was lower (Blazich and others 1993).

Seeds of rosebay rhododendron collected in Avery County, North Carolina, also required light for germination regardless of temperature. At 25 °C, increasing photoperiods increased germination, with 79 and 81% germination occurring by day 21 for the 12- and 24-hour photoperiods, respectively. The alternating temperature again enhanced germination when light was limiting. At the alternating thermoperiod, germination of 92 to 97% was reached by day 21 for photoperiods ≥ 4 hours (Blazich and others 1991).

Rowe and others (1994a) also found that seeds of Catawba rhododendron have an obligate light requirement for germination. In contrast, Blazich and others (1991), reported that without light, seeds of Catawba rhododendron collected in Buncombe County, North Carolina, germinated in the dark. However, germination at 25 °C was low (5%), with moderate germination (64%) occurring at 25/15 °C. At both thermoperiods, germination > 95% was attained by day 15 for photoperiods of $^1/_2$ to 12 hours. This suggests that the germination response of Catawba rhododendron in darkness may vary, depending on the provenance or on the environmental conditions under which the seeds developed. The work of Glenn and others (1998) has suggested that the light requirement does not disappear during dry storage.

In addition, Rowe and others (1994a) compared germination in seeds from 3 provenances of Catawba rhododendron—Johnston County, North Carolina (elevation 67 m); Cherokee County, Georgia (elevation 320 m); and Yancey County, North Carolina (elevation 1,954 m)—representing diverse geographical and altitudinal distributions. Generally, light and temperature requirements for germination of seeds

from all provenances were similar. Regardless of temperature, seeds required light for germination, and daily photoperiods as short as $^1/_2$ hour maximized germination. The major difference in germination response among provenances was related to seed vigor. Seeds from the Yancey County (higher-elevation) provenance germinated at a faster rate with greater cumulative germination than seeds from lower elevation provenances.

In studying effects of irradiance on seed germination of rosebay rhododendron, Romancier (1970) provided a range of irradiance levels to seeds during 16-hr photoperiods at 22 °C. He reported zero germination in total darkness but found no significant differences in germination with light intensities ranging from 1.6 μmol/m^2/sec (0.13 klux or 12 foot-candles) to 21.9 μmol/m^2/sec (1.72 klux or 160 foot-candles), indicating that very low levels of irradiance will stimulate germination. All seeds, including those in total darkness, had been exposed to light before the test began, so it is during the period following imbibition that light is essential. Glenn and others (1999) reported that dormancy was induced in seeds of Catawba and rosebay rhododendrons by not subjecting seeds immediately to light following inbibition. However, the degree of dormancy varied depending on (a) the length of time imbibed seeds were maintained in darkness and (b) the temperature at which the dark treatments were imposed and the seeds were germinated.

Nursery practice and seedling care. Rhododendrons may be propagated by seeds, stem cuttings (Dirr and Heuser 1987; Hartmann and others 2002), layering (Wells 1985), grafting (Wells 1985), and micropropagation (tissue culture) (Anderson 1984; McCown and Lloyd 1983). Commercially, plants usually are propagated by stem cuttings, although rooting ability is genotype specific. Procedures developed for micropropagation are currently being used with great success. Nevertheless, seed propagation is still practiced to develop new hybrids, raise understocks for grafting, and propagate wild species.

Seeds should be sown in January or as early as local conditions will allow. This is important to allow maximum growth the first year. The longer the growing period before mid-July (when growth normally ceases), the larger the seedlings will be at the end of the first season (Leach 1961). Many materials have been used as a germination medium, including vermiculite, perlite, sawdust, peat, and various soil mixes. Flats filled with peat moss and sand or perlite mixtures topped with 6 mm ($^1/_4$ in) of slightly firmed shredded sphagnum moss work well (Wells 1985). Many propagators are convinced that a medium consisting solely of shredded sphagnum moss provides the best results (Leach 1961; Wells 1985). Sphagnum moss is naturally acidic, retains water, and inhibits fungal organisms responsible for damping-off.

Seeds should be sown sparingly. Because of the need for light and their small size, seeds should not be covered with medium. Flats can then be placed in a greenhouse with moderate heat (24 °C), preferably under intermittent mist. Covering flats with glass or plastic may be advisable if mist is not available. Most seeds germinate in 1 to 3 weeks. In an additional 4 to 8 weeks, small seedlings will have 2 to 4 true leaves in addition to the cotyledons (Anderson and Anderson 1994). The time of germination and the first few weeks thereafter are critical. Seedlings must be shaded from direct sunlight, and the surface of the medium should never be allowed to become dry, not even briefly. Some growers sow about 1,000 seeds in a standard flat measuring 36 × 51 × 10 cm (14 × 20 × 4 in) and then transplant seedlings when they are still very small. Others sow them more sparsely and wait until the plants are about 2.5 cm (1 in) tall before transplanting.

In about 6 months, seedlings will be large enough to be transplanted. During the critical transplanting stage, young seedlings are carefully teased out from the sphagnum. The root system will separate easily if an underlying sand and peat mixture is used. Then, seedlings are transplanted into prepared flats containing an acidic medium (pH 4.0 to 5.5), taking care not to bury the cotyledons. Commercial growers usually put 108 seedlings into a standard flat filled with sterilized medium (Leach 1961). Flats may then be placed back in the greenhouse under shade, where they will remain for 9 months. Overwintering is seldom a problem in a greenhouse as long as plants are prevented from freezing. During seedling growth, plants may be fertilized with about 180 ppm N from a 15-45-5 ($N:P_2O_5:K_2O$) water-soluble fertilizer also containing 200 ppm calcium chloride ($CaCl_2$) and 75 ppm magnesium sulfate ($MgSO_4$). In addition, terminal growth often is pinched back to produce bushier plants. With flame azalea, Malek and others (1992a) reported that lateral shoot development in seedlings could be stimulated by either manual or chemical pinching. Generally, the number of lateral shoots increased with the leaf stage at which manual pinching was imposed. The highest number of shoots resulted by removing the terminal 2 nodes at the 16-leaf stage. Both pinched and nonpinched plants treated with dikegulac—2,3:4,6 bis-O-(1-methylethylidene) α-L-xylo-2-hexulofuranosonic acid—produced more lateral shoots than manual pinching alone. The number of shoots increased linearly with increasing concentrations of dikegulac over a range of 0 to 4,000 ppm, whereas responses to 4,000, 6,000, and 8,000 ppm were comparable. However, considerable

reduction in leaf, stem, and root dry weights occurred with increasing concentration. This research also demonstrated that pinching seedlings manually prior to dikegulac treatment did not result in significantly greater numbers of lateral shoots compared to dikegulac treatment of nonpinched plants.

In spring, 1-year-old seedlings are removed from the flats, graded, and planted into pots or prepared beds to grow 1 or 2 more years before planting in permanent locations. They can be placed outdoors to harden off when the chance of killing frost has past, but they must not be exposed to direct sunlight. When plants of Catawba rhododendron were grown in controlled-environment growth chambers under long days at 16 different day/night temperature combinations, Rowe and others (1994b) found that a day/night cycle of 22/22 °C to 26/22 °C was optimal for seedling growth, whereas cycles ranging from 30/22 °C to 26/22 °C optimized net photosynthesis (Rowe and others 1994c). Similar results were reported for flame azalea (Malek and others 1992b). Throughout propagation and subsequent culture, plants should be examined frequently for insect and disease problems. Rhododendrons can be raised successfully with proper handling of the tender and delicate young seedlings by using a porous, well-drained acidic medium high in organic matter, and by maintaining ample moisture at all times.

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Rosaceae—Rose family

Rhodotypos scandens (Thunb.) Makino

jetbead

Paul O. Rudolf and Peyton W. Owston

Dr. Rudolf (deceased) retired from the USDA Forest Service's North Central Forest and Range Experiment Station; Dr. Owston retired from the USDA Forest Service's Pacific Northwest Research Station

Synonyms. *R. tetrapetalus* (Sieb.) Makino

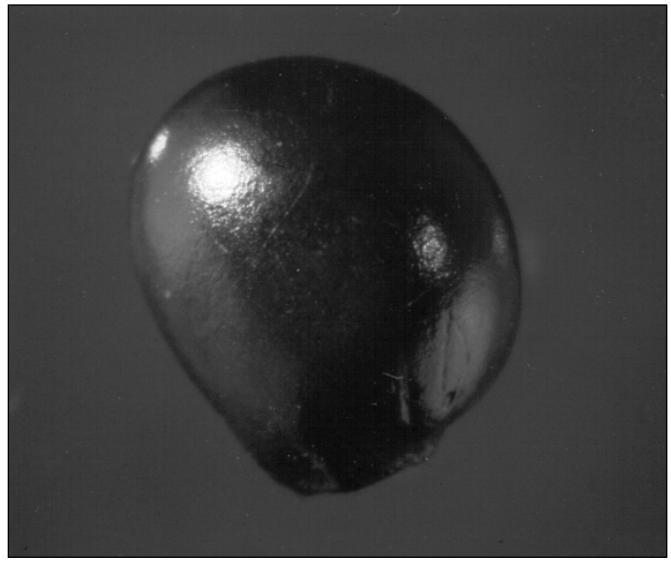
Growth habit, occurrence, and use. The only member of the genus *Rhodotypos* introduced to any extent in the United States is jetbead—*R. scandens* (Thunb.) Makino. Native to Japan and central China, jetbead is an upright, spreading, deciduous shrub usually 1 to 2 m tall; it reaches 5.5 m in Japan. It was introduced into cultivation chiefly for ornamental purposes in 1966 (Ohwi 1965; Rehder 1940) and is now considered invasive.

Flowering and fruiting. The showy, white, perfect flowers are 2.5 to 5 cm across and bloom from April to June (Ohwi 1965; Rehder 1940). Jetbead fruits are shiny, black, dry drupes, obliquely ellipsoid in shape (figure 1). They ripen in October or November and persist on the plant well into the winter; each contains 1 small stubby ellipsoidal stone (seed) about 6 mm long, dull tan in color, and characteristically sculpted in the manner of leaf venation, with the "midrib" extending around the longest periphery (figure 2) (Rehder 1940; Wyman 1947).

Collection of fruits, and extraction and storage of seeds. The fruits can be collected from the bushes by hand or flailed onto canvas from October to midwinter (Rudolf 1974). Extraction of stones from the fruits may not be necessary. In one sample, the number of cleaned seeds per weight was 11,488/kg (5,210/lb); purity was 89% and soundness 86% (Rudolf 1974). Seeds of this species are orthodox and can be stored air-dry in open containers at 1 to 10 °C for up to 9 months without loss of viability. Storage in sealed containers and in a vacuum at various humidities did not improve results (Flemion 1933).

Pregermination treatments. The seeds exhibit a combined dormancy that can be overcome by stratification in moist peat for 30 days at 25 to 30 °C, followed by 90 days of stratification at 5 °C (Barton 1961; Flemion 1933). Partially after-ripened seeds subjected to high temperature go into secondary dormancy (Flemion 1933).

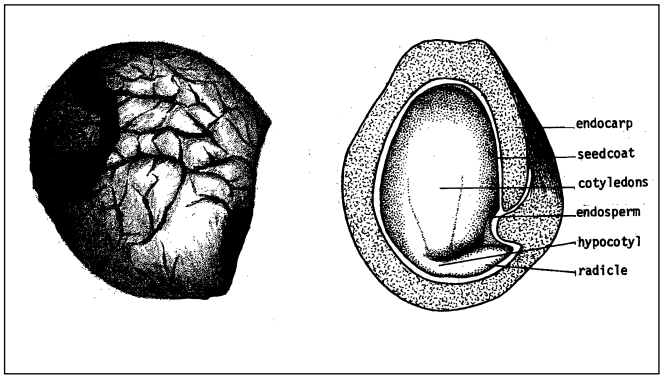
Figure 1—*Rhodotypos scandens*, jetbead: fruit.



Germination tests. Germination tests can be made in sand flats at temperatures of 20 °C (night) and 30 °C (day) for 90 days. In 3 tests, 81% (range 72 to 86%) of stratified seeds germinated, whereas only 16% of untreated seeds germinated (Flemion 1933; Rudolf 1974).

Nursery practice. Seeds should be sown in the fall in mulched or board-covered cold frames. A sowing depth of 12 mm ($^1/_2$ in) is suggested. Some germination will take place the second year (Flemion 1933). Slightly green (immature) seeds sown in the fall are reported to germinate in 1 year (Dirr and Heuser 1987). Presumably, stratified seeds could be sown in the spring. In a planting test of slightly green seeds collected in August and sown immediately, 100% germination was seen the next spring (Titus 1940). Stem cuttings of jetbead can be rooted any time that the plants have leaves, but June and July are best. A mistbed or shaded plastic tent is recommended (Dirr and Heuser 1987).

Figure 2—*Rhodotypos scandens*, jetbead: cleaned seed (**left**) and longitudinal section through a seed (**right**).



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Anacardiaceae–Sumac family

Rhus L.

sumac

D. Bradley Rowe and Frank A. Blazich

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Growth habit, occurrence, and use. The genus sumac—*Rhus* L.—consists of about 150 species of deciduous or evergreen shrubs, trees, and vines indigenous to temperate and subtropical regions of both hemispheres (LHBH 1976; Rehder 1990; RHS 1994). They occur frequently as pioneer species on disturbed sites and abandoned fields and along woodland borders. However, they are intolerant of shade and cannot compete with invading trees (Gill and Healy 1974). Sumacs are tolerant of poor, sandy, or rocky soils, and of soil moisture regimes ranging from dry to wet. For example, smooth sumac is adaptable to sites ranging from nearly bare rock to sand to heavy clay, and tolerates soil pH from acidic to slightly alkaline (Johnson and others 1966). Species native to North America are listed in table 1.

Three species of the genus *Toxicodendron*—poison-oak, *Toxicodendron diversilobum* (Torr. & Gray) Greene; poison-ivy, *T. radicans* (L.) Kuntze; and poison-sumac, *T. vernix* (L.) Kuntze—also are included because they are referred to frequently as *R. diversiloba* Torr. & Gray, *R. radicans* L., and *R. vernix* L., respectively. Laurel-sumac—*Malosma laurina* (Nutt.) Nutt. ex Abrams), until recently known as *Rhus laurina* Nutt.—is also included for the same reason.

Members of the sumac genus are shrubs, vines, or trees with alternate, simple, or featherlike (pinnate) compound leaves. Winter buds are minute, naked (without scales), and covered with dense hairs. Sumacs are fast growing and usually short-lived plants. Roots of sumac can spread more than 16 m in each direction, forming an extensive root network near the surface (Duncan 1935).

Sumacs are valuable for erosion control because of proliferation of rhizomes that results in an extensive root system. The species is ideally suited for roadside plantings, revegetation of areas of eroded or depleted soils, range reclamation and mine spoils restoration, and other conservation plantings (Brinkman 1974; Humphrey 1983). Some are grown as ornamentals for their pinnate foliage; persistent terminal showy fruits; and brilliant red, orange, or yellow fall color. This is especially true of the cutleaf staghorn sumac —*R. hirta* (L.) Sudworth 'Laciniata'— with its deeply cut, bright green leaves in summer; brilliant orange-red fall color; and twisted, exotic forms in winter (Cross 1988). Sumacs are recommended as ornamental shrubs for dry and open sites, but cultivation is easy in any garden soil.

Species of sumac also provide wildlife with habitat and an important source of food. Their thicket-forming growth provides excellent cover for birds and animals. The fruits, produced in large quantities each year, are eaten by over 30 species of birds, as well as rodents and other mammals. The twigs and leaves are browsed by deer (*Odocoileus* spp.), moose (*Alces americana*), and mountain sheep (*Ovis* spp.) (Elias 1989; Strauss 1988). The wood is soft, weak, and of no commercial value (Elias 1989). However, skunkbush was once used by Native Americans for food, as a tobacco substitute, and for making baskets. In addition, some species can be processed to yield tannin and lacquer (LHBH 1976).

Geographic races and hybrids. There is some disagreement among taxonomists as to the classification of genera (*Rhus* vs. *Toxicodendron*) and particular species. For example, prairie sumac is often considered to be a variety or race of shining sumac (Elias 1989). In addition, natural hybridization occurs in the wild (Johnson and others 1966).

Flowering and fruiting. Plants are dioecious (flowers imperfect, one sex) or polygamous (flowers imperfect and perfect, both sexes). Flowers are small and rather inconspicuous and are borne in terminal or axillary clusters in the spring (table 2). They are pollinated by bees. Fruits are small, hairy, berry-like drupes, rounded to egg-shaped, containing a single nutlet or seed without endosperm (figures 1–3) (Brinkman 1974; Elias 1989). In most species, fruits form a dense cluster and ripen in the fall and may persist on the plant through winter. Seeds are spread primarily by birds and small mammals (Brinkman 1974). Sumacs generally produce copious quantities of seeds with some seeds produced nearly every year.

Table 1—*Rhus,* sumac; *Toxicodendron,* poison-ivy, etc.; *Malosma,* laurel-sumac: nomenclature and occurrence

Scientific names & synonym(s)	Common name(s)	Occurrence
***R. aromatica* Ait.** *R. canadensis* Marsh.	**fragrant sumac,** lemon sumac, sweet-scented sumac	Vermont & Ontario to Minnesota, S to Florida & Louisiana
***R. choriophyllum* Woot. & Standl.**	**Mearns sumac**	S New Mexico & Arizona & adjacent Mexico
***R. copallina* L.**	**shining sumac,** winged sumac, mountain sumac, wing-rib sumac, dwarf sumac	Maine & Ontario to Minnesota, S to Florida & Texas
***R. glabra* L.** *Schmaltzia glabra* Small *R. borealis* Greene	**smooth sumac,** scarlet sumac	Maine to British Columbia, S to Florida & Arizona
***R. hirta* (L.) Sudworth** *R. typhina* L.	**staghorn sumac,** velvet sumac	Quebec to Ontario, S to Georgia, Indiana, & Iowa
***R. integrifolia* (Nutt.) Benth. & Hook. f. ex Brewer & S. Wats.**	**lemonade sumac,** sourberry, lemonade berry	S California & Baja Californa
***R. kearneyi* Barkl.**	**Kearney sumac**	Arizona & N Baja California
***R. lanceolata* (Gray) Britt.** *R. copallina* var. *lanceolata* Gray	**prairie sumac**	S Oklahoma & E Texas to S New Mexico & adjacent Mexico
***R. michauxii* Sarg.** *Schmaltzia michauxii* M. Small	**false poison sumac**	North Carolina to Georgia
***R. microphylla* Engelm. ex Gray**	**desert sumac,** scrub sumac, small-leaf sumac	SW US & adjacent Mexico
***R. ovata* S. Wats.** *R. ovata* var. *traskiae* Barkl.	**sugarbush,** sugar sumac	Arizona, S California, N Baja California
***R. trilobata* Nutt.** *Schmaltzia anisophylla* Greene *S. trilobata* var. *anisophylla* (Greene) Barkl.	**skunkbush,** ill-scented sumac	Illinois to Washington, California, & Texas
***R. virens* Lindheimer ex Gray**	**evergreen sumac,** tobacco sumac, lentisco	SW US
Related Taxa		
***Toxicodendron diversilobum* (Torr. & Gray) Greene** *R. diversiloba* Torr. & Gray *R. toxicodendron* ssp. *diversilobum* Torr. & A. Gray) Engl.	**poison-oak**	British Columbia to Baja California
***T. radicans* ssp. *radicans* (L.) Kuntze** *R. radicans* L.; *R. toxicodendron* L.	**poison-ivy**	Nova Scotia to Florida, W to Minnesota, Nebraska, & Arkansas
***T. vernix* (L.) Kuntze** *R. vernix* L.	**poison-sumac,** swamp sumac, poison elder	Swamps, Maine to Minnesota, S to Florida & Louisiana
***Malosma laurina* (Nutt.) Nutt. ex Abrams** *R. laurina* Nutt.	**laurel-sumac**	S California, Baja California

Sources: Elias (1989), LHBH (1976), Rehder (1990), RHS (1994).

Collection of fruits, seed extraction, and cleaning. Fruit clusters, which may be picked by hand as soon as they are ripe, are often available until late in the year. If collected early, fruits of smooth sumac and staghorn sumac, which occur in very dense clusters, may need additional drying and should be spread out in shallow layers for drying. However, fruits usually will be dry enough to process if they are collected in late fall or early winter (Brinkman 1974). Hybrid clumps often are found where smooth sumac and staghorn sumac occur near each other (Johnson and others 1966). These hybrid clumps may have seed-stalk heads that appear normal, but most seeds therein are generally empty, with the few full seeds usually infertile. Care must be taken to avoid such hybrid clumps. Even seeds of nonhybrid clumps should be checked carefully before collection to make certain that an excessive amount of empty seeds are not present. An estimate of the amount of empty seeds can be determined by crushing a small sample with a pair of pliers (Johnson and others 1966).

Dried fruit clusters can be separated into individual fruits by rubbing or beating the clusters in canvas sacks, followed by screening to remove debris (Brinkman 1974). Seeds can then be cleaned by running them through a macerator with water to remove remaining pieces of seedcoats

Table 2—*Rhus,* sumac; *Toxicodendron,* poison ivy, etc.; *Malosma,* laurel-sumac: growth habit, flowers, and fruits

Speicies	Growth habit & max height	Flowers	Fruits
R. aromatica	Shrub to 2.5 m	Yellowish, in clustered spikes 5–20 cm long, forming short panicles that appear before leaves	Red, hairy, 6 mm across; early summer, persist into early winter
R. choriophylla	Shrub or small tree to 5 m with an open irregular crown	Tiny, in dense branched clusters 5–6 cm long & wide from July–August	Red, hairy, 6-8 mm across
R. copallina	Shrub or small tree to 6 m	Greenish, in dense terminal panicles	Red, hairy; late summer, persist into winter
R. glabra	Shrub or tree to 6 m	Green, in dense panicles 10–25 cm long	Scarlet, hairy; summer
R. hirta	Shrub or tree to 9 m, twigs densely pubescent	Greenish in dense, terminal panicles 10–20 cm long	Crimson, densely hairy; late summer, persist on plant into winter
R. integrifolia	Evergreen shrub or tree to 9 m	White or pinkish in pubescent panicles	Dark red, hairy; spring
R. kearneyi	Large shrub or tree to 5 m	White in short, crowded clusters at tips of branchlets	Reddish, hairy
R. lanceolata	Thicket-forming shrub or small tree to 10 m	Yellowish-green to white in dense clusters at end of branchlets in July or August	Dark red, hairy; September or October
R. michauxii	Low stoloniferous shrub to 1 m	Greenish-yellow in panicles 10–20 cm long	Scarlet, densely hairy, in dense panicles
R. microphylla	Shrub, to 2 m, rarely treelike to 5 m	White in heads or spikes	Globose, to 0.1 cm diameter, orange-red
R. ovata	Evergreen shrub to 3 m, rarely a tree to 4.5 m	Light yellow, in short dense spikes	Dark red, hairy; spring
R. trilobata	Shrub to 2 m	Greenish, in clustered spikes, appearing before leaves	Red, hairy; spring
R. virens	Shrub	White to 4 cm long in terminal panicles	—
Related Taxa			
T. diversilobum	Shrub to 2.5 m, sometimes climbing	Greenish, in axillary panicles	Whitish
T. radicans ssp. *radicans*	Trailing or climbing vine, shrub, or rarely a tree	Greenish white in panicles 3–6 cm long	Whitish, berrylike 5–6 mm across, in axillary clusters; early summer, persisting into winter
T. vernix	Shrub or small tree to 9 m	Greenish, in slender panicles 8–20 cm long	Greenish white in pendent axillary panicles to 20 cm long; pedicles persist through winter
M. laurina	Shrub, 3–6 m	Greenish white, in dense panicles 5–10 cm long	Whitish; early summer

Sources: Elias (1989), LHBH (1976), Rehder (1990), RHS (1994).

and empty seeds. Such thorough cleaning is seldom practiced except for skunkbush; seeds of other species are sown with pieces of the fruit wall still attached (Brinkman 1974). Trials have shown that about 99% of the empty seeds of smooth sumac can be removed by flotation, as empty seeds float and filled ones sink (Johnson and others 1966). However, the flotation method of separating empty seeds is not always successful with seeds of staghorn sumac (Brinkman 1974). Number of seeds per unit weight and seed yields vary among species (table 3).

Storage. Seeds of sumac are orthodox in storage behavior and can be stored over winter and possibly for years without special treatment (Dirr and Heuser 1987). Seeds of smooth sumac stored at room temperature for 10 years still exhibited over 60% germination, suggesting that controlled storage conditions are not required. Seeds of shining sumac have even survived 5 years of burial in the soil in Louisiana (Haywood 1994). However, Farmer and others (1982) recommend storing dried seeds of smooth sumac and shining sumac in sealed glass containers at 3 °C. Seeds of other species should be stored under a temperature range from 0 to 5 °C.

Pregermination treatments. Seeds of sumac need to be scarified in concentrated sulfuric acid for 1 to 6 hours, depending upon the species—then either fall-planted out-of-doors or stratified for approximately 2 months at about 4 °C before planting (Hartmann and others 2002). Farmer and others (1982) reported that without scarification, < 5%

Figure 1—*Rhus,* sumac: fruits of *R. triblobata,* skunkbush (**left**) and *R. hirta,* staghorn sumac (**right**).

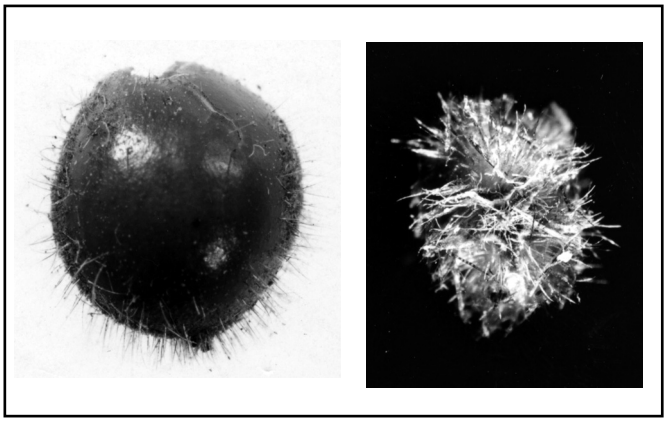


Figure 2—*Rhus,* sumac; *Malosma,* laurel-sumac: nutlets (seeds) of *R. glabra*, smooth sumac (**upper left**); *R. integrifolia,* lemonade sumac (**upper right**); *M. laurina*, laurel-sumac (**middle left**); *R. ovata*, sugarbush (**middle right**); *R. triblobata,* skunkbush (**bottom left**); *R. hirta*, staghorn sumac (**bottom right**).

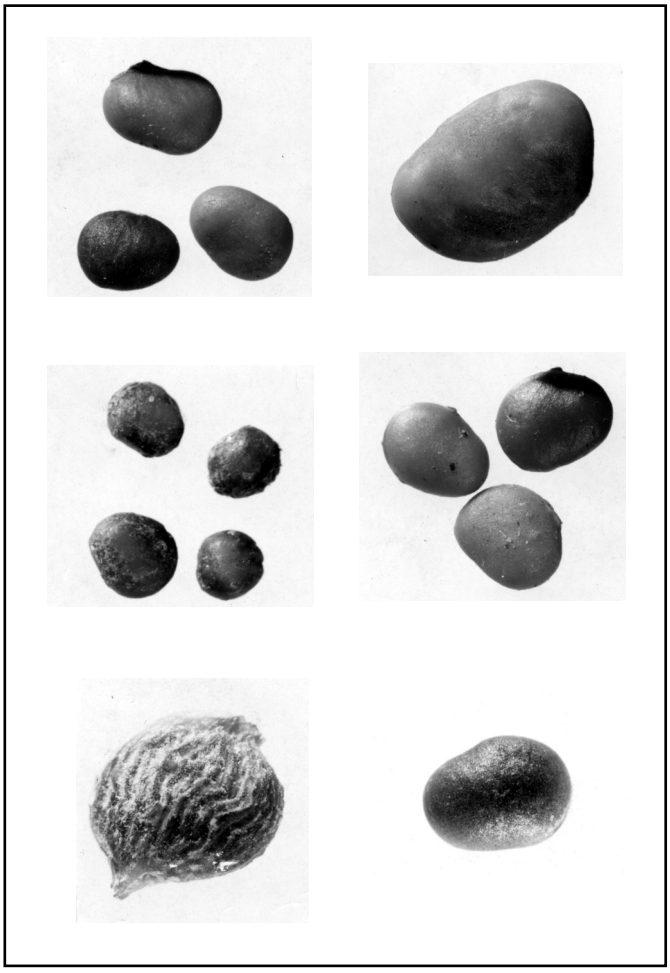
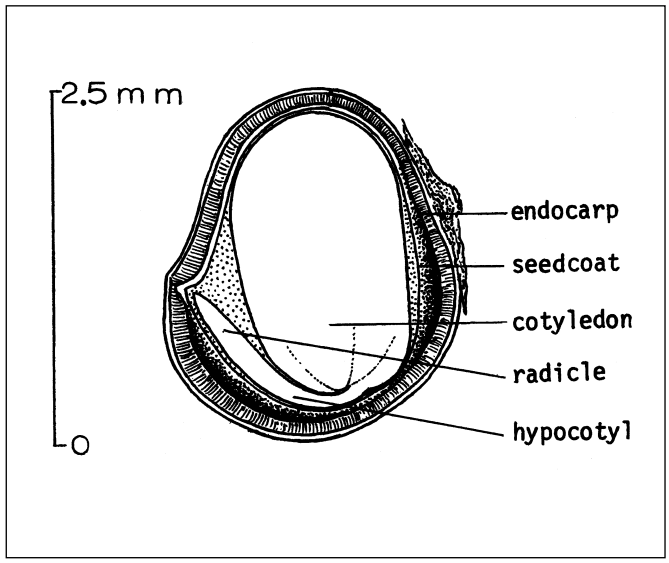


Figure 3—*Rhus hirta*, staghorn sumac: longitudinal section of a seed.



of seeds of smooth sumac germinated, but 3 to 4 hours of scarification in concentrated sulfuric acid promoted an average of 58% germination. Even after 20 years, without scarification, 3% of the seeds receiving no acid treatment germinated. However, there was a gradual increase in the number of decayed seeds with increasing durations of scarification (Farmer and others 1982).

In other species such as fragrant sumac and skunkbush, seed dormancy is caused by both a hard seedcoat and a dormant embryo, thus requiring both scarification and stratification for optimum germination (Heit 1967). These 2 treatments must be performed in proper sequence for spring-sown seeds, but the moist prechilling treatment is not necessary for fall-sown seeds. Scarification with sulfuric acid for about 1 hour followed by cold stratification at 1 to 4 °C for 1 to 3 months is recommended for seeds of fragrant sumac. Skunkbush requires 1.5 to 2 hours of scarification and 1 month or slightly longer of moist prechilling for maximum germination (Heit 1967; Weber and others 1982). Seeds of evergreen sumac need to be acid-scarified with concentrated sulfuric acid for 50 minutes and then cold-stratified for 73 days (Hubbard 1986; Tipton 1992).

High temperatures also are effective in removing seedcoat dormancy, a phenomenon that occurs naturally during wildfires. Germination of prairie sumac increases after seeds are exposed to fire (Rasmussen and Wright 1988). High temperatures scarified seeds of prairie sumac when temperatures reached 76 °C in wet environments or 82 °C in dry environments. Heat ruptures the seedcoats and waxy cuticle, enabling seeds to imbibe water. Heat generated on or near the soil surface by fire (82 °C) is sufficient to scarify seeds

Table 3—*Rhus,* sumac; *Malosma,* laurel-sumac: seed yield data

Species	Fruits (x1,000)/wt		Cleaned seeds (x1,000)/weight				Samples
			Range		Average		
	/kg	/lb	/kg	/lb	/kg	/lb	
R. copallina	—	—	81.4–173.8	37.0–79.0	125.4	57.0	4
R. glabra	50.6–105.6	23.0–48.0	52.8–277.2	24.0–126.0	107.8	49.0	28
R. hirta	66.0	30.0	107.1–148.7	48.7–67.6	117.3	53.3	5
R. integrifolia	6.6	3.0	15.0–17.6	6.8–8.0	16.7	7.6	2
R. ovata	37.4	17.0	41.1–57.2	18.7–26.0	—	—	2
R. trilobata	15.4–19.8	7.0–9.0	23.3–66.0	10.6–30.0	44.7	20.3	9
M. laurina	198.0	90.0	—	—	285.1	129.6	1

Source: Brinkman (1974).

(Rasmussen and Wright 1988). In seeds of nutgall tree, or Chinese gall, or nutgall tree—*R. chinensis* Mill., a species native to China that is often referred to incorrectly as *R. javanica* L.—a temperature of 55 ± 7.4 °C was successful in overcoming the impermeable seedcoat (Washitani 1988). With increasing temperature, shorter exposures became sufficient to render seeds permeable, but temperatures > 75 °C damaged seeds and resulted in lower germination. The most favorable regimes among those tested were temperatures of 65 to 75 °C for durations of 30 to 120 minutes, which frequently occur on denuded ground during the midday hours of clear spring and summer days (Washitani 1988).

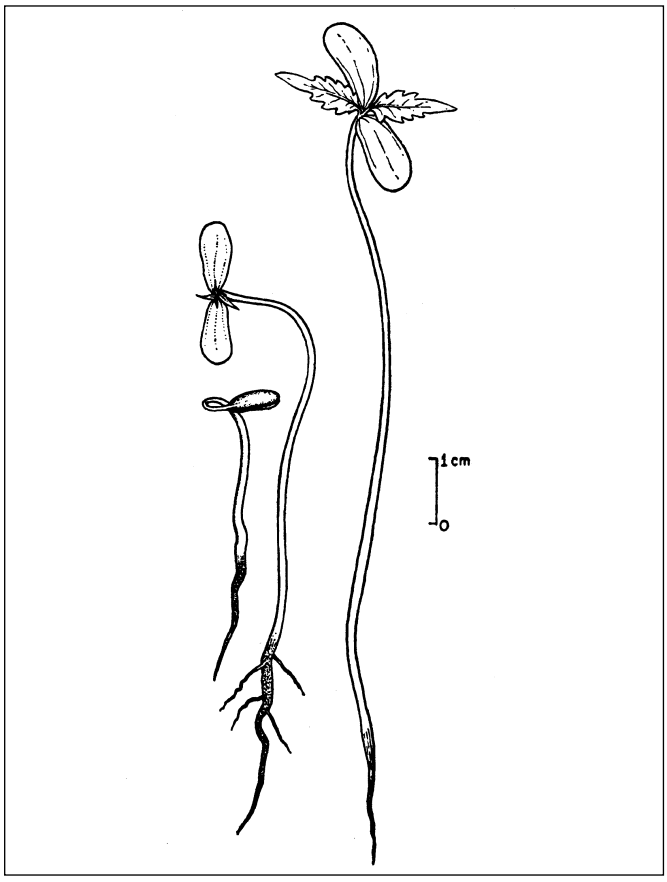
Other scarification treatments include hot water and mechanical scarification. A 2-minute submersion in boiling water was the most effective of timed heat treatments for seeds of smooth sumac (Johnson and others 1966). Germination of seeds of prairie sumac scarified with sulfuric acid was greatest when they were soaked for 60 minutes but was less than that of seeds that were mechanically scarified or treated with wet heat at 94 or 97 °C (Rasmussen and Wright 1988).

The degree of seedcoat hardness and embryo dormancy varies within and among seedlots for most species (Hartmann and others 2002; Krugman and others 1974). Seed sources also must be considered when determining scarification and stratification pretreatments. This is true for sumacs, as individual seedlots and seed sources vary in their acid treatment requirements to remove seedcoat dormancy (Heit 1967). Test averages alone are not a good representation of germination potential because of wide family differences and a significant family by treatment interaction (Farmer and others 1982). For example, germination of individual clonal seedlots of smooth sumac ranged from 25 to 75% (Farmer and others 1982). Family differences in germination are apparently based on variable susceptibility of individual seeds to scarification (Farmer and others 1982). The duration of scarification and stratification should be determined for each seedlot.

Germination tests. Light and temperature influence germination, which is epigeal (figure 4). When seeds were subjected to total darkness, the percentage germination of seedlots of smooth sumac (Brinkman 1974) and prairie sumac (Rasmussen and Wright 1988) were reduced. Heit (1967) also stressed the importance of germination in the presence of light. Likewise, temperature also is important. Evergreen sumac germinated at temperatures ranging from 21 to 30 °C (Tipton 1992), similar to that reported for other sumacs (Brinkman 1974). Final percentage germination declined with increasing temperature from a predicted maximum of 52% at 21 °C, whereas maximum germination rate increased with temperature to a predicted maximum of 69% germination at 31 °C. These results demonstrate that under low temperatures, germination would be delayed and slow, but eventually yield more seedlings. Under high temperatures, germination would also be delayed, but relatively rapid, yet it would yield few seedlings (Tipton 1992). In studies with alternating day/night temperatures, percentage germination of smooth sumac and shining sumac seedlots was significantly greater when they were subjected to an alternating temperature (16/8 hours) of 20/10 °C than at 15/5 °C or 30/20 °C. Germination rate was also affected—germination was completed within 10 days at 20/10 °C and 30/20 °C but took 20 days at 15/5 °C (Farmer and others 1982). Maximum germination of prairie sumac occurred when seeds were subjected to alternating temperatures of 20/10 °C with a short-day light cycle of 8 hours of light and 16 hours of darkness (Rasmussen and Wright 1988).

Gibberellins and ethylene or ethephon (2-chloroethyl phosphonic acid) are known to overcome dormancy in seeds of some species by completely or partially substituting for the moist-prechilling requirement (Hartmann and others 2002; Norton 1985). This was true for seeds of staghorn sumac, as germination after 30 days was higher for seeds

Figure 4—*Rhus hirta*, staghorn sumac: seedling development at 2, 4, and 17 days after germination.



incubated for 24 hours in 100 mg/liter gibberellic acid (GA) (26% germination) than 0, 1, 10, or 1000 mg/liter GA (19, 22, 24, and 22% germination, respectively). When seeds were stratified at 4 °C for 0, 10, 20, or 30 days, percentage germination increased with the length of the stratification period to a maximum of 48%. However, combining infusion of GA into seeds with cold stratification did not further enhance germination if the stratification period exceeded 10 days (Norton 1986, 1987). In contrast, promotion of germination due to ethephon was demonstrated only after 20 or 30 days of stratification, whereas no effect was observed in the absence of a cold treatment (Norton 1985). A combination of ethephon treatment at 200 mg/liter for 24 hours followed by 30 days of cold treatment at 4 °C increased germination to 60%.

Soil pH has some influence on germination. Once prairie sumac seeds were scarified, germination occurred under a wide range of pH (4 to 10), but highest germination occurred at a pH of 10 (Rasmussen and Wright 1988). In nature, soil pH increases for a short time following fire. Increased pH is attributed to ash deposition on burned areas. Fire enhances these conditions, thus aiding establishment following burning. Furthermore, seedling emergence and root growth of staghorn sumac were inhibited by simulated acid rain (Lee and Weber 1979), which tended to lower soil pH.

In addition, exudates from leaves of sumac (identified as miasmins and saprolins) inhibit germination and seedling growth of a number of other plants (Matveev and others 1975). Water-soluble extracts from leaves of shining sumac had an adverse effect on germination and radicle growth of loblolly pine—*Pinus taeda* L.—which suggests that shining sumac, a common shrub on southern pine sites, may interfere with regeneration of loblolly pine from seeds (Smith 1990). Furthermore, extracts from seeds of skunkbush inhibited growth of brome—*Bromus* L. spp.—either by killing newly germinated seeds or by reducing coleoptile growth by 30% compared to the control (Hampton and Singh 1979).

Nursery practice and seedling care. Sumacs can be propagated from seeds, by rooting stem cuttings (Hartmann and others 2002; Tipton 1990), or by field-planting root cuttings in early spring (Cross 1982, 1988; Jonsson and Zak 1975; Hartmann and others 2002). Although sumacs are heavy seed producers, commercially they are usually propagated vegetatively by root cuttings (Cross 1988; Jonsson and Zak 1975).

When propagating by seeds, the ideal sowing time depends on the species. Seeds that do not require stratification, such as those of shining, smooth, and staghorn sumacs, are sown best in the spring after a scarification treatment. Seeds scarified in sulfuric acid should be rinsed thoroughly with running water prior to sowing. Species that exhibit double dormancy, such as fragrant and skunkbush, can be either subjected to scarification and stratification and planted in spring or they can be scarified and sown in the fall, thus allowing winter temperatures to provide moist prechilling naturally (Dirr and Heuser 1987). In general, seeds should be sown at least 1.3 linear cm (1/2 in) deep at a rate of about 82 viable seeds/linear m (25/ft) (Brinkman 1974). However, depth of planting from 0 to 6 cm (0 to 2.4 in) did not affect percentage emergence of seeds of prairie sumac (Rasmussen and Wright 1988).

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Grossulariaceae—Currant family

Ribes L.

currant, gooseberry

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Growth habit, occurrence, and use. The currant and gooseberry genus—*Ribes*— includes about 150 species of deciduous, (rarely) evergreen, shrubs that grow in the colder and temperate parts of North America, Europe, Asia, and South America. The unarmed species are commonly called currants; the prickly species are gooseberries. Of the more important species for which seed data are available, 16 are native to the United States and 1 was introduced from Europe (table 1). These species generally occur as rather low-growing shrubs, although 3 species can attain heights of 3 to 4 m (table 2).

Six of the more showy species—alpine, American black, golden, wax, clove, and winter currants—are cultivated for their colorful fruit, attractive flowers, and ornamental foliage. Berries are made into jam, jelly, pie, juice, and syrup. All native species are valuable as food and cover for wildlifeand many provide browse for livestock (Plummer and others 1968). Golden and clove currants have been used in shelterbelt plantings in the prairie–plains and intermountain regions. The former also has been widely planted for erosion control (Pfister 1974). Golden, wax, white-stem, and gooseberry currants are valued as ornamentals in the United States and Canada (Barnes 1986). Currants are shade tolerant (Quick 1954). Many species regenerate vegetatively as well as from seed (Dittberner and Olson 1983; Wasser 1982). Most are rhizomatous (Lotan and others 1981). Seeds of currants remain viable in soil for long periods of time (Lyon and Stickney 1976).

Germination is stimulated by disturbances such as fire (Lotan and others 1981; Morgan and Neuenschwander 1985; Young 1983). Consequently, currants are common pioneer species on hot burns occurring on xeric sites (Hopkins and Kovalchik 1983). However, their seedcoats are relatively thin and may be destroyed by severe fires. Moist mineral soil with high amounts of humus provides a good seedbed for currants. Seeds are often introduced to the seedbank by birds and mammals that cannot digest the seeds (Lyon and Stickney 1984). Moss and Wellner (1953) suggested that, in the northern Rocky Mountains, seeds are also directly deposited simply by falling to the ground below parent plants. Seeds remain viable in the soil for long periods of time (Lyon and Stickney 1976). Moss and Wellner (1953) found soil-borne seeds of prickly currant more than 200 years old.

Many species serve as alternate hosts to white pine blister rust—*Cronartium ribicola* J.C. Fischer—a disease that has severely affected forest ecology and forest management practices (Ketcham and others 1968). Wax currant has also been shown to produce allelopathic effects (Heisey 1982).

Geographic races. Nine of the species listed (table 1) have recognized varieties; these species are pasture, Sierra, and Missouri gooseberries, and alpine, clove, winter, wax, Hudson Bay, and sticky currants. Distinctions in the first 5 species are not clearly related to geographic races, whereas the last 4 species contain geographic races (Hitchcock and others 1955; Rehder 1940; Steyermark 1963).

Flowering and fruiting. Flowers are bisexual (dioecious in alpine currant), usually small and greenish, but yellow to red in some species (Rehder 1940). The flowers are borne singly or in few- to many-flowered racemes from April to June (table 3). Flowers are often wind-pollinated (Quick 1954). Fruit is a green, many-seeded, glandular or smooth berry 6 to 13 mm in diameter (figure 1) that ripens in early to late summer. Mature fruits are red in some species, from purple to black in others, and occasionally red, yellow, or black within a species (table 4). Bees are very important to pollination of some European currants (Blasse and Hofman 1988). A mature seed (figure 2) is filled with a large endosperm containing a minute, rounded embryo (figure 3). Seeds are dispersed almost entirely by birds and mammals during the summer and fall.

The earliest seedcrops produced by Sierra gooseberry and prickly and sticky currants are borne when the plants are 3 to 5 years old. Good seedcrops are borne at intervals

Table 1—*Ribes,* currant, gooseberry: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***R. alpinum* L.** *R. opulifolium* L.	**alpine currant**	Europe to Siberia
***R. americanum* P. Mill.** *R. floridum* L'Herit.	**American black currant**	Nova Scotia to Alberta, S to Virginia & New Mexico
***R. aureum* Pursh** *Chrysobotrya aurea* (Pursh) Rydb. *R. flavum* Colla; *R. tenuiflorum* Lindl.	**golden currant,** slender golden currant, flowering currant	E Washington to Saskatchewan & South Dakota, S to California & New Mexico
***R. aureum* var. *villosum* DC.** *R. odoratum* H. Wendl. *Chrysobotrya odorata* (Wendl.) Rydb.	**clove currant,** buffalo currant	South Dakota & Minnesota, S to Missouri, W Texas, & Arkansas
***R. cereum* Dougl.** *R. churchii* A. Nels & Kenn. *R. inebrians* Lindl.; *R. pumilum* Nutt.	**wax currant,** squaw currant	British Columbia to central Montana, S to northern Mexico
***R. cynosbati* L.** *Grossularia cynosbati* (L.) Mill. *R. gracile* Michx.	**pasture gooseberry,** eastern prickly gooseberry	Nova Scota to Alberta, S to Virginia, Nebraska, & New Mexico
***R. hudsonianum* Richards.** *R. petiolare* Dougl.	**Hudson Bay currant,** wild black currant, northern black currant	Alaska to Hudson Bay, S to N California, Utah, Wyoming, & Minnesota
***R. inerme* Rydb.** *Grossularia inermis* (Rydb.) Cov. & Britt. *R. divaricatum* Dougl. var. *inerme* (Rydb.) McMinn *R. purpusii* Koehne ex Blank.	**white-stem gooseberry**	British Columbia to Montana, S to California & New Mexico
***R. lacustre* (Pers.) Poir.** *Limnobotrya lacustris* Rydb. *R. echinatum* Dougl.; *R. grossulariodes* Michx. *R. parvulum* Rydb.	**prickly currant,** swamp gooseberry, swamp black currant	Alaska to Newfoundland, S to California, South Dakota, & Pennsylvania
***R. missouriense* Nutt.** *Grossularia missouriensis* (Nutt). Cov. & Britt. *R. gracile* Pursh, not Michx.	**Missouri gooseberry**	Minnesota to Connecticut, S to Tennessee, Arkansas, & Kansas
***R. montigenum* McClatchie** *Limnobotrya montigena* McClatchie Rydb. *R. lacustre* var. *molle* Gray. *R. lentum* Cov. & Rose; *R. molle* Howell	**gooseberry currant,** alpine prickly currant, mountain gooseberry	British Columbia to Montana, S to S California & New Mexico
***R. nevadense* Kellogg** *R. ascendens* Eastw.; *R. grantii* Heller	**Sierra currant**	S Oregon, N California, & W Nevada
***R. oxyacanthoides* ssp. *irriguum* (Dougl.) Sinnott** *R. irriguum* Dougl. *R. divaricatum* var. *irriguum* (Dougl.) Gray *Grossularia irrigua* (Dougl.) Cov. & Britt.	**Idaho gooseberry,** inland black gooseberry	British Columbia, S to NE Oregon & E to W Montana
***R. roezlii* Regel** *Grossularia roezlii* (Regel) Cov. & Britt. *R. amictum* Greene; *R. aridum* Greene *R. urlsonianum* Greene	**Sierra gooseberry**	California & Nevada
***R. rotundifolium* Michx.** *Grossularia rotundifolia* (Michx.) Cov. & Britt. *R. triflorum* Willd.	**roundleaf gooseberry,** Appalachian gooseberry	Massachusetts to New York S to North Carolina
***R. sanguineum* Pursh** *Calobotrya sanguinea* (Pursh) Spach *Coreosma sanguinea* (Pursh) Spach *R. glutinosum* Benth.	**winter currant,** red flowering currant, Oregon currant, blood currant	W British Columbia, S to California
***R. viscosissimum* Pursh** *Coreosma viscosissima* (Pursh) Spach *R. halli* Jancz.	**sticky currant**	British Columbia to Montana, S to California & N Arizona

Source: Pfister (1974).

Table 2—*Ribes,* currant, gooseberry: growth habit, height at maturity and year of first cultivation

Species	Growth habit	Height at maturity (m)	Year first cultivated
R. alpinum	Dense, unarmed shrub	0.9–2.4	1588
R. americanum	Unarmed shrub	0.6–1.8	1727
R. aureum	Unarmed shrub	0.9–3.0	1806
R. aureum var. *villosum*	Unarmed shrub	0.9–3.0	1812
R. cereum	Unarmed shrub	0.3–1.5	1827
R. cynosbati	Prickly shrub	1.5	1759
R. hudsonianum	Unarmed shrub	0.3–1.8	1899
R. inerme	Prickly shrub	0.9–2.1	1899
R. lacustre	Prickly shrub	0.3–1.8	1812
R. missouriense	Prickly shrub	0.3–1.8	1907
R. montigenum	Low, very prickly shrub	0.3–0.9	1905
R. nevadense	Unarmed shrub	0.9–1.8	1907
R. oxyacanthoides spp. *irriguum*	Prickly shrub	0.3–2.4	1920
R. roezlii	Prickly shrub	0.6–1.5	1899
R. rotundifolium	Low, prickly shrub	0.9	1809
R. sanguineum	Unarmed shrub	0.9–3.6	1818
R. viscosissimum	Hardy, unarmed shrub	0.3–1.8	1827

Source: Pfister (1974).

Table 3—*Ribes,* currant, gooseberry: phenology of flowering and fruiting

Species	Location	Fruit ripening	Flowering
R. alpinum	Europe	Apr–May	July–Aug
R. americanum	—	Apr–June	June–Sept
R. aureum	—	Apr–May	June–July
R. aureum var.*villosum*	Wyoming	Late May	Late Aug
	Kansas	Mid–Apr	June
	—	Apr–June	June–Aug
R. cereum	—	Apr–June	Aug
R. cynosbati	—	Apr–early June	Late July–Sept
R. hudsonianum	—	May–July	—
R. inerme	—	May–June	—
R. lacustre	—	Apr–July	Aug
R. missouriense	—	Apr–May	June–Sept
R. montigenum	—	Late June–July	Aug–Sept
R. nevadense	—	May–July	—
R. oxyacanthoides ssp. *irriguum*	—	Apr–June	—
R. roezlii	—	May–June	—
R. rotundifolium	—	Apr–May	July–Sept
R. sanguineum	Oregon	Apr–May	July–Aug
	—	Mar–June	—
R. viscosissimum	—	May–June	Aug–Sept

Sources: Fernald (1950), Hitchcock and others (1955), Krüssmann (1960–1962), Loiseau (1945), Munz and Keck (1965), NBV (1946), Petrides (1955), Pfister (1974), Rehder (1940), Stephens (1969), Steyermark (1963), Symonds (1963), Wyman (1949).

of 2 to 3 years (Moss and Wellner 1953; Quick 1954). Clove currant, however, produces good crops annually (Pfister 1974).

Seed collection and extraction. The fruits should be picked or stripped from the branches as soon as they are ripe to preclude loss to birds. Unless the seeds are to be extracted immediately, fruits should be spread out in shallow layers to prevent overheating (Pfister 1974). Berries of alpine currant are often allowed to ferment in piles for a few days prior to extraction (NBV 1946). Maceration and washing are used to separate the seeds from the pulp. Dried fruits should first be soaked in water before cleaning. Small quantities of berries can be cleaned in a kitchen blender. The berries are covered with water and ground in the blender for 15 to 45 seconds. After the seeds have separated from the pulp, additional water is added to allow the sound seeds to settle. The pulp,

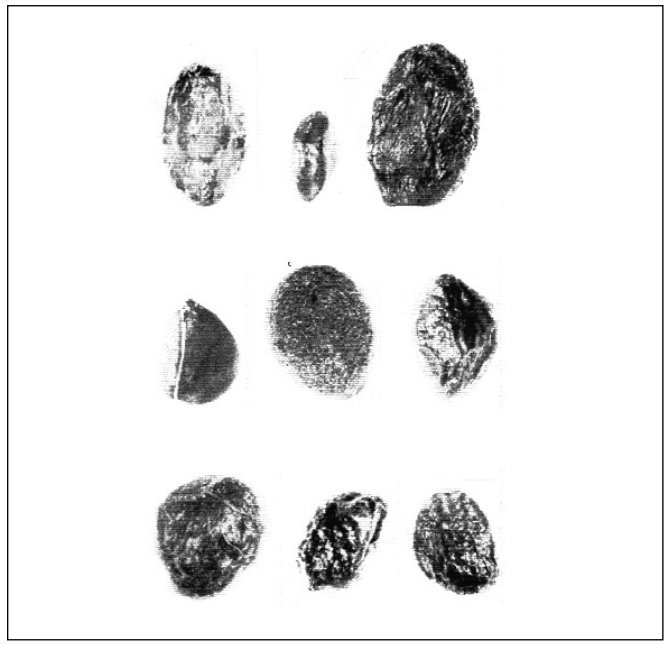
Table 4—*Ribes,* currant, gooseberry: fruit characteristics and seed storage conditions for air-dried seeds

Species	Fruit characteristics			Storage conditions		
	Surface	Diam (cm)	Ripe color	Temp (°C)	Duration (yr)	Viability at end (%)
R. alpinum	Glabrous	—	Scarlet	—	—	—
R. americanum	Glabrous	0.6	Black	6	4	38
R. aureum	Glabrous	0.6	Red, black, or yellow	21	17	89
R. aureum var. *villosum*	Smooth	1.0	Black, golden, or reddish brown	21	17	32
R. cereum	Glandular	0.6	Dull to bright red	21	27	4
R. cynosbati	Glandular	—	Reddish purple	21	7	8
R. hudsonianum	Smooth	1.0	Black	21	17	40
R. inerme	Smooth	0.6	Reddish purple	21	11	80
R. lacustre	Glandular	0.6	Purple to black	—	—	—
R. missouriense	Smooth	1.3	Purple to black	—	—	—
R. montigenum	Glandular	0.6	Red	—	—	—
R. nevadense	Glandular	—	Blue to black	Soil	4	81
	Glandular	—	Blue to black	21	4	88
R. oxyacanthoides ssp. *irriguum*	Smooth	1.0	Bluish purple	—	—	—
R. roezlii	Glandular	1.3	Purple or deep reddish brown	Soil	13	82
	Glandular	1.3	Purple or deep reddish brown	2	12	45
R. rotundifolium	Smooth	0.6	Purple	—	—	—
R. sanguimeum	Glandular	1.0	Blue to black	—	—	—
R. viscosissimum	Glandular	1.3	Black	21	17	23
	—	—	—	21	22	7

Sources: Hitchcock (1955), Jepson (1925), Ketchum and others (1968), Munz (1965), Pfister (1974), Quick (1945, 1947, 1954), Rehder (1940), Stephens (1969).

Figure 1—*Ribes*, currant, gooseberry: berries of *R. cereum*, wax currant (**upper left**); *R. cynosbati*, pasture gooseberry (**upper right**); *R. lacustre*, prickly currant (**middle left)**; *R. montigenum*, gooseberry currant (**middle right**); *R. sanguineum*, winter currant (**bottom left**); *R. viscosissimum*, sticky currant (**bottom right**).

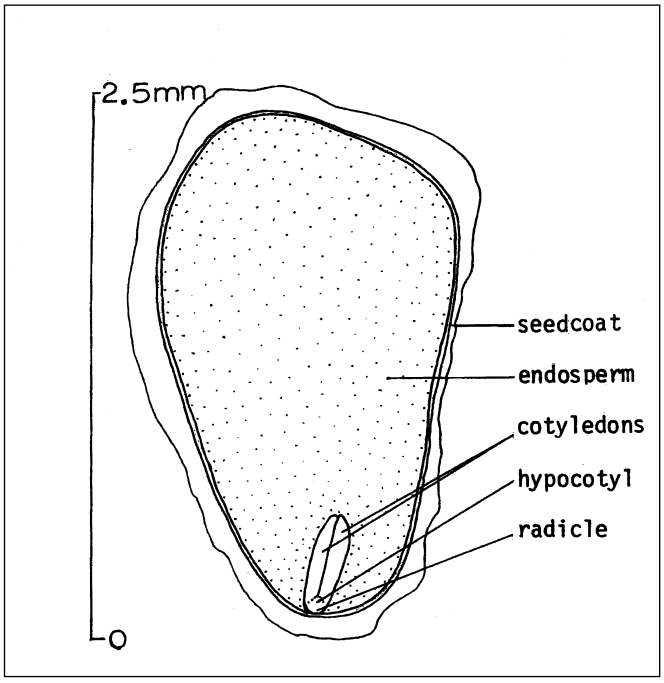
Figure 2—*Ribes*, currant, gooseberry: seeds of *R. cereum*, wax currant (**upper left**); *R. hudsonianum*, Hudson Bay currant (**upper center**); *R. oxyacanthoides* ssp. irriguum, Idaho gooseberry (**upper right**); *R. lacustre*, prickly currant (**center left**); *R. montigenum*, gooseberry currant (**center middle**); *R. nevadense*, Sierra currant (**center right**); *R. roezli*, Sierra gooseberry (**bottom left**); *R. sanguineum,* winter currant (**bottom center**); *R. viscosissimum*, sticky currant (**bottom right**).



empty seeds, and excess water can then be decanted. Seeds may be washed using a funnel lined with filter paper and then dried on the filter paper (Morrow and others 1954). Munson (1986) recommends replacing the blades in a food-processing blender or milkshake blender with a short length of plastic or rubber hose to extract the seeds. Data on the numbers of cleaned seeds per weight are listed in table 5.

Seed yields from 45 kg (100 lb) of berries was 1.8 kg (4 lb) for golden currant, 3.6 kg (8 lb) for clove currant, and 1.8 kg (4 lb) for winter currant (Pfister 1974). One liter of berries from winter currant weighs about 0.5 kg (1 bu weighs about 40 lb). Each prickly currant plant produces around 50 to 75 berries, and each berry has 8 seeds (Moss and Wellner 1953).

Figure 3—*Ribes missouriense*, Missouri gooseberry: longitudinal section through a seed.



Storage. Currant seeds are orthodox and remain viable for long periods when stored in sealed containers at a low moisture content. Temperature is evidently not critical. Samples of Sierra gooseberry seeds buried in soil in inverted open containers for 13 years exhibited 70 to 94% viability (Quick 1947b). Seeds of several species stored dry at room temperature also maintained high viability for periods up to 17 years (table 4).

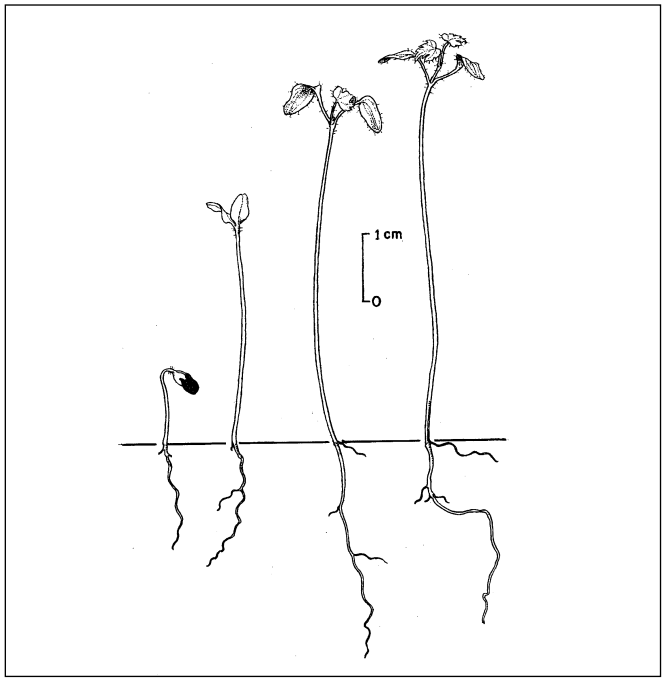
Germination. In nature, currant seeds normally germinate in spring following dispersal, although some seeds may remain dormant for many years (Moss and Wellner 1953; Quick 1954). The best seedbed appears to be mineral soil well supplied with humus. Germination is epigeal (figure 4). In the laboratory, seeds are slow to germinate except for those of Hudson Bay currant and roundleaf gooseberry. Most species require at least 1 stratification period of fairly long duration to break embryo dormancy (Rudolf 1949). Stidham and others (1980) achieved good germination of golden currant after 10 weeks of wet chilling in distilled water. Impermeable seedcoats also appear to be involved in dormancy of some seedlots of clove and American black currants (Pfister 1974). Germination rate and total can be increased by wet prechilling in sand, peat, or vermiculite or in a mixture of these media. Seed losses from damping-off fungi can be prevented by applying 646 mg of copper

Table 5—*Ribes*, currant, gooseberry: seed yield data

Species	Place collected	Cleaned seeds (x1,000)/weight				Samples
		Range		Average		
		/kg	/lb	/kg	/lb	
R. americanum	—	544–741	247–336	690	313	4
R. aureum	—	441–628	200–285	514	233	4
R. aureum var. *villosum*	North Dakota	234–395	106–179	368	167	8
R. cereum	California	443–624	201–283	553	251	5
R. cynosbati	—	417–487	189–221	452	205	2
R. hudsonianum	Idaho	1,389–2,703	630–1,226	2,127	965	12
R. inerme	Idaho & California	780–877	354–398	807	366	5
R. lacustre	California	—	—	1,135	515	1
R. missouriense	—	344–370	156–168	357	162	2
R. montigenum	Utah	—	—	313	142	1
R. nevadense	California	650–935	295–424	862	391	10
R. roezlii	California	388–650	176–295	520	236	10+
R. sanguineum	Oregon	—	—	626	284	1
R. viscosissimum	Idaho & California	562–769	255–344	657	298	5

Sources: Pfister (1974), Quick (1936, 1954).

Figure 4—*Ribes missouriense*, Missouri gooseberry: seedling development at 2, 7, 23, and 44 days after germination.



oxalate per 100 cm^2 of culture surface (Quick 1941). Optimal temperature and duration of stratification vary by species and, to a lesser degree, between seedlots within a species. For most species, a second wet chilling and a repeat germination test are necessary to obtain complete germination of viable seed (table 6). The dormancy irregularity within a seedlot provides a natural adaptive advantage: some seeds germinate immediately and some remain dormant in the forest soil until conditions are optimal for germination and development. Many methods of breaking dormancy have been tried on various species, including acid treatment of seedcoat, warm incubation, freeze-and-thaw, and stratification with alternating temperatures (Quick 1939a&b, 1940, 1941, 1943, 1945, 1947a&b). For most species these treatments offer little advantage over normal wet chilling. A lower temperature can improve germination and reduce wet-chilling requirements (Fivaz 1931; Pfister 1974). Stidham and others (1980) used potassium nitrate to improve early germination of golden currant. Most tests were conducted in a greenhouse using sand flats moistened with Hoagland's nutrient solution (Quick 1941). Some species showed considerable germination capacity without wet chilling when

Table 6—*Ribes,* currant, gooseberry: pregermination treatments and germination test results

Species	Pregermination treatment		Germination under test conditions*	Germination capacity†	
	Temp (°C)	Days	(%)	(%)	Samples
R. alpinum	0 to 10	90+	80	—	10
R. americanum	–2 to 2	90–120	68	76	39
R. aureum	–2 to 2	60	60	63	19
R. aureum var. *villosum*	20/0 (D/N)	120	94	98	3
R. cereum	–2 to 0	120–150	61	72	61
R. cynosbati	–2 to 5	90–150	69	72	19
R. hudsonianum	NP	NP	57	85	116
	0 to 2	90–120	69	76	42
R. inerme	0	120–200	60	74	54
R. lacustre	0	120–200	48	61	64
R. missouriense	–2 to 5	90+	73	—	3
R. montigenum	0	200–300	53	—	6
	0	120–150	8	33	15
R. nevadense	0	120	78	87	43
R. oxyacanthoides ssp. *irriguum*	0 to 5	90	79	81	11
R. roezlii	0	100–150	80	87	200
R. rotundifolia	–2 to 0	90+	80	81	10
R. sanguineum	0–2	100–140	61	64	55
R. viscosissimum	–2 to 0	140	58	67	88

Sources: NBV (1946), Pfister (1974), Quick (1939, 1940, 1941, 1943, 1945, 1947).

Note: D/N = day/night, NP = no pretreatment.

* Virtually all of the tested seeds were stratified and germinated in sand moistened with nutrient solution. The germination tests were conducted under greenhouse conditions for periods of 30 to 40 days.

† Germination capacity was determined by retrial stratification and a repeat germination test with conditions about the same as used initially.

investigators alternated diurnal temperatures (25 and 5 or 10 °C)—for example, prickly currant (Miller 1931), clove currant (Quick 1941), roundleaf gooseberry (Fivaz 1931), and sticky currant (Miller 1931). For these tests, 5 minutes of soaking in 2 to 10% sulfuric acid solution improved germination of prickly and sticky currant seeds (Miller 1931). Each species has its own unique germination characteristics, so that no procedure is best for all species. Additional work is needed to fully understand the dormancy mechanisms in the Ribes genus.

Nursery practice. Currant seeds are normally sown in fall, although they can be stratified and sown in spring. Few tests have been conducted to determine which species can be sown in spring without stratification; Hudson Bay currant may be one of these (table 6). Fall-sowing is recommended, especially if seedcoat dormancy is present (Heit 1968). However, Sierra gooseberry seeds must be dried before they are sown because fresh seeds will not germinate, even after stratification (Quick 1939). If fall-sowing is not possible, the seeds should be stratified before spring-sowing using the procedures summarized in table 6. Seeds should be sown at a rate of 646 to 860/m^2 (60 to 80/ft^2) (NBV 1946) or 130 viable seeds/m of row (40/ft) and covered to a depth of 3 to 6 mm ($^1/_8$ to $^1/_4$ in) (Pfister 1974). Seeds of Sierra gooseberry and wax and Sierra currants may be covered up to 1.3 cm (1/2 in) (Quick 1939a, 1940).

The only reported experience in nursery stock production is for clove currant (Pfister 1974). Seedbeds are fall-sown, mulched to a depth of 5 to 8 cm (2 to 3 in) and covered with snow fence. About 20,000 seedlings are produced per kilogram of seeds (9,000/lb) and the normal outplanting age is 2 years. Most species can be propagated readily from hardwood cuttings taken in autumn (Pfister 1974).

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Fabaceae—Pea family

Robinia L.

locust

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Growth habit, occurrence, and use. The locust genus—*Robinia*—includes 9 species, with 8 varieties native to the United States and Canada (BONAP 1996). Four species, 6 varieties, and 4 hybrids are considered here (table 1). Most of these species are shrubs and a few are deciduous trees. Black locust is a medium-sized tree 12 to 18 m high with a maximum of 30 m (Roach 1965). It reaches its best development in the Appalachian region and has been widely planted in the Western Hemisphere and Europe. The rapid growth of black locust on good sites, its nitrogen-fixing ability, and the durability of its wood (especially for fence posts) makes black locust one of the most valuable species in the genus. Bristly locust and its variety Kelsey locust are low shrubs, 0.6 to 3 m high (Fernald 1950). They are useful for erosion control because of prolific root sprouting. Growth of locust species is very good on calcareous soils, but bristly locust will grow also on strip mine spoils, where acid soils have pH values as low as 4.0. Bristly locust is a triploid and Kelsey locust is a diploid (Whitaker 1934). New Mexican locust is a small tree, 3 to 7.5 m high (Wooten 1913).

Flowering and fruiting. The perfect flowers occur in racemes originating in the axils of leaves of the current year; they appear in the spring and early summer (Radford and others 1964; Sargent 1965). Flowers are pollinated by insects, especially bees (Robertson 1928). The fruit, a legume (figure 1), ripens in the autumn and contains 4 to 10 dark brown to black seeds about 4.8 to 6 mm long (figure 2) (Olson 1974; Small 1933). When they ripen, the legumes (pods) become brown and open on the tree, releasing the seeds. Black locust begins seed-bearing at about 6 years of age and produces good crops every 1 to 2 years (Little and DeLisle 1962; Olson 1974). Seeds contain no endosperm (figure 3).

Collection, cleaning, and storage. Ripe seeds should be collected before the legumes open. Legumes can be picked from the trees by hand or flailed or stripped onto canvas or plastic sheets from late August throughout the winter (table 2). The legumes should be spread out to air-dry until they are brittle to facilitate breaking them open. Alternatively, they can be dried in a forced-air seed or cone drier if a faster result is needed or if natural drying conditions are too humid. Once the legumes are brittle, they can be threshed by flailing them in a bag or by running them through a macerator or brush machine (chapter 3). Chaff and light seeds can be removed by fanning or flotation in water. Legumes of New Mexican locust should be collected soon after ripening, because they open rapidly once ripening is complete (Olson 1974). Seed weights are similar among the locusts (table 3). Soundness and purity of seedlots is high. Seedlot purities of 97% and soundness of 90 to 99% have been obtained (Olson 1974). Locust seeds are orthodox in storage behavior. In prolonged storage, dry seeds retain their viability for 10 years or more if placed in closed containers at 0 to 4.5 °C. For periods of 3 to 4 years, open storage in a cool, dry place can be practiced (Olson 1974). Seeds can be stored dry and sown within a year (Wyman 1953).

Pregermination treatment. Dormancy in untreated seeds of locust is entirely due to impermeable seedcoats. Prompt germination can be induced by proper scarification. Several methods have been devised for this. The most well-developed treatment, with concentrated sulfuric acid, has been used on both New Mexican (Cox and Klett 1984) and black locusts (Brown 1973; Chapman 1936; Meginnis 1937; Olson 1974, Singh and others 1991). Myatt (1991) reports a much-refined acid scarification procedure. First the seeds are sized in a 2-screen cleaner using a 3.2-mm (#8) round-hole top screen and a 2.8-mm (#7) round-hole bottom screen. Larger seeds were found to require a shorter acid treatment than do small seeds. By treating the sizes separately, fewer of the seeds remain impermeable and fewer are damaged by too-long a treatment. Large seeds are treated for 45 to 60 minutes, medium seeds from 60 to 75 minutes, and small seeds from 75 to 90 minutes. Seeds are first wet with

Table 1—*Robinia,* locust: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***R.* × *ambiqua* Poir. (pro sp)** *R.* × *ambique* var. *bella-rosea* (G. Nicholson) Rehder *R.* × *dubia* Foucault	**locust**	North Carolina
***R. hispida* L.** *R. pallida* Ashe *R. speciosa* Ashe *R. grandiflora* auct. non Ashe nec L. nec Schneid.	**bristly locust**	Nova Scotia & Maine S to Florida, W to Ontario, Minnesota, & Texas
***R. hispida* var. *fertilis* (Ashe) Clausen** *R. fertilis* Ashe *R. grandiflora* Ashe *R. pedunculata* Ashe	**bristly locust**	Connecticut S to North Carolina, W to Iowa
***R. hispida* var. *kelseyi* (Colwell ex Hutchinson) Isely** R. kelsyi Cowell ex Hutchinson	**Kelsey locust**	Kentucky, Tennessee, North & South Carolina; also New Jersey
***R. hispida* var. *nana* (Ell.) DC.** *R. elliottii* (Chapman) Ashe ex Small *R. nana* Ell.	**bristly locust**	S Appalachian Mtns of Alabama, Georgia, North & South Carolina, Kentucky,& Tennessee
***R. hispida* var. *rosea* Pursh** *R. albicans* Ashe *R. boyntonii* Ashe *R. leucantha* Rehd.	**mossy locust,** bristly locust	S Appalachian Mtns of Alabama, Georgia, North & South Carolina, Kentucky, & Tennessee
R. x holdtii Beissn. *R.* x *coloradensis* Dode	**Holdt locust**	Colorado, Utah, & Wyoming
R. x longiloba Ashe (pro sp.)	**locust**	North & South Carolina
***R. x margarettiae* Ashe (pro sp.)** *R. x salvinii* Rehd.	**Margarett locust**	New Brunswick & Nova Scotia S to Georgia, W to Ontario & Ohio
R. neomexicana Gray *R. luxurians* (Dieck) Schneid. ex Tarouca & Schneid. *R. neomexicana* var. *luxurians* (Gray) Dieck *R. neomexicana* var. *subvelutina* (Gray) (Rydb.) Kearney & Peebles	**New Mexican locust**	Wyoming S to New Mexico & Texas, W to California
***R. neomexicana* var. *rusbyi* (Woot. & Standl.) Martin & Hutchins ex Peabody** *R. breviloba* Rydb. *R. rusbyi* Woot. & Standl.	**Rusby locust**	Arizona & New Mexico
***R. pseudoacacia* L.** *R. pseudoacacia* var. *rectissima* (L.) Raber	**black locust**	Nova Scotia & New Brunswick S to Florida, W to Washington & California
***R. viscosa* Vent.**	**clammy locust**	Nova Scotia & New Brunswick S to Georgia, W to Ontario, Wisconsin, & Tennessee
***R. viscosa* var. *hartwegii* (Koehne) Ashe** *R. hartwegii* Koehne	**Hartweg locust**	Georgia & North & South Carolina

Source: BONAP (1996).

water in a leak-proof plastic tub. The concentrated sulfuric acid is added at a rate of 720 ml/4.5 kg of seeds. This amount of seeds is easily worked. A small amount of additional water is added to allow the seeds to be stirred with a wooden slat during the treatment. Stirring should be almost constant to evenly distribute the acid and thus prevent burning of individual seeds. At the end of the prescribed time in the acid, the seeds should be rinsed thoroughly in running water, then next soaked overnight in water. Those that have been successfully scarified will swell. Air-drying the treated seeds just enough to surface-dry them will allow the swollen seeds to be screened from the non-swollen seeds using the 2-screen machine. The top screen for this second screening would be about a 4-mm (#10) round-hole screen. The non-swollen seeds can be retreated in acid for 45 to 60 minutes using the same procedure as with the full lot. Swollen seeds are now ready for planting. They may be temporarily placed in a cooler for a few days until planted. If only 1 cycle of

Figure 1—*Robinia*, locust: legumes (pods) of *R. hispida* var. *rosea*, mossy locust (**left**); *R. hispidus* var. *fertilis*, bristly locust (**top center**); *R. neomexicana*, New Mexican locust (**bottom center**); *R. pseudoacacia*, black locust (**right**).

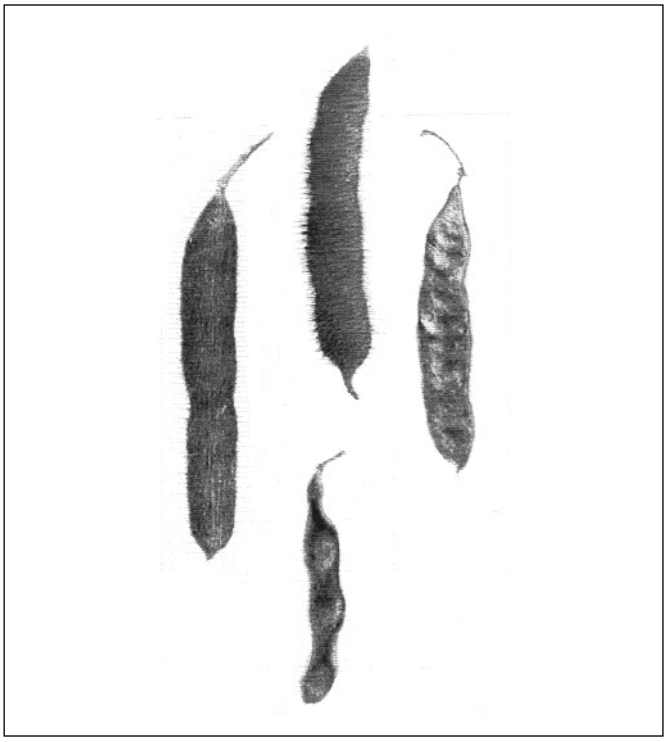


Figure 2—*Robinia*, locust: seeds of *R. hispidus* var. fertilis, bristly locust (**top left**); *R. hispida* var. *rosea*, mossy locust (**top right**); *R. neomexicana*, New Mexican locust (**bottom left**); and *R. pseudoacacia*, black locust (**bottom left**).

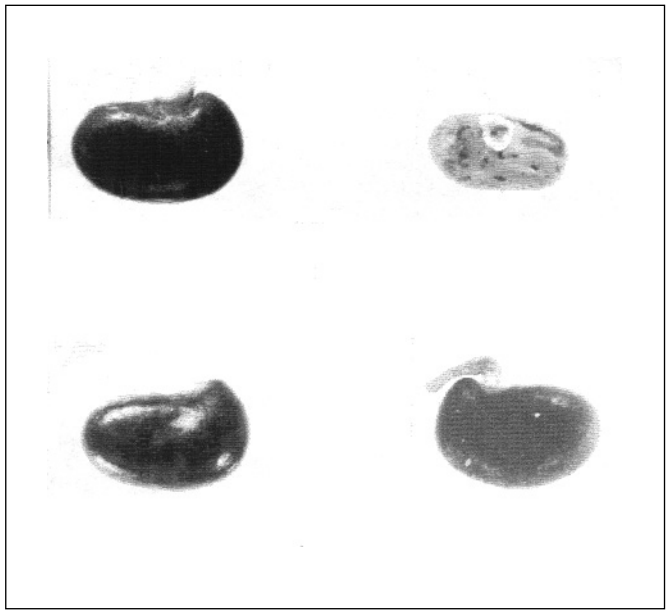
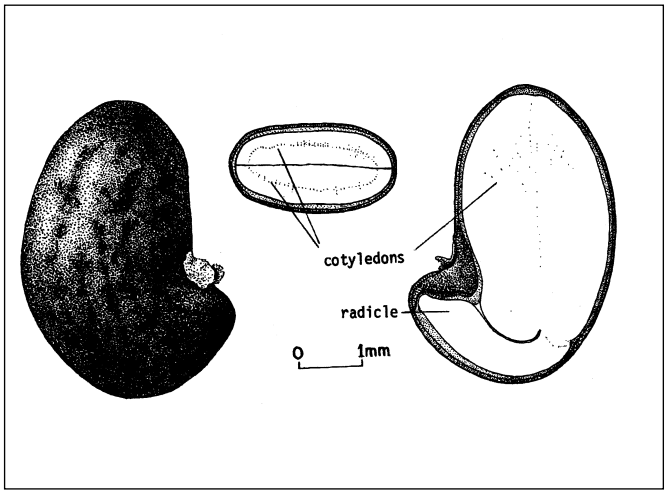


Figure 3—*Robinia pseudoacacia*, black locust: exterior (**left**) and longitudinal (**right**), and cross (**center**) sections of a seed.



acid is planned, a test sample should be run to determine the length of soak. Here small seed samples are soaked in acid for progressively longer intervals until a majority of the seeds are swollen following the water soak. Predetermined soaking times have varied from 10 to 120 minutes (Heit 1967; Meginnis 1937). Acid scarification is hazardous, so wearing adequate protective clothing—face shield and rubber gloves, boots, and apron—is mandatory.

A second widely used method is hot water treatment (Singh and others 1991; Wilson 1944). This procedure can be done by bringing a container of water to a boil, removing it from the heat, and pouring in the seeds. The water and seeds are then allowed to cool overnight. Although not practiced, it is reasonable to assume that the sizing of the seeds described above for acid would allow for a more complete scarification. Burning a hole in the seedcoat with a heated needle, nicking the seedcoat with a clipper, and heat shock (alternate boiling and cold water dips) have also been tried (Singh and others 1991). The nicking was as effective as the acid, burning less effective, and heat shock, even with multiple cycles of hot and cold, was still less effective.

Germination tests. Germination tests on scarified seeds may be made with any conventional medium. After 10 to 40 days at diurnally alternating temperatures of 30 °C in the day and 20 °C at night, germination capacities of several species of locust ranged from 10 to 93% (Olson 1974). Light is not required for germination (Heit 1968; Meginnis 1937). Germination capacity depends primarily on the effectiveness of the scarification treatment in making the seedcoat permeable to water without damaging the embryo (Meginnis 1937). For seeds used in a germination test, mechanical scarification with a needle, razor blade, or clipper can be done rapidly and without the hazards of handling acid. Acid-treated seeds have also been found to mold much more easily than mechanically treated seeds in germination tests at the USDA Forest Service's National Seed Laboratory (Karrfalt 1990).

Table 2—*Robinia,* locust: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
R. hispida	May–June	July–Sept	—
R. hispida var. *fertilis*	Early June	Sept	Oct–Nov
R. neomexicana	—	Sept	Sept–Oct
R. pseudoacacia	—	Sept–Oct	Sept–Apr

Sources: Olson (1974), Radford and others (1964), Sargent (1965).

Table 3—*Robinia,* locust: seed yield data

	Seed yield/fruit weight		Cleaned seeds/weight	
Species	/45.4 kg	/100 lb	/kg	/lb
R. hispida var. *fertilis*	—	—	50,715	23,000
R. hispida	—	—	61,080	27,700
R. neomexicana	9	20	47,630	21,600
R. pseudoacacia	6.8–15	15–33	52,920	24,000*

Sources: Sargent (1965), Small (1933), Swingle (1939).

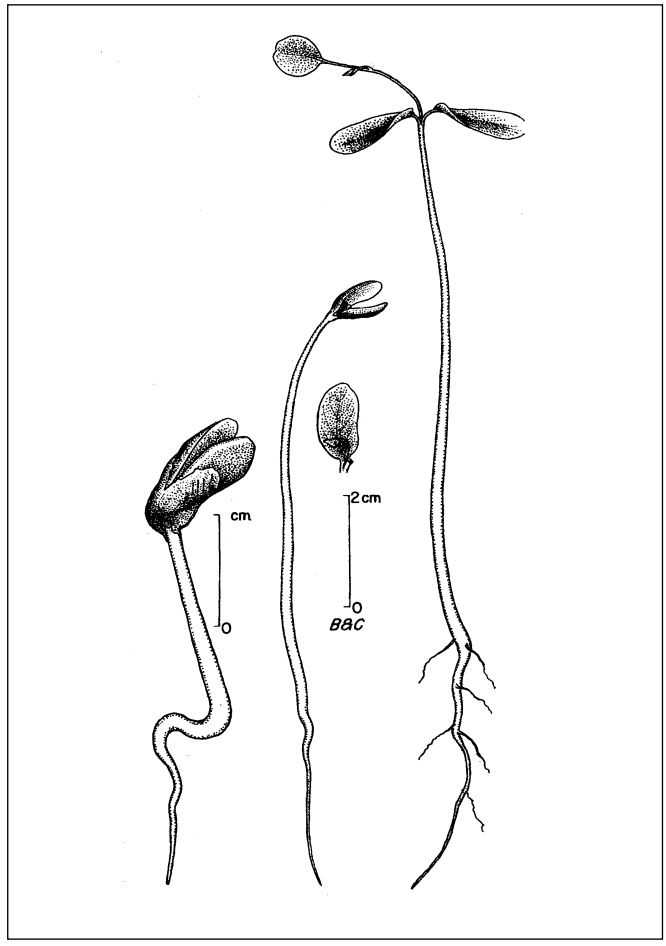
* Range was 16,000 to 35,000 seeds/lb.

For official germination testing, the Association of Official Seed Analysts (AOSA 1993) prescribe a pretreatment of a 1-hour soak in concentrated sulfuric acid, then chilling for 21 days at 20 °C. International rules (ISTA 1993) prescribe either scarification of the seeds at the cotyledon end or soaks in sulfuric acid until the surface of the seedcoats are pitted. Germination is then carried out at alternating temperatures of 20/30 °C for 14 days.

Nursery practice. Locust seeds may be drilled in rows 15 to 20 cm (6 to 8 in) apart at a rate of 65 to 100 seeds/m (20 to 30/ft), or broadcast in fertile soil from March to May. Seeds should be covered with about 6 mm ($^1/_4$ in) of soil, sand, or a mixture of sand and sawdust (McWilliams 1970; Olson 1974). Seeds should be treated with a nitrogen inoculant, especially if the seedbeds have been fumigated. Mulching is not mandatory, but a light straw mulch has been used advantageously in the culture of bristly locust in New York (McWilliams 1970). Germination is epigeal (figure 4). Seedlings of locust have large roots, and raising nursery beds 15 to 20 cm (6 to 8 in) facilitates lifting. One-year-old seedlings can be planted successfully on most fertile soils. Chaney and Kozlowski (1974) found that the addition of anti-transpirants to the nursery soil before sowing would reduce germination but had the potential to improve the growth and water balance of the surviving seedlings.

Direct seeding. Locust is often used in revegetating disturbed sites such as road cuts and strip mines. It is important in such areas to cover the seeds with about 6 mm

Figure 4—*Robinia pseudoacacia*, black locust: seedling development after 1, 3, and 8 days of germination.



($^1/_4$ in) of soil, as in the nursery. Brown (1973) reported a 10- to 60-fold improvement in germination from covering the seeds planted on West Virginia mine spoils. Brown also found (1973) that soil compaction from grading the sites and herbaceous competition resulted in poorer conditions for germination and seedling establishment. Salinity can also be a problem along highways and in dry countries where irrigation must be practiced in agroforestry applications. Under salinity levels of 0.05 to 0.80%, black locust germination was reduced and occurred more slowly (Bangash 1977; Bicknell and Smith 1975).

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Rosaceae—Rose family

Rosa L.

rose, briar

Susan E. Meyer

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Growth habit, occurrence, and uses. The genus *Rosa* is found primarily in the North Temperate Zone and includes about 200 species, with perhaps 20 that are native to the United States (table 1). Another 12 to 15 rose species have been introduced for horticultural purposes and are naturalized to varying degrees. The nomenclature of the genus is in a state of flux, making it difficult to number the species with precision. The roses are erect, clambering, or climbing shrubs with alternate, stipulate, pinnately compound leaves that have serrate leaflets. The plants are usually armed with prickles or thorns. Many species are capable of clonal growth from underground rootstocks and tend to form thickets. Usually found in the more moist but sunny parts of the landscape, wild roses provide valuable cover and food for wildlife, especially the birds and mammals that eat their hips and act as seed dispersers (Gill and Pogge 1974). Wild roses are also utilized as browse by many wild and domestic ungulates. Rose hips are an excellent source of vitamin C and may also be consumed by humans (Densmore and Zasada 1977). Rose oil extracted from the fragrant petals is an important constituent of perfume. The principal use of roses has clearly been in ornamental horticulture, and most of the species treated here have been in cultivation for many years (Gill and Pogge 1974).

Many roses are pioneer species that colonize disturbances naturally. The thicket-forming species especially have potential for watershed stabilization and reclamation of disturbed sites. If roses are to be used for these purposes, it is greatly preferable to utilize species native to the region rather than exotics, which can become serious pests. An

Table 1—*Rosa,* rose: scientific names and geographic distribution for 12 species native or naturalized in the United States

Scientific name	Common name(s)	Geographic distribution
***R. acicularis* Lindl.**	**prickly rose**	Circumboreal, S in North America to Utah, New Mexico, Nebraska, & New York
***R. blanda* Ait.**	**meadow rose,** smooth rose	E North America, S to Missouri & Nebraska
***R. californica* Cham. & Schlecht.**	**California rose**	S Oregon, S to Baja California
***R. canina* L.**	**dog rose**	Introduced from Europe; locally escaping in E North America
***R. eglanteria* L.**	**sweetbriar rose,** eglantine	Introduced from Europe; naturalized in the Pacific NW & in E North America
***R. gymnocarpa* Nutt.**	**baldhip rose,** dwarf rose	Pacific NW S to central California & E to Montana & Idaho
***R. multiflora* Thunb. ex Murr.**	**multiflora rose,** Japanese rose	Introduced from Japan; widely naturalized in E North America
***R. nutkana* K. Presl.**	**Nootka rose**	Alaska S to California, Utah, & Colorado
***R. rugosa* Thunb.**	**rugosa rose,** hedgerow rose	Introduced from E Asia; naturalized in E & mid-W North America
***R. setigera* Michx.**	**prairie rose,** climbing rose	Mid-W United States S to Texas; naturalized in E North America
***R. wichuraiana* Crépin.**	**wichura rose,** memorial rose	Introduced from E Asia; locally escaping in E North America
***R. woodsii* Lindl.**	**Woods rose**	Widely distributed in W & mid-W North America

Source: Gill and Pogge (1974).

example is the multiflora rose, a Japanese species that was widely promoted as a "living fence" in a previous era (Anderson and Edminster 1954). It has invaded thousands of acres of unimproved pastureland in the eastern United States and is now the target of a large and expensive control program (Mays and Kok 1988).

Flowering and fruiting. The large, perfect flowers are usually borne singly or in groups of 2 or 3, though some species (for example, wichura, multiflora, and prairie roses) have flat-topped inflorescences with few to many flowers. The flowers generally appear in late spring or early summer and are insect-pollinated. They are perigynous, with the 5 sepals, 5 to many petals, and many stamens inserted on the edge of the hypanthium and the many pistils borne within its cup. In fruit, the hypanthium enlarges to become the fleshy, berrylike hip (figure 1), and the pistils become single-seeded achenes (figures 2 and 3). The achene wall is usually hard, bony, and resistant to damage.

The fruits may ripen from late summer to fall, but they usually persist on the plants through the winter, presumably as an enticement to dispersers. The hips are often brightly colored in hues of orange, red, and purple that are attractive to birds. Those that have not been taken by spring are pushed off by the newly developing flowers of the next season. Once on the ground, the hips disintegrate quickly.

Figure 1—*Rosa*, rose: fruits (hips) of *R. eglanteria*, sweetbriar rose (**top**); *R. multiflora*, multiflora rose (**bottom left**); *R. nutkana*, Nootka rose (**bottom center**); and *R. setigera*, prairie rose (**bottom right**).

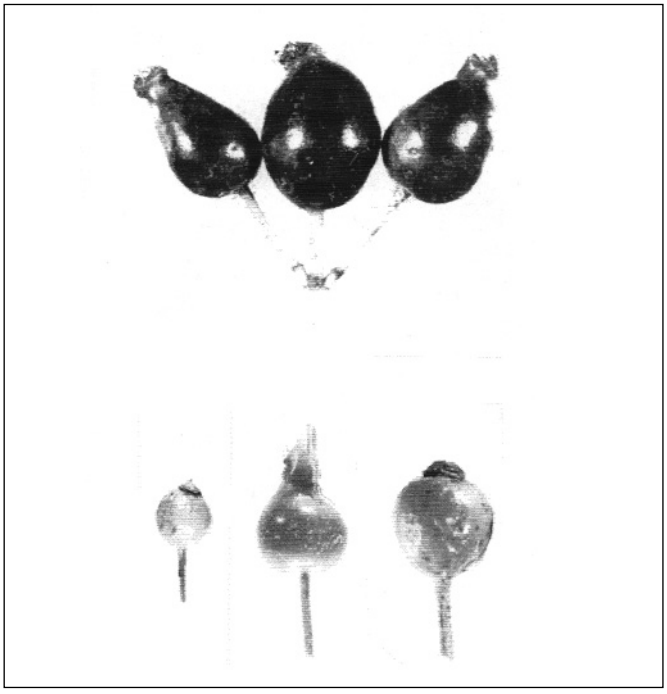


Figure 2—*Rosa*, rose: seeds (achenes) of *R. eglanteria*, sweetbriar rose (**top**); *R. gymnocarpa*, baldhip rose (**second**); *R. multiflora*, multiflora rose (**third**); *R. nutkana*, Nootka rose (**fourth**); and *R. setigera,* prairie rose (**bottom**).

Chalcid wasps of the genus *Megastigmus* (Torymidae) are important predispersal consumers of rose seeds (Mays and Kok 1988; Nalepa 1989). These wasps emerge as adults in spring and oviposit through the hip wall into the ovules of newly developing achenes. Their larvae develop by consuming the seeds over the summer, overwinter as late-instar larvae, pupate in early spring, and emerge as adults in time to repeat the life cycle. Chalcid infestations of 50 to 60% are common (Semeniuk and Stewart 1964; Svejda 1968) and infestations as high as 90% have been reported (Nalepa 1989). Achenes containing chalcid larvae appear normal in size and density and cannot be distinguished by inspection from viable achenes. The native chalcid *M. nigrovariegatus* Ashmead and the light form of the introduced rose seed chalcid *(M. aculeatus* Hoffmeyer) attack most if not all species of rose, whereas the dark form is apparently specific to multiflora rose and is being utilized in biocontrol programs (Mays and Kok 1988; Nalepa 1989).

Seed collection, cleaning, and storage. Rose hips may be collected by hand-stripping or by beating them into containers any time after the seeds are fully ripe. Ripeness is signaled by a change in the color of the hips from green to orange, red, or purple. If not processed right away, the hips

should either be refrigerated or spread out to dry, as otherwise they can overheat and the seeds become damaged. The hips should be soaked in water if they have been allowed to dry prior to processing, then macerated using a macerator or similar device. Small lots can be macerated by rubbing the hips through screens. The achenes may be separated from the pulp by flotation or the material may be dried and the achenes cleaned out using a fanning mill. Achene weights vary from 5 to 17 mg (1.8^{-4} to 6.0^{-4} oz) and they number 59,530 to 185,220/kg (27,000 to 84,000/lb), depending on species and seedlot (table 2). Rose seeds may have a limited storage life, with some loss of viability in laboratory or warehouse dry storage after as little as 2 to 3 years (Crocker and Barton 1931; Gill and Pogge 1974), but they are almost certainly orthodox in storage behavior. Seeds of Woods rose have been reported to retain viability in open warehouse storage for 15 years (Stevens and others 1981). Sealed storage of air-dried seeds at low temperature is recommended (Gill and Pogge 1974).

Germination and seed testing. Rose seeds are normally dormant at maturity and require some form of pretreatment in order to germinate. Release from dormancy is a complex process that may involve changes at the pericarp, testa, and embryo levels. The degree of dormancy and the principal level of dormancy control varies among species, cultivars, seedlots, and even among hips within a single bush. Because the achenes have a thick, hard pericarp and do not swell when placed in water, it is often assumed that they are water-impermeable. Work by Svejda (1972) and others has shown that this is not the case. The achenes do take up water, although the mechanical restriction presented by the pericarp can sometimes prevent full imbibition. Tincker and Wisley (1935) showed, for 10 rose species, that cracking the pericarp alone did not remove dormancy. The importance of including treatments that weaken the pericarp in efforts to remove rose seed dormancy depends on the species and the particular lot. In nursery propagation of the rootstock rose *R. dumetorum* (*R. corymbifera*) 'Laxa', sulfuric acid treatment before warm plus cold stratification improves germination (Roberts and Shardlow 1979). The acid scarification can be eliminated and the warm stratification period shortened if the achenes are warm-stratified with compost activator (Cullum and others 1990). The role of these treatments is apparently to weaken the pericarp along

Figure 3—*Rosa setigera*, prairie rose: longitudinal section through a seed.

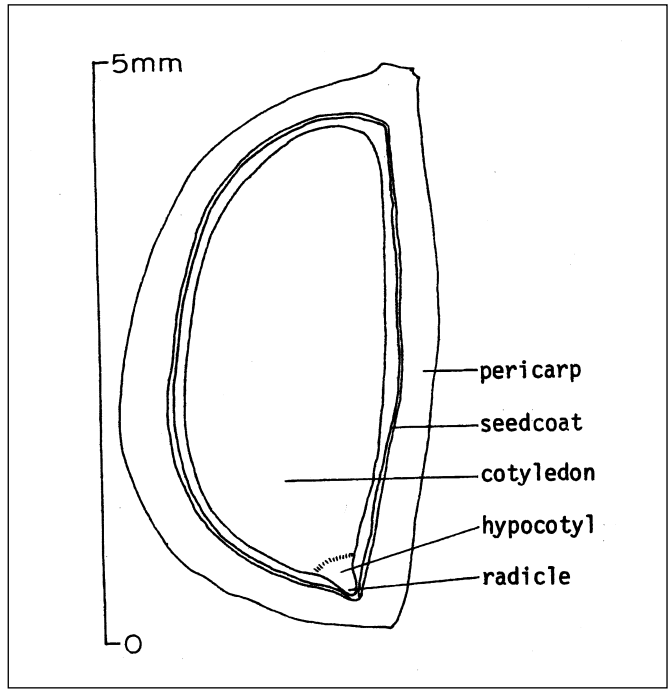


Table 2—*Rosa,* rose: achene weight data

Species	Mean weight		Achenes/weight	
	mg	oz	/kg	/lb
R. acicularis	25–28	0.9–1.0	35,940–40,130	16,300–18,200
R. blanda	9–12	0.3–0.4	81,580–116,860	37,000–53,000
R. californica	4	0.1	224,910	102,000
R. canina	13 (8–17)	0.5 (0.3–0.6)	59,530–119,070	27,000–54,000
R. eglanteria	15	0.5	68,355	31,000
R. gymnocarpa	16	0.6	61,740	28,000
R. multiflora	6–9	0.2–0.3	110,250–180,810	50,000–82,000
R. nutkana	8–15	0.3–0.5	66,150–132,300	30,000–60,000
R. rugosa	6–9	0.2–0.3	114,660–163,170	52,000–74,000
R. setigera	9	0.3	110,250	50,000
R. wichuriana	5	0.2	185,220	84,000
R. woodsii	9 (7–13)	0.3 (0.2–0.5)	77,170–143,320	35,000–65,000

Sources: Belcher (1985), Gill and Pogge (1974), Mirov and Kraebel (1939).

the sutures, whether with acid or through microbial digestion. Responsiveness to warm plus cold stratification can also be increased in *R. dumetorum* 'Laxa' by vacuum-infiltrating the achenes with growth hormones such as gibberellic acid or benzyladenine (Foster and Wright 1983), which suggests that something other than simple mechanical restriction may be involved. Similarly, in the relatively nondormant multiflora rose, the achenes may be induced to germinate without chilling either by treatment with macerating enzymes that weaken pericarp sutures or by leaching with activated charcoal to remove inhibitors from the incubation solution (Yambe and Takeno 1992; Yambe and others 1992). By using macerating enzymes to remove dormancy, these workers were able to demonstrate a phytochrome-mediated light requirement for germination in this species (Yambe and others 1995). Acid scarification (but not mechanical scarification) is reported to substitute for warm pretreatment in the cultivated rose *R. gallica* L. (Svejda 1968).

Chilling is the treatment most often applied to remove rose seed dormancy, and the achenes of most species will germinate eventually if chilled for long enough periods. For some species, periods of cold stratification corresponding to a single winter in the field are sufficient, as in prairie, multiflora, and wichura roses (table 3). Achenes of these species may show increased dormancy if the chilling period is preceded or interrupted by periods of incubation at warmer temperatures (Semeniuk and Stewart 1962; Stewart and Semeniuk 1965). Interruption of chilling with warm incubation resulted in secondary dormancy induction only if the temperature of warm incubation was too high. If the seeds were held below this 'compensating' temperature, no change in dormancy resulted, and the seeds could accumulate the effects of chilling across warm interruptions. Seeds whose chilling requirements had just barely been met germinated best at relatively low incubation temperatures, whereas those that had been in chilling for longer than necessary either eventually germinated in chilling or could germinate at a wide range of temperatures, including those above the compensating temperature. Semeniuk and others (1963) showed that, for prairie rose, the effect of the warm pretreatment

Table 3—*Rosa*, rose: stratification requirements

Species	Warm stratification		Cold stratification		Germination	Incubation
	Days	Temp (°C)	Days	Temp (°C)	temp (°C)	(%)
R. acicularis	—	—	365	5	5	57*
	118	25	90	5	20, 10/20	90*
R. blanda	—	—	90	5	13, 18	7†
	—	—	270	5	13, 18	53†
R. californica	—	—	90	5	—	62
R. canina	60	20	60	4	—	47
	90	20	150	4	—	34
R. eglanteria	—	—	570	5	5	24
	—	—	450	5	5	40
R. gymnocarpa	—	—	90	5	—	43
R. multiflora	—	—	90	5	15–18	45
	—	—	180	5	15–18	60
	—	—	120	5	5	72
R. nutkana	—	—	365	4.5	4.5	65
	—	—	128	4.5	18.5	48
	128	18.5	128	4.5	18.5	72
R. rugosa	—	—	90	3	20–29	32
	60	20	90	3	20–29	60
	—	—	210	4	20	85
R. setigera	—	—	120	5	15–18	90
	—	—	90	4.4	18.3	48
R. wichuriana	—	—	60	5	15–18	75
	—	—	45	5	18.3	76
R. woodsii	—	—	120	3	—	0
	60	20	90	3	—	49

Sources: Crocker and Barton (1931), Densmore and Zasada (1977), Gill and Pogge (1974), McTavish (1986), Mirov and Kraebel (1939), Rowley (1956), Semeniuk and Stewart (1962, 1964, 1966), Stewart and Semeniuk (1965), Svejda (1968), Tillberg (1983), Tinker and Wisley (1935).

* Based on total viable seeds.

† Total viability known to be about 55%; all other percentages based on total seeds, viability unknown.

above the compensating temperature was to induce secondary dormancy at the embryo level. Interestingly, this dormancy could be alleviated only by chilling whole achenes; chilling the embryos did not alleviate their dormancy.

Other species, such as prickly, Nootka, and Woods roses, show much increased germination percentages in response to chilling periods corresponding to a single winter if the chilling period is preceded by a period of warm incubation (table 3). This requirement for warm incubation before chilling would effectively postpone seedling emergence in the field until the second spring after seed production (Densmore and Zasada 1977). The temperature and duration of the warm treatment is sometimes important. In rugosa rose, a warm pretreatment of 60 days at 20 °C before 90 days of chilling at 3 °C increased germination over chilling alone, but longer periods resulted in decreased germination (Svejda 1968). The effect of warm pretreatment on chilling response has been formally documented for only a few rose species, but it is likely that high-viability lots of any species that show minimal germination after 6 months of chilling would be benefitted by a warm pretreatment.

Exactly what changes take place in rose seeds during warm pretreatment or chilling is not known. In many cases, the warm pretreatment seems to have effects at the seed level rather than simply providing an opportunity for pericarp weakening (Densmore and Zasada 1977). Hormonal balance has been implicated in the imposition of dormancy in rose seeds by several workers. Substances leached from dormant rose achenes or obtained from them by grinding have been shown to suppress germination of otherwise non-dormant excised rose embryos (Jackson and Blundell 1963, 1965; Svejda and Poapst 1972). Excised seeds with physically disrupted testas showed much lower germination than embryos with testas removed, suggesting that inhibitors leaching from the testa suppressed germination (Jackson and Blundell 1963). Other workers have shown that, although inhibitory substances are present in dormant achenes and may disappear during dormancy loss, their removal alone is not sufficient to induce germination (Julin-Tegelman 1983; Tillberg 1983).

Variation in dormancy-breaking requirements both within and among lots of any rose species make it difficult to predict effective treatments. One of the causes of this variation has been quite well-studied in cultivated tea roses, and the results probably apply to wild species as well. Von Abrams and Hand (1956) were the first to demonstrate that seeds of a given cultivar matured in the field at warmer temperatures were less dormant (that is, had a shorter chilling requirement) than seeds matured at cooler temperatures. This result has been confirmed by De Vries and Dubois (1987), who also found that warmer maturation temperatures were associated with higher hip set and higher numbers of achenes per hip. Gudin and others (1990) examined the relationship of maturation temperature with developmental rate, endocarp thickness, and dormancy status. They also looked at the effect of the pollen parent in controlled crosses. They found that achenes matured at cooler spring temperatures had slower development, thicker endocarps, and higher levels of dormancy than those matured at warmer summer temperatures. Pollen parent also had an effect on both dormancy and endocarp thickness, presumably through its effect on developmental rate. These workers concluded that the higher dormancy associated with lower maturation temperature was mediated through endocarp thickness, but slow development could also have effects at the testa or embryo level. For example, Jackson and Blundell (1963) reported that excised embryos of rugosa rose grown in Wales were non-dormant, whereas Svejda (1972) and Julin-Tegelman (1983), working with lots grown in Canada and Sweden, reported that excised embryos of this species required 3 to 4 weeks of chilling to become germinable.

Another source of variation in dormancy status for rose achenes is a consequence of the post-maturation environment. Semeniuk and Stewart (1960, 1966) showed for several species that achenes from hips that had overwintered on the bush were more dormant than achenes from those same bushes collected and tested in the fall or stored dry and tested along with the field-overwintered achenes. This effect has also been noted by other workers (Jackson and Blundell 1963; Roberts and Shardlow 1979). It is probably best to collect rose hips soon after they reach maturity and to clean the collections immediately if seed dormancy status is an issue.

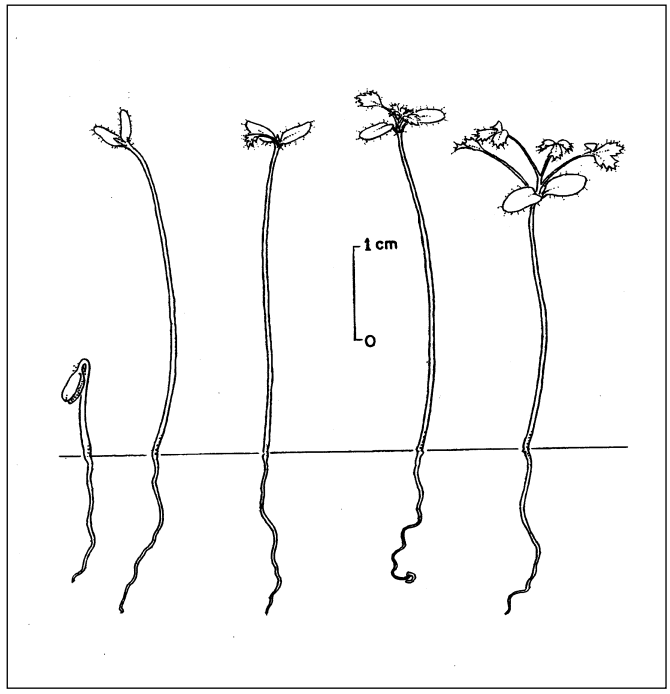
Because of the wide variation in dormancy-breaking requirements within each species, quality evaluations of rose seeds are usually carried out using tetrazolium staining (Gill and Pogge 1974). The achenes are first soaked in water for 24 hours. Firm pressure with a knife on the suture or a tap with a small hammer is used to split open the pericarp. The testa is then scratched or clipped at the cotyledon end and the seed is immersed in 1% tetrazolium chloride for 6 hours at room temperature. The testa is slit along the side and the embryo, which fills the seed cavity, is squeezed or teased out for evaluation (Belcher 1985). The excised embryo method may also be used, although it has little advantage over tetrazolium staining (Gill and Pogge 1974). For purposes of determining fill and chalcid infestation levels, x-radiography is suitable (Belcher 1985).

The preferred method in official testing is also tetrazolium staining (ISTA 1993), although stratification for 28 days at 3 to 5 °C is suggested for multiflora rose (AOSA 1993). For other rose species, the international rules (ISTA 1993) suggest an alternate method of 12 months of stratification, followed by germination in sand at 20 °C for 70 days. Germination is epigeal (figure 4).

Field seeding and nursery practice. Woods rose has been fall-seeded as a part of mixes for revegetation of deer winter ranges in pinyon-juniper and mountain brush communities of the Intermountain West (Plummer and others 1968). It is recommended for areas with more than 300 mm of annual precipitation, and should be broadcast-seeded or drilled with other small-seeded shrubs at rates of 0.5 to 1 kg/ha (0.45 to 0.9 lb/ac). It reportedly is relatively easy to establish from seeds and persists very well after initial establishment. Other native rose species could probably also be direct-seeded successfully in wildland settings.

Planting rose seeds in a nursery setting may be carried out in fall for outdoor cold stratification or in summer for warm followed by cold stratification. Seedlings will emerge the following spring. For spring plantings, the achenes must be appropriately stratified or otherwise pretreated prior to planting. Recommended planting depth is 5 to 10 mm (1/5 to 2/5 in), depending on seed size. Bareroot plants may be produced successfully as 1+0 stock, and container stock can be produced by 3 to 5 months after germination (Landis and Simonich 1984; Shaw 1984). Roses are also readily propagated from cuttings.

Figure 4—*Rosa blanda*, meadow rose: seedling development at 1, 3, 6, 26, and 41 days after germination.



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Arecaceae—Palm family

Roystonea O.F. Cook

royal palm

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Synonyms. *Oreodoxa regia* (H.B.K.) for Cuban royal palm; *Roystonea elata* (Bartr.) F. Harper for Florida royal palm. Note that Little (1979) states that the Cuban royal palm has been united with the Florida royal palm, *R. elata*. However, all articles written before and some articles written after 1979 do not unite these 2 species.

Growth habit, occurrence, and use. There are 2 noteworthy species of *Roystonea* palms grown in the United States and its territories (table 1). Puerto Rico royal palm is native to Puerto Rico and Vieques, St. Croix in the U.S. Virgin Islands, and possibly Tortola in the British Virgin Islands (Francis 1992; Little and Wadsworth 1964). It has possibly naturalized in the British Virgin Islands and in St. Thomas and St. John in the U.S. Virgin Islands (Francis 1992). The smooth gray trunk with its swollen base and the gracefully drooping fronds are a common sight in the island cities. Its ability to withstand a polluted atmosphere and to grow well on either moist, well-drained soils or nutrient-deprived fill dirt enhances its value as a landscape plant. Francis (1992) reports heights of 26.4 m and diameters of 25 to 70 cm in Puerto Rico. Maximum age is 80 to 110 years, and flowering can begin as early as the seventh year. Little and Wadsworth (1964) and Braun (1983) note heights reaching only 18 m and diameters of 30 to 61 cm for the species, whereas LHBH (1977) reports heights reaching at least 15 m. Because of its ability to withstand hurricane-force winds, it is able to become dominant in the forest canopy despite its short stature (Francis 1992). In addition to its importance as an ornamental, the palm's lumber is widely used in rural construction, the leaves as a roof thatch, the flowers as an important nectar source for honey bees (*Apis mellifera* L.), and the fruits as a fat-rich food source for birds (Francis 1992; Little and Wadsworth 1964). The tree apparently has no serious insect pests, but the lumber is susceptible to attack by the dry-wood termite *Cryptotermes brevis* (Walker) (Francis 1992; Little and Wadsworth 1964; Wolcott 1946).

Cuban royal palm is a native of Cuba that is now naturalized in Hawaii (Neal 1965) and in Collier, Dade, and Monroe Counties in Florida (Little 1979; West and Arnold 1952). Like its relative, it too is a widely planted ornamental. There is some variation in reported height growth for the species: Neal (1965) noted heights reaching only 15 to 21 m in Hawaii, but West and Arnold (1952) reported heights of 24 to 34.5 m and diameters up to 61 cm in Florida. LHBH (1977) lists maximum heights of at least 23 m.

Both species grow in the subtropical moist and subtropical wet life zones (Holdridge 1967). Moore (1973) describes other species of royal palm growing on the eastern coast of Mexico, Guatemala, and Honduras, and in Venezuela. Their upper trunks are encased in a green column of leaf sheaths 1 to 3 m long. The pinnate leaves have short petioles, and a sheath and blade 2.4 to 3.7 m long. In Puerto Rico royal palm, the youngest leaflet projects as a spire above the oth-

Table 1— *Roystonea,* royal palm: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***R. borinquena* O.F. Cook**	**Puerto Rico royal palm**	Puerto Rico & Vieques; St. Croix, U.S. Virgin Islands; Tortola, British Virgin Islands
***R. elata* (Bartr.) F. Harper** *R. regia* (H.B.K.) O.F. Cook *Oreodoxa regia* (H.B.K.)	**Cuban royal palm,** Florida royal palm	Cuba; naturalized in S Florida & Hawaii

Sources: Francis (1992), Little (1979), Little and Wadsworth (1964), Neal (1965), West and Arnold (1952).

ers (Little and Wadsworth 1964), and pinnae grow from the rachis in 2 planes (LHBH 1977). Pinnae grow in several planes along the rachis of each Cuban royal palm leaf. Little and Wadsworth (1964) contend that another characteristic distinguishing Puerto Rico royal palm from Cuban royal palm is that the latter lacks the swollen trunk of the former; however, both West and Arnold (1952) and Neal (1965) report the swollen base—and Neal (1965) and Braun (1983) the swollen middle trunk—in Cuban royal palm.

Flowers and fruits. Flowers of both species develop from buds formed at the base of the leaves. Whitish male and female flowers form on the same panicle, with male flowers of each tree opening and falling before the female flowers to prevent self-fertilization. Generally, each female flower forms between 2 male flowers on the panicle (Francis 1992; Little and Wadsworth 1964). The male flowers have 3 small broad sepals and 3 blunt-pointed petals; the females have 3 small broad sepals and a tubular corolla (Little and Wadsworth 1964).

In Puerto Rico royal palm, the twice-branched drooping panicles develop from large narrow buds. The panicles develop inside a dark brown sheath that is 0.9 to 1.5 m long (Francis 1992; Little and Wadsworth 1964). According to LHBH (1977) and Braun (1983), one feature that distinguishes this species from the Cuban royal palm is the presence of scales on the axes bearing the flowers (rachillae). The length of the inflorescence also seems to differ, with that of Puerto Rico royal palm reaching up to 1 m (Little and Wadsworth 1964) and that of Cuban royal palm reaching only 60 to 80 cm (Braun 1983; West and Arnold 1952). The panicle of Puerto Rico royal palm bears stalkless male flowers measuring 13 mm across, smaller female flowers,

Figure 1—*Roystonea borinquena*, Puerto Rico royal palm: fruit.

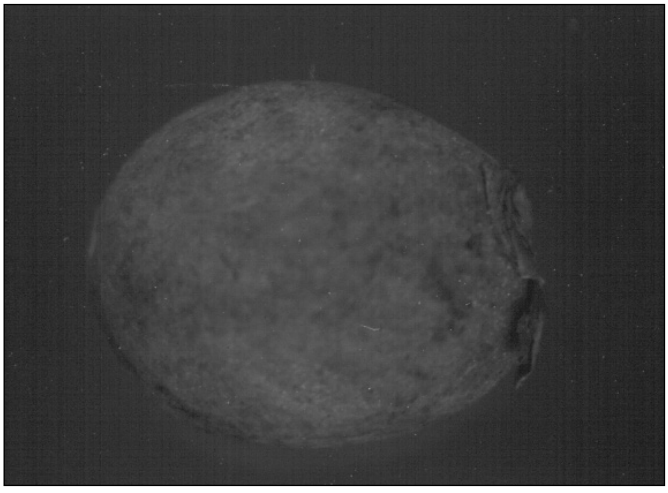
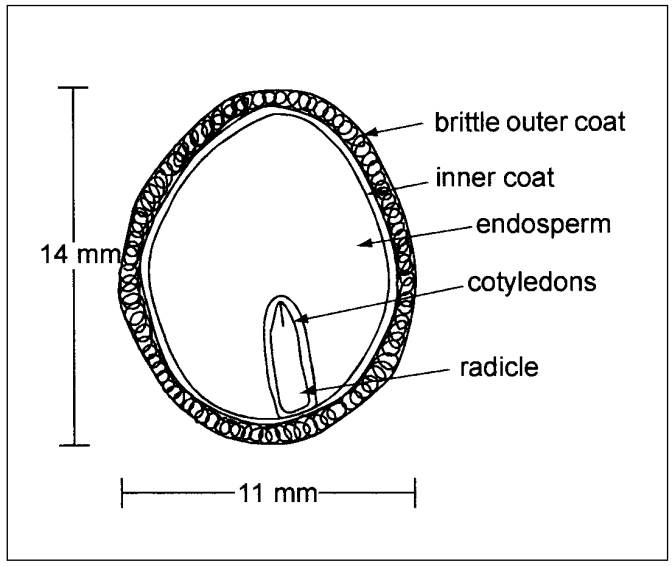


Figure 2—*Roystonea borinquena*, Puerto Rico royal palm: seeds.

Figure 3—*Roystonea borinquena*, Puerto Rico royal palm: longitudinal section through a seed.



and, eventually, greenish yellow fruits that are 13 mm long and about 10 mm in diameter (Little and Wadsworth 1964). Fruits (figure 1) ripen to a brownish purple color and contain 1 light brown elliptic seed that is 8 mm long, hard, and oily (figures 2 and 3). Flowers can occur throughout the year.

The Cuban royal palm bears white, fragrant flowers on a many-branched panicle. Male flowers measure 6 mm across and the violet-purple fruits are smooth, ovate, and measure 13 mm in length. Each fruit bears a single light brown, thin seed that is embedded in brown fibrous flesh (Neal 1965; West and Arnold 1952). The seeds contain oil that may be sold commercially (Moscoso 1945).

Collection, storage, and germination. Francis (1992) reports that, in a survey of 100 Puerto Rico royal palm trees, 35% bore no fruit whereas others produced massive quantities of fruit and seeds (6,000 to 12,000/tree). Seeds are commonly dispersed by water, birds, rodents, and domestic animals but are easily collected for propagation on the ground beneath open-grown trees. Francis and Rodriguez (1993) estimate an average of 2,980 seeds/kg (1,352/lb). Seeds can be stored for 1 to 2 months in sealed containers at room temperature and for longer periods of time under refrigeration. Seeds sown in trays of sand with no pretreatment and kept at ambient temperatures (24 to 30 °C) averaged 80% germination after 14 days. Germination is hypogeous (Francis 1992) and may take up to 2 months after sowing. The radicle emerges first, the shoot about 3 weeks later. Under natural conditions, germination of both species may not begin for 50 to 60 days and may not be completed for an additional 100 days (Braun 1983). Broschat and Donselman (1988) found that soaking Cuban royal palm seeds in 1,000 ppm GA_3 solution for 48 hours slightly increased the rate of germination but also resulted in abnormally elongated seedlings. The best results were obtained if seeds were cleaned and then germinated at temperatures between 30 to 35 °C. They also determined that the best method for long-term storage for Cuban royal palm was to place clean, half-ripe to ripe seeds (air-dried at 80 to 90% relative humidity and treated with a fungicide, for example, thiram) in tightly sealed polyethylene containers held at room temperature (23 °C). The seeds of royal palm may be intermediate in their storage behavior. Ellis and others (1991) put forth the idea that seeds of the Cuban royal palm are not truly orthodox nor recalcitrant. Apparently, drying the seeds to a low moisture content or storing them below
0 °C may result in damage.

Nursery practices. Puerto Rican royal palm seedlings kept in full sunlight averaged 30 cm (12 in) in height after 6 months and 90 cm (36 in) after 15 months; they can be grown to heights of 1.5 m (60 in) or more in 4-liter (1-gal) containers (Francis 1992). Even large trees can be dug up with a backhoe and transplanted. Survival is high as long as they are braced and watered frequently. High mortality results if young trees with only a few basal leaves or short trunks are moved without a protective ball of earth and left without shade and water (Francis 1992).

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Rosaceae—Rose family

Rubus L.

blackberry, raspberry

John C. Zasada and John C. Tappeiner III

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Growth habit, occurrence and use. *Rubus* is a large and complex genus with 12 subgenera. The 2 largest subgenera and those most important in North America are *Eubatus* (blackberries) and *Idaeobatus* (raspberries). There are about 200 species in *Idaeobatus* and perhaps as many as 1,000 or more in *Eubatus* (Fernald 1950; Jennings 1988). There are 3 other subgenera—*Chamaemorus* (cloudberries), *Cyclatis* (Arctic berries), and *Anoplobatus* (flowering raspberries)—that include 1 or more North American species. Blackberries are distinguished from raspberries by the presence of a core or torus that fills the center of the berry when it is removed from the plant; the ripe fruits of raspberries have no core and are shaped like a thimble when removed from the plant. Most species are native to the cool, temperate regions of the Northern Hemisphere; a few are found in the tropics and the Southern Hemisphere (Jennings 1988). The occurrence, general uses, and growth form of some species common in North America are listed in tables 1 and 2.

Although more than 1 species may occur on a given site within a specific geographic area, each species has a specific site-type on which it achieves best development. For example, in Wisconsin there are 6 *Rubus* spp. (Curtis 1959). Allegheny blackberry, trailing raspberry (*R. pubescens* Raf.), and red raspberry are the most widespread and occur together on some sites, but the maximum presence for each is in southern dry, northern wet-mesic, and boreal forests, respectively. The other 3 species—swamp dewberry, blackcap raspberry, and thimbleberry—attain maximum presence in northern dry, southern dry-mesic, and boreal forest types, respectively (Curtis 1959). Most species occur on relatively similar sites throughout their ranges. However, thimbleberry occurs on very different sites over its natural range. For example, in western Oregon it occurs in areas generally free of frost, whereas in Wisconsin and northern Michigan, maximum presence is in areas receiving significant amounts of snow and having prolonged winter air-temperatures well below freezing. Species distribution for various geographic regions can be found in works by Hickman (1993), MacKinnon and others (1992), Meades and Moores (1994), USDA Forest Service (1993), and Viereck and Little (1972), as well as in other regional flora and site classification manuals.

Rubus spp. are a major fruit crop in the North Temperate Zone in Europe and North America; this is their dominant use. Because the primary product is a fruit, there has been a large amount of research focusing on factors limiting fruit production, and thus directly and indirectly seed production. In this chapter, we can only briefly summarize the available literature; a more complete discussion can be found in Ourecky (1978), Moore and Janick (1983), and Jennings (1988). Jennings (1988) provides a very thorough discussion of *Rubus* breeding and cultivation.

The many growth forms of the various species, and the wide range of site conditions on which they occur, make the species useful in reclamation, revegetation, and erosion control projects. Because of the stout spines on some species, dense stands make good barriers to restricted areas as well as providing cover and food for many animal species. Stems and leaves are browsed by a large number of animals. Palatability varies among species and seasons of the year and by site conditions for a species. The fruits are eaten by animals ranging in size from insects to birds to small mammals to the Alaska brown bear (*Ursus middendorfii*). Fruit and bark of the roots and stems have medicinal properties and were used by Native Americans to cure a variety of ailments (Coladonato 1990a&b; Krochmal and others 1969; MacKinnon and others 1992; Meeker and others 1993; Snow and Snow 1988; Tirmenstein 1990a–f). Salmonberry was introduced in Great Britain and has become a weed problem in lowland forests and plantations (Paterson 1996).

Rubus spp. native to North America and some naturalized exotic species can be found at all stages of forest succession (table 1). The most impressive communities in terms

Table 1—*Rubus,* blackberry, raspberry: nomenclature and occurrence

Scientific name & synonym(s)	Common names	Occurrence
SUBGENUS: *Eubatus* (blackberries)		
R. allegheniensis Porter	**Allegheny blackberry,** sow-teat blackberry	New Brunswick to Minnesota, S to Missouri, Arkansas, E to North Carolina
***R. canadensis* L.** *R. millspaughii* Britt. *R. randii* (Bailey) Rydb. *R. amabilis* Blanchard	**smooth blackberry,** thornless blackberry, mountain blackberry	Newfoundland to Ontario & Minnesota, S to Tennessee & Georgia
***R. hispidus* L.** *R. obovalis* Michx. *R. sempervirens* Bigel.	**swamp dewberry**, running blackberry	Prince Edward Island to Ontario, S to Wisconsin, E to Maryland & mtns of North Carolina
***R. laciniatus* Willd.** *R. fruticosus* var. *laciniatus* West. *R. vulgaris* Weihe & Nees	**cutleaf blackberry**, evergreen blackberry	Old-World origin; escaped from cultivation in Massachusetts to Michigan & S; also W of Cascade Mtns from British Columbia to California
***R. procerus* P.J. Müll. & Boulay**	**Himalayan blackberry**	Europe; naturalized from Delaware to Virginia, S British Columbia to California W of Cascade Mtns
***R. ursinus* Cham. & Schlect.** *R. macropetalus* Dougl. ex Hook	**trailing blackberry**, Pacific blackberry	British Columbia to California & Idaho
SUBGENUS: *Idaeobatus* (raspberries)		
***R. idaeus* L.**	**red raspberry**	Present in all states (but SE US, Texas, & Oklahoma) & all provinces of Canada
***R. occidentalis* L.**	**blackcap raspberry**, black raspberry, thimbleberry	New Brunswick to Minnesota, S to Colorado, E to Georgia
***R. spectabilis* Pursh** *R. stenopetalus* Cham.	**salmonberry**	SE Alaska to Idaho & California; becoming naturalized in Great Britain
SUBGENUS: *Chamaemorus* (cloudberry)		
***R. chamaemorus* L.**	**cloudberry**, bake-apple	Alaska, New England, & all Canada
SUBGENUS: *Anoplobatus* (flowering raspberries)		
***R. odoratus* L.** *Rubacer odoratus* (L.) Rydb.	**fragrant thimbleberry,** flowering raspberry, purple-flowering raspberry	S Quebec to Ontario S to Michigan & E to Georgia
***R. parviflorus* Nutt.**	**thimbleberry**, western thimbleberry	SE Alaska to California, New Mexico, Dakotas to N Great Lakes area
SUBGENUS: *Cyclatis* (Arctic berries)		
***R. arcticus* L.**	**nangoon berry,** arctic bramble, wineberry	North America from Alaska to Labrador & Newfoundland; also Minnesota

Sources: Brinkman (1974), Curtis (1959), Fernald (1950), Hickman (1993), Jennings (1988), MacKinnon and others (1992), Viereck and Little (1972).

of sheer abundance and site domination are found after major disturbances such as forest harvesting and fire and on abandoned agricultural land and along roadsides, where light, water, and nutrients are readily available. These stands originate from soil seedbanks, with subsequent clonal development (as in the case of red raspberry in north temperate and boreal forests) or from vegetative reproduction (as in salmonberry in the coastal forests of the Pacific Northwest) (Lautenschlager 1991; Ruth 1970; Tappeiner and others 1991; Whitney 1978, 1982, 1986; Zasada and others 1992, 1994) (figures 1 and 2). Dense stands can prevent or greatly delay establishment of trees and other species (Tappeiner and others 1991; Lautenschlager 1990). Trailing raspberry in north temperate forests, cloudberry and nagoonberry in boreal forests and tundra, and five-leaf bramble (*R. pedatus* Sm.) in coastal forests of the Pacific Northwest and Alaska are perennials with a low or trailing growth form and are present in understory plant communities in mature and old growth forests (Coladonato M 1990a&b; Graber and Thompson 1978; Tappeiner and Alaback 1989; Mackinnon and others 1992; Maxwell 1990; Maxwell and others 1993; Meeker and others 1993; Meidinger and Pojar 1991; Piroznikov 1983; Tirmenstein 1990a–f; Viereck and Little 1972; Viereck and others 1992; Whitney 1978).

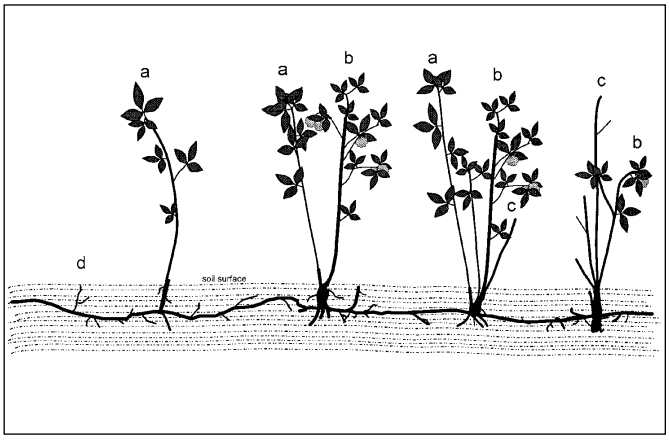
Rubus spp. collectively have one of the most versatile systems for reproduction, colonization, and species maintenance among woody plants. In addition to sexual reproduction, asexual reproduction (apomixis) is well-developed in most species. Asexual reproduction also includes all forms of vegetative reproduction and agamospory (formation of

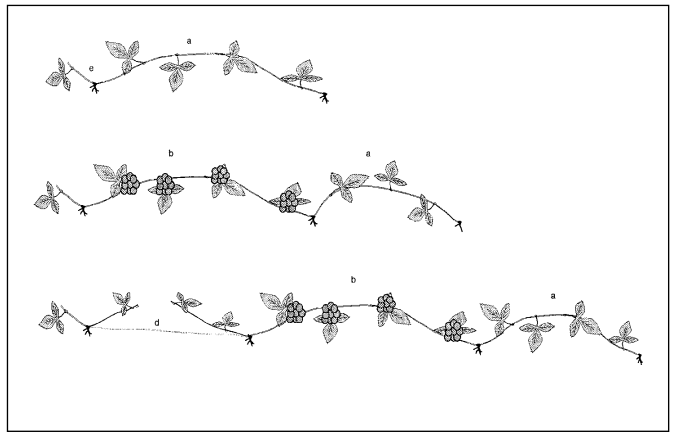
Table 2—*Rubus,* blackberry, raspberry: height or length at maturity and fruit ripeness criteria

Species	Growth habit	Height or length at maturity (m)	Year first cultivated	Fruit ripeness criteria	
				Preripe	Ripe
SUBGENUS: *Eubatus*					
R. allegheniensis	Shrub	1.8	1905	Red, hard	Black-purple
R. canadensis	Shrub	2.8	1727	Red, hard	Black, soft
R. hispidus	Vine	1.8–2.5	—	Red, hard	Reddish purple to black
R. laciniatus	Vine	2.8–4.6	1770	Dull red	Black, sweet, shining
R. procerus	Vine	6.2–9.2	1890	Red, hard	Black, soft
R. ursinus	Vine	4.6–6.2	—	Red, hard	Black, shining, soft
SUBGENUS: *Idaeobatus*					
R. idaeus	Shrub	2.2	—	Pink, hard	Red, sweet
R. occidentalis	Shrub	1.5–2.2	1696	Bright red, hard	Purple-black, soft
R. spectabilis	Shrub	2.8–4.6	1827	Pink, hard	Orange or red, soft
SUBGENUS: *Chamaemorus*					
R. chamaemorus	Perennial forb, below-ground rhizome	0.1–0.2	—	Red, hard	Orange, soft
SUBGENUS: *Anoplobatus*					
R. odoratus	Shrub	1.8	1635	Pink, hard	Red, soft
R. parviflorus	Shrub	0.5–2.5	—	Pink, hard	Red, soft

Sources: Brinkman (1974), Fernald (1950), Jennings (1988), MacKinnon and others (1992), Viereck and Little (1972).

Figure 1—*Rubus*, blackberry, raspberry: general structure of ramets in populations with different growth habits. Diagram (**left**) for species—in this case red raspberry, a biennial cane species—in which clone development occurs in the soil by development of root (for example, red raspberry) or rhizome (for example, salmonberry) systems. Diagram (**right**) for species in which clones expand by layering of above ground stems (for example, trailing raspberry). KEY: **a** = primocanes, **b** = florocanes, **c** = dead canes, **d** = part of stem or root system that is either dead or non-flowering. (Drawings are based on observations by Whitney (1982, 1986), Suzuki (1987, 1989, 1990), and the authors.)





seeds without sexual reproduction) (Grant 1981; Richards 1986). These various modes of reproduction affect the frequency and distribution of genotypes in natural populations; sexually reproducing species have more genotypes than those where apomixis is common (Nybom and Schaal 1990).

Although a detailed description of all aspects of vegetative reproduction is beyond our scope, a general knowledge of these characteristics is necessary to understand spatial and temporal variation in fruit and seed production. There are 3 basic types of clone development, each producing ramets with different life expectancies and flowering potential. These are layering, development from roots or rhizomes, and basal sprouting (figures 1 and 2). The longevity of ramets within a clone varies from 1 growing season to 15 years or more, depending on the species and site conditions (Jennings 1988; Rantala 1976; Ryynanen 1973; Suzuki 1987, 1989, 1990; Tappeiner and others 1991, 2001; Whitney 1978, 1982, 1986; Zasada and others 1992, 1994). Salmonberry has relatively long-lived ramets developing from rhizomes, whereas red raspberry ramets are biennial and produced from a spreading root system. Even in red raspberry, however, ramets may be produced by basal sprouting from one point on the root system, giving that physical position a life-span of more than 2 years (figure 1). Yet another pattern is that of cloudberry, an herbaceous, perennial species with a well-developed rhizome system from which leaves and flowers are produced annually (Jennings 1988; Rantala 1976; Rynnanen 1973). Clonal expansion in other species, for example trailing raspberry and Himalaya blackberry, occurs by layering at the tip or other nodes (figure 1) (Jennings 1988; Whitney 1978, 1986).

Although most species are deciduous, several are evergreen—for example, cutleaf blackberry and Himalayan blackberry, both exotic species that have become naturalized in the western United States. Stems of some species lack spines or bristles whereas others are very well-armed. Dense thickets of Himalayan blackberry and Allegheny blackberry can be very difficult and painful (!) to walk through. The density of spines for a given species can vary with site conditions (Zasada 1996) and the genes controlling spine production are known (Jennings 1988).

Humans have a mixed relationship with *Rubus* spp. On the one hand, they provide a highly edible and nutritious fruit in cultivation and in native plant communities. On the other hand, they can be competitors for growing space, often retarding or (in the extreme case) preventing the establishment of commercially valuable trees. In this case, significant measures are taken to reduce their density and biomass. An understanding of seed production, seed longevity, germination, and seedling establishment is necessary for benefitting from all of the values of these plants while minimizing their development on sites where their presence may prevent achieving management goals.

Geographic races. The genetics of *Rubus* is complex because of the presence of sexual and asexual reproduction. This appears to be particularly true in the *Eubatu*s subgenus, where hybrids with varying degrees of sterility are produced sexually. Sterility is to a significant degree dependent on ploidy levels and these range from 2 to 7x (x = 7). Once produced, these hybrids reproduce asexually by vegetative reproduction and agamospermy. The subgenus *Idaeobatus* is predominantly diploid and sexual reproduction is most common. Crossability among species within both subgenera has been studied (Brainerd and Peitersen 1920; Grant 1981; Jennings 1988; Peitersen 1921).

Flowering and fruiting. Most *Rubus* species are monoecious, but there are dioecious species—for example, cloudberry (Agren and others 1986) and other Arctic spp. (Jennings 1988). Flowering occurs during the spring or summer and rarely in the fall (table 3). Flowers normally have 5 sepals and petals. Size of the flowers varies with subgenus, and *Anoplobatus* flowers generally are the largest.

Pollination by insects is common, and pollinators have been identified for some species—for example, cloudberry (Hippa and Koponen (1976), salmonberry (Barber 1976), and red raspberry (Whitney 1978). *Rubus* flowers produce large quantities of nectar, thus attracting insects (Jennings 1988). In blackberries, self-pollination is often adequate to provide the stimulus necessary for asexual seed production, but a mixture of self-pollination and cross-pollination often occurs. Fertilization occurs about 1 day after pollination (Jennings 1988; Nybom 1985, 1986, 1988; Ourecky 1975).

Pollen can be collected and stored for use at a later time. Maintenance of viability during storage varies with temperature and humidity, and species (Otterbacher and others 1983; Ourecky 1975; Perry and Moore 1985). Perry and Moore (1985) concluded that pollen should be collected every few days to assure that pollen is fresh for crossing and that if pollen must be stored, then subfreezing temperatures (–5 to –40 °C) and low humidities provided the best conditions. Nybom (1985) described methods for assessing pollen viability in subgenus Rubus.

A raspberry or blackberry fruit is an aggregate of small, usually succulent drupelets (figure 3), that each contain a single hard-pitted pyrene or nutlet (figure 4). [The words "nutlet" and "seed" can be used interchangeably, but we

Table 3—*Rubus,* blackberry, raspberry: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
SUBGENUS: *Eubatus*				
R. allegheniensis	—	May–July	Aug–Sept	Aug–Sept
R. canadensis	—	June–July	July–Sept	July–Sept
R. laciniatus	NE US	June–Aug	July–Oct	Sept–Oct
R. hispidus	—	June–early Sept	Mid-Aug–Oct	Aug–Oct
R. procerus	Washington	June–Aug	Aug–Sept	—
R. ursinus	Pacific Coast	June–July	Aug–Sept	Oct–Nov
SUBGENUS: *Idaeobatus*				
R. idaeus	Rangewide	Late May–July	Late June–Oct	July–Oct
R. occidentalis	—	Apr–June	June–Aug	June–Aug
R. spectabilis	Alaska	May–June	June–Aug	June–Aug
	Oregon–Washington	Apr–May	May–July	June–July
SUBGENUS: *Chamaemorus*				
R. chamaemorus	Boreal North America	June–July	July–Aug	Aug–Sept
SUBGENUS: *Anoplobatus*				
R. odoratus	—	June–Sept	July–Sept	July–Sept
R. parviflorus	Pacific Northwest	May–June	June–July	July–Aug

Sources: Barber (1976), Brinkman (1974), Coladonato (1990a), Hippa and Koponen (1976), Viereck and Little (1972), Whitney (1978).

Table 4—*Rubus,* blackberry, raspberry: fruit weight and number of seeds/fruit

Species	Fresh fruit weight (g)	Seeds/fruit Avg	Seeds/fruit Range	Source
R. spectabilis	—	62	28–128	W Oregon
		40	17–65	SE Alaska
R. parviflorus	—	190	127–246	W Oregon
R. idaeus	1.3 (0.8–2.4)	36	28–47	British Columbia & N Alberta
General (N = 8 cv)	—	63	27–103	Norway
Restricted pollination	—	13	—	Norway
Open-pollination	—	32	—	Norway
R. arcticus	0.37–1.09	25	10–35	Finland
R. chamaemorus				
Full light	—	11	7–13	Sweden
Shade	—	14	10–16	Sweden
Hand-pollination	—	11	—	Sweden
Open-pollination	—	8	—	Sweden
No defoliation	—	8	—	Sweden
50% defoliation	—	8	—	Sweden
General	2.5	18	—	Finland
General	—	10	3–18	Alaska
Rubus subgen. *Eubatus*	1.2–6.8	56	27–83	Arkansas

Sources: Ågren (1989), Moore and others (1974a), Nybom (1986), Rantala (1976), Redalen (1977), Ryynänen (1973), Staniforth and Sidhu (1984), Suzuki (1990), Van Adrichem (1972), Willson (1996), Whitney (1978), Zasada (1996).

have used seed.] Each drupelet is a complete fruit, a miniature version of a cherry or plum (which are drupe-type fruits). Each aggregate fruit is the product of 1 flower and the number of drupelets per aggregate varies with species, pollination success, and environmental conditions (figure 3 and table 4). Ripening occurs 30 to 36 days and 40 to 70 days after pollination in raspberries and blackberries, respectively. Drupelets within an aggregate fruit ripen uniformly, but there can be considerable variation among fruits. Three phases of development are recognized: rapid fruit growth following pollination, slow growth as the seed develops, and a final period of rapid growth before the fruit is fully mature (Jennings 1988). In natural populations, the interaction between microclimate and genetic variation in

flowering and fruit ripening usually spreads the timing of aggregate maturation over a period of several weeks or more.

Figure 2—*Rubus*, blackberry, raspberry: red raspberry clone showing distribution of ramets (**circles**) as they were in a clone excavated on an upland site in central Alaska. This plant was about 5-years-old and originated from seed. Red raspberry clones develop by expansion of the root system. Salmonberry, thimbleberry, cloudberry, and other species may develop clones with similar ramet distribution, but clone expansion occurs by the growth of rhizomes. Ramet longevity in these latter species is also different.

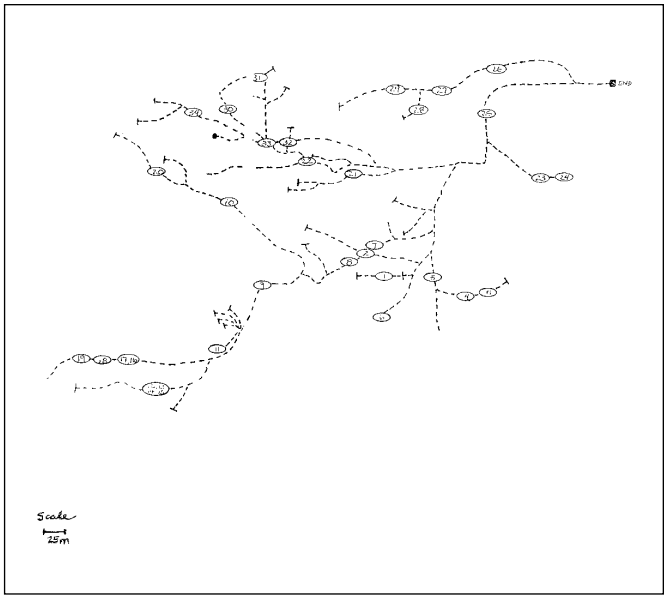
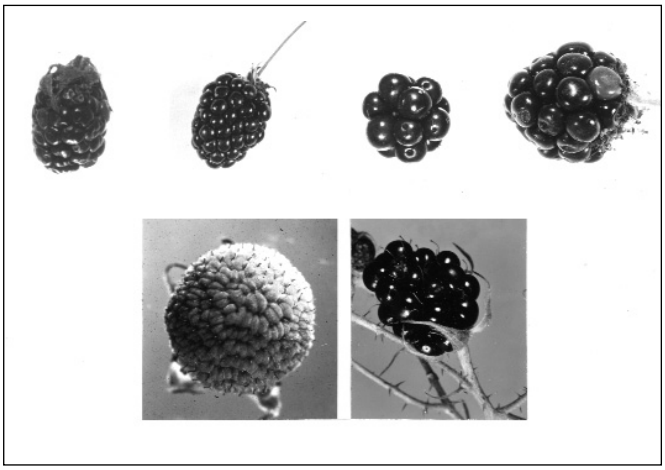


Figure 3—*Rubus*, blackberry, raspberry: fruits of *R. alleghensis*, Allegheny blackberry (**upper far left**); *R. canadensis*, smooth blackberry (**upper middle left**); *R. hispidus*, swamp dewberry (**upper middle right**); *R. procerus*, Himalayan blackberry (**upper far right**); *R. parviflorus*, thimbleberry (**lower left**); and *R. ursinus*, trailing blackberry (**lower right**).



The breeding system in *Rubus* is often described as versatile because seeds are formed sexually and asexually. The relative importance of these two types of seeds varies within and among subgenera and species and may differ within a plant depending on the pollen source. In the *Idaeobatus* group, seeds are normally formed sexually. In *Eubatus* species, seeds are produced sexually and asexually (Jennings 1975; Nybom 1985, 1986, 1988). In most cases, pollen is required to produce seed asexually, but the embryo is not produced by the fusion of male and female gametes (pseudogamy). Parthenogenesis (seed formation without pollination) occurs in some species. Seeds of both sexual and asexual origin may be present in the same fruit (Jennings 1975; Nybom 1985, 1986, 1988).

The abscission layer that develops as the fruit ripens differs in raspberries and blackberries. Fruits may drop from the plant or be removed by various animal species. The number of drupelets or entire aggregates removed at any one time depends on the size of the fruit and the size and eating habits of the animal (Snow and Snow 1988). Seeds are usually deposited with other materials in the feces. Large animals such as the grizzly bear (*Ursus arctos*), may deposit 50,000 to 100,000 salmonberry seeds in a single pile of feces. Seeds may be secondarily consumed or moved from the feces piles by small rodents and birds. Brunner and others (1976), Jordano (1984), Gervais (1996), and Traveset and Willson (1997, 1998) discuss other aspects related to selection and dispersal of *Rubus* seeds by animals. The amount of fruit removed has been found to vary from near 100 to 40% and will depend on habitat type and type of animal feeding on the fruits (Jordano 1982; Snow and Snow 1988). In British Columbia, forest silvicultural practices are being altered in coastal riparian areas to provide for adequate fruit production by salmonberry and other species that are important food sources for grizzly bear (McLennan and Johnson 1993).

Although fruit consumption is often viewed as a loss of seeds, in *Rubus* spp. consumption of seeds is important to the reproductive biology of the plant. Several examples are described below. Dispersal of seeds away from parent plants depends on animals. The distribution of seeds in space and time depends on the size and eating habits of the animal (for example, bears deposit large quantities of seeds in one place, whereas small birds deposit only a few seeds at a time), and the movement habits of the animal following feeding. Seeds that pass through the digestive tract of animals receive varying degrees of scarification (for example, salmonberry seeds in bear feces may have had the fleshy fruit wall completely removed or be little affected, as evidenced by the presence

of complete fruit aggregates) and as a result have potentially different germination patterns. Deposition in feces of differing composition and chemistry affects the germination substrate, and physical and chemical environment available for seedling establishment. If animals are feeding simultaneously on fruits of different plants, fecal deposits may affect competitive and other interactions between *Rubus* spp. and other genera.

Good seedcrops occur nearly every year. Environmental factors affect the amount of flowering and fruit production. In northern Wisconsin, red raspberry crop failures may occur in clearcut areas as a result of severe frosts in mid- to late June, whereas in adjacent areas with 50 to 75% canopy cover, frost may have little effect (Zasada 1996). There are a host of fungi, bacteria, viruses, and insects that affect fruit production in domesticated cultivars and varieties (Jennings 1988; Mason and others 1981; Ourecky 1975).

Flowering occurs on perennial stems (salmonberry), biennial canes (red raspberry), and flower buds produced annually from rhizomes (cloudberry) (figures 1 and 2). Because of the importance of biennial caned species for fruit production, considerable information exists (Jennings 1988; Ourecky 1975; Whitney 1978; Zasada 1996). Briefly, the first-year vegetative canes in red raspberry are termed "primocanes." During the second growing season, they flower ("florocanes"), produce a fruit crop, and die. Within a natural stand of red raspberry, primocanes usually outnumber florocanes by a factor of 2 or more (Whitney 1978, 1982, 1986; Zasada 1996). Primocanes do produce flowers on occasion, and this trait has been developed into a fall-producing cultivar (Prive and others 1993a&b).

The rate of node production is about constant in primocanes. Node density, and thus density of potential flower buds, is determined by the rate of internode elongation. Flower bud initiation occurs at about the time that canes become dormant and may continue in the spring after a period of dormancy. Nodes can have primary, secondary, and tertiary flower buds; the secondary and tertiary buds develop if the primary bud is damaged or dies (Hudson 1959; Jennings 1988).

In florocanes, there is little or no height growth. Fruiting laterals develop from the nodes. The number and distribution of fruiting laterals is dependent on genotype, node position, and microclimate. Fruit production per lateral may vary from 10 to 100 in domestic cultivars of raspberry and blackberry (Jennings 1988).

Primocanes and florocanes may compete for resources, and fruiting may be reduced on individual florocanes. Similarly, in the absence of florocanes more primocanes are produced. Clones vary considerably in the effects of this interaction on fruiting (Crandall and others 1974; Waister and others 1977). Vegetative characteristics of salmonberry and red raspberry stems are affected by light and other resource availability in forest stands where they commonly grow (Lautenschlager 1990; Tappeiner and others 1991; Zasada 1996).

Collection of fruits. During the maturation process, fruits change from green to their characteristic color (table 2). Although all species have a characteristic fruit color when ripe, there can be variation among genotypes. For example, in salmonberry, there are 2 mature fruit color polymorphisms—red and orange. The orange form is generally more common in the southern part (that is, Oregon) of the range, and the red form in the northern part (southeastern Alaska) of the range, although clones with red and orange fruits intermingle in both areas (Gervais 1996). The red fruit form passes through an orange stage on the path to maturation (Gervais 1996; Traveset and Willson 1998), but at maturity there is a distinct and easily observed difference in color. The amount of variation in fruit color may also vary among sites and geographic areas. Thus, to use fruit color as an index of maturity, one needs to know the color variation that occurs in a species. Although fruits are usually collected when they are fully ripe, Ourecky (1975) suggested that fully developed green fruits contain well-developed seeds and could be picked in that condition. Another index of ripeness is the ease with which fruits can be picked as a result of the development of the abscission layer. Fruits in natural populations will be available for picking over a period of several weeks to a months because of the variation in maturation due to the effect of genotype and microclimate on flowering and fruit development. Because of the importance of fruits as animal food, it may be important to closely monitor an area in order to collect adequate quantities before animals take them (Snow and Snow 1988). For salmonberry, it has been shown that the red-fruited form may be preferred to the orange-fruited type in some cases and may vary by species of birds and mammals (Traveset and Willson 1998).

Rubus fruits are usually picked by hand, but machines have been developed to mechanically harvest commercial crops (Ourecky 1975). They can also be picked after they have dropped from the plant. The number of seeds per fruit varies considerably among species (table 4). Within a species, seeds per fruit may also vary by a factor of 2 or more depending on microclimate, pollination, and genetic variability. Seed weight also varies considerably among and within species (table 4). For example, in *R. ulmifolius*

Table 5—*Rubus*, blackberry, raspberry: seed yield data

Species	Place collected	Seed wt/fruit wt g/kg	Seed wt/fruit wt lb/100 lb	Seeds (x1,000)/weight Range /kg	Range /lb	Average /kg	Average /lb
SUBGENUS: *Eubatus*							
R. allegheniensis	—	40	4	370–724	168–329	574	262
R. canadensis	—	40	4	458–495	208–225	476	216
R. hispidus		—	—	282–513	128–233	408	185
R. laciniatus	Washington	7	0.7	—	—	301	137
R. procerus	—	—	—	—	—	323	147
R. ursinus	Washington	58	5.8	—	—	845	384
Rubus (general European)*	Sweden	—	—	359–869	163–395	480	219
SUBGENUS: *Idaeobatus*							
R. idaeus	Minnesota	30	3	667–845	303–384	722	328
	British Columbia/Alberta	46	4.6	469–794	213–397	632	288
R. occidentalis	Minnesota	30–80	3-8	629–845	286–384	735	334
R. spectabilis	Oregon 1	—	—	251–528	115–240	354	162
	Oregon 2	—	—	189–321	87–146	240	109
	Oregon 3	—	—	270–45	123–157	316	144
	Oregon 4	—	—	216–298	98–135	265	120
	Alaska	—	—	—	—	315	143
SUBGENUS: *Chamaemorus*							
R. chamaemorus	Sweden/Finland	59	(5.9)	—	—	122	56
	Alaska	—	—	80–101	37–45	90	40
SUBGENUS: *Anoplobatus*							
R. odoratus	Pennsylvania	—	—	—	—	1,085	493
R. parviflorus	Oregon	—	—	357–806	162–367	611	278
	Washington	—	—	719–1201	327–546	20	418
SUBGENUS: *Cyclatis*							
R. arcticus	Sweden/Finland	76	(7.6)	—	—	980	446

Sources: Brinkman (1974), Lautenschlager (1990), Nybom (1980), Rantala (1976), Zasada (1996).

* Seeds of 20 species in Sweden.

Schott., the individual seed weight with the highest frequency was 2 to 2.5 mg, whereas weights ranged from 1 to 5 mg (Jordano 1984).

Extraction and storage of seeds. Seeds may be extracted by macerating the fruits in water then floating off or screening out the pulp and empty seeds (Brinkman 1974). Because of the high strength of the endocarp (figure 5), maceration does not damage the seeds (Rose 1919). Small lots of fruit may be covered with water and macerated in a blender until the pulp and fiber are separated (Morrow and others 1954). Additional water is then added, the sound seeds allowed to settle, and the pulp and empty seeds decanted. Several changes of water will yield cleaner seeds. Seed yield data are presented in tables 4 and 5.

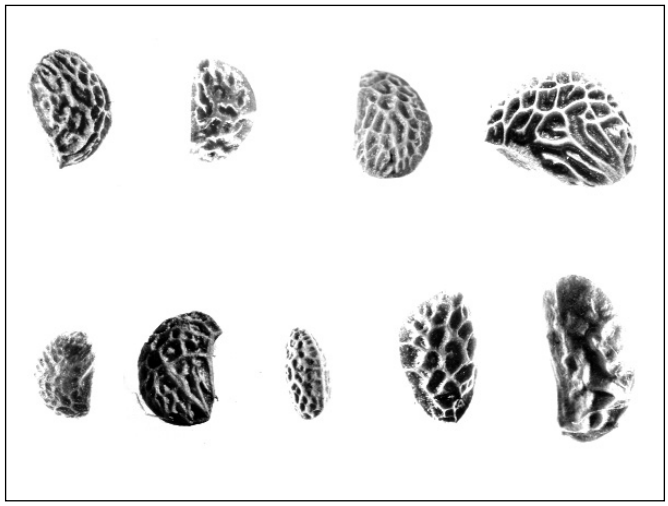
The cleaned seeds should be dried before storage. Clark and Moore (1993) reported that seeds from raspberry cultivars germinated well after storage for 26 years at 4 to 5 °C.

Rubus seeds can be present in the forest floor of many forest types in North America (Barber 1976; Graber and Thompson 1978; Granstrom 1982; Maxwell 1990; McGee 1988; Moore and Wein 1977; Peterson and Carson 1996; Piroznikov 1983; Quick 1956; Ruth 1970; Whitney 1978; Yokohama and Suzuki 1986; Zasada 1996) long after the species has disappeared from the site. The longevity of seeds in the forest floor is believed to be on the order of decades to a century or more, indicating that seeds can be stored for long periods of times under seasonally alternating temperature and moisture conditions.

Understanding longevity of seeds in the forest floor is complicated for at least 2 reasons. First, Graber and Thompson (1978) found that 6,000 to 7,000 viable *Rubus* seeds/ha (2,400 to 2,800/ac) were deposited annually in northern hardwood forests in New England, making it difficult to determine the age of the seed population. Second, few controlled experiments have been conducted to demonstrate seed longevity in the soil; Granstom (1987) reported that artificially buried seeds remain viable for at least 5 years.

Germination. Raspberry and blackberry seeds are described as having deep dormancy caused by one or more of the following: impermeable seedcoat (endocarp), mechan-

Figure 4—*Rubus*, blackberry, raspberry: nutlets (seeds) of *R. alleghensis*, Allegheny blackberry (**upper far left**); *R. canadensis*, smooth blackberry (**upper middle left**); *R. hispidus*, swamp dewberry (**upper middle right**); *R. lacinatus*, cutleaf blackberry (**upper far right**); *R. ursinus*, trailing blackberry (**lower far left**); *R. occidentalis*, blackcap raspberry (**lower middle left**); *R. odoratus*, fragrant thimbleberry (**lower center**); *R. procerus*, Himalayan blackberry (**lower middle right**); *R. spectabilis*, salmonberry (**lower far right)**.

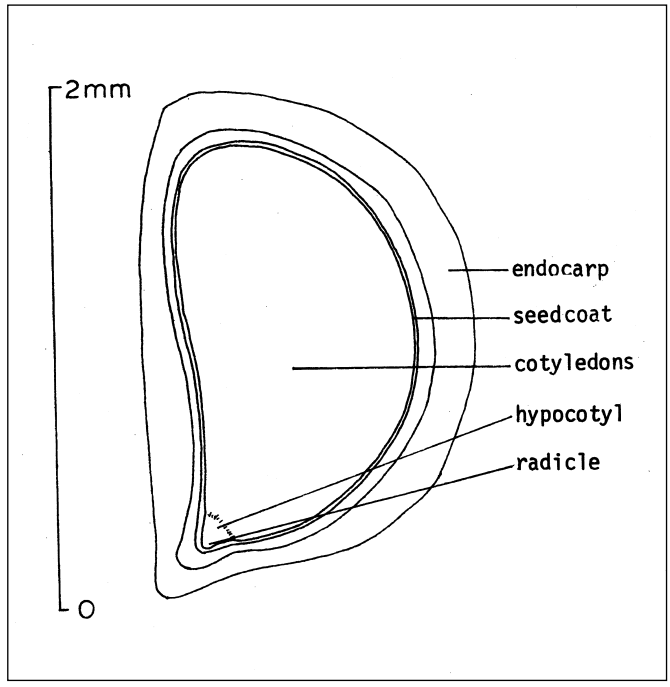


ical resistance of the seedcoat to growth, chemical inhibitors in the seedcoat and endocarp and the presence of a dormant embryo (Jennings 1988; Nybom 1980; Ourecky 1975). Under natural conditions, dormancy is broken by a combination of factors, including exposure to freeze-thaw cycles, diurnal and annual changes in temperature, cycles of wetting and drying of the seedcoat, passage thru the digestive system of animals, and activity of fungi and insects on the seedcoat. A given cohort of seeds germinates over a period of 2 to 3 or more years under field conditions, with some seeds apparently lying dormant for decades. The germination pattern will vary by species, microclimate, and condition of seeds when dispersed, among other factors (Barnes 1985; Dale and Jarvis 1983; Krefting and Roe 1949; Maxwell 1990; Nybom 1980; Tappeiner and Zasada 1993). It is commonly believed that passage through the digestive tract of an animal speeds germination. However, the importance of this treatment appears to be dependent on the species and the type of animal passing the seeds (Barber 1976; Lautenschlager 1990).

There may be an interaction between the way in which seeds are handled and dried and the type of dormancy seeds exhibit. For example, Dale and Jarvis (1983) indicate that raspberry seeds that do not undergo a prolonged period of drying germinate better that those that are dried. Rantala (1976), however, indicates that some species may germinate better after prolonged drying. The point is that dormancy may be manageable to some degree for some species during the handling process. Depth of dormancy may also be affected by the temperature at which fruits develop (Dale and Jarvis 1983).

The list of treatments used to improve overall germination and rate of germination is comprehensive to say the least. These have included the following by themselves or in various combinations: chemical scarification with sulfuric acid or sodium hypochlorite (either used alone or both sequentially); mechanical scarification by removing part of the endocarp, seedcoat, and endosperm; hormone treatment (gibberellic acid); warm temperature incubation; immersion in boiling water; cold stratification; incubation in oxygenated water; treatment with nitrate; and recovery of seeds from feces of various animals (Barber 1976, 1978; Brinkman 1974; Campbell and others 1988; Dale and Jarvis 1983; Galletta and others 1989; Jennings 1988; Ke and others 1985; Lautenschlager 1990; Lundergan and Carlisi 1984; Maxwell 1990; Moore and others 1974a&b; Nesme 1985; Nybom 1980; Ourecky 1975; Rantala 1976; Rose 1919; Scott and Ink 1957; Traveset and Willson 1998; Warr and others 1979). In spite of the efforts to improve the uniformity of germination, results are highly variable within and among species and no standard method seems to be available for germination of species in the genus.

Figure 5—*Rubus canadensis*, smooth blackberry: longitudinal section of a seed.



Some form of sulfuric acid treatment followed by cold stratification is a common treatment prior to germination. Sulfuric acid significantly changes the structure and thickness of the endocarp and the weight of the seed (Lautenschlager 1990; Moore and others 1974b). Some important considerations for acid treatment mentioned in the above references are listed below:

- The seed surface should be dry, otherwise the reaction between water and acid will result in temperatures lethal to the embryo.
- Raspberry seeds should be treated for no more than 15 to 20 minutes, whereas blackberry seeds require up to several hours. Seeds should be stirred frequently during treatment.
- It may be necessary to immerse the container with seeds and acid in an ice bath to keep the temperature at safe levels for the embryo.
- Seeds should be thoroughly washed following treatment to remove acid. Although some seeds will germinate with acid treatment alone (which essentially removes the seedcoat as a barrier) (Nesme 1985), 60 to 120 days of cold stratification seems to improve germination for some species.

Various concentrations of sodium or calcium hypochlorite can be used as an alternative to sulfuric acid (Campbell and others 1988; Galletta and others 1989). Sometimes calcium hydroxide is used in combination with the hypochlorite. Hypochlorites also significantly alter the endocarp but

Table 6—*Rubus*, blackberry, raspberry: germination results

Species or variety & source	Germination temp (°C)	Total germination (%)	Time to 50% germination
*R. idaeus**	10	69 (18–94)	28 days
	20	93 (84–96)	6 days
	30	60 (40–88)	33 days
R. idaeus† 'Glen Cova'			
No stratification	—	48	—
Stratification	—	53	—
R. idaeus‡			
Bear feces			
Acid scarification	21	6	—
No scarification	21	0	—
Coyote feces			
Acid scarification	21	10	—
No scarification	21	0	—
Fresh seed			
Acid scarification	21	8	—
No scar.ification	21	0	—
R. spectabilis§			
Fresh seeds			
Acid scarification	21–28	0	—
Scarification & 2-mon stratification	21–28	0	—
Scarification & 4-mon stratification	21–28	62	—
Scarification & 6-mon stratification	21–28	81	—
Bird feces			
No stratification	21–28	0	—
4-mon stratification	21–28	25	—
6-mon stratification	21–28	73	—
Coyote feces			
6-mon stratification	21–28	6	—
R. chamemorus‖			
3–5-mon stratification	Variable	<1	—
6–9-mon stratification	Variable	3–10	—
10–13-mon stratification	Variable	30–31	—

Sources: Barber (1996), Dale and Jarvis (1983), Lautenschlager (1990), Lundergan and Carlisr (1984); Moore and others (1974); Nesme (1985), Rantala (1976).

* Seeds were treated as follows: surface sterilized in 1% sodium hypochlorite (NaClO) for 10 minutes, nicked to expose radicle; soaked for 3 min in 1% NaClO, and incubated in the dark for 1 year.

† Seeds were extracted and air-dried, treated for 20 minutes with sulfuric acid and 7 days with calcium hypochlorite; stratified at 5 °C or unstratified. Fruits were collected 43 days after anthesis. Seeds were from fruits collected earlier or later differed in germination response.

‡ Seeds were from natural populations in Maine; they were stratified for 2 to 6 months after acid treatment; tests were conducted for 30 days.

§ Fresh seeds from Washington state populations; stratified at 2 to 5 °C.

‖ Seeds stratified at 1 °C and germinated monthly in a mist propagation chamber.

do not carbonize it as does sulfuric acid. Duration of the treatment is several days as opposed to minutes or several hours for sulfuric acid. Solutions of 12 to 15% appeared to work best for raspberry but were not as effective with blackberries (Galletta and others 1989). Seeds should be thoroughly washed after treatment.

Plant breeders often excise embryos or "nick" the endocarp of individual seeds to improve germination when seed supply is limited or when seeds from particularly valuable controlled crosses are being grown (Ke and others 1985; Nesme 1985; Warr and others 1979). This is generally not possible for large seedlots.

The effectiveness of the cold stratification treatment depends on the stratification temperature and the length of stratification (Rantala 1976). The optimum temperature may differ among species. Cloudberry, for example, seems to germinate better following stratification at 1 °C than at 4 °C. Rantala (1976) and Barber (1976) have demonstrated the value of stratifying seeds for 6 months or more for cloudberry and salmonberry, respectively.

Seed quality can be can be estimated from cutting tests and x-radiography (Nesme 1985). Seeds that sink when placed in water contained what appeared to be viable embryos, and a general separation of high from low-quality seeds is possible in this way (Lautenschlager 1990; Nybom 1980).

Germination following the above described treatments that attempt to alter the condition of the seedcoat and eliminate inhibitors or other conditions by cold stratification is highly variable among species and within species. In table 6 are listed a few examples of the variation in germination that may be encountered in seeds collected from natural populations and from varieties produced for fruit production. Generally, treatments that mechanically remove the endocarp improve germination above the values in table 6. Rate of germination is generally slow; in tests conducted out-of-doors and allowed to run for a year or more, germination will commonly occur over at least 1 or 2 growing seasons for many species (Barnes 1985; Nybom 1980; Tappeiner and Zasada 1993; Traveset and Willson 1997, 1998). Graber and Thompson (1978) concluded that seeds are most likely to germinate after being in the soil at least 5 years. It seems safe to conclude that many of the tests that are conducted do not stratify seeds long enough to remove the impediment to germination. Brinkman (1974) provides general germination information for several other species.

The examples shown in table 6 were generally conducted in a constant temperature environment. For some species, diurnally fluctuating temperatures result in better germination than constant temperatures (Campbell and others 1988).

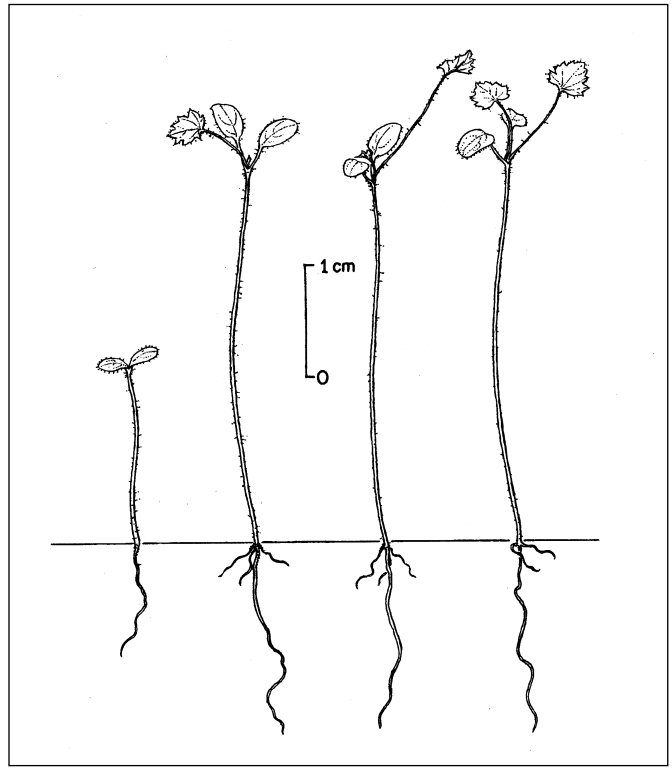
Light appears to improve germination in many species (Nybom 1980; Ourecky 1975). However, some species (for example, red raspberry, cloudberry, and salmonberry) do not require light to germinate (Warr and others 1979; Lautenschlager 1990).

Germination is epigeal (figure 6). Cotyledons are normally 2, but Nybom (1980) observed that seedlings with more than 2 cotyledons were fairly common and that treatments increasing germination increased cotyledon number. Polyembryony has been reported in cloudberry (Rantala 1976).

Nursery practice. The best germination usually follows sowing of scarified seeds in the late summer or early fall (Wroblowna 1949), although spring-sowing scarified and stratified seeds is also recommended (Heit 1967). Seeds should be sown in drills and covered with 3 to 5 mm ($^1/_8$ to $^3/_8$ in) of soil (Brinkman 1974). Mulching over winter reduces drying and soil-freezing (Hill and Beattie 1956).

Barnes (1985) recommends the following schedule for production of *R. deliciosus* Torr. from seed: gather seeds in late summer, clean and store them at near freezing; sow from October–December in unfertilized sand beds and cover with sand; wet down and firm soil over seeds; once

Figure 6—*Rubus occidentalis*, blackcap raspberry: seedling development at 1, 13, 22, and 36 days after germination.



seeds have germinated and reached a height of 5 to 7 cm (2 to 3 in) transplant to deep 15 cm (6 in) pots to promote both lateral and vertical root development. Fall-sowing produces better results than spring-sowing of stratified seeds. Seeds germinate over several growing seasons and the beds are usually not resown for at least 2 seasons in order to get better return of seedlings from sown seeds.

Ourecky (1975) found that full-sized green fruits can be collected cleaned, treated, and sown. Moist vermiculite and finely shredded sphagnum are both good planting media. Seeds should not be covered with more than 2 to 8 mm ($^1/_{10}$ to $^3/_{10}$ in) of the medium. As soon as the second true leaf appears (figure 6), seedlings can be transplanted to individual containers.

Vegetative propagation—by tip-layering, rooting suckers, and crown division and by taking leaf-bud and stem cuttings—is used to increase availability of desirable varieties (Ourecky 1975). Salmonberry can be established in coastal Oregon under field conditions with little post-planting care from crowns or rhizome cuttings if planted in the winter during the wet season (Maxwell 1990).

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Arecaceae—Palm family

Sabal Adans.

palmetto

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Growth habits, occurrence, and use. Palmettos—genus *Sabal*—are native to the Western Hemisphere and are distributed from the Bermuda Islands and the South Atlantic and Gulf States through the West Indies to Venezuela and Mexico (Sargent 1965). Five species inhabit the southeastern United States, Puerto Rico, and the Virgin Islands (table 1). Cabbage palmetto has tree form and attains a height at maturity of 12 to 27 m (Sargent 1965); it is found from North Carolina to south Florida, in low flatwoods and on offshore islands in the north, and becoming common throughout the lower part of the Florida peninsula. Cabbage palmetto has few commercial uses but is used extensively by rural residents for a variety of purposes—the trunk for timber, the bud for food, and the leaves for craft weaving. Cabbage palmetto has been planted widely as an ornamental. It has no forage value and only limited usefulness for wildlife. Scrub palmetto has a low, spreading form and attains a height at maturity of about 1.3 m (Bailey 1939; McCurrach 1960). It has a restricted range in the dry pinelands and scrub of central Florida (Small 1933). The bud is eaten as a salad vegetable, and the fruits are eaten by animals and birds.

Flowering and fruiting. The perfect white flowers of cabbage palmetto measure about 6 mm in diameter and are borne in drooping clusters 1.3 to 1.8 m long from June to August, depending upon latitude (Sargent 1965; Snyder 1952; West and Arnold 1947). The flowers are pollinated by insects (Knuth 1906). The fruit is a berry, subglobose or slightly obovoid, about 8 mm in diameter. The fruit is dark brown to black and ripens in late autumn or winter (Bailey 1939). Each fruit contains 1 light brown seed about 6 mm in diameter (Sargent 1965). Fruits and seeds of scrub palmetto are slightly larger (figure 1). Embryos are minute (figure 2).

Collection, cleaning, and storage. The fruits of these palms may be picked from the plants when ripe, and the

Table 1—*Sabal,* palmetto: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***Sabal causiarum* (O.F. Cook) Becc.**	**Puerto Rico palmetto,** Puerto Rico hat palm	Puerto Rico & the Virgin Islands
***Sabal etonia* Swingle ex Nash** *S. miamiensis* Zona	**scrub palmetto,** etonia palmetto	Florida
***Sabal mexicana* Mart.** *S. exul* (O.F. Cook) Bailey *S. texana* (O.F. Cook) Becc. *Inodes exul* O.F. Cook; *Inodes texana* O.F. Cook	**Rio Grande palmetto** Mexican palmetto, Oaxaca palmetto	Texas
***Sabal minor* (Jacq.) Pers.** *S. deeringiana* Small *S. glabra* Sarg., non P. Mill. *S. louisiana* (Darby) Bomhard *Corypha minor* Jacq.	**dwarf palmetto,** Sonoran palmetto	Florida and Louisiana, N to North Carolina, W to Oklahoma, Arkansas, & Texas
***Sabal palmetto* (Walt.) Lodd. ex J.A. & J.H. Schultes** *S. jamesiana* Small *Inodes schwarzii* O.F. Cook *Corypha palmetto* Walt.	**cabbage palmetto,** cabbage palm, palmetto	Florida, Georgia to Louisiana, North Carolina, & South Carolina

Source: Wasson (2001).

Figure 1—*Sabal*, palmetto: fruits (**left**) and seeds (**right**) of *S. etonia*, scrub palmetto (**top**) and *S. palmetto*, cabbage palmetto (**bottom**).

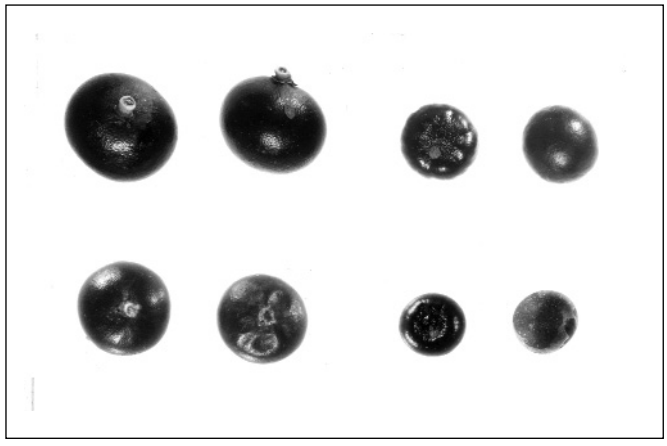
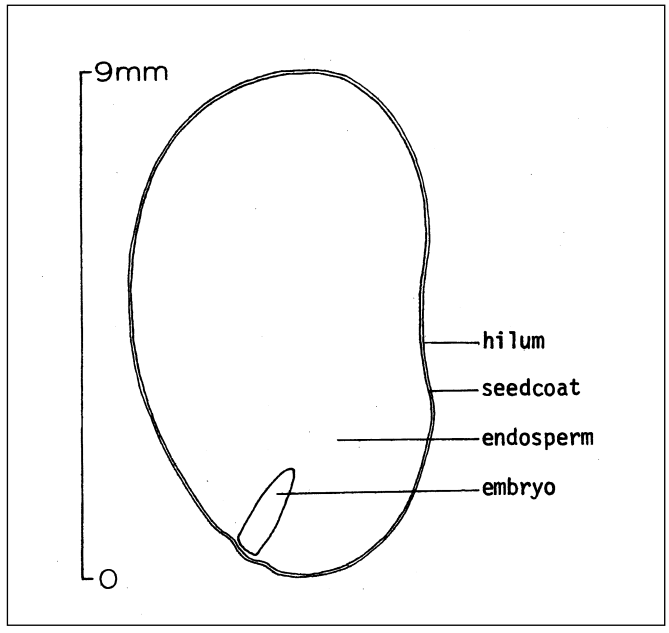


Figure 2—*Sabal etonia*, scrub palmetto: longitudinal section through a seed.



seeds separated from the pulp by running them through a macerator or rubbing them on hardware cloth. The purity of seed samples was 100% for seedlots used to determine seed weight (table 2) (Olson and Barnes 1974). Palmetto seeds are orthodox in storage behavior. Cabbage palmetto seeds have been stored successfully at 5 °C for up to 8 weeks (Carpenter 1987). Seeds of Rio Grande palmetto were found to tolerate desiccation, a prerequisite to dry, cold storage (Dickie and others 1993). Seeds of seamberry—*S. parviflora* Becc.—have survived dehydration to 12% moisture content and submersion in liquid nitrogen, indicating that this species, and possibly others in the genus, could be stored either under conventional freezer storage or liquid nitrogen (Becwar and others 1983).

Germination tests. The seeds of palmetto require no pretreatment to break dormancy, but 30 days of stratification in moist sand at 4 °C increases the speed of germination. For example, the average germinative capacity of 4 samples of fresh, unstratified cabbage palmetto seeds was 91% in 120 days (Olson and Barnes 1974). Four samples of stratified seeds had an average germinative capacity nearly as high (89%) in half the time (Olson and Barnes 1974). The tests were carried out at an alternating night–day temperature regime of 20 to 30 °C with 8 hours of daylight. Germination tests were conducted for cabbage palmetto in south Florida on seeds that had the micropyle caps removed and on untreated seeds (Olson and Barnes 1974). The germination percentage was 84 to 95% in 4 days with the micropyle cap removed and only 36% in 100 days for untreated seeds. Carpenter (1987) germinated cabbage palmetto at a constant soil temperature of 30 °C in a greenhouse and found that 7 days of water soaking at 35 °C boosted germination significantly, from 65 to 85%. Speed of germination was also improved by this water soaking. Unstratified seeds of scrub palmetto averaged 72% germination in 82 days at a constant temperature of 22 °C, and only 64% in the same period with alternating 20/30 °C for 16 and 8 hours, respectively (Olson and Barnes 1974). Carpenter (1988) found, in a series of constant-temperature studies of scrub palmetto, that 30 °C was optimal for both germination percentage and speed of germination. This optimal temperature is substantially higher than that reported by Olson and Barnes (1974). The benefit in speed of germination from prechilling seeds reported by the latter authors might be explained by the fact that they reported on germination at about 7 degrees below the optimum. Slow germination has been reported for Puerto Rico, Rio Grande, and dwarf palmettos. Germination of untreated seeds of the first 2 species took from 6 to 18 weeks for completion, whereas dwarf palmetto needed 7 to 24 months of moist prechill before germination at 25 °C (Ellis and others 1985).

Nursery practice. Seeds should be planted 13 to 25 mm ($^1/_2$ to 1 in) deep in light textured soil, soon after collection (Jordann 1949). The seeds should not be permitted to dry.

Table 2—*Sabal,* palmetto: seed data

Species	Cleaned seeds/weight: Range /kg	Range /lb	Average /kg	Average /lb	Samples	Moisture content (%)
S. etonia	—	—	1,280	581	8	9.8
S. palmetto	758–763	1,668–1,682	1,675	7,600	2	19.3

Sources: Olson and Barnes (1974).

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Salicaceae—Willow family

Salix L.

willow

John C. Zasada, D.A. Douglas, and W. Buechler

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Growth habit, occurrence and use. The willow genus—*Salix*—includes 350 to 400 species (Argus 1996). The majority are in the Northern Hemisphere, from arctic through temperate latitudes (table 1). Three species are native south of Mexico (Dorn 1976) and 67 found in the contiguous 48 United States, where tree and shrub forms predominate. The 39 species found in Alaska are mostly tall to medium shrubs; prostrate growth forms are mostly on the tundra. Shrub and prostrate shrub forms constitute a dominant portion of the vegetation of the Circumpolar Arctic (defined as north of the treeline) and include about 29 species in the North American Arctic (Argus 1996). These tundra species are segregated into a variety of habitats (Argus 1973; Viereck and Little 1972). General information on the genus worldwide can be found in Warren-Wren (1972) and Newsholme (1992); the taxonomy and distribution of American species is covered by Argus (1973, 1986, 1995), Dorn (1976), MacKinnon and others (1992), and Viereck and Little (1972). General reviews of ecological characteristics and effects of fire on more than 20 species are available in the Fire Effects Information System Database (Fisher 1992). Seed characteristics of poplar (*Populus,* the other North American genus in the Salicaceae) are very similar to those of willows, and information for poplar is applicable to willow (Schreiner 1974; Zasada and Wyckoff 2002). The uniformity in seed characteristics, particularly germination, in the Salicaceae is remarkable considering that the family comprises several hundred species.

The importance of willows as a component of regional vegetation varies geographically and with the mix of habitat types within the region (Fisher 1992). In particular, willows become more important with increasing latitude in North America. In the boreal forests of northern Canada and Alaska, willows are the most common tall and intermediate shrubs; they fill niches occupied by hazel (*Corylus* spp.), maple (*Acer* spp.), and cherry and plum (*Prunus* spp.) in more southern parts of the boreal forest. In the tundra, willows are often the only woody species present; in riparian areas, they are, along with alder (*Alnus* spp.), the largest plants in these important tundra habitats.

Willows have a variety of growth forms (Brinkman 1974; Newsholme 1992; Viereck and Little 1972; Warren-Wren 1972). The tallest attain heights of 30 m, whereas prostrate tundra willows attain heights of a few centimeters to little more than 30 cm. Crown spread and shape is variable; the weeping willow is a popular ornamental tree. "Diamond" willow wood (of various species), named for the diamond-shaped stem lesions that expose the heartwood, is sought after in some areas for making furniture, walking canes, and lamp bases, and for ornamental woodwork.

In natural regeneration, the relative importance of seed versus vegetative propagation varies between species and between locations for a given species (for example, feltleaf willow) (Bliss and Cantlon 1957; Moore 1982; Walker and others 1986). Under appropriate moisture conditions, seeds germinate and seedlings establish in riparian and upland habitats (Densmore and Zasada 1983; Krasny and others 1988; McBride and Strahan 1984; McLeod and McPherson 1972; Walker and others 1986; Zasada and others 1983). Mineral soil is the most suitable substrate because of its water-holding characteristics, but other substrates are adequate if water is available. After seedling establishment, some species (coyote willow and related species) develop clones by suckering from root systems and others by downward bending and layering of stems and branches; however, most species capture space by crown expansion from a multiple-stemmed clump (Douglas 1989; Krasny and others 1988; Ottenbreit and Staniforth 1992). Some species are important colonizers in early stages of primary succession on floodplains, whereas others colonize in later stages of floodplain succession (Argus 1973; Viereck 1970; Viereck and Little 1972; Walker and others 1986).

The majority of species reproduce vegetatively. The most common form of vegetative regrowth is sprouting from

Table 1—*Salix,* willow: nomenclature and occurrence

Scientific name & synomyn(s)	Common name	Occurrence
***S. alaxensis* (Anderss.) Coville**	**feltleaf willow**	Throughout Alaska, Yukon Territory, & N British Columbia; scattered E across Canadian Arctic & S in Rocky Mtns. to Jasper National Park
***S. amygdaloides* Anderss.**	**peachleaf willow**	S Quebec, W to SE British Columbia, S to E Washington, Nevada, & Arizona, E to Kentucky & Pennsylvania
***S. arctica* Pallas**	**arctic willow**	Alaska E to Quebec, S to California,, N Europe, & Asia
***S. babylonica* L.**	**weeping willow**	China; naturalized from s Quebec, S Ontario, & S Vermont SW to Missouri, Georgia, & South Carolina
***S. bebbiana* Sarg.**	**Bebb willow**	Newfoundland, W to Hudson Bay & Alaska, S to New Mexico, N to Montana & E to Iowa, Maryland, & New England
***S. boothii* Dorn.**	**Booth willow**	British Columbia to Alberta, S through Washington & Montana to New Mexico, Arizon, & California
***S. caroliniana* Michx.**	**coastal plain willow**	Maryland to E Kansas, S to E Texas & E to S Florida; also in Cuba
***S. discolor* Muhl.**	**pussy willow**	Labrador W to central British Columbia, S to Idaho, E to Delaware & in mtns. S to E Tennessee
***S. eriocephala* Michx.** *S. cordata* Muhl.; *S. rigida* Muhl.	**cordate willow**	S Newfoundland to E Saskatchewan & Montana, S to Kansas, E to Virginia
***S. exigua* Nutt.**	**coyote willow**	Montana, Alberta to British Columbia &Washington, S to S California, E to W Texas & W South Dakota
***S. geyerana* Anderss.**	**Geyer willow**	Montana W to British Columbia, S to California & Arizona; also Colorado & Wyoming
***S. glauca* L.**	**white willow**	Alaska, S to British Columbia & in Rocky Mtns to New Mexico & W Texas; also N Mexico
***S. interior* Rowlee**	**sandbar willow**	E Quebec, W to central interior Alaska, S to E Colorado & New Mexico, E to Louisiana, Tennessee, & Maryland; also N Mexico
***S. lasiolepis* Benth.**	**arroyo willow**	Idaho & Washington, S to S California, SE Arizona & W Texas; also N Mexico
***S. lucida* Muhl.** [incl. *S. lasiandra* Benth.]	**Pacific willow**	Saskatchewan to interior Alaska, S to S California; scattered E to New Mexico & N to Wyoming & Idaho
***S. lutea* Nutt.**	**yellow willow**	Manitoba & Saskatchewan, w to Yukon & British Columbia, S to E Washington & E Oregon & to S California, Arizona, & New Mexico; also E Nebraska & North Dakota
***S. nigra* Marsh.**	**black willow**	Maine to E Minnesota, S to E Kansas & S Texas, E to N Florida; also in N Mexico, Arizona, & California
***S. petiolaris* Sm.**	**meadow willow**	New Brunswick W to Alberta; scattered S to Colorado & E to New Jersey
***S. planifolia* Pursh.**	**diamondleaf willow**	Throughout Alaska & Yukon Territory, N British Columbia
***S. repens* L.**	**creeping willow**	Wet areas in Europe & Asia
***S. scouleriana* Barratt ex Hook.**	**Scouler willow**	E Manitoba to S Alaska, S to S California; scattered E to New Mexico & N to Montana

Sources: Argus (1973, 1975), Brinkman (1974), Cooper and Van Havern (1994), Hillier and sons (1989), Little (1979), MacKinnon and others (1992), Newsholme (1972, 1992), Viereck (1987), Viereck and Little (1972), Vogel (1990).

buds located at the base of the stem. Other types of vegetative regeneration found in a limited number of species include sprouting from roots, layering of stems, and rooting of broken stem and branch segments. In riparian areas, whole plants are sometimes dispersed by water after being washed out by erosion. Artificial regeneration can be achieved by seeding or by planting seedlings and stem cuttings. Willows regenerate quickly after natural disturbances such as flooding (Krasny and others 1988; Shafroth and others 1994; Viereck 1970) and fire (Lyon and Stickney 1976; Viereck and Dyrness 1979; Zasada and others 1983; Zedler and Sheid 1988). They also regenerate on sites disturbed by humans, including mine tailings (Chose and Shetron 1976; Holmes 1982); thermally polluted lands (McLeod and Sherrod 1981); and construction sites (Bishop and Chapin 1989). Willows are used to artificially revegetate areas of natural and human disturbance such as those indicated above and for dune stabilization (Fisher 1992; Westoby 1975).

Hybridization occurs in willows but the extent to which it is present is not well established (Argus 1973, 1974; Mosseler and Zsuffa 1989). Hybridization experiments by Argus (1974), Mosseler and Zsuffa (1989), and Mosseler (1987, 1990) conducted with North American willows have

confirmed that hybridization occurs among some native species. Barriers to natural hybridization include phenological differences in flowering times, differences in pollen morphology, and other pre- and post-pollination limitations (Kim and others 1990; Mosseler 1987, 1990; Mosseler and Papadopol 1989).

Uses of willows include wood and fiber production, watershed and soil stabilization, habitat and food for wildlife, environmental restoration, landscaping, basketry and furniture making (MacKinnon and others 1992; Newsholme 1992; Viereck and Little 1972; Warren-Wren 1972). Because of the ease of rooting of stem cuttings, rapid early growth and biomass production, and prolific coppicing following cutting, willows are used in short-rotation forestry (Mitchell and others 1992; Sennerby-Forse 1986; Siren and others 1987; Zsuffa and others 1993). Willows were used by Native Americans and Eskimos for medicinal purposes and construction materials (Fisher 1992; MacKinnon and others 1992; Meeker and others 1993; Viereck 1987; Vogel 1990).

Flowering and fruiting. Willows are dioecious (figure 1). The sex ratio in natural populations is often female-biased, with ratios as high as 4:1 (Alliende and Harper 1989; Begin and Payette 1991; Crawford and Balfour 1983, 1990; Fox 1992; Kaul and Kaul 1984; Kay and Chadde 1992; Moore 1982). Because of irregular flowering, at least several years may be required to accurately assess the sex of individual shrubs and determine sex ratios in natural populations; this is particularly true on less productive sites. There is no definitive biochemical test or molecular genetics technique available for distinguishing male and female plants.

Figure 1—*Salix bebbiana*, Bebb willow: male (**right**) and female (**left**) catkins, which consist of a varying number of flowers depending on sex of the flower and species. The mature female flower produces a capsule (**see figure 3**) containing variable numbers of seeds depending on species, pollination success, and post-pollination predation.

Mosseler (1987) and Mosseler and Zsuffa (1989) found highly skewed sex ratios resulting from controlled inter- and intraspecific crosses. Sex ratios in naturalized exotic species—for example, *S.* × *rubens* Schronk (pro spp.) and *S. alba* spp. *vitellina* (L.) Arcang. in riparian areas in Colorado—are often highly skewed toward one sex because of vegetative reproduction (Shafroth and others 1994).

There have been reports of differences in vegetative characteristics and growth rate between male and female plants, but these differences are not well-established (Alliende and Harper 1989; Crawford and Balfour 1983, 1990). Male plants usually produce more flowers per unit of crown area than female plants (Kay and Chadde 1992; Zasada 2000).

Although the dioecious trait is universal across the genus, hermaphrodite plants (individuals with separate male and female flowers) and catkins (male and female flowers on the same catkin) have been observed in a number of species (Alliende and Harper 1989; Crawford and Balfour 1983; Mosseler and Zsuffa 1989). Mosseler and Zsuffa (1989) observed hermaphroditic plants in both natural populations and in controlled inter- and intraspecific crosses. Plants that are hermaphroditic initially sometimes become completely male as they mature sexually (Mosseler and Zsuffa 1989).

Seed-bearing age in willows depends on species and site conditions. Following disturbances such as fire and logging, willows of vegetative origin (for example, stump sprouts developing from the basal bud bank) flower sooner than plants of seed origin. Sprouts often produce seeds 1 to 2 years after a fire that kills the mature plant, whereas seedlings of the same species require 5 to 10 years before the first seeds are produced. In controlled environments, Mosseler and Zsuffa (1989) reported that coyote willow plants flowered several months after germination in a controlled environment and Mosseler (1996) found that 6 of 7 native willows flowered within 2 years of germination. Zasada (2000) has also observed flowering in 1-year-old creeping willow seedlings.

Catkins bearing several to many staminate or carpellate flowers (figure 1) appear before or after leaf appearance, depending on the species (Mosseler 1987; Viereck and Little 1972). Each carpellate flower contains 2 carpels. The number of ovules per carpel may vary considerable within and among species. Argus (1996) observed the following variation in ovules per carpel: feltleaf willow, 6 to 9; peachleaf willow, 8 to 11; arctic willow, 6 to 7; Bebb willow, 3 to 8;

Booth willow, 6 to 9; pussy willow, 3 to 9; coyote willow, 6 to 15; Geyer willow, 3 to 6; Pacific willow, 16 to 20; yellow willow, 3 to 9; meadow willow, 3. Hand-pollination can significantly affect seed production (it increases the number of flowers producing seeds and the number of fertilized ovules per flower), suggesting that insufficient pollination is common in natural populations (Fox 1992). Species vary in their dependence on insect- or wind-pollination, though the former predominates across the genus (for example, Argus 1974; Mosquin 1971; Vroege and Stelleman 1990). The female catkin, when adequately pollinated, produces several to many capsules (fruits) with multiple seeds (figures 2 and 3 and table 2). Moore (1982) observed that 24, 38, 67, and 62% of the capsules (flowers) matured and produced viable seeds in feltleaf willow. Zasada (2000) found that between 80 to 90% of the capsules in creeping willow produced seeds. Jones (1995) found that between 28 to 88% of capsules on arctic willow catkins produced seeds.

Primary dispersal of willow seeds is by wind. The hairs or "cotton"—which give the seeds great buoyancy—develop on the seedcoat as opposed to being a modification of the seedcoat, as is the case with the wings and other structures that facilitate dispersal in other species (Bewley and Black 1994). The seed separates easily from the hairs. Although willows have the potential to travel great distances (many kilometers), depending on wind and weather conditions, large quantities are deposited under the plant (Zasada 2000). Seeds can also be carried long distances over water, either by the wind or by the water itself. Measuring seed-rain for willows is not as easy as in other species because of the nature of the dispersal unit and the short life of the seeds. Various sized containers filled with water or a soil mix in which germination occurs have been used successfully (Walker and others 1986; Zasada and Densmore 1979) and sticky traps are also effective in catching and hold seeds. Water and wet soil appear to be particularly good media for catching and holding the dispersal unit.

Flowering and fruiting can be reduced significantly by biotic and abiotic factors. Zasada (2000) observed mortality due to frost of 0 to 38% for female flowers and 0 to 68% for males. Herbivores—for example, moose (*Alces alces*) and elk (*Cervus elphus*)—can reduce flower production by browsing twigs, and birds such as ptarmigan (*Lagopus leucurus*) specifically eat flower buds. Kay and Chadde (1992) found essentially no catkins outside of exclosures protected from elk browsing, whereas inside exclosures there were an average of 1,445 (137/ft^2), 583 (55/ft^2), 694 (66/ft^2), and 1336 (126/ft^2) catkins/m^2 of canopy for Bebb, Booth, yellow, and Geyer willows, respectively. Insect galls in arroyo willow reduced reproductive bud production by 43% compared to unaffected stems and seed production potential of individual clones by 10 to 50% (Sacchi and others 1988).

Collection of fruits and seeds. There are 2 broad groups of willows relative to seed dispersal patterns—those with seeds that are dispersed in late spring or summer and those with seeds that are dispersed in the fall, mainly after leaves have been shed (Chmelar and Meusel 1979; Densmore and Zasada 1983; Junttila 1976; Lautenschlager 1984; Poptsov and Buc 1957; Toepfer 1915; Viereck and Little 1972; Zasada and Densmore 1980; Zasada and

Figure 2—*Salix glauca*, white willow: catkin just beginning to open.

Figure 3—*Salix*, willow: capsule at various stages of opening (**a–e**) and the dispersal unit at different stages; **f** = hairs in capsule; **g** = hairs fully deployed and separated from the seed. When seeds land on water, hairs may remain attached to the seed, giving it buoyancy; based on Lautenschlager (1984) and Lautenschlager and Lautenschlager (1994).

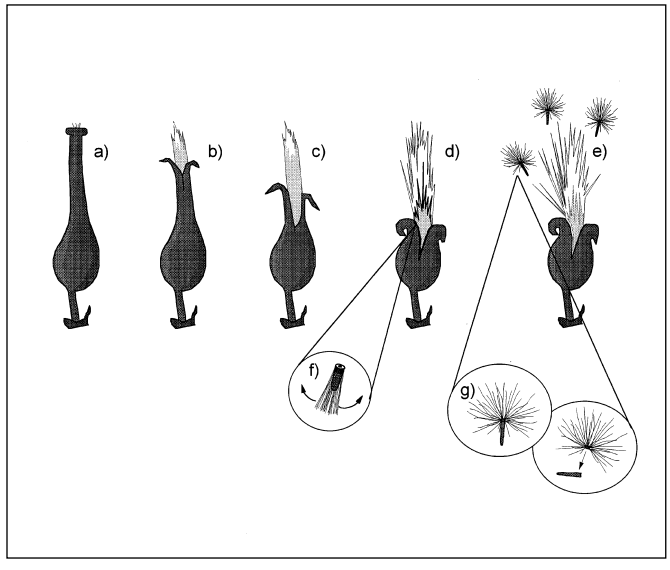


Table 2—*Salix*, willow: seed quantity in catkins

Species	Location	Capsules in catkin with seeds	Seeds/capsule	Seeds/catkin
S. alaxensis	Alaskan Arctic Slope			
	Site 1	45 (35–61)	8 (7–8)	333 (245–427)
	Site 2	71 (61–80)	9 (8–10)	673 (488–800)
	Site 3	119 (92–137)	10 (8–11)	1,174 (736–1,280)
	Site 4	98 (82–109)	7 (6–8)	600 (492–763)
S. amygdaloides	Ontario, Canada	—	16 (14–18)	—
S. arctica	Canadian high Arctic—Ellesmere Island			
	Dry site (year 1)	24 (8–40)	18 (10–25)	432
	Dry site (year 2)	65 (60–70)	9 (8–10)	595
	Wet site (year 1)	7 (2–12)	12 (5–18)	84
S. bebbiana	Yellowstone National Park	37 (24–48)	6 (5–7)	218 (144–311)
S. boothii	Yellowstone National Park	64 (43–79)	6	400 (286–427)
S. discolor	Ontario, Canada	—	10 (8–12)	—
S. exigua	Ontario, Canada	—	25 (15–36)	—
S. geyeriana	Yellowstone National Park	18 (12–29)	5 (4–6)	81 (42–171)
S. lucida	Ontario, Canada	—	17 (12–20)	—
S. lutea	Yellowstone National Park	74 (69–78)	11 (11–12)	841 (754–925)
S. petiolaris	Ontario, Canada	—	3 (2–5)	—
S. repens	Newborough, Warren, North Wales	4 (3–4)	22 (19–25)	82 (50–110)

Sources: Jones (1995), Kay and Chadde (1992), Moore (1982), Mosseler (1987), Zasada (2000).
Note: Values are means with ranges in parentheses.

Viereck 1975). Fall-dispersers comprise about 11% and about 20% of the species in North America and Alaska, respectively. Fall-dispersers are most common in the tundra regions of Alaska and Canada, but some species occur in the boreal forest (Argus 1973; Densmore and Zasada 1983; MacKinnon and others 1992; Viereck and Little 1972).

The seeds of the summer-dispersers live up to about 8 weeks; the rate at which seeds lose viability differs among species and is related to ambient temperature and relative humidity. No seeds in this group have been observed to overwinter and germinate the year after dispersal (Densmore 1979; Densmore and Zasada 1983; Ebersole 1989; Martens and Young 1992; Moss 1938). The rapid loss of viability is a critical consideration when collecting and handling fruits and seeds.

Catkins should be collected as close to the time of seed dispersal as possible. Timing of collection can be based on catkin color and condition of the capsule. Catkin color changes from green to yellow or yellow-brown at maturity. It is best to wait until the capsules begin to open (figure 3), as collection at this stage usually results in the most rapid opening of capsules and the most efficient seed extraction. One note of caution: insect-damaged capsules may *appear* to be dispersing seeds but are often still green and capsules are not opening normally (figure 3). There can be variation of a month or more in timing of dispersal for a species with a wide altitudinal or elevational range (table 3). Once capsules are ripe and begin to open, the rate of seed dispersal is determined by weather conditions: under warm, dry, windy conditions all seeds may be dispersed within a few days. Under wetter, cooler conditions, dispersal may be spread out over a month. If a small amount of seeds is all that is required, stems with immature catkins can be collected and placed in a greenhouse in water; seeds can then be collected when the capsules open (Marten and Young 1992).

After catkins have been removed from the plant they should be placed in a paper bag that allows the catkin-drying process to continue during transport. Catkins should not be packed tightly because air circulation may be restricted. Bags containing catkins must be kept out of direct sunlight.

To obtain seeds from a specific inter- or intraspecific cross, dormant stem cuttings (50 cm or less in length) with reproductive buds should be obtained from female and male plants in late winter (Mosseler 1987). These cuttings should then be placed in a greenhouse or growth chamber, where they will flower within 2 weeks. Male clones are often forced to flower before females and the pollen stored until the females are ready for pollination. This avoids pollination from unwanted sources. Willow pollen may be frozen for 1 to 2 months without losing its viability. There is a period of 3 to 6 days, depending on species, during which flowers can be pollinated (Mosseler 1987). Catkins will produce viable

Table 3—*Salix, willow*: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
S. alaxensis	Alaska—Brooks Range	May–June	June–July	July–Aug
	Alaska—Tanana River	Apr–May	May	May–June
	Alaska—central Interior*	May–June	June–July	July–Aug
S. amygdaloides	NE Minnesota	May–June	—	—
S. arctica	Canadian high Arctic—			
	Ellesmere Island	July	Aug–Sept	—
	Interior Alaska	June–July	July–Aug	Aug–Sept
S. bebbiana	—	Apr–June	May–June	May–June
S. caroliniana	North & South Carolina	Mar–April	Mar–Apr	—
S. discolor	N Ontario & British Columbia	May	—	—
	Rocky Mtns, USA	Mar–April	Apr–May	Apr–May
S. eriocephala (as *S. rigida*)	NE Minnesota & N Ontario	Apr–June	June	June-July
S. exigua	—	May–July	June–July	June–July
S. fragilis	US & Europe	Apr–May	May–June	May–June
S. glauca	Alaska—Brooks Range	June–July	July–Aug	Sept–Nov
	Alaska—mid-boreal forest	May–June	July–Aug	Sept–Nov
	Alaska—Denali National Park	June–July	July–Aug	Sept–Nov
S. interior	N Ontario		Aug 13	—
S. lucida†	Idaho	Apr–May	June–Aug	June–Aug
S. nigra	In north	Feb–April	Apr–May	Apr–May
	In south	May–June	June–July	June–July
S. petiolaris	General	May–June	June–July	June–July
S. scouleriana	General	Apr–June	May–July	May–July

Sources: Brinkman (1974), Densmore and Zasada (1983), Jones (1995), Viereck and Little (1972).

* High elevation. † As *S. lasiandra.*

seeds within 3 to 5 weeks using these procedures. It may be necessary to remove some catkins from the branch in order to assure that enough water and other resources are available for complete development of some catkins. Stems can be kept in aerated or unaerated water; water should be changed 2 to 3 times per week. At each change of water, 1 to 2 cm of stem should be trimmed from the base to expose fresh xylem to assure efficient water uptake. Stems of some species will root readily under these conditions (Densmore and Zasada 1978; Haissig 1970; Mosseler 1987). Mosseler (1987) reported that stem cuttings that rooted were more likely to produce seeds.

The seeds of the fall-dispersers are not as short-lived as summer-dispersers and thus there is more leeway in collecting catkins and handling seeds (Zasada and Densmore 1977). Seeds of fall-dispersers may disperse quickly during warm weather in September, but it is often possible to find seeds in late fall after the first snowfall.

To estimate the number of catkins necessary for a desired quantity of seed, it is important to know the seed yield per catkin (table 2). As in other genera with multiple-seeded fruits, seed yield per catkin varies among species, among sites for a species, among years, and with condition of the catkin (for example, amount of insect infestation or disease).

Although willows generally produce seeds annually, the variation among years is not well-documented. Moore (1982) found that some female feltleaf willows produced relatively large numbers of catkins (200 to 500) over a 2-year period, whereas others of the same age and stature produced no catkins in either year. Within Moore's 3 study areas, 22 of 66% of the mature shrubs did not produce flowers. Jones (1995) found that annual variation in seed production occurred on both wet and dry sites during 2 years of study and that no seeds were produced on their wet site in one of the years. Walker and others (1986) observed similar levels of willow seed production on riparian sites in Alaska during a 2-year period. In addition to genetic and physiological factors that control flowering and seed production, animal browsing, insects, and disease can significantly affect annual variation in seed availability (Kay and Chadde 1992). Though some level of variation in seed production should be expected among years, it is usually possible to find some individuals of a species with a collectible seedcrop in a given year on most sites.

Extraction and storage of seeds. Simak (1980) stated that the following conditions were key for extraction and storage of Salicaceae seeds: (1) placement in proper conditions as soon as possible (catkins cannot necessarily be stored at ambient air or room temperatures and be expected to have viable seeds); (2) separation of seeds from the cotton using methods that minimize mechanical damage to seeds; (3) pre-drying to about 6 to 10% of dry weight and storage in sealed containers that will maintain a constant humidity; and (4) storage of seeds at subfreezing temperatures to maintain seed viability for time periods of 6 months or more.

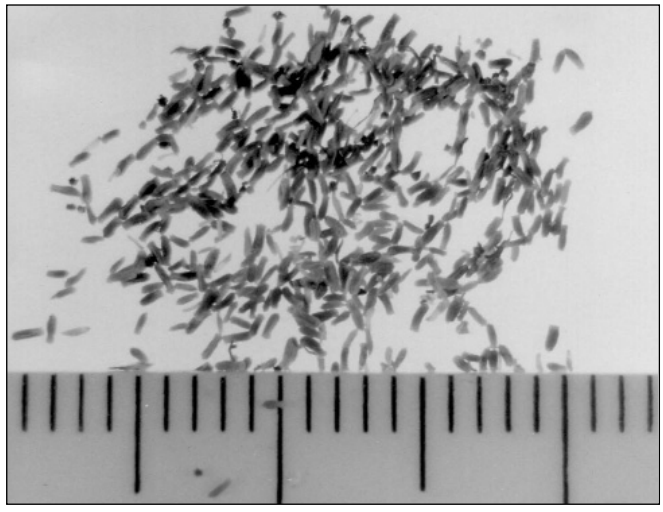
There is some difference of opinion regarding the need to separate seeds from the cotton (figure 4) (Martens and Young 1992; Simak 1980). We agree with Simak (1980) that seeds should be separated because doing so reduces the bulk of the material to be stored. There is some indication that storage with the cotton may reduce viability, particularly in the summer-dispersing species (Simak 1980).

Small- to medium-sized lots of seeds can be cleaned according to the following steps:

- Catkins should be placed in a single layer in screen-covered boxes in a relatively warm, dry area, with temperature at 20 to 24 °C and relative humidity at 25 to 35%. Air should be able to circulate around the catkins to allow rapid drying. If capsules are beginning to open when collected, opening will be completed in 2 to 3 days. Green catkins open more slowly and incompletely and seed recovery is low.
- Then, the catkins and cotton-containing seeds should be placed in a container so that material can be shaken or tumbled in an airstream or tumbled as in a cement mixer (Einspahr and Schlafke 1957; Fung and Hamel 1993). The seeds separate easily from the cotton (figure 4) under these conditions.
- Seeds can be separated from coarser and finer residue by passing the mixture through a screen or sieve.
- Seeds extracted in this way have a moisture content very close to the 6 to 8% recommended by Simak (1980).

Seeds should be stored at temperatures from –5 to –40 °C immediately after cleaning. They can be stored for up to 6 months at 1 to 5 °C but not for longer. Storage in containers with a dessicant such as calcium chloride ($CaCl_2$) does not appear to prolong seed life (Martens and Young 1992; Simak 1980). However, storage with a dessicant appears to provide long-term benefit for poplar (*Populus* spp.) (Zasada and Wyckoff 2003) and additional work is needed on use of desiccants for storing willow seeds. The longest periods of successful storage reported are 44 months at –20 °C (Simak 1980) and 36 months at –10 °C (Zasada and Densmore 1980). Viability of poplar seeds with characteristics similar to summer-dispersing willows has been maintained for 10 to 12 years when stored at –10 to –20 °C (Wyckoff and Zasada 2003). The small seed size (figure 5 and table 4) makes it easy to store very large quantities of seeds in a limited space.

Figure 4—*Salix alaxensis*, feltleaf willow: seeds, divisions on scale each = 1 mm.



Germination tests. Willow seeds are very small, usually 1 to 2 mm long and less than 1 mm wide (figures 5 and 6). The seedcoat is transparent and the green cotyledons are readily visible. The seeds appear to contain a functional photosynthetic system, with the following levels (chlorophyll a, 1.45 mg/g, and chlorophyll a:b, about 2.4 mg/g) for dormant seeds of white willow, a fall-disperser (Zasada and Coyne 1975). Green color is an indicator of potential seed viability.

Germination requirements differ for summer and fall dispersers (figure 7) (Densmore and Zasada 1983; Juntilla 1976; Poptsov and Buch 1957; Zasada and Viereck 1975). Under natural conditions, seeds of summer dispersers germinate in 12 to 24 hours after dispersal with adequate moisture (figure 7). Seeds will even germinate underwater (Densmore and Zasada 1983; Moore 1982). Germination may be reduced on substrates with a substantial content of salt (Jackson and others 1990; Krasny and others 1988). All tested species—from climates as different as the Arctic, coastal rain forest, and plains areas of the western United States—appear to exhibit a similar response to temperature and do not exhibit any signs of dormancy (Densmore and Zasada 1983; Juntilla 1975; Krasny and others 1988; Martens and

Table 4—*Salix*, willow: cleaned seed data

Species	Place collected	Cleaned seeds (x 1,000)/weight /kg	/lb	Samples
S. amygdaloides	Minnesota	5,720	2,600	1
S. bebbiana	Idaho (770 m)	5,500	2,500	2
S. caroliniana	South Carolina	18,260	8,300	1
S. exigua	Washington (615 m)	22,000	10,000	1
S. fragilis	Minnesota	7,040	3,200	1
S. lasiandra	Idaho (770 m)	25,300	11,500	1
S. petiolaris	Minnesota	1,100	500	1
S. scouleriana	Idaho (770 m)	14,300	6,500	1

Source: Brinkman (1974).

Figure 5—*Salix*, willow: seed; there is no endosperm and the seed is attached to the hairs at the radicle end. Viable seeds are green due to the presence of chlorophyll; the shade of green is determined by the species, seed water content, and length of time in storage (Simak 1980).

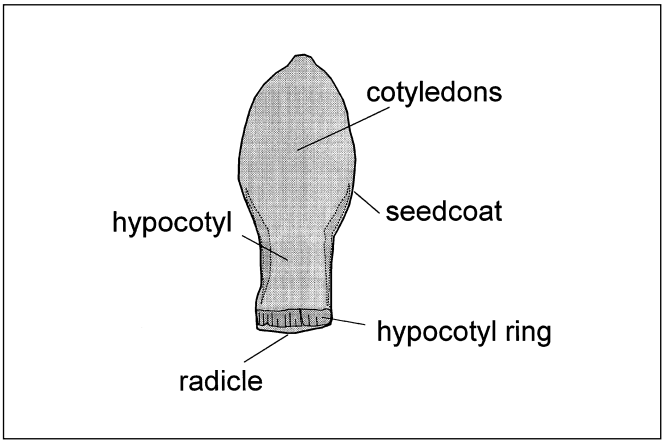
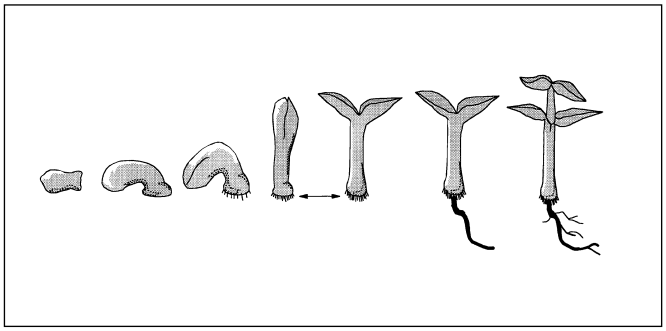


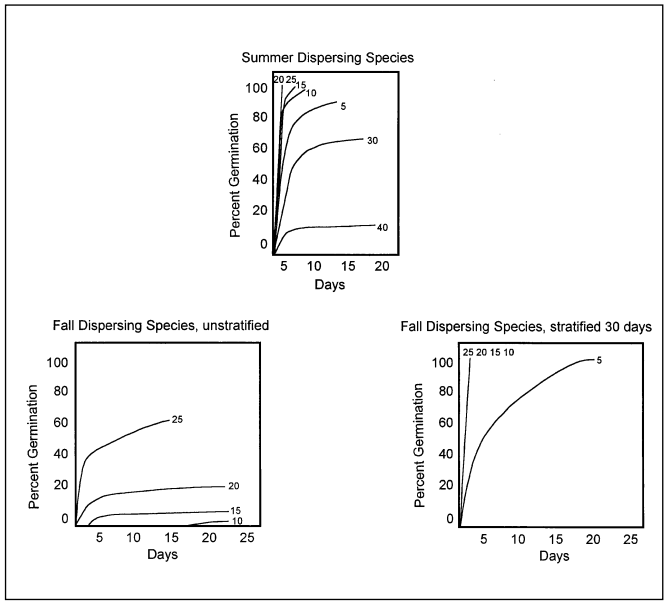
Figure 6—*Salix*, willow: seeds; note development of hypocotyl hairs (**arrow**) from the hypocotyl ring (see figure 5); adapted from Simak (1980).



Young 1992; Zasada and Viereck 1975). Germination is complete between 5 to 30 °C but declines rapidly at temperatures above 30 °C. Temperatures of 20 to 25 °C appear to be optimum (figure 7). Germination may be tested on a variety of substrates (Brinkman 1974). Seeds germinate completely in the dark, but rate of germination may be higher in the light (Densmore and Zasada 1983; Zasada and Viereck 1975). Official seed testing recommendations call for a 14-day test on moist blotter paper with alternating temperatures of 20 to 30 °C, and light during the 8 hours at 30 °C; no pretreatments are needed (ISTA 1993).

Fall-dispersers exhibit seed dormancy (figure 7). Under natural conditions, seeds overwinter and germinate quickly following snowmelt (Densmore 1979; Densmore and Zasada 1977). Germination of unstratified seeds occurs between 5 to 30 °C, with the highest germination at the warmest temperatures. Stratification widens the range of temperatures over which seeds germinate and increases the rate of germination (Densmore 1979; Densmore and Zasada 1977; Juntilla 1976; Zasada and Viereck 1975; Zasada and Densmore 1983). After 30 days of stratification, the germination pattern at all temperatures resembles that of summer dispersers (Densmore and Zasada 1983). The length of strat-

Figure 7—*Salix*, willow: generalized patterns of temperature and stratification effects on germination of seeds of summer- and fall-dispersing willows; numbers indicate germination temperatures (°C).



ification required for complete germination increases prior to the onset of dispersal, reaching a maximum as dispersal begins in the fall, and declining in seeds dispersed late in the fall (Densmore 1979; Densmore and Zasada 1983; Zasada and Viereck 1975). The International Seed Testing Association (1993) did not consider fall-dispersed seeds in their testing rules.

Willow germination, though epigeal, does not follow the usual pattern. Hypocotyl hairs attach the seedling to the substrate and the radicle shows delayed development. Simak (1980) has proposed appropriate criteria for evaluating willow germinant quality (figure 7).

Nursery practice. Contrary to earlier beliefs (Brinkman 1974), seeds can be sown after being stored. Although seed viability may decline during 3 to 4 years of storage, vigorous seedlings can be produced with seeds stored for at least this long. Seedlings can be produced as bareroot stock or in containers and much of the information for poplars applies to willows (Schreiner 1974; Wyckoff and Zasada 2002). Although opened capsules containing seeds and cotton can be broadcast on well-prepared beds, seedling density and distribution can be better controlled if the cotton is removed.

After sowing, seeds can be gently pressed into the soil. Seeds should not be buried, however, as a soil covering of 2 to 4 mm (0.09 to 0.2 in) will significantly reduce seedling emergence (McDonough 1979; Zasada 2000). Seedbeds must be kept moist until the seedlings are well-established; a fine spray of water is preferable. To conserve moisture and maintain a high relative humidity near the bed surface, close shading often is provided with slats and burlap. These covers should be removed as soon after germination as possible, for willows grow best under full light. Seedling growth is relatively rapid, and plantable container seedlings can be produced in 1 growing season.

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Lamiaceae—Mint family

Salvia L.

sage

Susan E. Meyer

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Growth habit, occurrence, and use. The sage genus—*Salvia* contains about 700 species of annual and perennial herbs and shrubs and is worldwide in distribution. There are perhaps 20 woody species in the United States, principally in the Southwest and California (table 1) (Correll and Johnson 1970; Munz and Keck 1959). They are intricately branched, rounded or sprawling shrubs or subshrubs with often leathery, opposite, leaves. The foliage is usually strongly aromatic. Members of the sage genus are used medicinally and as culinary herbs; many of the native species have been locally adopted for these uses. Native sages are often fast-growing and freely reseed themselves onto disturbed lands (Keeley and Keeley 1984). They could be useful in the stabilization of disturbed land. Several California species are dominant components of coastal sage scrub communities and are also significant in chaparral. They also head the list of wild California bee plants for honey production (Jepson 1951). In addition, sages are showy in flower and have interesting foliage, giving them great potential as ornamentals for low-water-use landscaping (ANPS 1990). Most are native to warm winter areas, but Dorr sage occurs throughout the Great Basin and is quite cold hardy.

Flowering and fruiting. Sages tend to flower after the principal rainy season. Thus, California and Mojave Desert species are spring-flowering, whereas Sonoran and Chihuahuan Desert species are usually late-summer-flowering. The flowers are often large and showy, borne in interrupted spikes or terminal heads, and attractive to many native bees and other pollinators. The corollas are strongly 2-lipped and range from white through red, blue, or violet in color, depending on the species. The superior ovary is deeply 4-lobed, and after fertilization it develops into 4 easily separable nutlets that ripen within the papery calyx cup. Fruits toward the base of each inflorescence ripen first, perhaps 2 to 3 weeks earlier than those at the upper end (Nord and Gunter 1974). The nutlets usually ripen about 6 weeks after full flower. Each nutlet contains a single seed (figures 1 and 2) . The ripened nutlets are shaken from the plant by wind or raindrops. Once on the ground they may be eaten by ants, rodents, or birds. They have no special mode of dispersal.

Seed collection, cleaning, and storage. The procedures of Nord and Gunter (1974) for the harvest, cleaning, and storage of Sonoma sage could probably be applied to most shrubby species. The seeds are harvested by clipping, hand-stripping, or beating into containers as soon as nutlets

Table 1—*Salvia,* sage: nomenclature, habit, habitat, and geographic distribution

Scientific name	Common name(s)	Habit	Habitat	Distribution
***S. apiana* Jepson**	**white sage**	Subshrub	Coastal sage scrub, chaparral, pondersoa pine forest, warm desert shrub margins	Coastal & cis-montane S California S to Baja California
***S. dorrii* (Kellogg) Abrams**	**Dorr sage,** purple sage	Shrub	Warm & cold desert shrub communities, piñyon–juniper woodland	W Washington to SE California, Arizona, Utah, & Idaho
***S. mellifera* Greene**	**black sage**	Subshrub	Coastal sage scrub, chaparral, warm desert shrub margins	Coastal & cis-montane central California S to Baja California
***S. sonomensis* Green**	**creeping sage**	Mat-forming suffrutescent	Chaparral, oak woodland, ponderosa pine forest	Coastal & cis-montane California, mostly in N

Source: Munz and Keck (1959).

Figure 1—*Salvia sonomensis*, creeping sage: nutlets.

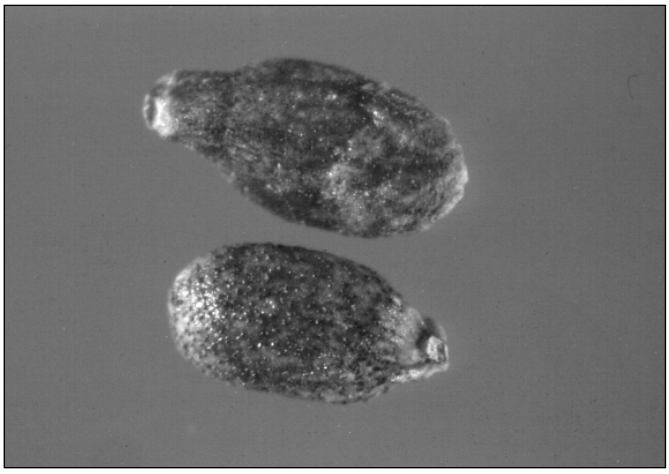
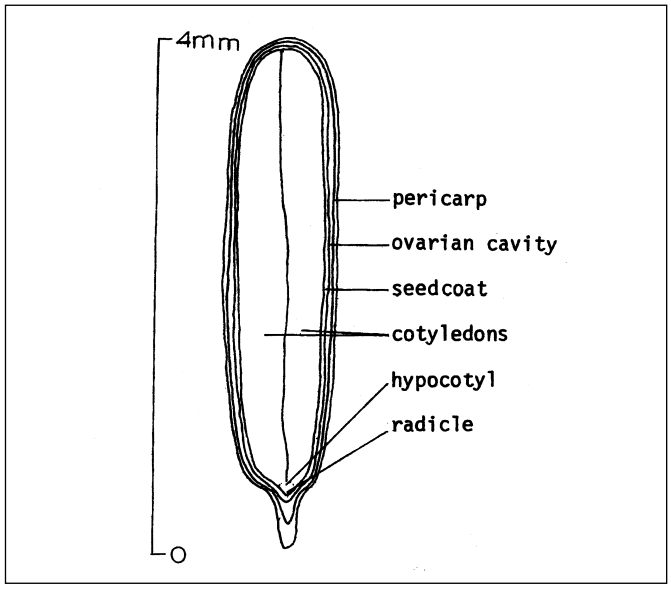


Figure 2—*Salvia sonomensis*, creeping sage: longitudinal section through a seed.



can be dislodged from the lower parts of the inflorescences. These early seeds are apparently larger and of better quality than those produced later in the season. If harvesting is delayed, most of the crop could be "stormed-off" and lost. The harvested material should be thoroughly dried and passed through a hammermill or barley debearder. Small lots may be handrubbed. The seeds may then be cleaned-out by screening or with a fanning mill. For creeping sage, a #1 (1-mm) screen retained a high proportion of filled nutlets while allowing most unfilled nutlets to pass through. The optimal screen size for this purpose will depend on species and possibly on the seedlot (table 2). Fill percentage can be increased by blowing or screening out smaller nutlets, so that this value is somewhat an artifact of the cleaning procedure. The importance of high fill depends on the intended use of the seedlot. The reported weights for individual nutlets of different species vary from 0.8 to 2.4 mg, and number of seeds per weight varies from 416,750 to 1,250,230/kg (189,000 to 567,000/lb) (table 2).

Sage species may form persistent seedbanks in the field (Keeley and Keeley 1984; Malanson and O'Leary 1982), so it is likely that they remain viable for considerable periods in dry storage (orthodox behavior). Kay and others (1988) reported that seeds of Doff and white sages showed little loss of viability during 5 to 7 years of sealed warehouse or 4 °C storage, whereas in unsealed warehouse storage (where moisture levels were allowed to fluctuate) some loss of viability was observed. Nord and Gunter (1974) reported no loss of viability for seeds of creeping sage stored at 4 °C for over 2 years.

Germination and seed testing. Seeds of shrubby sage species are generally relatively easy to germinate (table 3). Seed collections of cis-montane California and desert species generally contain a readily germinable fraction (Kay and others 1988; Keeley 1986, 1987)), whereas seeds of other species, such as creeping sage, may have a chilling requirement (Nord and Gunter 1974). A desert population of black sage showed increased germination in the light in response to heat-shock treatments (1 or 5 hours at 70 °C or 5 minutes at 115 °C) that may have simulated summer soil heating (Keeley 1986). Seeds of desert populations of the related annual species chia—*S. columbariae* Benth.—are known to have an after-ripening requirement that is met more quickly at high temperatures (Capon and others 1978). White sage is also reported to respond positively to heat shock (Keeley 1987, 1991). Coastal sage scrub and chaparral populations of black sage germinated well in light without pretreatment but required a charate stimulus (a leachate made from charred wood) to germinate in the dark (Keeley 1986). This response is apparently an adaptation that permits seedlings to germinate and establish from persistent seedbanks after wildfire (Keeley 1986). Chilling and alternating temperature regimes sometimes increased germination percentages for black sage, but the results were inconsistent (Keeley 1986). Kay and others (1988) reported that a seedlot of Doff sage germinated to 28% at 15 °C in the dark after a summer of warehouse storage and that its germination increased to 53% after 5 years in storage, suggesting that seeds of this species also have a dry after-ripening requirement. They obtained a similar increase (from 19% to 43%) for seeds of white sage during a single year of warehouse storage. Sage seed dormancy that is overcome in nature by

Table 2—*Salvia,* sage: seed weights and maximum germination percentages

Species	Seed weight mg	Seed weight oz	Seeds/weight /kg	Seeds/weight /lb	Max germination %
S. apiana	1.4	.05	714,400	324,000	42
	1.9	.07	511,600	233,000	43
S. dorrii	2.4	.08	416,800	189,000	53
S. mellifera	1.1	.04	911,000	413,000	69
S. sonomensis	1.5	.05	685,800	311,000	90
	0.8	.03	1,212,800	550,000	70

Source: Kay and others (1988), Keeley (1986, 1987), Nord and Gunter (1974).

Table 3—*Salvia, sage*: seed germination responses to pretreatments and incubation conditions

Species	Light	Alternating temp	Chilling	Heat shock	Dry storage	Charate	GA
S. apiana	+	+	+	+	+	nd	+
S. mellifera	+	+	+	+	nd	+	nd
S. sonomensis	nd	nd	+	nd	nd	nd	+

Sources: Emery (1988), Kay and others (1988), Keeley (1986, 1987), Nord and Gunter (1974).
Notes: nd = no data; see text for details.

either dry after-ripening or chilling may be circumvented through a 1-hour soak in gibberellic acid (GA) at 100 to 500 ppm (Nord and Gunter 1974) and 400 ppm (Emery 1988). The seeds may be dried for sowing following the GA treatment.

For recently harvested seedlots of sage species, a cut test is a good indicator of viability. Tetrazolium (TZ) staining may also be used, either to evaluate the viability of ungerminated seeds at the end of a germination test or in lieu of a germination test. Belcher (1985) recommends the following procedure for the herbaceous blue sage, *S. azurea* Michx. ex Lam.: soak seeds overnight in water, clip at cotyledon end, place in 1% TZ solution for 6 hours and then slice them lengthwise for evaluation. The embryo in sage seeds is well-developed and fills the seed cavity, but the endosperm is rudimentary or absent. Until more specific recommendations can be made, a generic germination test for shrubby sage species (as recommended for blue sage) is incubation at 15/25 °C or 20/30 °C in the light, with first count at 7 days and last count at 21 days and with post-test viability evaluation as described above.

Field seeding and nursery practice. Shrubby sage species can be direct-seeded in early to late fall in winter rainfall areas such as cis-montane and coastal California (Emery 1988). Sonoran and Chihuahuan Desert species would probably best be seeded before summer rains. Sages are often early seral species adapted to disturbance and establish more readily if seeded in the absence of heavy herbaceous competition (Nord and Gunter 1974). Spring-seeding of chilled or GA-treated seeds was recommended for creeping sage, on the argument that rodent predation would be decreased and that field chilling conditions were unreliable (Nord and Gunter 1974).

Shrubby sages are readily produced from seed as container stock in a nursery setting. In California, seeds are sown outdoors in flats in early fall (Emery 1988). More dormant seedlots may be treated with GA or subjected to a chilling treatment before sowing. Seedlings are then transplanted to larger containers when at the 6- to 8-leaf stage. Sages may also be direct-seeded or planted as germlings in tube containers such as those used for conifer seedlings.

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Caprifoliaceae—Honeysuckle family

Sambucus L.

elder

Kenneth A. Brinkman and W. Gary Johnson

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Mr. Johnson retired from the USDA Forest Service's National Seed Laboratory

Growth habit, occurrence and use. The elder genus—*Sambucus*—includes about 20 species of deciduous shrubs or small trees, rarely herbs, native to temperate and subtropical regions of both the Eastern and Western Hemispheres. The fruit of most species is used by birds and mammals as well as by humans, but some species have poisonous fruits. Some species have medicinal properties; others are planted for their attractive foliage and colorful fruit. Plants are often browsed by deer (*Odocoileus virginianus*) and livestock (Plummer and others 1968; Van Dersal 1938). In the United States, 3 native varieties and subspecies have potential value for wildlife and environmental plantings (table 1). American elder and blue elder have been used more than the other species for these purposes.

Flowering and fruiting. The large clusters of small, white or yellowish white, perfect flowers bloom in the spring or summer (table 2). The fruit is a berrylike drupe (figure 1) containing 3 to 5 one-seeded nutlets or stones (figures 2 and 3). When ripe, the fruits vary from red to nearly black, depending on species (table 3). Dispersal is chiefly by birds and animals.

Geographic races. Regional floras do not agree on the taxonomy of this genus. There is great confusion on delimiting the species, subspecies, and varieties (LHBH 1976). Two varieties of blue elder have definite geographic limits and these may be climatic races. Both American and scarlet elders have developed varieties, but these do not appear to be related to climate.

Collection of fruits. Elder fruits are collected by stripping or cutting the clusters from the branches. Collection should be made as soon as the fruits ripen to reduce losses to birds. If the seeds are not to be extracted immediately, the fruits should be spread out in thin layers to prevent heating. Scarlet elder fruits can be harvested before

Table 1—*Sambucus,* elder: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***S. nigra* spp. *canadensis* (L) R. Bolli** *S. canadensis L.*	**American elder,** common elder, sweet elder, elderberry, black elderberry	Nova Scotia to Manitoba, Florida to Texas
***S. nigra* spp. *cerulea* (Raf.) R. Bolli** *S. caerulea* Raf.; *S. glauca* Nutt.	**blue elder,** blue elderberry, blueberry elder, elder blueberried	British Columbia & W Montana S to California & New Mexico
***S. racemosa* var. *racemosa* L.** *S. callicarpa* Greene; *S. pubens* Michx.	**scarlet elder,** red elder, redberried elder	Newfoundland to Alaska, S to Georgia, W Oregon & mtns of central & S California

Table 2—*Sambucus,* elder: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
S. nigra			
spp. *canadensis*	June–July	July–Sept	Aug–Oct
spp. *cerulea*	May–July	Aug–Sept	Aug–Oct
S. racemosa var. *racemosa*	Apr–July	June–Aug	June–Nov

Sources: Harris (1969), Hitchcock and others (1959), LHBH (1976), Plummer and others (1968), Rehder (1940), Van Dersal (1938).

Figure 1—*Sambucus nigra* spp. *cerulea*, blue elder: fruit cluster (**top**) and single fruit (**bottom**).

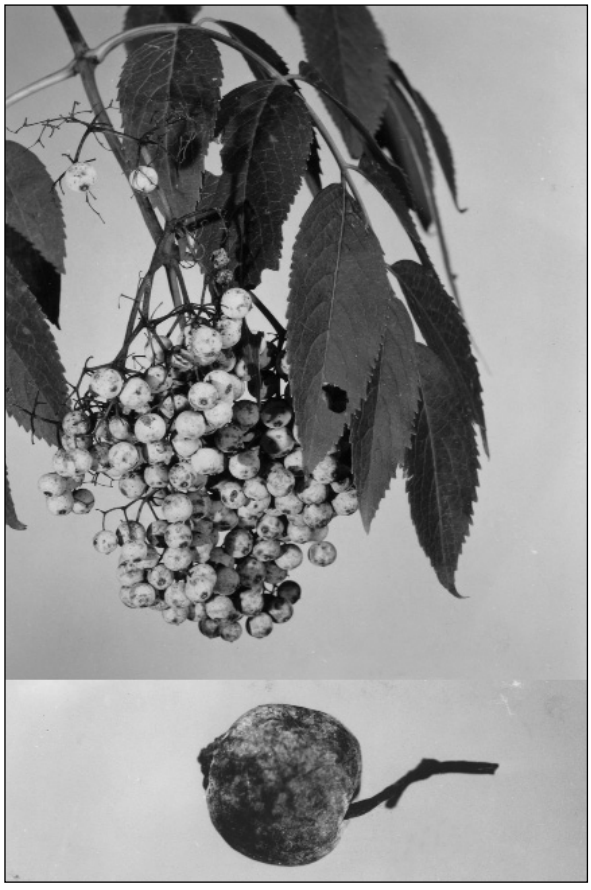
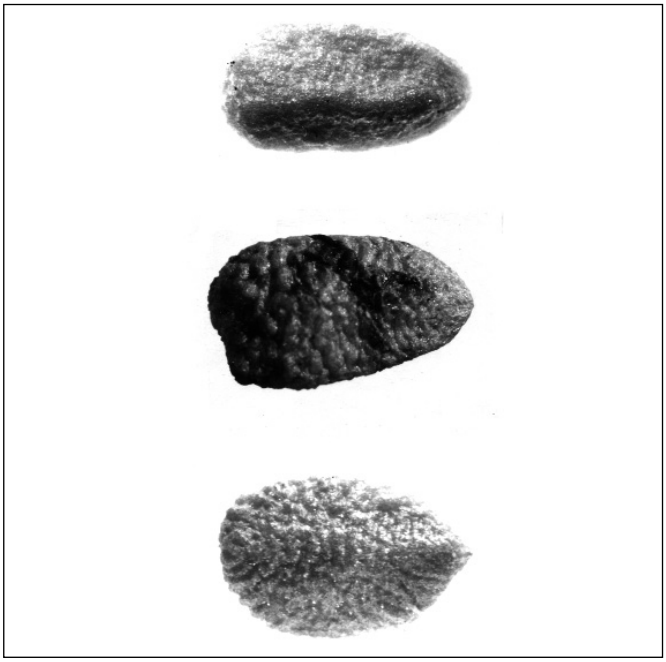


Figure 2—*Sambucus*, elder: seeds of *S. racemosa* var. *racemosa*, scarlet elder (**top**); *S. nigra* spp. *canadensis*, American elder (**center**); and *S. nigra* spp. *cerulea*, blue elder (**bottom**).



maturity and the seeds will still germinate (Dirr and Heuser 1987). Cram (1982) found that seeds harvested on August 5 in Saskatchewan before the fruit was color ripe showed 95% germination after 90 days of cold stratification, whereas seeds harvested on August 25 showed only 76%. Increased dormancy or harder seedcoat may be the cause of the lower germination in the seeds harvested August 25 (Cram 1982). Specific gravity or moisture content of the fruits did not decrease during maturation but fluctuated up and down, apparently in response to rainfall (Cram 1982).

Extraction and storage of seeds. The fruits (figure 1) may be (a) dried; (b) run through a macerator with water and the pulp and empty seeds floated off (Plummer and others 1968); or (c) crushed, dried, and used without further cleaning. Commercial seedlots may consist of either dried fruits or cleaned seeds (figures 2 and 3). After a short period of drying, lots of freshly extracted seeds may be fanned or screened to remove debris. Excessive drying should be avoided. Seed yields and number of seeds per weight vary among species (table 4).

Small lots of fruit may be cleaned in a food blender (Morrow and others 1954). The berries are covered with water, the blender is run long enough to macerate them, and more water is added to float off the pulp and debris. Several changes of water will result in cleaner seeds. The seeds are separated from the last change of water in a filter-line funnel and can be dried on the filter paper.

Elder seeds may be stored dry at 5 °C for several years (Morrow and others 1954). Seeds of American elder showed

Figure 3—*Sambucus racemosa* var. *racemos*a, scarlet elder: longitudinal section through a nutlet.

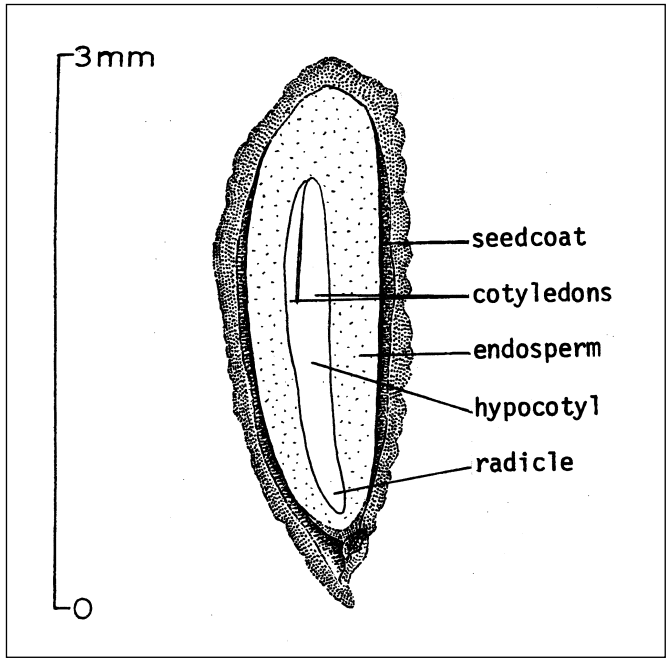


Table 3—*Sambucus,* elder: height, seedcrop frequency, and fruit ripeness criteria

Species	Height at maturity (m)	Year first cultivated	Years between large seedcrops	Ripe fruit color
S. nigra				
spp. *canadensis*	2.7	1761	1	Purplish black
spp. *cerulea*	9	1850	—	Blue-black
S. racemosa var. *racemosa*	3.0	1812	1	Scarlet, bright red

Sources: Brinkman (1974), Fernald (1950), LHBH (1976), Rehder (1940), Rydberg (1965).

Table 4—*Sambucus,* elder: seed yield data

Species	Seeds/wt of fruit		Cleaned seeds/weight				Samples
			Range		Average		
	kg /45 kg	lbs/100 lbs	/kg	/lb	/kg	/lb	
S. nigra							
spp. *canadensis*	3.2–8.2	7–18	385–713	175–324	510	232	14
spp. *cerulea*	2.7	6	257–570	117–259	451	205	23
S. racemosa var. *racemosa*	1.8	4	422–829	192–377	629	286	6

Sources: Brinkman (1974), McKeever (1938), Plummer (1968), Rydberg (1965), Swingle (1939).

little loss in viability after 2 years (Brinkman 1974). Seeds of scarlet elder have been kept satisfactorily in moist sand at 5 °C for a year, but cold, dry storage probably is adequate.

Pregermination treatments. Elder seeds are difficult to germinate because of their dormant embryos and hard seedcoats. Although response varies among species and seedlots, good germination of dried seeds usually results after warm stratification for 60 to 90 days followed by at least 90 days at 5 °C (table 5). Heit (1967) suggested that 10 to 15 minutes of soaking in sulfuric acid, followed by 2 months of chilling at 1 to 4 °C or by late summer planting, would give optimum seedling production. Some seedlots, however, germinated better when treated for 5 minutes with acid, followed by 2 days of water soaking and then by warm and cold stratification (Brinkman 1974). American elder seeds from southern sources of usually do not need acid treatment (Dirr and Heuser 1987). For blue elder, treatment with 1,000 mg of gibberellic acid per liter for 24 hours followed by 30 days of stratification at 4 °C yielded 55% germination. Combining 100 mg of ethephon (an ethylene-releasing compound) per liter with the gibberellic acid treatment and stratification resulted in a 69% germination (Norton 1986a&b).

Germination tests. Tests can be made in sand or on germination paper at alternating temperatures of 30 and 20 °C, but lower temperatures are equally successful for some species (table 6). Although most tests were made with

Figure 4—*Sambucus nigra* spp. *canadensis,* American elder: seedling development at 2, 20, 33, and 45 days after germination.

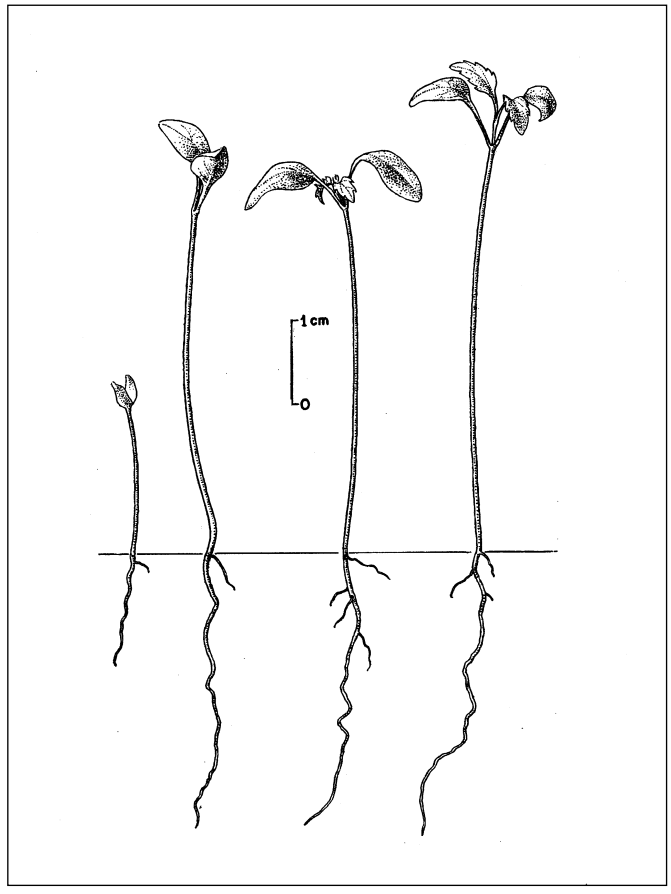


Table 5—*Sambucus,* elder: stratification treatments

Species	Medium	Warm period		Cold period	
		Temp (°C)	Days	Temp (°C)	Days
S. nigra					
spp. *canadensis*	Sand	20–30	60	5	90–150
spp. *cerulea*	Sand	Room*	450*	5	98
S. racemosa var. *racemosa*	Sand	20–30	30–60	5	90–150

Sources: Adams (1927), Brinkman (1974), Davis (1927), McKeever (1938).
* Dry seeds were stored, but not stratified, for 450 days at room temperature.

Table 6—*Sambucus,* elder: germination test conditions and results

Species	Germination test conditions				Germination speed		Germination avg		Purity
	Medium	Temp (°C)		Days	Percent	Days	(%)	Samples	(%)
		Day	Night						
S. nigra									
ssp. *canadensis*	Sand or soil	30	20	60	32	16	63	7	80
spp. *cerulea*	Sand	21	21	35	55	12	79	3	80–90
S. racemosa var. *racemosa*	Sand	30*	20*	60	50	27	47	6	97

Sources: Adams (1927), Brinkman (1974), Davis (1927), McKeever (1938), Plummer (1968).
* Day and night temperature of 77 and 50 °F were used on some samples.

at least 16 hours of light, the need for light has not been established. Germination is epigeal (figure 4).

Nursery practice. Elder seeds can be sown in the fall soon after collection, or they can be stratified and sown in the spring. In either case, germination often is not complete until the second spring. At the USDA Forest Service's nursery in Coeur d'Alene, Idaho, dried seeds of blue elder usually are soaked in water for 3 days, then stratified in vermiculite for 3 months at 1 °C before spring-sowing (Brinkman 1974). A seedling density of 375/m^2 (35/ft^2) is sought. Seeds are sown 5 mm ($^1/_4$ in) deep in drills and covered with about 8 mm ($^3/_8$ in) of sawdust mulch. Two reported tests of American elder sown soon after collection resulted in 92 to 95% (Adams 1927) and 60 to 70% germination (Davis 1927). Fall-sown seedbeds should be mulched. One-year-old seedlings usually are large enough for field planting. Elders also can be propagated from cuttings (Dirr and Heuser 1987; LHBH 1976).

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Sapindaceae—Soapberry family

Sapindus saponaria var. *drummondii* (Hook. & Arn.) L. Benson

western soapberry

Ralph A. Read and John C. Zasada

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Other scientific and common names. Previously classified as *Sapindus drumondii* Hook. & Arn. Other common names include wild China-tree, soapberry, Indian soapplant, cherrioni, jaboncillo (Little 1950; Tirmenstein 1990; Vora 1989).

Growth habit, occurrence, and use. Western soapberry grows on clay soils and on dry limestone uplands from southwestern Missouri to Louisiana, and westward through Oklahoma and Texas to southern Colorado, New Mexico, southern Arizona, and northern Mexico. It is used as an indicator species for riparian habitats in parts of the southwestern United States (Tirmenstein 1990). The soapberry family comprises nearly 2,000 species, which are primarily tropical (Watson and Dallwitz 1992). Western soapberry is similar to wingleafed soapberry (*Sapindus saponaria* L. var. *saponaria*), which is found from Arizona to Florida.

Soapberry is a small to medium deciduous tree, 7.7 to 15.4 m tall (Dirr 1990; Little 1950; Phillips and Gibbs 1953). It was first introduced into cultivation in 1900. Soapberry is planted for its environmental and wildlife value and, to a small extent, for shelterbelts in the southern plains (Tirmenstein 1990; Vora 1992). It is also a useful shade and ornamental tree in dry, windy, landscape sites (Khatamian and Abuelgasim 1986). The glossy, yellow fruit and long, pinnate leaves make it especially attractive. The fruit contains about 37% saponin and was used locally in the past for making soap (Tirmenstein 1990). The heavy, strong, close-grained wood splits into thin strips that have been used in basketry (Read 1974).

Flowering and fruiting. Western soapberry is described as polygamo-dioecious. That is, individual trees in a population may be truly dioecious (having only male or female flowers) or they may contain flowers with both male and female functions (Dirr 1990). The small, white flowers, borne in rather large clusters of terminal or axillary panicles, open during May to July (Read 1974). The fruit, a yellow, translucent, globular drupe measuring 10 to 14 mm in diameter, usually contains a single, dark brown, hard-coated seed (figures 1 and 2), but occasionally 2 or 3 seeds are present (Khatamian and Abuelgasim 1986; Preston 1940). The fruits ripen during September to October and persist on the tree until late winter or spring. Seedcrops are usually abundant each year (Engstrom and Stoeckeler 1941).

Collection, extraction, and storage. Fruits may be collected any time during late fall or winter by hand-picking or flailing them from the trees onto canvas. Although fruits are fairly dry by this time, they still need to be spread in shallow layers to keep them from heating. A bushel of fresh fruits from a central Oklahoma source had a calculated weight of 18.6 kg (41 lb) (Read 1974). Seed extraction is facilitated by sprinkling the fruits with water twice daily until pulp softens. Pulp can then be removed and floated away by running the fruits through a macerator with water. After drying, the seeds are ready for storage or use (Read 1974).

Forty-five kilograms (100 lb) of fruit will yield 13.6 to 16 kg (30 to 35 lb) of clean seeds (Read 1974) with a maximum of 37.2 kg (82 lb) reported (Swingle 1939). There are 950 to 1430 fruits/kg (430 to 650/lb) (Read 1974). Clean seeds per weight (based on 8 samples) varied from 1,510 to 4,360/kg (685 to 1,980/lb) (Engstrom and Stoeckler 1941; Read 1974; Swingle 1939). A fresh collection from central Oklahoma ran 1,540 seeds/kg (700/lb), with 104% moisture (percentage of dry weight) after 7 days of water-soaking followed by a de-pulping treatment (Reed 1974). Soundness of 12 samples averaged 77% (Read 1974). No data are available on seed longevity in cold storage, but it is likely that dry storage at low temperatures would be satisfactory.

Pregermination treatments. Germination of stored seeds may be slow and delayed. The chief cause is embryo dormancy, often accompanied by an impermeable seedcoat. Some seedlots require only stratification, whereas others

Figure 1—*Sapindus saponaria* var. *drummondii*, western soapberry: fruit and seed.

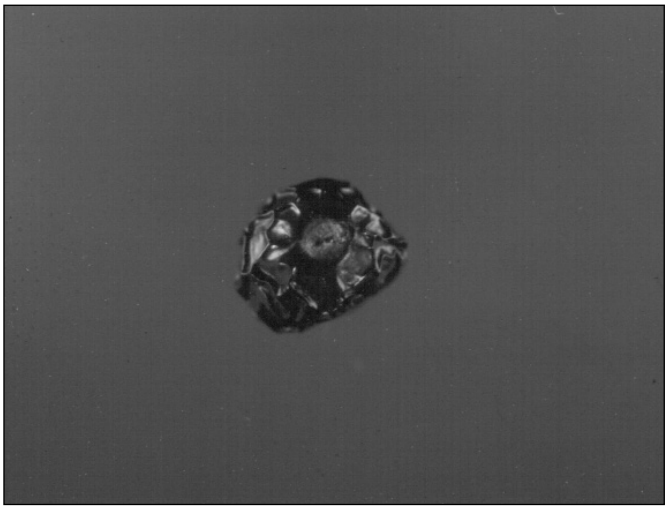
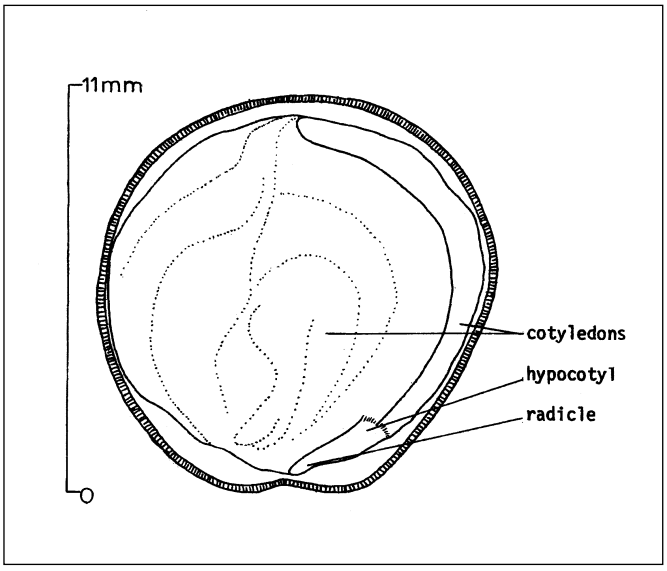


Figure 2—*Sapindus saponaria* var. *drummondii*, western soapberry: longitudinal section through a seed.



may need a prestratification treatment (Afanasiev 1942; Munson 1984; Vora 1989). Germination of western soapberry and other species in the genus may be improved by pretreatment with concentrated sulfuric acid (Munson 1984; Read 1974; Sheikh 1979; Vora 1989). The need for acid scarification can be determined by soaking a few seeds in cold water for 5 to 7 days. If the seeds swell, only stratification is needed. If the seeds remain small and hard, they should be pretreated with acid; however even seedlots responding to acid treatment contain some seeds that will germinate without treatment (Munson 1984; Vora 1989). The length of time that seeds need to be acid-scarified for maximum germination has varied among studies. Thirty to 45 minutes seems to be a minimum amount of time, with 60 to 180 minutes as times necessary for maximum germination (Munson 1984; Read 1974; Sheikh 1979; Vora 1989). Stratification following scarification may or may not improve germination. Hot water scarification and freezing seeds in conjunction with 90 days of stratification at 5 °C also improved germination but not as effectively as acid treatment with or without stratification (Munson 1984). A warm stratification of dried fruits for 6 to 10 weeks at 21 to 30 °C often has the same effect as pretreating cleaned seeds with acid. After such treatment, the pulp is decayed or partially decomposed and can be washed off without difficulty. Seedlots should then be stratified at a low temperature for 90 days (Afansiev 1942). Freshly collected, clean seeds germinated better without pretreatment (Read 1974).

Germination tests. Germination tests have been run in sand flats and combinations of peat moss and vermiculite at temperatures alternating diurnally from 20 to 30 °C (Munson 1984; Read 1974; Sheikh 1979; Vora 1989). Germination varies with quality of the seedlots. In addition, there will be large variability within a seedlot depending on pretreatment. For example, germination of acid-treated seeds was 88%; hot water–treated, 65%; frozen, 58%; and untreated, 44% (Munson 1984). In another comparison, germination of untreated seeds was 17% and acid-treated seeds about 70% (Vora 1989).

Nursery practice. Because western soapberry apparently varies considerably in seed hardness and response to pregermination treatments, examination tests before nursery sowing are essential. If seeds of freshly picked and dried fruits absorb moisture during 5 to 7 days of water soaking for de-pulping, they may be sown in the fall or spring with no further treatment. If seeds remain small and hard after water-soaking, they should be scarified for 2 to 2 $^1/_2$ hours unless previous tests have shown shorter times are better (Munson 1984) and stratified (60 to 90 days) to ensure adequate germination in spring-sowing. Seeds should be sown at a density of about 211 viable seeds/m^2 (20 seeds/ft^2) at a depth of 2 cm ($^3/_4$ inch) in a firm seedbed. Seedlings have a strong taproot, and top growth is slow in the nursery (Read 1974).

Seedlings can be grown in containers in a greenhouse environment. Davis and Whitcomb (1974) found that containers that were 6.35 cm^2 (2.5 in^2) top area and 15 to 30 cm deep (6 to 12 in)—with volumes of 605 and 1,210 cm^3 (37.5 and 75 in^3), respectively—were the most promising size. Seedlings grown in containers reached a height of 25 cm (9.8 in) in 80 days. Soapberry can also be propagated from stem cuttings (Dirr 1990; Dirr and Heuser 1987; Khatamian and Abuelgasim 1986).

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Chenopodiaceae—Goosefoot family

Sarcobatus vermiculatus (Hook.) Torr.

black greasewood

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Other common name. Greasewood.

Growth habit, occurrence and use. Black greasewood—*Sarcobatus vermiculatus* (Hook.) Torr.—is an erect to spreading, multi-branched, brittle, spinescent, and deciduous shrub that grows up to 2.5 m tall. It reproduces by seeds and by sprouting from its root crown and widespread root system (Branson and others 1967; Eddleman 1977; Robertson 1983). Black greasewood is widespread throughout western North America from southern Alberta, Saskatchewan, and British Columbia to Texas, northern Mexico, and eastern California (Branson and others 1967; Munz 1973; Stephens 1973; Stubbendieck and others 1994). Rickard (1982) classified this species as a phreatophytic halophyte–osmophyte. The shrub may grow on sandy soils in the northeastern part of its range (Stephens 1973), but it is most commonly associated with heavy textured soils of high salt content (0.05 to 1.6%) on flood plains that are either subject to periodic flooding or have a water table less than 10.5 m deep. Black greasewood frequently occurs in nearly pure stands in saline conditions. It also grows in nearly all the less-saline salt desert shrub types (Eddleman 1979; Robertson 1983; Romo and Eddleman 1985; Shantz and Piemeisal 1940). A narrow endemic form found in western Nevada—*S. vermiculatus* var. *Baileyi* (Cov.) Jep.—is recognized by Kartesz (1987) and Munz (1973), although it appears to integrate with the typical form.

Black greasewood is used as wood for fuel and the sharpened spines were used for painting by Native Americans (Stubbendieck and others 1994). Seeds, leaves, and new leaders are consumed by a variety of small mammals (Van Dersal 1938). It is an important browse plant and is rated from good to useless as forage for cattle, sheep, and big game animals in the winter and provides good cover and food for small mammals and birds (Blauer and others 1976). Sheep have been poisoned by rapidly consuming large amounts of new leader growth, which contains high levels of soluble oxalate (Kingsbury 1964; Stubbendieck and others 1994).

Flowering and fruiting. Black greasewood is usually monoecious, with the staminate flowers borne as catkin-like axillary spikes. Solitary green pistillate flowers are borne in leaf axils below staminate catkins (Munz 1973; Welsh 1987). Flowering occurs as early as June and as late as August (Eddleman 1979; Munz 1973; Romo 1985). The perianth is persistent, forming a circular winged coriaceous utricle containing an achene (figure 1). Achenes are composed of a thin outer membranous pericarp surrounding a coiled embryo (figure 2). Mature utricles are tan to light brown. Not all fruits ripen at the same time. Earliest maturation may be in late September; all fruits reach maturity by late November. Fruit dispersal begins in late September and may extend over the winter with a few fruit remaining on the plant in early summer the following year (Eddleman 1977, 1979; Romo 1985).

Collection, extraction, and storage of fruits. Mature fruits can be knocked from the plant with a flail. The best time for harvest is late October through November. A flail or de-winger can be used to remove the wings from well-dried fruits, which after being run through a fanning mill or seed

Figure 1—*Sarcobatus vermiculatus*, black greasewood: winged and de-winged utricles.

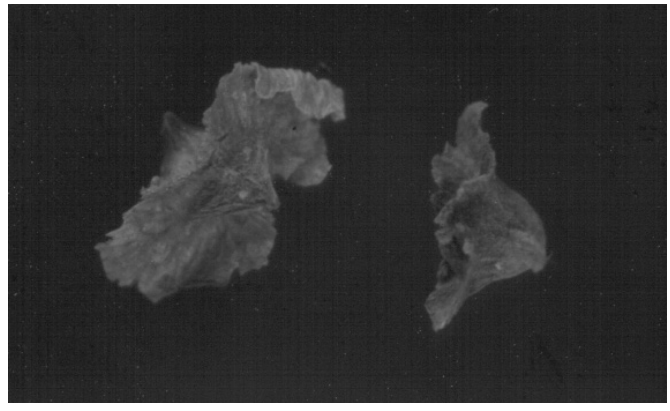
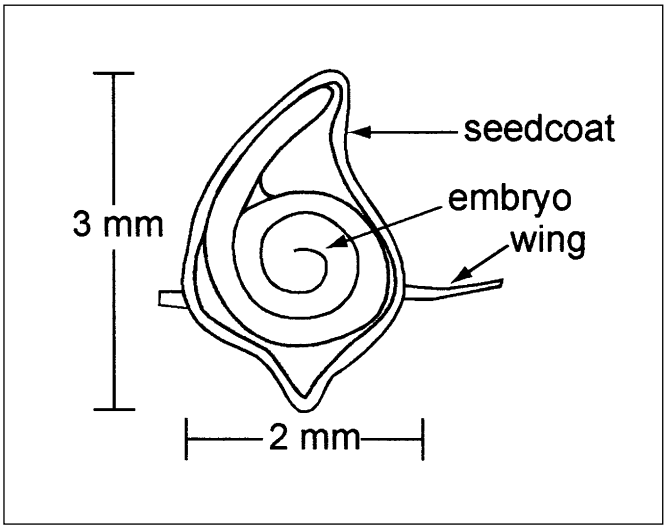


Figure 2—*Sarcobatus vermiculatus*, black greasewood: longitudinal section through a utricle with bracts removed.



blower can yield good-quality seedlots (Eddleman 1977; Romo 1985). Cleaned seeds number from 425 to 628/g (193,000 to 285,000/lb) (Blauer and others 1976; Eddleman 1977, 1979; Romo 1985).

Germination tests. Seeds germinate well at cooler temperatures and rates of germination are high (table 1). Laboratory tests have shown optimum germination temperatures range from 10 to 25 °C (Eddleman 1979; Robertson 1983; Romo and Eddleman 1985; Romo and Haferkamp 1987; Sabo and 1979). Seeds from New Mexico germinated poorly at temperatures above 19 °C; seeds from Montana germinated at temperatures ranging from 5 to 40 °C. In the latter case, high temperatures (especially those above 25 °C) reduced both germination rate and percentage germination and abnormal seedlings developed (Romo and Eddleman 1985). Seeds from an Oregon source germinated best at 20 °C (Romo and Haferkamp 1987).

Stratification does not appears to be necessary, but incubation at 4 °C for 30 or 60 days may improve percentage germination at warmer temperatures (Eddleman 1979). Seeds germinate well at 30 to 60 days following maturation. Long viability is possible: seeds stored in the laboratory for 4 years reached germination of 70% in 4 days (Eddleman 1982). Romo and Eddleman (1985) have made the distinction between viable embryos (that is, the imbibed radicle tip is white) from non-viable embryos (that is, the imbibed radicle tip is brown). It is uncertain whether removal of the bracts (wings) affects germination. These bracts contain high levels of sodium which is rapidly absorbed by the seedling, presumably as a means of adjusting its osmotic potential to cope with saline conditions during establishment (Eddleman and Romo 1987; Rickard 1982; Romo and Eddleman 1985).

Table 1—*Sarcobatus vermiculatus*, black greasewood: germination tests, conditions, and results

Seed source	Germination test conditions			Germination rate		Average % germination	Samples
	Medium	Temp (°C)	Days	Amt (%)	Days		
Montana	Kimpak	10	30	67	2	100	4
Montana	Kimpak	10	30	91	10	98	4
	—	5–25	30	—	—	80–93	4
New Mexico	Filter paper	11	25	—	—	100	—
		11	26	66	4	88	3

Sources: Eddleman (1979), Romo and Eddleman (1985), Sabo and others (1979).

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Lauraceae—Laurel family

Sassafras albidum (Nutt.) Nees

sassafras

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Synonyms. *Sassafras albidum* var. *molle* (Raf.) Fern., *S. sassafras* (L.) Karst., *S. officinale* Nees & Eberm.

Other common name. white sassafras.

Growth habit, occurrence, and use. Sassafras—*Sassafras albidum* (Nutt.) Nees—is a short to medium-tall, deciduous tree that is native from southwestern Maine to central Michigan and southeastern Iowa, and south to east Texas and central Florida. It is little more than a shrub at the northern portion of its range, but on more fertile sites, trees may reach heights of 30 m at maturity. Sassafras is valuable for timber and wildlife. The light brown wood is soft, lightweight, and very durable. Bark from the roots has been used for making tea, sassafras oil, and perfume for soap and other articles. There is some evidence that extracts of the roots have some insecticidal properties (Jacobson and others 1975). The species has been cultivated since 1630 (Griggs 1990; Little 1979).

Flowering and fruiting. The dioecious, greenish yellow flowers, 12 mm in length, are borne in 5-cm-long axillary racemes in March and April as the leaves appear. The drupaceous fruits are borne on thick red pedicles in clusters (Vines 1960). The single-seeded drupes are ovoid, dark blue, and about 8 to 13 mm long (figure 1). The pulpy flesh covers a hard, thin endocarp that encloses the seed (figure 2). The fruits mature from June to September, depending on latitude, and are dispersed within a month. Primary dispersal is by birds, which often eat the fruits before they fall (Little and Delisle 1962). Minimum seed-bearing age is 4 years for open-grown trees (Halls 1973), and good crops are produced every 1 or 2 years (Bonner and Maisenhelder 1974).

Collection, extraction, and storage. Fruits may be picked from the trees or knocked onto sheets of plastic or canvas by flailing the branches. The fruits are green before maturity, and the change to dark blue indicates that they are ready for collection (Bonner and Maisenhelder 1974). The pulpy flesh is usually removed before storage or sowing by rubbing the fruits over hardware cloth by hand or by breaking them up with mechanical macerators and washing the debris away with water. In the South, there are about 6,200 fruits/kg (2,800/lb) (Halls 1973). In the North, seeds collected and cleaned averaged 13,000/kg (5,900/lb). In Pennsylvania, 45 kg (100 lb) of fruit yielded about 14 kg (31 lb) of cleaned seeds (Bonner and Maisenhelder 1974).

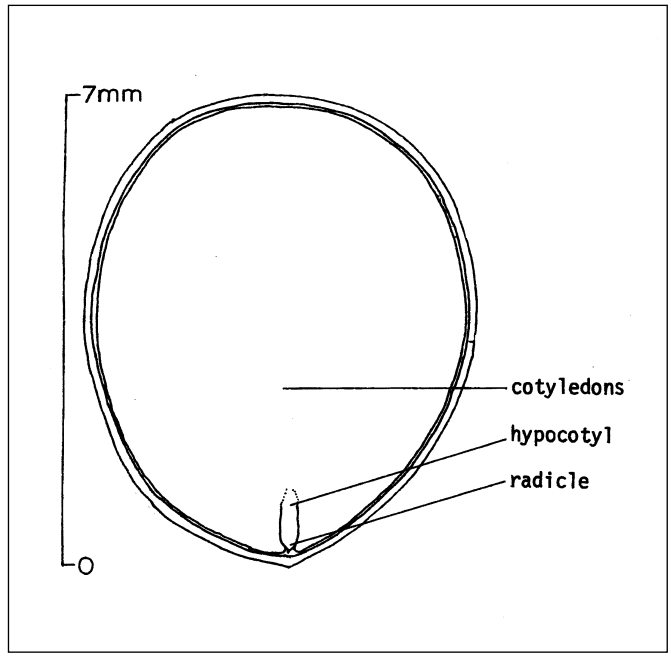
There are no known storage tests for sassafras, but the seeds can apparently be stored successfully for a few years at 2 to 4 °C and low moisture contents (Bonner and Maisenhelder 1974). This behavior should place sassafras in the orthodox seed storage grouping, although the very high lipid content (47%) of the seeds (Bonner 1971) suggests that long-term storage would be difficult. Soil seedbank studies have demonstrated that seeds buried in litter retained viability for 4 years in Louisiana (Haywood 1994) and for 6 years in West Virginia (Wendel 1977).

Figure 1—*Sassafras albidum*, sassafras: fruits and seed (**lower right**).

Germination. Sassafras seeds exhibit strong embryo dormancy, which can be overcome with moist stratification at 2 to 4 °C for 120 days. Germination can be tested in moist sand or other media at temperatures of 22 to 30 °C for up to 120 days. The common laboratory test regime of alternating 20/30 °C will probably produce good results also.

Nursery practice. Although sowing has been done with both cleaned and uncleaned seeds and dried fruits, better results were obtained with cleaned seeds. Because seeds sown early in the fall often germinate before cold weather, unstratified seeds should be sown as late in the fall as possible. It may be necessary to store the seeds for a short period between collection and fall-seeding. Stratification is recommended for seeds to be sown in the spring. The seeds should be drilled in rows 20 to 30 cm (8 to 12 in) apart and covered with 6 to 12 mm ($^1/_4$ to $^1/_2$ in) of firmed soil. Beds should be mulched with burlap, straw, or leaf mulch held in place by bird or shade screens until after spring frosts (Bonner and Maisenhelder 1974). Sassafras can also be propagated by layering and by root cuttings (Dirr and Heuser 1987).

Figure 2—*Sassafras albidum*, sassafras: longitudinal section through a seed.



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Anacardiaceae—Sumac family

Schinus L.

peppertree

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Growth habit, occurrence, and use. There are 3 species of the genus *Schinus* that have been introduced into the United States (table 1). They are members of the Anacardiaceae family and closely related to poison ivy—*Toxicodendron radicans* ssp. *radicans* (L.) Kuntze. Peruvian peppertree is native to South America and is grown in Mediterranean climates in Europe and in USDA Hardiness Zone 9 in North America. It has been naturalized in southern California for 100 to 200 years (Nilsen and Muller 1980b). This species is grown as an ornamental and is popular for its gnarled trunk and branches, with droopy, weeping branchlets and cascades of red berries. The trees reach a height and equal spread of 35 to 40 feet in 20 years (Johnson 1973).

Although early reports (Nilsen and Muller 1980a&b) stated that Christmasberry tree had not become naturalized, it has since widely naturalized in peninsular Florida and Hawaii. Its common name is derived from its use in making Christmas wreaths. The plant was first introduced in the United States in 1898 (Morton 1978). Unfortunately, many landowners who planted it as an ornamental have found that in a few years the tree outgrows its allotted space and is difficult to prune or cut down because of its tangle of branches. Mockingbirds (*Mimus polyglottis*), cedar waxwings (*Bombys cedrorum*), and robins (*Turdus migratorius*) feed on the berries and then drop the seeds in harvested fields, pastures, roadsides, canal banks, pinewoods, and hammocks (Morton 1978). Chrismasberry tree now covers thousands of acres in south and central Florida and the Florida Keys (Ewel 1979, 1986; Ewel and others 1989; Lemke 1992; Workman 1979). The plant has been designated a noxious weed throughout the Hawaiian Islands (Morton 1978). In California, it is recommended for planting in substitution for Peruvian peppertree, which is a host of black scale (*Saissetia olea* Oliver), an enemy of the citrus industry (Morton 1978).

The leaves, wood, and berries of Christmasberry tree are toxic to humans, animals, and birds. In Florida, a fine, itching body rash, with swelling of the face and eyelids, is commonly experienced by anyone who cuts down the tree or cuts off even a single branch while the tree is in bloom (Morton 1978). Children who ingest the berries experience digestive upsets and vomiting, along with a rash and swelling of the hands, arm, and face. Calves that have eaten the leaves develop enteritis, a swollen head, and hemorrhages in the eyes. Goats are immune to the tree's effects. Birds that feed excessively on the berries become intoxicated and unable to fly.

Most widespread are the respiratory difficulties that occur when the tree is in bloom. The airborne chemical from the blooms causes sinus and nasal congestion, rhinitis, headache, sneezing, eye irritation, tightness in the chest, and labored breathing (Morton 1978). Physicians are sometimes successful in relieving their patients' symptoms by administering desensitization injections of extracts made from the inflorescences.

Table 1—*Schinus*, peppertree: nomenclature and occurrence

Scientific name	Common name(s)	Occurrence
***S. molle* L.**	**Peruvian peppertree,** *molle, pirul,* California peppertree, Peruvian mastic tree	Andes of Peru; naturalized in S California
***S. polygamus* (Cav.) Cabrera**	**peppertree,** *huigen*	W South America
***S. terebinthifolius* Raddi**	**Christmasberry tree**	Brazil; naturalized in S Florida & Hawaii

Source: LHBH (1976), Wasson (2001).

The eradication of the larger trees by harvesting for pulpwood has been explored. The strength properties of the pulp are low: 40 burst factor, 70 tear factor, 8,500 tensile strength (Morton 1978). The fibers are about 0.8 mm long. The strength characteristics of Christmasberry tree would rank it with the poorest of native hardwoods and the extractives could pose a serious processing problem.

Flowering and fruiting. The leaves have 3 to 13 sessile, finely toothed leaflets 2.5 to 5 cm long that are dark green above and paler underneath (Morton 1978). The ivory white flowers are borne profusely in racemes or panicles up to 15 cm long along the outer branches and at the branch tips. The flowers have 5 petals about 3 mm wide and 10 stamens situated on a 5-parted calyx (LHBH 1976). *Schinus* species are dioecious. Peruvian peppertree flowers yield a small amount of nectar for bees, but the species is important because it has a long flowering period (mainly of the male flowers) (Eisikowitch and Masad 1980).

The fruit is a 1-seeded drupe borne in compact masses. At first the berry is green and juicy, then it turns bright red on ripening and dries and remains on the tree for weeks (Johnson 1973).

Extraction and storage. Fruits of Christmasberry tree are collected by hand in the winter before Christmas, then dried and sold in the United States as a spice called "pink peppercorn" (Jones and Doren 1997). Seeds can be collected anytime between January and February by cutting the branches and stripping the berries from the branch (Perekins 2002). Fruits may persist on the shrub until May. A macerator is used to remove the sticky pulp. The seeds are surface-dried naturally by the sun until dry to the touch (Anderson 2002).

Christmasberry tree produces 54,400 cleaned seeds/kg (24,675/lb); Peruvian peppertree and peppertree yield 22,000 cleaned seeds/kg (9,980/lb). Viability of seeds may be maintained by storage at 3 °C or lower and 30% humidity (Eizenbrand 2002). In California, Christmasberry tree seeds can be stored for up to 60 to 90 days in cold storage (Anderson 2002). After 6 months of storage, the germination drops off 50% or more. At room temperature, the seeds grow mold, so cloth or polypropylene bags are used for seed storage to allow air to circulate (Anderson 2002).

Germination tests. The seed germination characteristics that differentiate Peruvian peppertree and Christmasberry tree may be the factors inhibiting the naturalization of Christmasberry tree in southern California (Nilsen and Muller 1980). The latter species may be excluded from the California vegetation because of its slow germination rate, which could preclude its establishment during the periods of brief rainfall and intermittent drought (Nilsen and Muller 1980).

Germination treatments carried out in the dark at 24 °C were performed on the seeds of both species. Peruvian peppertree seeds germinate best after soaking for 5 minutes in a 10% solution of sulfuric acid (H_2SO_4) (Nilsen and Muller 1980); imbibition for 24 hours and stratification (30 days at 2 °C) did not break dormancy in seeds of this species.

Seeds of Christmasberry tree germinate equally well with imbibition or acid treatment, and a significant amount of germination occurred after 30 days of 2 °C stratification (Nilsen and Muller 1980). Seeds of Peruvian peppertree are more inhibited by cold conditions than are those of Christmasberry tree. Seeds of neither species germinated when incubated to 70 °C for 1 hour. Laboratory germination of Peruvian peppertree began on the 17th day and that of Christmasberry tree began on day 28.

Germination tests performed in native soil delayed germination of Peruvian peppertree and inhibited that of Christmasberry tree. In both greenhouse soil mix or field soil, seeds of Peruvian peppertree germinated better than those of Christmasberry tree, except when seeds were germinated in a winter-regimen growth chamber (15/2 °C) (Nilsen and Muller 1980a).

Nursery practices. *Schinus* seeds are usually grown in pots filled with sandy clay loam. In southern California, the seeds germinate in the winter at about 50% relative humidity and 18/10 °C temperatures (Nilsen and Muller 1980a). Christmasberry tree has a higher root net accumulation ratio, which gives it a greater drought tolerance than Peruvian peppertree. Both *Schinus* species show positive relative growth rates within and below the common irradiances under canopies of southern California coastal communities (Nilsen and Muller 1980a).

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Taxodiaceae—Redwood family

Sciadopitys verticillata (Thunb.) Sieb. & Zucc.

umbrella-pine

Paul O. Rudolf and Peyton W. Owston

Dr. Rudolf (deceased) retired from the USDA Forest Service's North Central Forest Experiment Station; Dr. Owston retired from the USDA Forest Service's Pacific Northwest Research Station

Growth habit, occurrence, and use. Native to the mountains of central and southern Japan at elevations of 200 to 1,500 m, the umbrella-pine (also known as Japanese umbrella-pine or parasol-pine)—*Sciadopitys verticillata* (Thunb.) Sieb. & Zucc.—is a pyramidal conifer from 20 to 40 m tall. It is most commonly grown in the United States for ornamental purposes, but it is also planted for erosion control. In Japan, the decay-resistant wood is used for lumber and the bark provides oakum for calking boats (Bailey 1939; Dallimore and Jackson 1967; McClintock 1992; Rehder 1940). Umbrella-pine is the only species in its genus.

Flowering and fruiting. Flowers of both sexes occur at the ends of branchlets in the spring. The male flowers are in clusters and the female flowers, which develop into ovoid cones, are solitary. When the cones ripen in the fall of the second season, they become gray-brown and are about 76 to 127 mm long and 38 to 51 mm wide. Each cone scale bears 5 to 9 ovoid, compressed, narrowly winged seeds (figure 1) about 13 mm long (Dallimore and Jackson 1967; McClintock 1992; Rehder 1940).

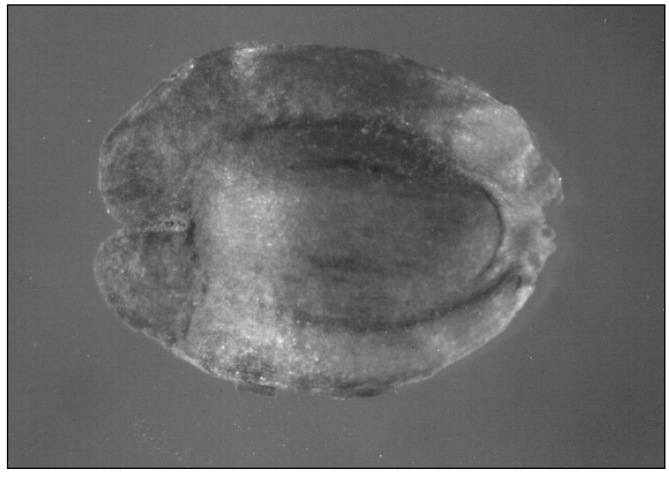
Collection of fruits; extraction and storage of seeds. Ripe cones may be picked in the fall from the trees and placed in a warm, dry place to open; seeds are removed by shaking and then de-winged. Numbers of cleaned seeds per weight ranged from 32,600 to 42,800/kg (14,800 to 19,400/lb) and averaged about 38,150/kg (17,300/lb) in more than 30 samples. Purity averaged 96% in 10 samples (Rafn and Son nd; Swingle 1939). Seeds stored at moisture contents of 10% or less in sealed containers at temperatures of 5 °C or lower will probably retain good viability for at least 2 years. Long-term storage data are not available, but the seeds appear to be orthodox in storage behavior.

Pregermination treatments. The existing literature is somewhat contradictory. Some authors report reasonable success with 100 days of stratification in moist sand at 17 to 21 °C (Swingle 1939); 90 days of stratification in moist, acid peat at 0 to 10 °C (Barton 1930); and 1 month of stratification at 25 °C followed by 4 to 5 months at 2 °C or a constant 2 °C for 5 to 6 months (Asakawa 1973). Asakawa (1973) also obtained germination rates between 56 and 70% of filled seeds without prechilling. He concluded that their dormancy is not deep.

On the other hand, Hatano (1972) states that it is "well known" that the seeds are deeply dormant and that the dormancy is difficult to break with stratification. He tried a number of pretreatments, including pre-chilling and seedcoat treatments. The only success he had was with 24 hours of pretreatment with 0.02 to 0.10% silver nitrate before stratification, and that success was partial and varied (from 1 to 65% germination).

Germination tests. Germination of umbrella-pine seeds seems to require 2 months or more, even after pretreatment (Asakawa 1973). Germination of pretreated seeds can be tested in germinators or sand flats at a temperature of about 20 °C (night) to 30 °C (day) for 60 to 75 days. Average germination in 14 early tests was 45% (Barton

Figure 1—*Sciatopitys verticillata*, umbrella-pine: seed



1930; Rehder 1940; Waxman 1957). Waxman (1957) obtained best results (76% in 77 days) when seeds were germinated on a sand surface under mist with 9 hours of light daily. In a later test, Asakawa (1973) obtained up to 76% germination on agar with 8 hours of light. Germination is poor in continuous light (Asakawa 1973; Hatano 1972).

Nursery practice. The seeds should be sown in the fall or stratified for sowing in the spring. Umbrella-pine is not easy to grow and is extremely slow-growing when propagated from seeds (Halladin 1991). It has a tendency to form several leaders. Field planting has been done with 3+2 and 4+2 stock (Dallimore and Jackson 1967). Umbrella-pine can also be propagated by layers or by cuttings of half-ripened wood in summer (Bailey 1939). A nursery in Oregon propagates solely by cuttings because of faster results; Halladin (1991) describes the technique in detail.

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Fabaceae—Pea family

Senna armata (S. Watson) Irwin & Barneby

senna

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Synonyms. *Cassia armata* S. Watson

Other common names. spiny senna, armed senna, bladder senna, partridge pea.

Growth habit, occurrence and use. The genus *Senna* can be found in herb, shrub, or tree form with even-pinnate leaves; although generally unarmed, it may have weak spines. This large genus is found in the American tropics, temperate zones, and occasionally, the desert (Jepson 1993). This discussion will focus on the Mojave and Colorado species of senna—*Senna armata* (S. Wats.) Irwin & Barneby—which has grooved prominent branches with inconspicuous leaves (Benson and Darrow 1954). The inflated tubular hairs that cover the stem slow air movement, providing some protection against the hot drying air (Bainbridge and Virginia 1989). Senna is common on road berms and edges, preferring a well-drained, gravelly soil (CALR 1995). Senna is an attractive shrub that should be given greater attention in landscaping (Perry 1987).

Flowering and fruiting. Flowers are yellow to salmon in color with a pleasant fragrance, occurring solitary or several in the axils of the upper leaves (Kay and others 1977). Blooms appear in May to July. The linear, light tan legumes (pods) are 2.5 to 4 cm long and may be somewhat constricted between seeds (Kay and others 1977). Seeds (figures 1 and 2) have a thick, grayish membrane covering a brown surface and are irregularly obovoid, 7 to 9 mm long (Kay and others 1977).

Collection, extraction, and storage. Seeds may be hand-picked, usually beginning in June and July when they ripen. They should collected from the bushes, not the ground, to avoid insect infestations. Seed collection must be timed to gather the ripe seeds before they attract small rodents and are eaten by them. Seeds should be dried, then cleaned; freezing may be used to kill pests (Bainbridge and Virginia 1989). Kay (1975) used a belt harvester and fanning mill with a 5.6-mm (#14) top and 7.1-mm (#18) bottom seed-cleaning screens to extract and clean seeds. Yields were 38,800 seeds/kg (17,600 seeds/lb), 94% undamaged.

Figure 1—*Senna armata*, senna: mature seed.

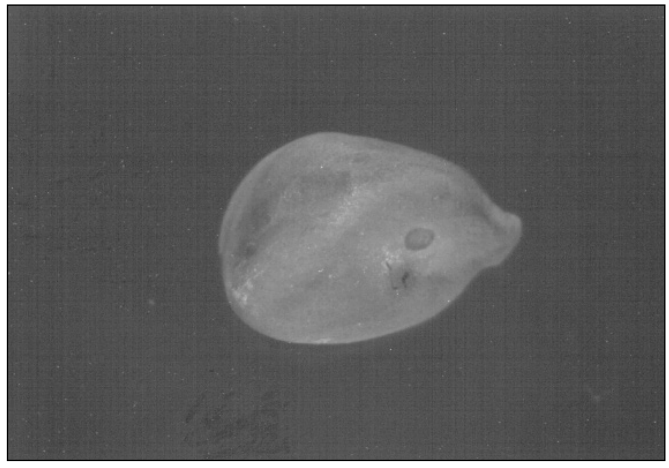
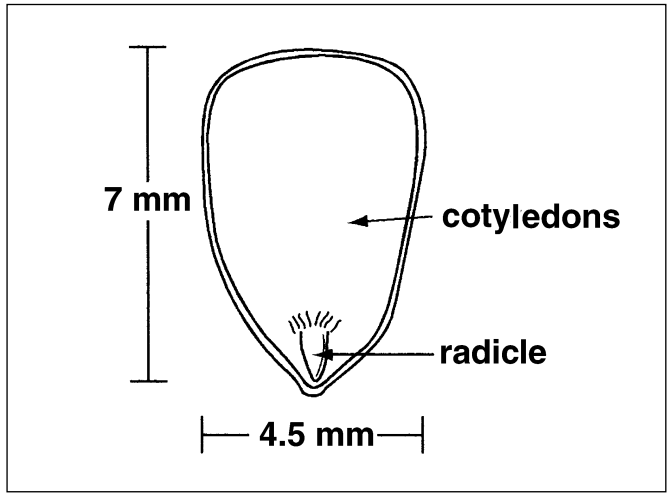


Figure 2—*Senna armata*, senna: longitudinal section through a seed.



The seeds are orthodox in storage behavior. In long-term storage trials by Kay (1988), seeds were stored at room tem-

perature, 4 °C, –15 °C, and in warehouse conditions, with germination rates tested annually over 14 years. The results indicated that, as is common with many legumes stored under low moisture conditions, the already high percentage of hard seeds can increase in cooler temperatures. Bainbridge and Virginia (1989) observed that storage was best in mesh bags stored in a warehouse. In Kay's experiments, decreases in germination rates in sealed containers may reflect some need for after-ripening.

Pregermination treatments. According to Stark (1966), no seed treatment is required for senna, and planting done under optimal conditions produces germination in 2 to 5 days. At the U.S. Department of the Interior, National Park Service's Joshua Tree National Park (JTNP), seeds have been germinated using a 1-hour soak in water or a 1:1 bleach–water solution, followed by leaching for 12 to 24 hours. This method has produced an average germination rate of 50%.

Germination tests. Germination tests at JTNP include direct-sowing to blotter paper, soaking overnight in cold water, and soaking initially in cold water followed by overnight leaching. All 3 methods had moderate success, indicating that no treatment is necessary when seeds are placed directly onto moist toweling; average germination 50% (CALR 1995). Other trials by Kay and others (1988) refer to initial germination of seeds using 4 replications of 100 seeds in damp paper toweling placed in a growth chamber at 15 °C. Test conditions were maintained for 28 days, with germination percentages recorded every 7 days; initial germination rate for senna was 75%. Germination tests, conducted annually to test the effects of storage, were then averaged to a "best germination" of 92%. These annual tests consisted of 4 replications of 50 seeds using the same initial testing methods. The effects of temperature on germination rates were also tested, with the following results (Kay and others 1988):

Temperature (°C)	2	5	10	15	20	25	30	40
Germination (%)	0	0	19	41	46	20	28	0

Nursery practice and seedling care. In direct-seeding trials, germination in Nevada seedlots was best at 15 to 20 °C, but seeds collected at lower elevations may need higher temperatures; no germination was observed at 5 or 40 °C (Bainbridge and Virginia 1989). Nursery stock has been outplanted at JTNP using 3.8-liter (1-gal) and 6.8-liter (1.8-gal) containers that were 35 to 37 cm (14 to 15 in) deep. The plants monitored after 10 months (before late winter precipitation) had respective survival rates of 7 and 14% (CALR 1995). Monitoring continues at the site, and figures may be different after the winter and spring rains. Senna seedlings were noted to be susceptible to rot and should be planted into a well-drained soil with conservative watering (CALR 1995).

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Taxodiaceae—Redwood family

Sequoia sempervirens (Lamb. ex D. Don) Endl.

redwood

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Other common names. coast redwood, California redwood.

Growth habit, occurrence, and use. Redwood is one of the largest trees in the world. It commonly grows to 60 to 84 m in height and 2.4 to 3.6 m in diameter, with the current champion reaching 101 m in height (Van Pelt 2001). Its relatively shallow but wide-spreading root system rises into a buttressed and somewhat tapering trunk that supports a short, narrowly conical crown (Harlow and Harrar 1969). Individual trees can live 2,000 years or longer. It grows naturally in the summer fog belt of the coastal range from Little Redwood Creek on the Chetco River in southwestern Oregon to Salmon Creek in the Santa Lucia Mountains of southern Monterey County, California. This redwood belt is an irregular coastal strip about 725 km long and 8 to 56 km wide (Roy 1966). Elevation ranges from sea level to 915 m and averages from 635 to 3,100 mm annual precipitation, most of it falling as winter rain (Olson and others 1990).

Redwoods reach their maximum development in the northern part of their range, where the climate is cool and moist and sedimentation from successive floods has created deep fertile alluvial flats. They are smaller and give way to other species as altitude, dryness, and slope increase (Olson and others 1990). Since 1843, redwood has been cultivated outside its natural range, in parts of Europe and New Zealand (Boe 1974; Olson and others 1990).

The wood is used where decay resistance is important. It is made into lumber, plywood, pulpwood, grape stakes, fencing, roof shakes, and other specialized products. Bark is used for insulation and garden mulch (Boe 1974; Harlow and Harrar 1969; Olson and others 1990).

Flowering and fruiting. The tiny male and female flowers grow separately on different branches of the same tree. Ovulate conelets lead to broadly oblong cones with thick scales that are closely packed, woody, and persistent. Each cone scale bears a crescent-shaped row of ovules (Buchholz 1939). Flowering may occur over several months from November to March (Metcalf 1924), but ovules are usually fertilized in May (Buchholz 1939). Dry weather during pollination permits better pollen dispersal and improves seed viability (Olson and others 1990). Cone ripening time can range from late September to mid-January, depending on latitude, elevation, and weather (Lippitt 1996).

Trees begin to bear seeds at 5 to 15 years of age (Boe 1974). Good seedcrops occur every 5 to 7 years (Lippitt 1996), with light crops intervening. Fair to abundant crops occurred for 5 consecutive years in north-coastal California (Boe 1968); however, this is unusual (Lippitt 1996). Further south in the redwood type, some stands produce seed poorly and irregularly, whereas others frequently have fair to abundant crops (Muelder and Hansen 1961). A mature seed has a brown wing and a slightly darker seedcoat. The wing, which is part of the seedcoat, is about equal in width to the seed (figure 1). Embryos have 2 cotyledons (figure 2). Opened cones often persist through the next growing season (Boe 1974). Cones have the following quantitative characteristics (Lott 1923; Munz 1959; Olson 1990; Roy 1965):

Seeds per cone scale	2–5
Average seeds per cone	60
Cone length	1.3–2.8 cm
Cone diameter	1.3–2.5 cm
Average fresh cones per weight	500/kg (227/lb)

Because of the polyploid chromosomal make-up of redwood, care should be taken to avoid in-breeding in seed orchards. Seedlings from self-crossed seeds had lower nursery survival under stress and grew slower in the field than those from out-crossed seeds (Libby and others 1981).

A technique for making controlled pollinations on detached redwood cuttings has become practical. Pollination was most effective when dry pollen was brushed between the open scales of the female strobili. In subsequent years, cuttings that have rooted successfully can be pollinated and will produce viable seeds (Libby and McCutchan 1978; Libby and others 1972).

Figure 1—*Sequoia sempervirens*, redwood: seed.

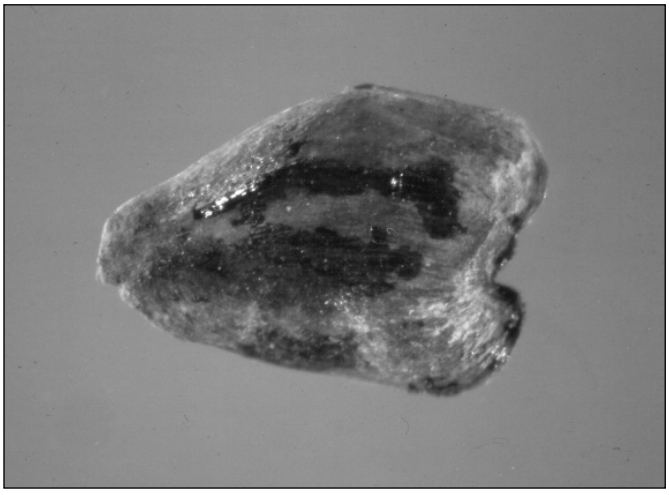
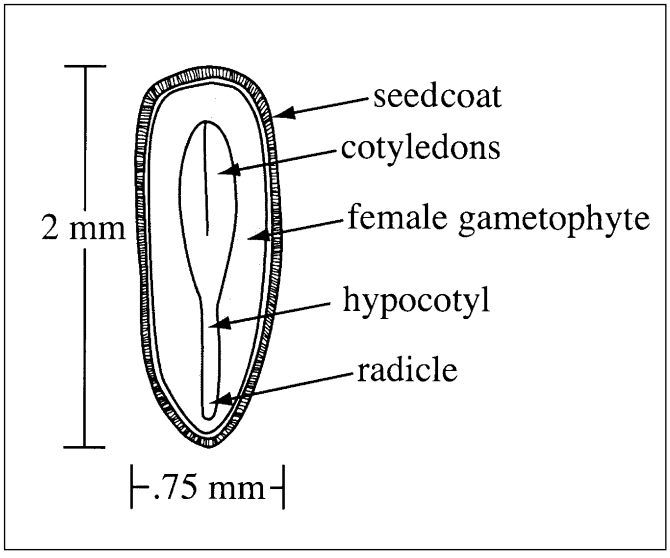


Figure 2—*Sequoia sempervirens*, redwood: longitudinal section through a seed.



Collection of cones and extraction of seeds. Seeds are mature when cone color changes from green to greenish yellow or when cone scales slightly separate (Roy 1965). In the northern part of the redwood's range, cone collections should begin in October (Lippitt 1996). Natural seed dispersal proceeds rapidly after October, reaching a peak from November to February (Boe 1968).

Cones can air-dry in 5 to 8 days at 21 to 24 °C with good air circulation (Lippitt 1996). Large nurseries use a kiln set at 38 to 43 °C to open cones in 24 hours (Lippitt 1996). Seeds are extracted with a screen tumbler. At the L.A. Moran Reforestation Center, Davis, California, the seedlots are repeatedly passed through a 4-way air separator to obtain a high percentage of filled seeds with high germination rate. Experience with a magnified x-ray makes it possible to distinguish tannin-filled seeds and filled but less viable seeds from seeds that will produce vigorous germinants.

The following seed data have been noted by Lippitt (1996) for cleaned seedlots:

Cleaned seeds per weight		
Low	167,372/kg	(75,920/lb)
High	259,297/kg	(117,617/lb)
Average (N = 37)	194,000/kg	(88,000/lb)
Purity	98%	
Germination	60%	

Storage of seeds. Redwood seeds are orthodox in nature and store well for long periods of time. The L.A. Moran Reforestation Center of the California Department of Forestry and Fire Protection has stored seeds with 5 to 9% water content at –17.8 °C for over 10 years with no loss in viability (Lippitt 1996). Storage of seedlots above freezing has not been successful (Boe 1974; Metcalf 1924; Olson and others 1990; Schubert 1952).

Germination. A 5-year record of seed dispersal in old-growth redwood showed that, of the total seeds dispersed, only 2.5 to 12.4% were sound (Boe 1968). In seeds collected from branch cuttings, Libby and others (1972) measured percentage germination at 5 to 21%. Identification of unsound seeds is often difficult because many seeds that appear to be good are actually filled with tannin (Olson and others 1990). Germination is readily tested in covered petri or plastic dishes on filter paper, vermiculite, or Sponge Rok®. Satisfactory germination has been obtained at a constant temperature of 21 °C as well as at temperatures alternating diurnally from 30 to 20 °C. The International Seed Testing Association (ISTA 1993) prescribes the alternating temperatures on the top of moist paper for 21 days; no pretreatment is needed. Germination speed can be increased by soaking the seeds overnight in aerated water (Olson and others 1990). Germination is epigeal.

Germination capacity has typically been low in the past, but this can be corrected by thorough seed processing. Redwood seed germination can be improved by 24 hours of water soaking followed by 4 weeks of stratification (Lippitt 1996).

Nursery practice and seedling care. Redwood seeds may be sown from March to May. Seeds are sown by drilling to a depth of 3 mm ($^1/_8$ in) and at a rate calculated to give a density of 323 seedlings/m^2 (30/ft^2) for either 1+0

or 2+0 planting stock. All seedbeds are fumigated as standard practice. Mineral soil provides the best seedbed, but seeds will germinate in duff, on logs, and on most moist surfaces. Seeds can germinate in either shade or sunlight (Olson and others 1990), but frost protection is important (Lippitt 1996). Redwood seedlings need a greater supply of soil water than most associated species (Fritz 1966). The roots lack root hairs and, therefore, are not efficient in extracting water from the soil (Olson and others 1990). If the seeds are sown in fumigated beds, the beds should be inoculated with endomycorrhizae (Lippitt 1996). From 10 to 20% of the seedlings may be culled at the time of lifting (Boe 1974). Redwood seedlings are especially susceptible to damping-off, which is caused by gray mold (*Botrytis cinerea* Pers.:Fr.) and a blight caused by *Cercospora sequoiae* Ellis & Everh. (Sinclair and others 1987).

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Taxodiaceae—Redwood family

Sequoiadendron giganteum (Lindl.) Buchholz

giant sequoia

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Synonyms. *Sequoia gigantea* (Lindl.) Decne., *Sequoia washingtoniana* (Winslow) Sudw.

Other common names. bigtree, Sierra redwood.

Growth habit, occurrence, and use. This species grows to heights exceeding 76 m in central California on the western slopes of the Sierra Nevada in more or less isolated groves at 1,400 to 2,300 m of elevation. Its north–south range is about 420 km (Schubert and Beetham 1965; Weatherspoon 1990). It has been cultivated rather widely since 1853 for landscaping, watershed planting, and lumber (Boe 1974).

Geographic race. On the basis of differences of cotyledon number, isoenzyme allele frequencies, variation in germination percentage, and observed heterozygosity in 35 natural populations, a level of genetic variation was detected. Relatively higher levels of heterozygosity were found in the southern parts of the range, suggesting different local selection pressures. Low heterozygosity among embryo samples suggests that inbreeding and/or population substructuring has taken place (Fins and Libby 1982). Field studies in Germany further support the concept that there are provenance differences in this species. Best growth was found in seedlings grown from seed sources from the central and southern portions of the natural range (Dekker-Robertson and Svolba 1993).

Flowering and fruiting. Flowering is monoecious. The small, enclosed terminal buds differentiate in late summer, and flowering and pollination occur the following spring between mid-April to mid-May, when conelets are quite small. Conelets are about half size in July and reach full size in August, when fertilization takes place. At the start of winter the embryos have only a few cells, and they remain this way overwinter. Embryos develop rapidly the following summer and by late August, the second year after pollination, they are morphologically mature (Buchholz 1938). Young trees start to bear cones about age 20 (Stark 1968).

Cones may remain attached to the tree for many years, and most seeds are retained. During late summer, however, when cone scales shrink, some seeds are shed. As soon as cones become detached, they dry out, and the seeds are liberated within a few days (Buchholz 1938). This fruiting characteristic provides seeds every year in the groves. Cones show the following quantitative characteristics (Munz 1959; Schubert and Beetham 1965):

Scales per cone	25–40
Seeds per scale	3–9
Seeds per cone (average)	230
Cone length	5–9 cm

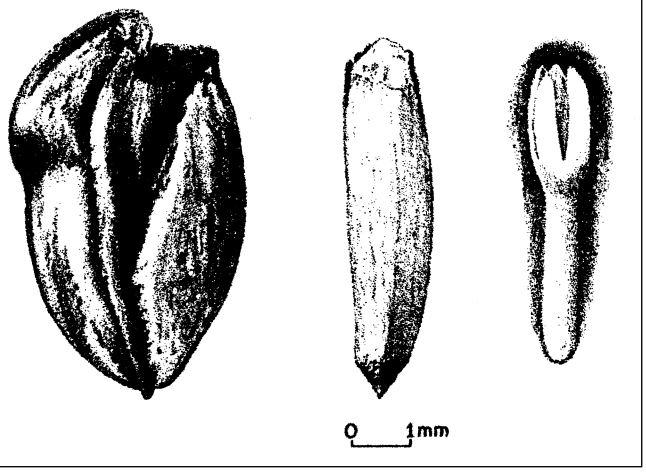
Seeds measure 3 to 6 mm long and are compressed and surrounded by laterally united wings that are broader than the body of the seed (figure 1). Embryos have 3 to 5 cotyledons (Boe 1974).

Collection, extraction, and storage. The old, persistent cones can be collected at any time; but for fresh cones, collections should be made in September and later. Squirrels cut and cache cones that furnish considerable quantity for collection (Boe 1974). Cones should be air-dried at 30 °C for about 7 days, or heated in a cone kiln at 38 to 40 °C for 24 hours. Seeds can be then extracted in a tumbler and screened to remove cones and other debris. Underdeveloped and resin-filled seeds can be removed with pneumatic cleaners. Multiple passes through a cleaner should yield seedlots with > 99% purity (Lippitt 1996). Yield and size of cleaned seeds are as follows (Lippitt 1996):

Average weight of seeds per volume of cones	402 g/hl	5 oz/bu
Cleaned seeds per weight		
Low	113,625/kg	51,530/lb
High	199,810/kg	90,620/lb
Average (29 samples)	173,100/kg	78,500/lb

Giant sequoia seeds are orthodox in storage behavior. They can be stored for 10 years or more at –18 °C with

Figure 1—*Sequoiadendron giganteum*, giant sequoia: seed with wings (**left**), seed with outer coat removed (**center**), and excised embryo (**right**).



seed moisture of 5 to 9% (Lippit 1996).

Germination. Germination values of giant sequoia seedlots has been reported from 30 to 73%. Optimum constant temperature for germination seems to be between 15 and 21 °C, but diurnally alternating temperatures of 30 to 20 °C are also satisfactory (table 1). A temperature of 6 °C was too cool and continuous 30 °C was too warm. Continuous light (day and night) or alternating light and dark periods produced about the same results. There is some dormancy in these seeds and stratification is needed for prompt germination. Good results (55% average germination) have been obtained by leaching seeds in running water for 24 hours, surface-drying them, and stratifying them in plastic bags without medium for 6 weeks at 2 °C (Lippitt 1996). Average germination values of 41 and 35% were obtained following overnight soaking and stratification at 2.2 to 2.8 °C for 91 days with or without a fungicide. The rate of germination is reduced in the presence of the fungicide (Fins 1981).

Nursery practice. For bareroot production, stratified seeds should be sown between mid-March and mid-April on the surface of the bed and covered with about 6 mm ($^1/_4$ in) of aged sawdust. In the absence of fumigation, seeds should be sown in soil that has been used recently to grow an endomychorrizal species—for example, giant sequoia, coast redwood (*Sequoia sempervirens* (D. Don) Endl., or incense-cedar (*Calo cedrus decurrens* Torr.)—or that has been inoculated with soil from such beds. The target bed density should be 245 seedlings/m^2 (23/ft^2) (Lippitt 1996).

For container production, stratified seeds should be sown in May. Seeds should be covered very lightly, about 3 mm ($^1/_8$ in). Damping-off and other fungi can be serious problems with this species. Infection can be reduced by minimizing water on the foliage by irrigating early in the day, "wanding" the foliage after irrigation, and using fans to maintain good air circulation (Lippitt 1996).

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Table 1—*Sequoiadendron*, giant sequoia: pregermination treatments, germination test conditions, and results

Cold stratification period (days)	Germination test conditions*				Avg % germination	Samples
	Daily light (hr)	Temp (°C)		Days		
		Day	Night			
0	<16	15	15	32	43.1	10
0	24	5	5	32	4.1	10
0	24	20	20	32	40.9	10
0	24	30	30	32	5.6	10
28	—	30	20	28	38.5	2
0	—	30	20	28	30.3	3

Sources: CDF (1968), Stark (1968).

* Tests were made on filter paper in petri dishes (Stark 1968) or on vermiculite (CDF 1968).

Arecaceae—Palm family

Serenoa repens (Bartr.) Small

saw-palmetto

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Synonym. *Serenoa serrulata* (Michx.) Nichols.

Growth habit, occurrence, and use. Saw-palmetto usually is an evergreen shrub, 0.6 to 2.1 m tall, with creeping, horizontal stems. Occasionally, the species attains the size of a small tree, reaching a height of 1.8 to 2.3 m, with an erect or oblique stem (Bailey 1976; Vines 1960). The common name, saw-palmetto, derives from the ascending, palmate leaves, which are rather stiff and have long petioles heavily armed with sharp, rigid, recurved teeth. These armed petioles are capable of severely scratching the skin and ripping clothing and shoes.

Saw-palmetto occurs from coastal South Carolina southward to Florida and westward to eastern Louisiana (Bailey 1939). It reaches its most extensive development in the pine flatwoods of the lower coastal plain of Georgia and Florida. Along Florida's eastern seaboard ridge grows a silver leaf variety that is highly prized for ornamental use. Saw-palmetto occurs in highest densities in flatwoods that have been burned annually or biannually (Abrahamson 1984). Saw-palmetto provides wildlife habitat for over 100 animal species (Carrington and others 2000; Hilmon 1986). Fatty acid extracts from the partially dried, ripe fruits (called "serenoa") are used as a phytotherapeutic agent in treating certain irritations of the bladder, prostate gland, and urethra (Ganzera 1999; Vines 1960). In some places, the large fan-shaped leaves (fronds) are used to thatch roofs on temporary structures, and larger stems are occasionally used for crude logs.

Large quantities of saw-palmetto leaves are shipped north for Christmas decorations; the flowers are a significant source of honey; and the stems are a source of tannic acid extract (Vines 1960). Saw-palmetto is increasingly used as a landscape plant to provide a naturalistic effect.

Flowering and fruiting. The numerous, small, white flowers are borne in panicles that emerge in February and March in southern Florida and in April in southern Georgia (Carrington and others 2000; Hilmon 1968; Vines 1960). The panicles appear on branches that are shorter than the leaves. The inflorescences and vegetative branches arise from buds identical in their position in the leaf axil and indistinguishable in their early development. In an adult plant, as much as half of the axillary buds abort; of those remaining, most (~80%) become inflorescences and the others (~20%) become vegetative suckers (Fisher and Tomlinson 1973). The inflorescence bud's first leaf is called a prophyll and its mouth splits as younger bracts grow through it; subsequent bracts are distichously arranged and encircle the main axis of the inflorescence (Fisher and Tomlinson 1973).

The flowers are perfect with 6 stamens and 1 stigma within 1 style (Radford and others 1964). Several thousand flowers per inflorescence are produced from buds at the bases of the previous year's leaves. Saw-palmetto plants must be at least 60 cm high to flower in the wild (Carrington and others 2000). The number of leaves produced per year after a disturbance is a good indicator of flowering.

Fire stimulates the initiation of inflorescences in sexually mature saw-palmettos by reducing the canopy and thus increasing light availability. Although a burn at any time of year stimulates flowering within 1 year of the fire, frequent burning reduces flower and fruit production. Two sites of 40 saw-palmetto plants were studied in a 6-year period and burned every 2 years. The plants flowered 36 times, with approximately 40% flowering occurring within 1 year of burning (Hilmon 1968). Saw-palmetto plants flowered 65% of the time following a burn on flatwood sites, and 85 to 90% bloomed after 2 or 3 burns (Abrahamson 1999). On scrub stand sites, saw-palmetto flowered 56% after a prescribed burn, 62% after the second-season burn, then returned to preburn levels (≥ 12%) by the third season after burning (Abrahamson 1999). The saw-palmettos produced more inflorescences per plant following the second and third fires. To maximize flower and fruit production, a site should be burned no more than every 4 years (Abrahamson 1999; Hilmon 1968). Stands of saw-palmetto on scrub and sandhills that had not been burned in a long time had relatively closed canopies and low reproductive frequencies (≥ 16%).

Cultural treatments have been used to stimulate flowering. Fertilizer (10% N, 5% P_2O_5, 5% K_2O) and dolomite lime (49% $CaCO_3$), 36% $MgCO_3$, and 10% Mg) applied at a rate of 155 g per plant around the plant's drip line, did not influence flowering. But when crowns were clipped and plants fertilized, there was a significant elevation in flowering during the second growing season: 18% flowering in treated plants compared to 4% flowering in control plants (Abrahamson 1999). Saw-palmettos that were only clipped had a 22% flowering response.

The fruit is a drupe measuring about 1.5 to 3 cm long and 15 to 20 mm in diameter, that is ovoid-oblong, green or yellow before ripening, and bluish to black when ripe (Hilmon 1968; McCurrach 1960; Vines 1960) (figure 1). Immature green fruits are present from May through July, turn orange by August, and ripen to bluish-black in September and October (Carrington and others 2001). Each drupe contains a single globose seed (figures 1 and 2), and the embryo is laterally oriented (Bailey 1976).

Each inflorescence typically produces 4 to 5 kg (9 to 11 lb) of fruits (Vines 1960) and can produce up to 12 kg (27 lb) in a good year (Carrington and others 2000). The average fruit yield for a site is 200 kg/ha; yields can vary from 150 kg/ha to over 1,500 kg/ha (Carrington and others 1997).

In Florida, anthracnose infection—by *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc.—has been identified as a major factor (90%) in fruit loss. The remaining 10% of the loss is caused by a caterpillar (*Atheloca* sp.) (Carrington and others 2001).

Collection of fruits. In south Florida, fruit harvesting begins in August, when fruits turn orange. In south Georgia, harvesting begins in early September, when fruits begin to turn black. The fruits are collected by snapping the panicles by hand, cutting them with pruning shears, or shaking the attached fruits into burlap bags, plastic sheets, or the bed of a truck. Seeds are available commercially within the natural range of the species.

Extraction and storage of seeds. Palmetto fruits can be dried in the sun or in indoors in bins or tobacco barns. The fruits are piled about 0.6 to 1.0 m high (Carrington and others 2000). Fruits are dried at 54 °C (not to exceed 60 °C) for about 3 days; fruits in bins are turned every 12 hours (Carrington and others 2000). The initial moisture content is about 66% fresh weight; the fruits are then dried to a maximum of 10% for storage.

Large suppliers store the freshly harvested fruits in wet tanks holding 100,000 kg (250,000 lb). The berries are conveyed to a stainless steel dryer with a capacity of drying 300,000 kg (750,000 lb) per day. The dryer takes an hour to dry a batch of fruits, thus preserving more of the fatty acids used for phytopharmaceuticals. After drying, a blower is used to remove leaves, stems, and other trash (SPHC 2002).

Seeds must be extracted from the fruits or germination will not occur, even after 222 days (Hilmon 1968). If high temperatures (35 °C) are maintained throughout the germination period, dried fruits will germinate in a greenhouse (Perkins 2002). Seed may be extracted by running the fruits through a macerator or other suitable device for separating the seeds from the pulp. Dried saw-palmetto fruits average 720/kg (326/lb); the dry seeds average 2,380/kg (1,081/lb) (Hilmon 1968).

Steel silos holding 100,000 kg (250,000 lb) are used for storing dried fruits. In a "low-tech" method, the dried fruits are stored in burlap bags and housed where they will not freeze. Seeds stored dry at room temperature for 3 months retained their viability (Hilmon 1968). After 1 year of storage, viability drops slightly; after the second year, viability drops about 50% (Perkins 2002). No tests of seed storage under a variety of conditions or different time periods have been reported.

Pregermination tests. Pregermination treatments of saw-palmetto seeds indicate that they require high temperatures throughout the germination period. Pretreatment temperatures (25, 35, and 45 °C) were significantly different for maximum germination and days to 50% final germination. Average germination for all treatments at 25 °C was 52.3% and 72 days to 50% final germination; germination at 35 °C was 60.8% and 47 days to 50% final germination; and germination at 45 °C was 41.9% and 61 days to 50% final germination (Carpenter 1986).

Non-imbibed seeds required significantly more time to achieve 50% final germination than did imbibed seeds at 25, 35, and 45 °C. Seed weights increased from 34 to 39% for imbibed seeds (Carpenter 1987). Seedlots that were soaked for 7 days in water or wet peat moss reached 50% final germination in 39.8 and 33.7 days at 35 °C, with maximum germination values of 75 and 80%, compared to lots of unimbibed seeds, which took 53 days to 50% final germination with 46% germination (Carpenter 1987). Soaking seeds in water for 7 days at 35 °C resulted in 10% higher germination and 27 days earlier germination when compared with soaking seeds in water at 25 °C (Carpenter 1986). There was also a 20% higher germination at 35 °C and 15 days earlier germination when compared with 45 °C soaking temperature (Carpenter 1986). There was no significant difference in germination and days to 50% final germination between seeds soaked for 7 days in water were compared to seeds stored in damp peat moss for 7 days at 25, 35, and 45 °C (Carpenter 1986). There was no interaction in germination response between temperature and seed soaking treatments.

Figure 1—*Serenoa repens*, saw-palmetto: fruit (**top**) and seed (**bottom**).

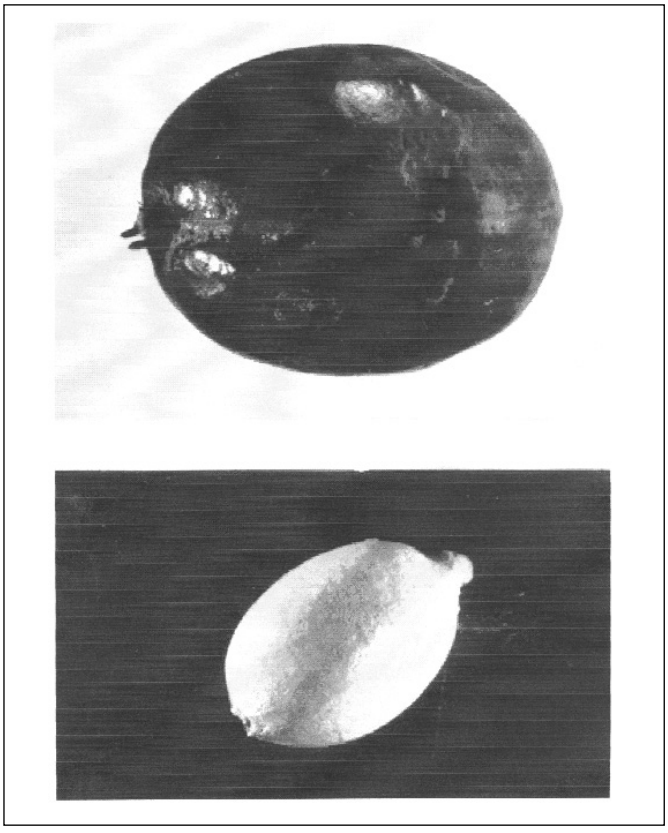
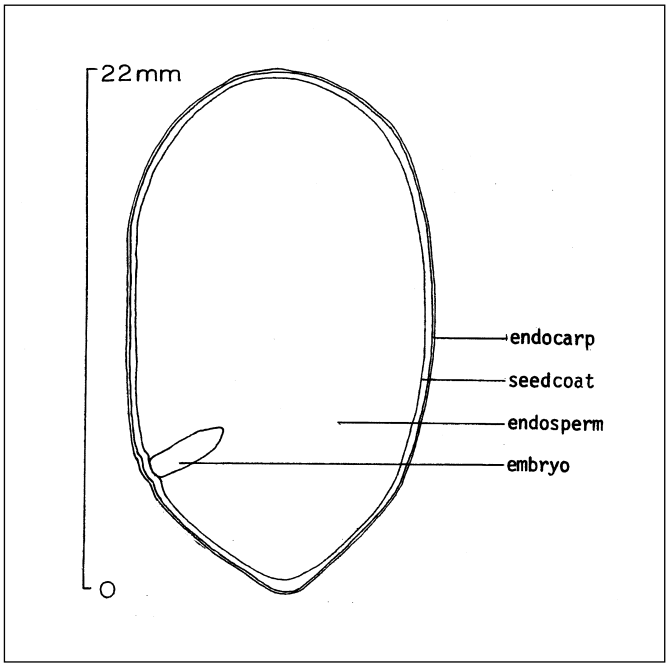


Figure 2—*Serenoa repens*, saw-palmetto: longitudinal section through a seed.



All seed treatments resulted in lower germination values than those of controls at each temperature. The germination over all temperatures dropped from 76% for no treatment to 13% for a 15-minute soak in sulfuric acid (H_2SO_4). Seed embryos were injured and killed by soaking in the acid for 15 minutes and to a lesser degree for 5 minutes (Carpenter 1986). Gibberillic acid and mechanical scarification treatments did not increase the total germination or reduce the days to 50% of final germination. Seed germination was reduced and delayed by 15 minutes of scarification (Carpenter 1986). The germination temperatures used in experiments Carpenter (1986 and 1987) were 34 and 21 °C with bottom heat at 30 °C provided to the propagation medium in the greenhouse. Seeds were planted 6 cm deep in clean builders' sand.

Germination tests. Germination tests were made with fresh seedlots treated in several ways—with and without pulp, endocarp intact and crushed, or with embryo and endosperm exposed (Hilmon 1968). Only extracted seeds germinated. The tests were made on moist filter paper with daytime temperatures of 26 to 28 °C and nighttime temperatures of 13 to 22 °C. Seeds with the micropyle cap removed and the embryo exposed began to germinate in 11 days; it took seeds with the cap intact 45 to 66 days to germinate. After 222 days, however, the germinative capacity of all extracted seeds was similar and ranged from 50 to 60%.

In another test, 5 replications of 20 seeds each from 3 different seed sources were tested under conditions nearly identical to those just described (Hilmon 1968). First germination occurred between 45 and 66 days. A period of slow germination was followed by a period of rapid germination (optimum period), during which approximately half of the seeds germinated. Optimum germination began $4^1/_2$ to 6 months after planting. Germinative capacity after 231 days ranged from 65 to 85%, and all ungerminated seeds appeared viable. The germination temperatures used in the experiments cited above (Carpenter 1986, 1987) were 34 and 21 °C, with bottom heat at 30 °C provided to the propagation medium in the greenhouse. Seeds were planted 6 cm deep in clean builders' sand.

Nursery practices. Freshly cleaned seeds are placed in large vats for a week to ferment. Without rinsing, the seeds are sown 1.25 to 2.5 cm ($^1/_2$ to 1 in) deep in a seedbed in the greenhouse. Dried seeds are soaked in water for 5 to 7 days at 32 to 38 °C before they are sown in the seedbed.

Seeds should not be sown until the nighttime temperature is constantly above 21 °C. Germination of fresh seeds averaged from 50 to 70%, compared to that of dried seeds, which averaged 30 to 50%. The first leaf of the seedling emerges above the soil 1 to 2 months after germination (Fisher and Tomlinson 1973). It takes 90 days to reach peak germination in the greenhouse (Perkins 2002).

After peak germination, the seedlings are transplanted to liners in a well-drained medium and grown with liquid fertilizer for 6 months. They are then transferred to 3.8-liter (1-gal) containers to grow for 12 to 16 months. The final step is transplanting the saw-palmetto into 11.4-liter (3-gal) containers to grow 12 to 16 months before they are finally ready to sell (Perkins 2002). Slow-release fertilizers are used for both sizes of containers.

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Elaeagnaceae—Oleaster family

Shepherdia Nutt.

buffaloberry

Scott C. Walker

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Growth habit, occurrence, and use. The genus *Shepherdia*—commonly called buffaloberry—is found wholly in the north and west of North America. It includes 3 species with varying distributions and uses (table 1). All are capable of fixing nitrogen in root nodules that contain bacteria (Mozingo 1987; Thilenius and others 1974).

Silver buffaloberry is a shaggy-barked, thorny, deciduous, large shrub to small tree up to 6 m tall, that often forms thickets. Plants spread by underground stems and readily sucker. Leaves are silvery and scurfy; both surfaces are covered with small star-shaped scales that reflect the light and account for the shrub's rusty silver aspect. These scales undoubtedly help reduce water loss during the summer (Knudson and others 1990; Lackschewitz 1991; Mozingo 1987; Wasser 1982; Welsh and others 1987).

Habitat includes moderate-textured soils at 1,100 to 2,300 m, along moist stream banks, terraces, and hillsides to open dry regions of the plains, and frequently on valley bottoms where the soil is not too saline (Knudson and others 1990; Smith 1987; Wasser 1982; Welsh and others 1987).

Silver buffaloberry with its strong grazing resistance, aided by thorny branches and root sprouting, has considerable potential for shelterbelts and for game food and cover plantings. It often forms single-clone patches and nearly impenetrable clumps. It is an important source of cover and food for small and large game animals (Knudson and others 1990). This species is regarded as poor to fair forage for sheep, deer (*Odocoileus* spp.), and elk (*Cervus elaphus*), and generally considered worthless for cattle. The fruits provide abundant and nutritious food and are highly sought after by birds (Mozingo 1987; Wasser 1982). The berries are edible and were used by Native Americans and are still commonly used as they make excellent jelly (Borland 1994; Knudson and others 1990; Lackschewitz 1991).

Russet buffaloberry is a thornless, deciduous, small to medium shrub with a characteristically spreading growth form, 1 to 3 m tall at maturity (Lackschewitz 1991; Mozingo 1987; Stubbendieck and others 1986). Twigs are slender, round, and densely scurfy with rusty, bran-like scales. Leaves, which are paired, have a bright green upper surface and paler lower surface with conspicuous brown scales (Lackschewitz 1991; Welsh and others 1987). This species is very cold and drought hardy and it can grow in a variety of habitat types. It is typically found along the banks of streams, and on moist open wooded slopes at 1,000 to 3,400 m. It can also be found on sandy or rocky, often sterile, soils. At its southern extremity, it is confined to the higher vegetation zones in the mountains (Link 1993; Mozingo 1987; Thilenius and others 1974).

Table 1—*Shepherdia,* buffaloberry: nomenclature and occurrence

Scientific name & synonym(s)	Common name	Occurrence
***S. argentea* (Pursh) Nutt.** *Lepargyrea argentea* (Pursh) Greene *Elaeagnus utilis* A. Nels.	**silver buffaloberry,** buffaloberry, redberry, silverberry, bullberry, wild-oleaster	Manitoba to Alberta, to Oregon & California, through the Great Basin to New Mexico, Kansas & the Dakotas
***S. canadensis* (L.) Nutt.** *Lepargyrea canadensis* (L.) Greene *Elaeagnus canadensis* (L.) A. Nels.	**russet buffaloberry,** Canadian buffaloberry, thornless buffaloberry, wild-oleaster, wild-olive, nannyberry, *soapolalillie*, soapberry	Newfoundland to Alaska, from central Maine, to Washington, through Oregon, Utah, & New Mexico
***S. rotundifolia* Parry** *Lepargyrea rotundifolia* (Parry) Green	**roundleaf buffaloberry**	S Utah, N Arizona

Source: Thilenius and others (1974).

Russet buffaloberry has little or no browse value for cattle and is only fair for sheep before frost. The berries are bitter and though not highly palatable to humans are eaten by birds and other wildlife (Lackschewitz 1991; Stubbendieck and others 1986).

Roundleaf buffaloberry has a low sprawling habit and is mainly 1 to 2 m tall, and 1 to 4 m wide. The thornless brachlets are covered with small white to yellowish hairs often appearing silver. The thick, persistent, somewhat evergreen leaves are silvery green above, and pale densely scurfy beneath, and as the name implies, circular or oval in outline (Welsh and others 1987). This species inhabits warm, dry, sandy or rocky slopes and occurs from southern Utah into the Grand Canyon region of Arizona throughout the saltbrush, sagebrush, and piñyon zones. Welsh and others (1987) describe roundleaf buffaloberry thusly: "This is a beautiful shrub. It festoons slopes with silvery clumps." It is reported to have some value as a winter browse in southeastern Utah.

Flowering and fruiting. Buffaloberries are dioecious. The small, petal-less, yellow to yellowish green flowers are borne single or clustered at the nodes. Plants resume growth in very early spring, usually soon after snowmelt. Flowering occurs quite early in the season (March to April), before or soon after the leaves appear. Fruits mature in late summer and fall (late June to September), varying with environment and source of planting stock (Borland 1994; Mozingo 1987; Thilenius and others 1974; Vories 1981; Wasser 1982).

Fruits are 3.2 to 8.5 mm in diameter and drupe-like, with a solitary smooth achene or small nutlet enveloped in a fleshy perianth. Color of mature fruits vary from orange-red (silver buffaloberry), red-yellow (russet buffaloberry), to silvery (roundleaf buffaloberry) (McTavish 1986; Mozingo 1987; Smith 1987; Wasser 1982; Welsh and others 1987). Cleaned achenes are used as seeds (figures 1 and 2). Minimum seed-bearing age is 4 to 6 years (Thilenius and others 1974).

Seedcrop quality and quantity can vary from year to year. McTavish (1986) reports that one of the major propagating problems with russet buffaloberry is poor seed quality. Researchers have obtained widely varying germination percentages from year to year under identical treatments. This seems to be due to poor embryo development. Therefore, it is suggested that seed collectors check the seeds before collection to ensure that proper embryo development has taken place (McTavish 1986).

Collection of fruits. The fruits may be harvested by stripping or flailing them from the bushes onto canvas; they may also be picked by hand or collected from the ground. The use of mechanical shakers has shown to be effective in harvesting the seed of silver buffaloberry (Halderson 1986). Heavy gloves should be used when collecting this species to avoid injury from the thorns. Care should be taken when collecting seeds of roundleaf buffaloberry as the silvery hairs that cover the fruit, branches, and leaves can be very irritating to the eyes and skin.

Figure 1—*Shepherdia argenta*, silver buffaloberry: exterior view of cleaned achenes.

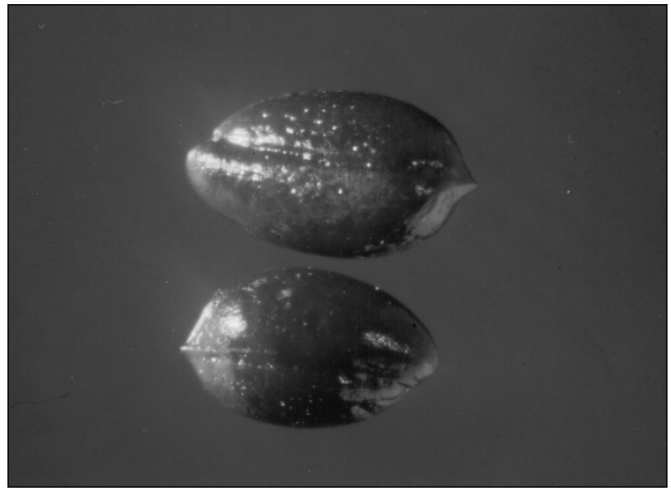
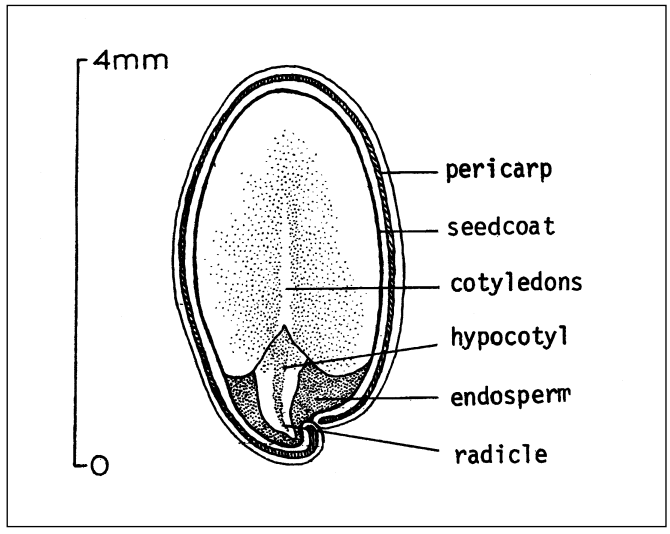


Figure 2—*Shepherdia argenta*, silver buffaloberry: longitudinal section through the embryo of an achenes.



Cleaned seeds can range from 28,600 to 147,700 seeds/kg (13,000 to 67,000/lb), varying with ripening, environmental conditions, and seed source (Jorgensen 1995; Link 1993; Smith 1987; Thilenius and others 1974; Vories 1981; Wasser 1982).

Extraction and storage of seeds. Twigs, leaves, and other debris are removed by running material over an air-screen cleaner. Fruit is then put through a macerator with water, and dried. The dried pulp and seeds can be hand-rubbed or lightly chopped, and again run over the cleaner to separate out the seeds (Link 1993; Thilenius and others 1974; Vories 1981; Wasser 1982).

The seeds are orthodox and should be stored dry, in cool conditions, optimally at 5 °C. Seed can be stored for 4 to 5 years while maintaining good viability (Thilenius and others 1974; Vories 1981). For short-term storage, seed extraction is not necessary. The fruits may be spread out in a thin layer and dried. For short-term storage of fruits, place them in open plastic bags under cool-dry conditions. Care should be taken to prevent heating of the collected fruits (Link 1993; Thilenius and others 1974). Seed quality has not been standardized. Minimum standards established by the USDI Fish and Wildlife Service (Wasser 1982) are 90% purity and about 60% germination.

Germination. A physiologically dormant embryo, and physical dormancy due to impenetrable seedcoats, are the major problems affecting germination (McTavish 1986; Thilenius and others 1974). Two generally accepted methods of breaking dormancy are scarification with sulfuric acid and moist cold stratification (table 2). After pretreatment, the majority of viable seeds of silver buffaloberry germinate in 20 days. Some seeds do delay germination up to 60 days (Wasser 1982). Germination is epigeal (figure 3).

Nursery practice and seeding. In nursery practice, seeds are planted 6 mm ($^1/_4$ in) deep and covered with up to 2.5 cm (1 in) of mulch. This suggests that seeds could be planted, perhaps to advantage, at depths up to 2 cm ($^3/_4$ in) in coarse, dry, and loose soil or in fall under wildland conditions. About half of the viable seeds sown produce usable 1+0 seedlings in nurseries, whereas only 5 to 15% establishment would be good survival from seeding under dryland field conditions (Thilenius and others 1974; Vories 1981; Wasser 1982).

The recommended seeding rate for wildland seedings is 1.1 to 2.2 kg/ha (1 to 2 lb/ac) in seeding mixtures totaling 11 to 34 kg/ha (10 to 30 lb/ac) (Wasser 1982). In nursery row plantings, seeds can be sown in rows at a rate of 100 to 160 viable seeds/m (30 to 50/ft). Seeds should be sown in the fall, but seeds that are prechilled for 3 months can be sown in spring, or probably later where late summer moisture is more reliable, or with irrigation (Thilenius and others 1974).

Silver buffaloberry can be propagated by cuttings, and wildlings can be transplanted successfully. Success of propagating russet buffaloberry from cuttings can vary. Vories (1981) reports that it roots well from cuttings, whereas McTavish (1986) reports that attempts at propagation by cuttings were largely unsuccessful. Roundleaf buffaloberry is generally grown from seeds because cuttings do not do well (Borland 1994; Vories 1981; Wasser 1982).

Figure 3—*Shepherdia argenta*, silver buffaloberry: seedling development at 1, 9, and 38 days after germination.

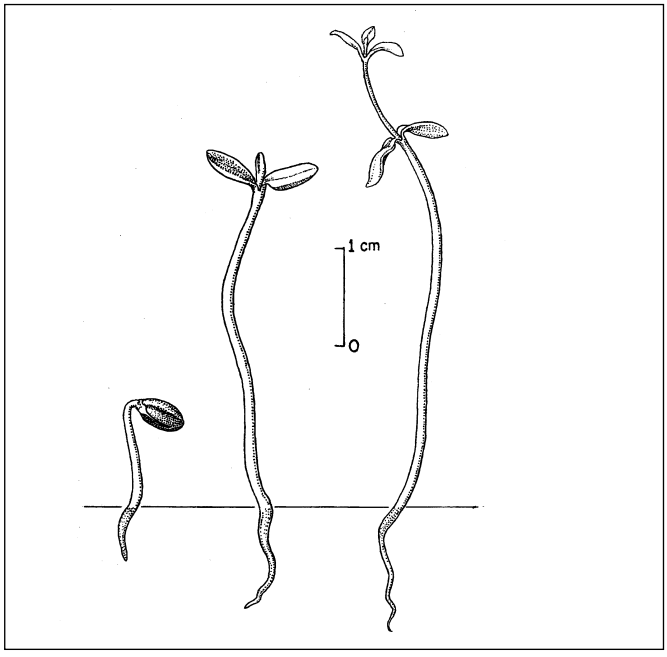


Table 2—*Shepherdia*, buffaloberry: germination treatment conditions and results

Species	Pretreatment	Germination treatment	Percent germination
S. argentea	Moist chill (3 °C for 90 days)	20–30 °C (18 days)	93
	Acid soak (20–30 min)	20–30 °C (21 days)	71–86
	None	Moist chill (3 °C for 170 days)	94
S. canadensis	Acid soak (15 min)	Moist chill (3 °C for 30 days)	89
	Acid soak (20–30 min)	20–30 °C (21 days)	80
	None	Moist chill (3 °C for 170 days)	80
S. rotundifolia	Acid soak (15–30 min)	20–30 °C	80–90
	Moist chill (3 °C for 30–60 days)	20–30 °C	80–90
	None	Moist chill (3 °C for 170 days)	86

Sources: Borland (1994, 1996), Jorgensen (1995), McTavish (1986), Thilenius and others (1974), Vories (1981).

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Sapotaceae—Sapodilla family

Sideroxylon lanuginosum (Michx.)

gum bumelia

Franklin T. Bonner and R. C. Schmidtling

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Synonyms: *Bumelia lanuginosa* (Michx.) Pers., *B. rufa* Raf.

Other common names. Woolly buckthorn, buckthorn, gum elastic, chittamwood.

Growth habit, occurrence, and use. Gum bumelia is a spiny shrub or small tree found from southern Georgia to southern Illinois and west to southern Kansas, southern Arizona, and northern Mexico. Reaching heights of up to 18 m, it is deciduous in its northern range and evergreen in its southern range. Gum bumelia has some value as wildlife food. It has been planted as an ornamental and to some extent for shelterbelts. It has a deep taproot and is extremely resistant to drought (Bonner and Schmidtling 1974).

Flowering and fruiting. The perfect, white flowers are borne on small fascicles 6 to 38 mm across and open during June and July (Bonner and Schmidtling 1974; Vines 1960). The fruit is a single-seeded drupe 8 to 25 mm long. It turns purplish black as it ripens in September and October and persists on the tree into winter (Bonner and Schmidtling 1974; Vines 1960). The single seed is 6 to 13 mm long and is rounded, brownish, and shiny (figures 1 and 2) (Vines 1960).

Collection, extraction, and storage. Fruits should be picked as soon as they turn purplish black. The fleshy outer coat may be removed by careful maceration in water. The following data were obtained on 4 samples from Texas and Oklahoma (Bonner and Schmidtling 1974):

Cleaned seeds per weight of fresh fruit	10–12 kg/50 kg (10–12 lb/50 lb)
No. of cleaned seeds	12,500/kg (5,700/lb)
Purity	94%
Sound seeds	88%

Figure 1—*Sideroxylon lanuginosum*, gum bumelia: seed

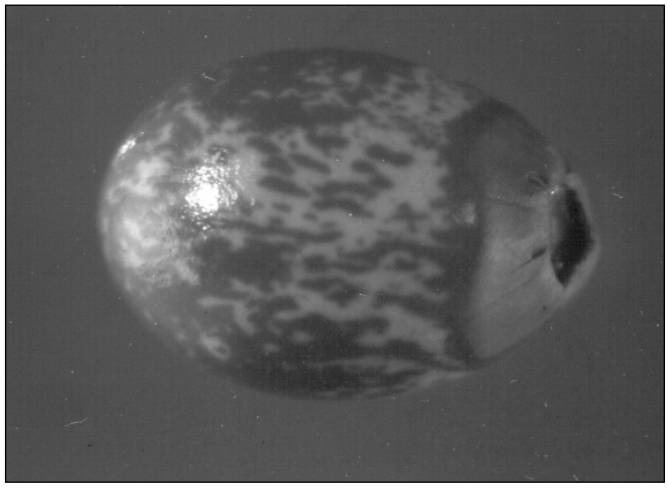
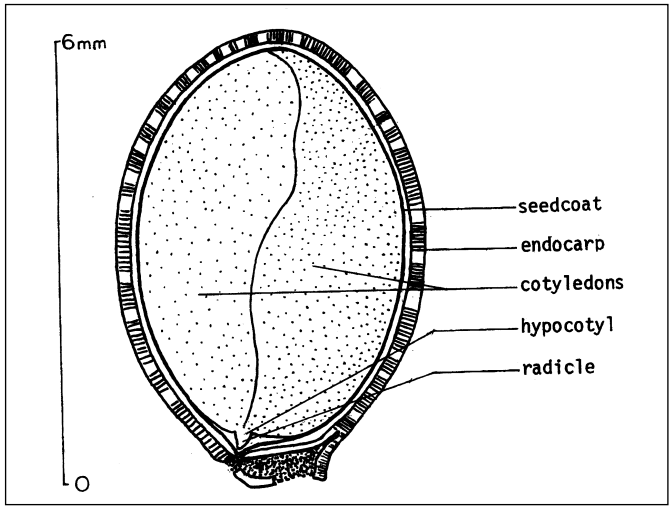


Figure 2—*Sideroxylon lanuginosum*, gum bumelia: longitudinal section through a seed.



Longevity of seeds in storage is not known.

Germination. Gum bumelia seeds germinate slowly and may be influenced by the seedcoat and internal conditions. Stratification for 60 days at 5 °C has been successful in promotion of germination (Bonner and Schmidtling 1974). Scarification by soaking in concentrated sulfuric acid for 20 minutes, followed by 4 to 5 months of stratification at 2 to 7 °C, has also been recommended (Afanasiev 1942). Preliminary trials on samples of each seedlot are desirable to determine whether the acid treatment is necessary.

Germination may be tested in flats of sand or sand and peat at temperatures of about 20 °C at night and 30 °C during the day. Test periods of 60 to 90 days are needed for complete germination of stratified seeds. Percentage germination of 21 to 44% was reported for 13 samples from Texas and Oklahoma (Afanasiev 1942). Untreated seed from Missouri had a percentage germination of 51% after 150 days (Clark 1940).

Nursery practice. Eighty-two viable seeds should be sown per linear meter (25/ft) and covered lightly with soil. Outplanting at the age of 2 years is suggested (Clark 1940).

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Simmondsiaceae—Jojoba family

Simmondsia chinensis (Link) Schneid.

jojoba

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Other common names. goatnut.

Growth habit, occurrence, and use. The Simmondsiaceae *(*jojoba family), has only 1 genus, *Simmondsia,* which consists of only 1 species, jojoba—*S. chinensis* (Link) Schneid. Once considered an isolated member of the box family (Buxaceae), jojoba is now regarded as sufficiently distinct to be placed in its own family. Jojoba is found from coastal and cis-montane southern California east to central Arizona and south to Sonora and Baja California (Munz 1974; Yermanos 1974). It is a characteristic plant of upland shrub communities in the Sonoran and Colorado Deserts and is also quite common as a component of chaparral.

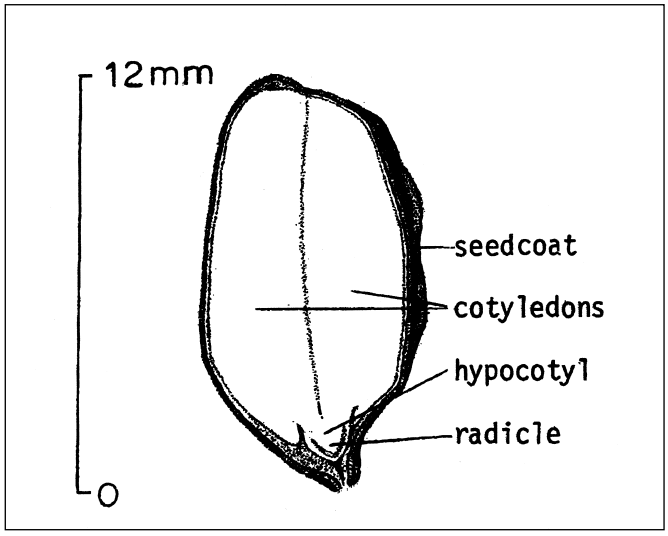
Jojoba is a sparsely branched, decumbent to erect shrub that grows to 2 or rarely 3 m in height. Its large (2- to 4-cm-long), opposite, entire leaves are evergreen, leathery, and dull gray. Plants are extremely tolerant of drought (Al-Ani and others 1972) and their foliage is a source of nutritious forage for sheep, goats, and cattle, as well as for wild ungulates and smaller browsers such as rabbits. The large seeds have been used locally as a food source by indigenous people (Brooks 1978).

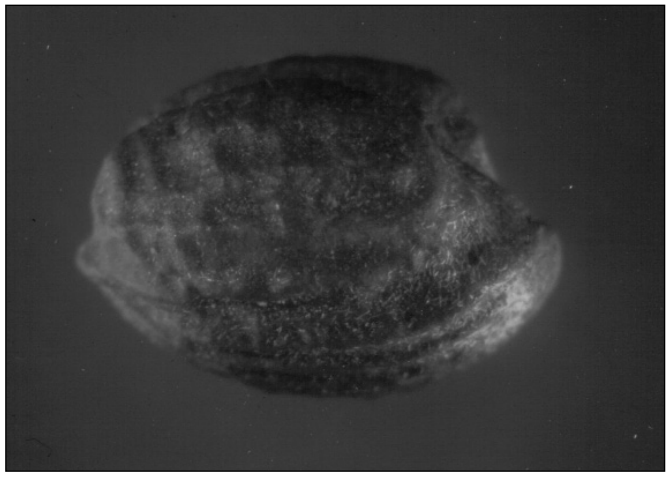
The most noteworthy feature of jojoba from a human perspective is the unusual liquid wax that makes up the storage reserve of its seeds. This substance, a fatty acid ester of a long-chain alcohol, is unique in the plant kingdom. It has chemical and rheological properties similar to those of sperm whale oil, which make it useful in a host of applications (Brooks 1978). Interest in commercial production of jojoba seed was greatly increased in the mid-1970s, when import of sperm whale oil into the United States was banned. First efforts were focused on harvesting seeds from wildland stands, but it was soon realized that for cost-effective production, cultivation in an agronomic setting would be necessary (Foster 1980; Yermanos 1979). Since that time, jojoba has been successfully cultivated in many semi-arid regions of the world (Ismail 1988; Kumari and others 1991; Milthorpe 1989; Muthana 1981; Nimir and Ali-Dinar 1991), where it has the advantage of low water requirements and the ability to grow on agriculturally marginal land. Selection on natural variability and breeding have given rise to improved cultivars (Dunstone 1990, 1991; Palzkill and others 1989).

Flowering and fruiting. Jojoba is dioecious and relies on wind for successful pollination (Niklas and Buchmann 1985). The flowers, which are greenish yellow, inconspicuous, and without petals, are borne in the axils of the leaves. The male flowers are clustered at the nodes, and the female flowers are usually borne singly. Flowering occurs in March through May in response to winter rains. Plants of most populations appear to have a short (2-week) vernalization requirement for induction of flowering (Nord and Kadish 1974). Under plantation conditions, jojoba usually begins producing seeds the second or third year after planting (Nord and Kadish 1974; Yermanos 1974). Seeds ripen during the summer. The endosperm is absent (figure 1), and the cotyledons (which function as the storage organs) contain about half of their weight as wax (Brooks 1978). Good seedcrops are produced at intervals of 2 to several years (Brooks 1978; Castellanos and Molina 1990). Some individuals appear to be genetically predisposed to be more productive than others, making selection for higher yield possible (Nord and Kadish 1974; Yermanos 1974).

The 1 to 3 large seeds are borne in a capsule that superficially resembles an acorn. This splits open apically and down the sides to release the seeds. As is the case with many large-seeded North American desert species, jojoba seeds are dispersed by scatter-hoarding rodents that are also their principal consumers (Castellanos and Molina 1990). Sherbrooke (1976) reported that only 1 heteromyid species in southern Arizona—Bailey's pocket mouse (*Peragnathus baileyi*)—was able to utilize jojoba seeds. The seeds contain a unique toxic cyanogenic glucoside (simmondsin). He concluded that Bailey's pocket mouse had evolved a detoxifica-

Figure 1—*Simmondsia chinensis*, jojoba: longitudinal section through a seed (**top**) and exterior view of a seed (**bottom**).





tion mechanism, enabling it to eat the seeds without harm. The seeds are, however, not particularly toxic to humans.

Jojoba seedlings emerge in response to autumn, winter, or spring rains (Castellanos and Molina 1990; Sherbrooke 1977). Germination is hypogeal. Wildland stands are often strongly male-biased—sometimes as many as 4 males to 1 female—but in cultivation the sex ratio is more equal (Brooks 1978). Male plants are thought to be more stress-tolerant as seedlings and thus to have higher survival rates under natural conditions. Seedling survival depends principally on weather patterns (Castellanos and Molina 1990) but may be higher in the protection of nurse plants or other sheltering objects (Sherbrooke 1977).

Seed collection, cleaning, and storage. Seeds of jojoba are most readily collected by raking or vacuuming after they have fallen to the ground, but where rodents are active, seeds do not remain on the ground for long (Castellanos and Molina 1990). Also, the growth form may or may not be conducive to this activity, a problem that is solved in cultivation by bottom-pruning (Yermanos 1974). For small lots, seeds can be collected by beating the branches over a hopper or by hand-stripping them when still slightly green, the "hard-dough" stage (Nord and Kadish 1974). Seeds picked green should be allowed to dry in a shady, well-ventilated area. A pneumatic device has been developed for commercial harvest (Coates and Yacizi 1991). If collected intact, the capsules may be broken up using a barley de-bearder or hammermill. The seeds can then be cleaned of debris and unfilled seeds in a conventional fanning mill or air-screen cleaner. The purity and viability of cleaned seedlots are usually high (Nord and Kadish 1974).

Jojoba seeds are quite variable in size, both within and among seedlots (Yermanos 1979). Nord and Kadish (1974) report an among-lot mean seed weight range of 660 to 3,300/kg (300 to 1,500/lb). Ismail (1988) sorted seeds of a single lot into 3 size classes with the following mean values:

	Seeds/weight		Length	
	/kg	/lb	cm	in
small	2,300	1,045	0.93	1/3
medium	1,300	590	1.38	1/2
large	1,060	480	1.84	3/4

Castellanos and Molina (1990) reported an even wider spread in the size of viable seeds, 670 to 20,000/kg (305 to 900/lb). Jojoba seeds lose viability relatively rapidly in laboratory storage at room temperature (from 100% to <60% after 2 years), but they are apparently still orthodox in storage behavior. When stored at low moisture content and temperature (3 °C), seedlots have retained high viability for 10 to 12 years (Nord and Kadish 1974). Under natural conditions, jojoba seeds do not form a persistent seedbank; all seeds either germinate, lose viability, or are consumed within a year of production (Castellanos and Molina 1990).

Germination. Jojoba seeds require no pretreatment and are usually readily germinable immediately after harvest (Nord and Kadish 1974; Rao and Iyengar 1982). They are protected from premature summer germination by a requirement for relatively cool temperatures—an optimum 15 to 23 °C (Nord and Kadish 1974), with no germination at 30/40 °C (Ismail 1988)—and slow germination rates. It takes 3 days for the first emergence of the radicle at 20/30 °C and 7 days at 10/20 °C) (Ismail 1988). Seedlots of large seeds germinated more quicky and to higher percentages than did lots of small seeds, suggesting that seed size is associated with germination polymorphism (Ismail 1988). This may function to reduce germination risk under field conditions by spreading out germination across rain events

(Castellanos and Molina 1990). Dormancy could be removed in most seeds by breaking the testa at the radicular end. Nord and Kadish (1974) reported that jojoba seeds could germinate at 5 to 10 °C but only after an 8-hour pretreatment at 20 °C. Germination is hypogeal (figure 2).

Nursery practice and field seeding. Jojoba may be direct-seeded if the plots are protected from seed predation and seedling grazing by rodents. The seeds should be planted in spring, when daytime soil temperatures are above 60 °C, at a depth of 2.5 to 5 cm (1 to 2 in) (Nord and Kadish 1974). Although mature plants can tolerate some freezing, the seedlings do not, perishing at temperatures below –2 °C.

Seedlings may also be readily be produced as container stock (Yermanos 1974). Seedlings emerge in 7 to 12 days at 60 to 75 °C. The plants may be held in 3.8-liter (1-gal) pots outdoors for 8 to 24 months. With the longer period, flowering takes place in the pots, making it possible to optimize sex ratios in plantation plantings. Another alternative is to establish plants from cuttings of known sex. Jojoba can be propagated from softwood stem cuttings taken in the spring or summer (Nord and Kadish 1974).

Figure 2—*Simmondsia chinensis*, jojoba: seedling development at 3, 7, and 14 days after germination.

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Solanaceae—Nightshade family

Solanum dulcamara L.

bitter nightshade

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Growth habit, occurrence, and use. Bitter nightshade—*Solanum dulcamara* L., also known as European bittersweet—is a climbing perennial vine, somewhat woody at the base. It grows to a height of 1.8 to 3.6 m. It is native in Europe, northern Africa, and eastern Asia. In its natural range in Europe, it occurs on sites ranging from wet and shaded to dry and exposed. Its presence indicates a habitat in which the moisture regime may fluctuate from moist to waterlogged. It occurs on mineral to peat soils characterized by a high nitrogen supply and with a pH range of 4.8 to 7.9 (Pegtel 1985). Pegtel (1985) has briefly summarized many aspects of the species biology within its natural range.

Naturalized in North America, it is often found in moist thickets, from Nova Scotia to Minnesota, south to North Carolina and Missouri (Curtis 1959; Gleason 1958) and from Idaho to Washington and California (Crossley 1974). Bitter nightshade has been cultivated since 1561, chiefly for ornamental purposes, but is now often considered invasive. The fresh berries are poisonous to most humans and fatal to rabbits, but some birds and other wildlife eat them with impunity. Gunn and Gaffney (1974) state that any medicinal values are offset by the poisonous properties of the fruits and berries. Recommendations for medicinal use are only for external application; it has been used as an ingredient in ointments.

Leaves of the typical variety are minutely pubescent or nearly glabrous. Many plants from Nova Scotia to Ontario, however, have distinctly hairy leaves and branches. These plants have been segregated as the variety *villosissimum* Desv. (Gleason 1958). Mathe and Mathe (1973) found that plants from western and eastern European sources differ in their alkaloid chemistry, suggesting the presence of chemical taxa within the species.

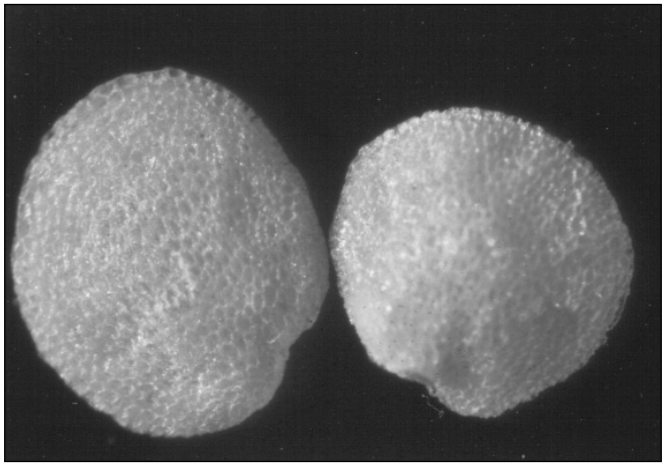
Bitter nightshade is 1 of 1,200 species in the genus, most of which occur in the tropical and subtropical regions of both hemispheres (Crossley 1974). The genus contains economically important agricultural species—such as potato (*S. tuberosum* L.) and eggplant (*S. melongena* L.)—that have been domesticated through plant breeding and for which there is a large amount of information available. (The tomato genus—*Lycopersicon*—is also a member of the Solanaceae.) The nightshade genus also contains a number of agricultural weed species that affect the production of crops such as sorghum, soybeans, and cotton, and for which there is a significant amount of information available on various aspects of seed biology (for example, Rogers and Ogg 1981). Some of the information may be useful for understanding the seed biology of bitter nightshade, but we did not review this information in detail. Seed characteristics of 42 economically important *Solanum* spp., including bitter nightshade, have been described (Gunn and Gaffney 1974).

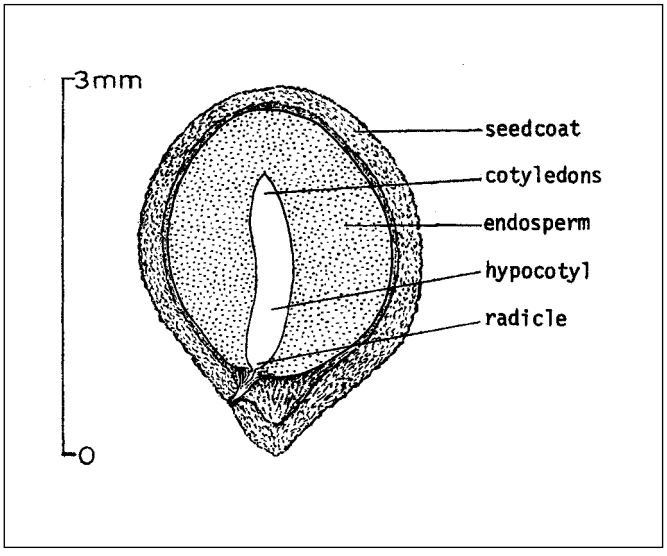
Flowering and fruiting. The violet flowers, which occur in long peduncled cymes, bloom from July to August. Bumble bee species—*Bombus* spp.—are important pollinators (Liu and others 1975). The ovoid to ellipsoid scarlet berries ripen from August to October.

The fruit is a juicy berry 8 to 11 mm in diameter that contains from 40 to 60 seeds. The seeds are 2 to 3 mm by 1.7 to 2.5 mm by 0.7 to 1 mm, strongly flattened, tannish pink, irregular disks, and dully glistening as if coated with fine sugar. The embryo is coiled within the seed (figure 1) (Gleason 1958; Gunn and Gaffney 1974). In cross-section, the embryo is seen as 4 small round structures within the endosperm; the presence of 2 or 3 sections of embryo in a cross-section of the seed is common in the genus (Gunn and Gaffney 1974). Good seedcrops are borne almost annually.

Collection of fruits; extraction and storage of seeds. Seeds may be collected from July to September by hand-picking the ripe berries (Crossley 1974). The fruits may be rubbed through a 10-mesh (2-mm) soil screen, and the pulp and empty seeds floated off with water. Large-scale extraction can be done in a macerator. Parts of the fruit may adhere to the seed (Gunn and Gaffney 1974). Crossley (1974) found in 1 collection that there were about 700,00 seeds/kg (350,000/lb) and that, after careful cleaning, purity should be 99 to 100% and soundness from 92 to 99%. Seeds from genetically transformed plants had seed weights that

Figure 1—*Solanum dulcamara*, bitter nightshade: exterior view of seeds (**top**); longitudinal section through seed (**bottom**). A cross-section of the seed would intersect the coiled embryo 4 times. Longitudinal section based on Crossley (1974) and Gunn and Gaffney (1974).





were 40 to 70% of those of normal plants (Lee and Davey 1988).

Seeds have maintained high viability when stored in airtight containers for 1 year at either 2 to 3 °C or room temperature (20 °C). A moisture content of 6% has been satisfactory for storage periods of less than 1 year (Crossley 1974; Roberts and Lockett 1977). Information is lacking on viability after longer periods, but these seeds appear to be orthodox in storage behavior and should keep well as described above.

Germination. Freshly collected seeds have a high germination capacity with no pretreatment. Seeds germinate at constant temperatures of 30 to 35 °C, but the best germination occurs at alternating temperatures (Crossley 1974; Pegtel 1985; Roberts and Lockett 1977) (table 1). There are no official test prescriptions for bitter nightshade, but other species of nightshade tested at alternating temperatures of 20 and 30 °C (AOSA 1993). Stratification (4 to 5 °C) increases germination at constant temperatures but not at alternating temperatures. Germination of fresh and 1-year-old unstratified seeds at constant temperatures of 20 to 30 °C was greater than 95%; treatment with potassium nitrate improved germination at 30 °C but not at lower temperatures (Roberts and Lockett 1977). Pegtel (1985) found no effect of potassium nitrate on germination. Stratification did not significantly widen the range of constant temperatures at which seeds would germinate (Crossley 1974; Roberts and Lockett 1977; Pegtel 1985). Seeds appear to germinate well without light, however light requirements have not been studied in detail. Seeds will germinate completely in 5 to 6 months under field conditions when covered by 5 cm (2 in) of soil (Roberts and Lockett 1977). Seeds collected from plants growing in a variety of microclimatic conditions did not differ in their response to constant and alternating temperature conditions (Pegtel 1985). Germination is epigeal (figure 2).

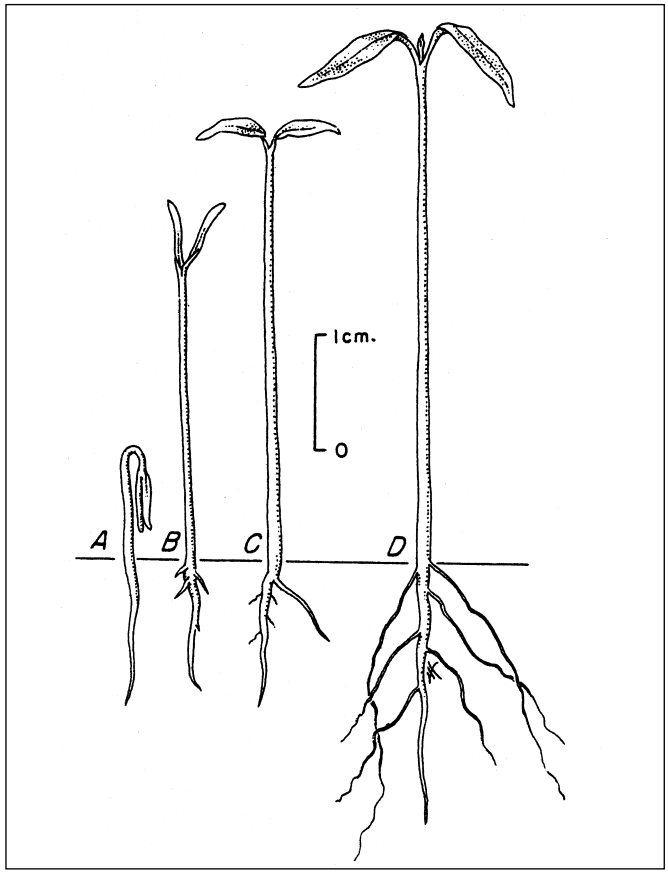
Table 1—*Solanum dulcamara*, bitter nightshade: pregermination treatments and germination

Storage (months)	Stratification (days)	Germination conditions*		Total germination (%)
		Days	Temp (°C)	
0	0	ND	20/30	95
3	0	ND	20/30	95
6	0	ND	20/30	95
0	0	ND	25	5
1	1	ND	25	80
3	3	ND	25	85
6	6	ND	25	75
0	0	ND	15	0
1	1	ND	15	5
3	3	ND	15	30
6	6	ND	15	65

Source: Roberts and Luckett (1977).

* ND = exposed to natural daylight for short periods but no light in germination incubators; 20/30 = 16 hours at low temp and 8 hours at high temp (10/25 °C and 10/30 °C were also used but they made little difference).

Figure 2—*Solanum dulcamara*, bitter nightshade: seedling development at 1, 2, 6, and 12 days after germination.



Nursery practice. It is suggested that seeds be sown in the fall if untreated or if stratified, sown in the spring and covered with about 0.3 cm (0.1 in) of soil. Seeds mixed thoroughly in the surface 7.5 cm (3 in) of soil in September–October and kept under field conditions (in Great Britain) began to emerge in late March; 6, 41, and 2% of seedlings appeared in March, April, and May, respectively. Forty-nine percent of the seeds planted produced germinants; 95% of seeds germinated in laboratory tests (Roberts and Lockett 1977). In other nightshade species, maximum seedling emergence occurred when seeds were covered by 1 to 2.5 cm (0.4 to 1.0 in) of soil (Boyd 1981). Root or stem cuttings can be used for vegetative propagation (Crossley 1974).

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Fabaceae—Pea family

Sophora L.

sophora

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Growth habit, occurrence and use. There are 50 to 70 woody and herbaceous species of the sophora genus found in the warm temperate and tropical regions of the world (Little 1979). Of the species found in the United States, 2 are discussed in detail here.

Mescalbean (also known as *frijolito* and Texas mountain-laurel)—*Sophora secundiflora* (Ortega) Lag. ex DC.—is a small tree of western Texas, New Mexico, and northern Mexico (Little 1976; Ruter and Ingram 1990). *Mamane*—*Sophora chrysophylla* (Salisb.) Seem.—is found in the forests of Hawaii. Mescalbean is a favored tree for landscaping in areas with alkaline soils and moderate drought (Ruter and Ingram 1990). Its seeds reportedly have hallucinogenic properties (Murakoshi and others 1986) and contain many alkaloids (Hatfield and others 1977; Izaddoost 1975; Keller 1975; Keller and others 1976). Vines (1960) lists 2 other southwestern species: silverbush (*Sophora tomentosa* L.), an evergreen shrub, and Texas sophora (*Sophora affinis* Torr. & Gray), a small tree. The Japanese pagoda tree (or Chinese scholar tree) (*S. japonica* L.) is planted in the United States as an ornamental (LHBH 1976; Wasson 2001).

Flowering and fruiting. The fragrant violet flowers of mescalbean appear in terminal clusters 5 to 12 cm in length during March and April. Fruits mature in September as brown pubescent legumes (pods) 2.5 to 13 cm long, usually containing 3 or 4 red globose seeds that are about 12 mm long (figures 1 and 2) (Vines 1960). Mamane racemes are 5 cm in length and golden yellow in color. The legumes are 10 to 15 cm long, and contain 4 to 8 flattened, yellow seeds that are about 8 mm long (Little and Skolmen 1989). Wagner and others (1989) describes the seeds as brown to grayish black.

Storage and germination. There are no long-term storage data on sophora seeds, but they are probably orthodox in storage behavior. Fresh mescalbeans and seeds stored for 1 year at 20 °C successfully germinated when given an acid pretreatment (Ruter and Ingram 1990). Germination rate was best in seeds soaked for 120 minutes in concentrated sulfuric acid. Pretreatment in hot water was unsuccessful. Wang (1991) reported that germination of red, untreated fresh and untreated 1-year-stored seeds was 50 and 8%, respectively. Treating fresh seeds with undiluted (93%) sul-

Figure 1—*Sophora secundifolia*, mescalbean: seed.

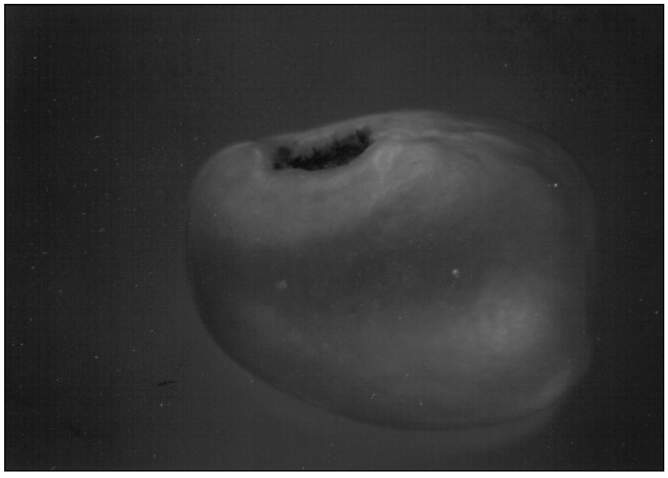
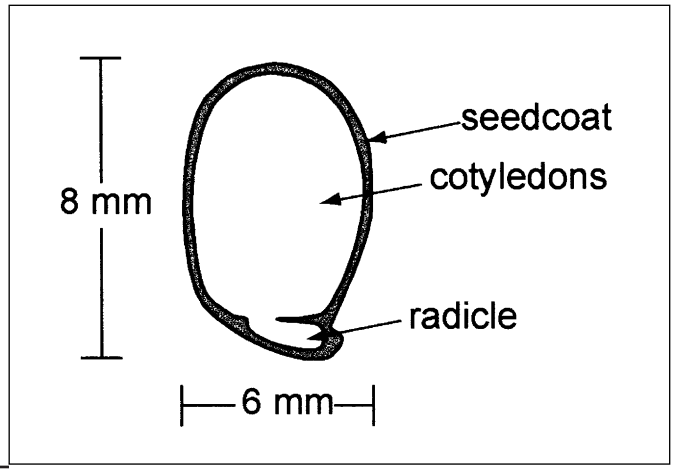


Figure 2—*Sophora*, sophora: longitudinal section through a seed.



furic acid for 10 minutes and stored seeds for 60 minutes increased germination to 80 and 70%, respectively, and reduced germination time to within 14 days. Highest germination values were obtained by drilling a small hole in the seedcoat (>83%). There were also differences in germination between the red seeds and those with a light yellow seedcoat which were harvested 10 days earlier. Untreated red seeds reached maximum germination (99%) within 24 days of sowing, whereas untreated yellow seeds reached maximum germination (93%) within 14 days.

Nursery practice. Field tests of mamane seeds showed that seeds that were pretreated either by sanding or by soaking in sulfuric acid and then were sown in the spring at a depth of 3.8 or 6.4 cm (1 $^1/_2$ to 2 $^1/_2$ in) had the highest percentage emergence and 1-year survival rates (Scowcroft 1981). Of the 2 treatments, spring survival was significantly lower for acid pretreated seeds than for untreated seeds, but sowing depth had no effect. However, mortality was thought to be due to low rainfall and extreme soil surface temperatures.

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Rosaceae—Rose family

Sorbaria sorbifolia (L.) A. Braun

false spirea

Paul O. Rudolf and Peyton Owston

Dr. Rudolf (deceased) retired from the USDA Forest Service's North Central Forest and Range Experimental Station; Dr. Owston retired from the USDA Forest Service's Pacific Northwest Research Station

Synonyms. *Spiraea sorbifolia* L., *Schizonotus sorbifolius* (L.) Lindl.

Other common names. Ural false spirea.

Growth habit, occurrence, and use. False spirea—*Sorbaria sorbifolia* (L.) A. Braun—is native to northern Asia from the Urals to Kamchatka, Sakhalin, and Japan. It is a deciduous shrub from 1 to 3 m tall, usually grown as an ornamental for its bright-green foliage and conspicuous panicles of white flowers (Krüssmann 1960; LHBH 1976; Rehder 1940; Schnelle 1990); the species has been planted for watershed protection and wildlife habitat. It is 1 of about 8 species native to northern and eastern Asia (Rehder 1940; Rosendahl 1955). False spirea often escapes from cultivation in the eastern United States.

Flowering and fruiting. The shiny, white, bisexual flowers bloom in May, June, and July in the northern United States (Rehder 1940; Rosendahl 1955). The fruits are small shiny follicles that ripen in August in Minnesota (Rehder 1940; Rosendahl 1955; Rudolf 1974). Good seedcrops are borne almost every year (Rudolf 1974). Seeds are small and fusiform (figures 1 and 2).

Collection, cleaning, and storage. The ripe fruits should be picked from the bushes by hand and separated from the panicles. The fruits may be kneaded in a bag or rubbed to break them up and then fanned carefully to separate the seeds from the debris. Rudolf (1974) reported that there were about 416,750 dried follicles/kg (189,000/lb) and about 1,667,000 seeds/kg (756,000/lb). No data on seed purity or soundness are available. Seeds may be stored dry in sealed containers at 1 to 5 °C if they are to be held longer than overwinter. Duration of viability under these conditions is not known, but the seeds appear to be orthodox in storage behavior, making a long duration probable.

Figure 1—*Sorbaria sorbifolia*, false spirea: seeds.

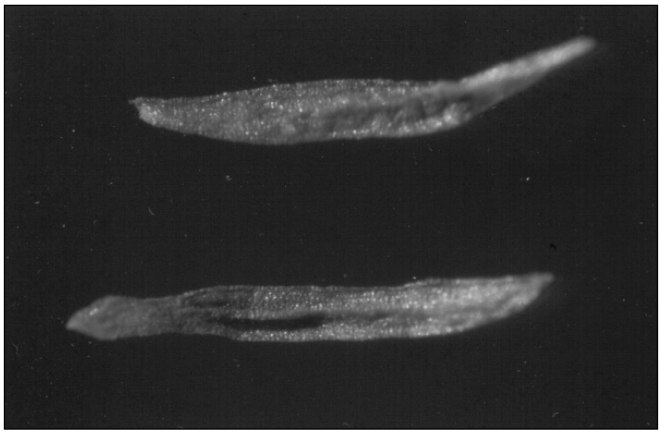
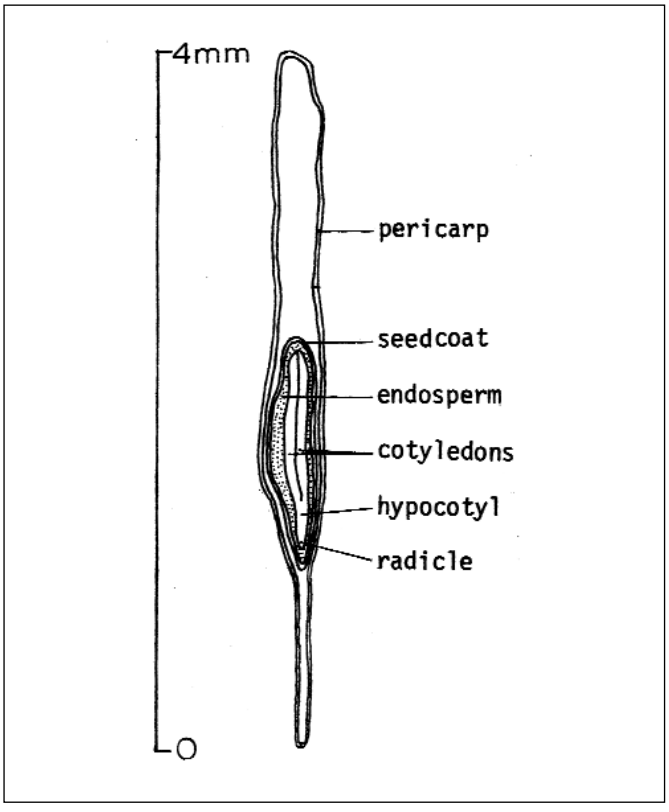


Figure 2—*Sorbaria sorbifolia*, false spirea: longitudinal section through a seed.



Germination. Apparently, some of the seeds have internal dormancy and it is suggested that they be stratified in a moist medium for 30 to 60 days at 1 to 5 °C. Germination test data are unavailable, but it is suggested that tests be made in germinators or sand flats, using pretreated seeds at a temperature of about 20 °C (night) to 30 (day) °C for 40 days. Seeds should be sown immediately after collection in the late summer or stratified seeds used in the spring (Swingle 1939). The seeds should be covered only lightly with soil (LHBH 1976).

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Rosaceae—Rose family

Sorbus L.

mountain-ash

William I. Stein

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Growth habit, occurrence, and uses. The mountain-ash genus—*Sorbus*—includes 80 to 100 species of deciduous trees and shrubs that are distributed in the Northern Hemisphere (Chalupa 1992; Little 1979). Mountain-ash, like other genera in the Rosaceae, is a plastic genus comprised of poorly defined taxa that show extensive introgression where their ranges meet or overlap (Calder and Taylor 1968; McAllister 1985). Geographic races probably have developed, especially in European mountain-ash, as evidenced by its wide range and its several forms and varieties. Hybrids are common among species of mountain-ash, yet the seeds of several species are produced asexually and the resulting progeny are always true to the parent (McAllister 1985; Wright 1981). Hybrids between species of mountain-ash and chokeberry (*Aronia*) or serviceberry (*Amelanchier*) also occur (Rehder 1940).

In growth form, the various species of mountain-ash range from low shrubs to medium-sized trees. Many tend to be multiple-stemmed. Four tree and 3 shrub species are native to North America. A species native to Eurasia, European mountain-ash, has been most widely planted and has become naturalized in parts of the United States and Canada (Calder and Taylor 1968; Little 1979; Viereck and Little 1972). The 5 species listed in table 1 are widely distributed and may be found from low to alpine elevations and ecosystems.

Graceful foliage, showy flowers, brightly colored fruits, hardiness, and a choice of sizes make mountain-ash species especially desirable for ornamental plantings (Wright 1981). The fruits are an important food for birds and rodents (Englund 1993; Van Dersal 1938) and those of some species are consumed by humans, either directly or in preserves and

Table 1—*Sorbus*, mountain-ash: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***S. americana* Marsh.** *Pyrus americana* DC.	**American mountain-ash,** mountain-ash, small-fruited mountain-ash	Newfoundland W to Manitoba, S to E Tennessee, N Georgia, & N South Carolina
***S. aucuparia* L.** *Pyrus aucuparia* (L.) Gaertn.	**European mountain-ash**, rowan-tree, rowan	Native of Eurasia; widely cultivated & naturalized across S Canada & N US, including California & SE Alaska
***S. decora* (Sarg.) Schneid.** *Pyrus americana* DC. var. *decora* Sarg. *S. americana* var. *decora* (Sarg.) Sarg *Pyrus decora* (Sarg.) Hyland	**showy mountain-ash,** mountain-ash, large-fruited mountain-ash	S Greenland to W Ontario, S to NE Iowa, & E to New York
***S. scopulina* Greene** *S. cascadensis* G.N. Jones *Pyrus scopulina* (Greene) Longyear *S. andersonii* G.N. Jones	**Greene mountain-ash,** western mountain-ash	NW Alaska S & E to Saskatchewan, South Dakota, & New Mexico to central California
***S. sitchensis* M. Roemer** *S. californica* Greene *Pyrus sitchensis* (Roem.) Piper *S. cascadensis* G.N. Jones	**Sitka mountain-ash,** Pacific mountain-ash, western mountain-ash, California mountain-ash	Yukon to S Alaska S to central California & W Nevada; N to Idaho, W Montana, & Alberta

Sources: Chalupa (1992), Little (1979), Rosendahl (1955), Viereck and Little (1972).

alcoholic beverages (Chalupa 1992; Pojar and Mackinnon 1994). The foliage and twigs are important browse for deer (*Odocoileus* spp.) and moose (*Alces americana*) and to a lesser extent, for domestic livestock (Van Dersal 1938). The wood of European mountain-ash is hard and tough and is used for production of household utensils and tool handles (Chalupa 1992); this species tolerates atmospheric pollution and is used to reforest areas where such conditions exist (Chalupa 1992).

Flowering and fruiting. The creamy white, complete flowers of mountain-ash are borne in large flattened clusters. Flowering occurs during mid-spring to mid-summer, depending on species and location (table 2). Kronenberg (1994) determined that European mountain-ash flowers in Europe after first fulfilling a 750-hour cold requirement under 7 °C and then a sum of 160 degree-days (with 6 °C as the base temperature) in a period when mean day temperatures are above 6 °C.

Fruits ripen from July to November (table 2). The showy fruits are scarlet to bright red when ripe (table 3). Fruits are fleshy, 2- to 5-celled, berrylike pomes (figure 1) with each cell containing 1 or 2 small, brown seeds (figures 2 and 3). Fruits may remain attached until late winter and are thus available for birds during critical forage periods. Seeds are chiefly dispersed by birds.

European mountain ash begins bearing seeds at about 15 years of age, and good seedcrops occur almost annually (Harris and Stein 1974). Mountain-ash seeds are subject to attack by several species of chalcidid flies (Chalcididae) (Rohwer 1913), and the fruits are damaged by a fungus and a bacterium (Chalupa 1992).

Collection, extraction, and storage. Fruits should be picked, shaken, or raked from the trees or shrubs as soon as

Figure 1—*Sorbus decora*, showy mountain-ash: a cluster of fruits, which are vermillion red when ripe.

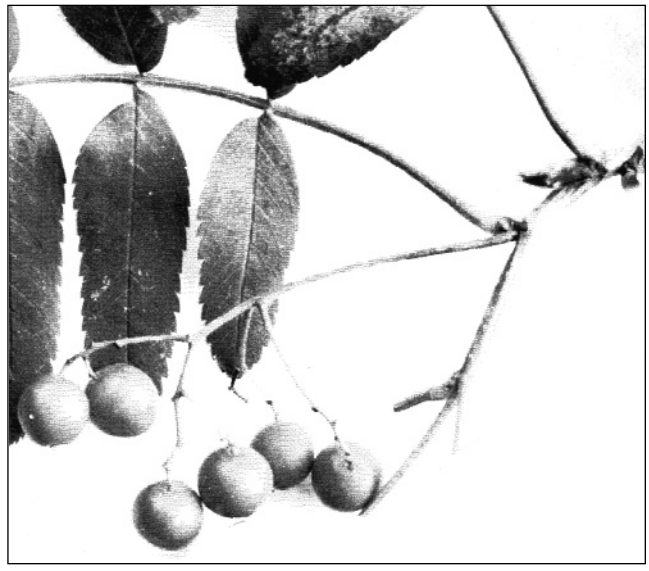


Table 2—*Sorbus,* mountain-ash: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
S. americana	May–July	Aug–Oct	Aug–Mar
S. aucuparia	May–July	Aug–Oct	Aug– winter
S. decora	May–July	Aug–Nov	Aug–Mar
S. scopulina	May–July	July	July–Dec
S. sitchensis	June–Aug	Aug–Oct	Aug–late winter

Sources: Fernald (1950), Harris and Stein (1974), Hitchcock and others (1961), Miller and others (1948). Rehder (1940), Rosendahl (1955), Van Dersal (1938), Viereck and Little (1972).

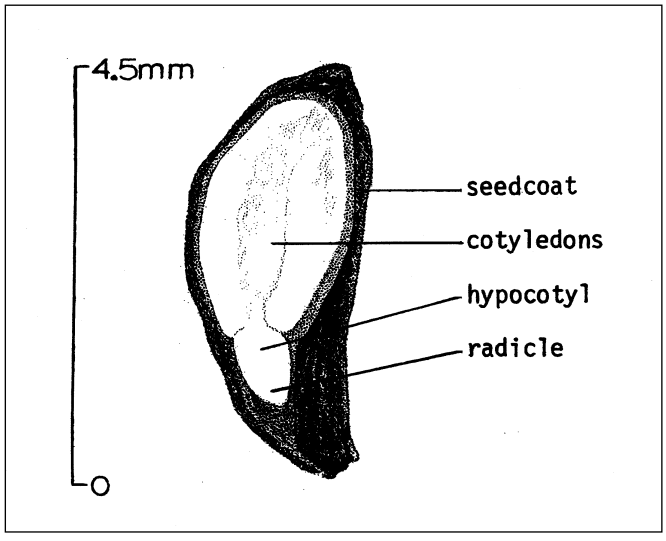
Table 3—*Sorbus,* mountain-ash: growth habit, height, fruit diameter, and color of ripe fruit

Species	Growth habit	Height at maturity (m)	Fruit diameter (mm)	Color of ripe fruit
S. americana	Shrub or tree	4–10	4–6	Bright red
S. aucuparia	Tree	5–20	8–10	Scarlet–bright red
S. decora	Shrub or tree	6–12	8–12	Vermillion red
S. scopulina	Shrub or tree	1–6	8–10	Orange–bright red
S. sitchensis	Shrub or tree	1–6	10–12	Red with bluish cast

Sources: Fernald (1950), Hitchcock and others (1961), Rehder (1940), Rosendahl (1955), Viereck and Little (1972).

Figure 2—*Sorbus*, mountain-ash: two seeds of *S. americana*, American mountain-ash (**left**) and one of *S. sitchensis*, Sitka mountain-ash (**right**).

Figure 3—*Sorbus aucuparia*, European mountain-ash: longitudinal section through a seed, showing large cotyledons.



they are ripe to prevent losses to birds and other foragers. They may be picked slightly immature (Shoemaker and Hargrave 1936) but they then require after-ripening. One suggested method is to pile immature fruits in heaps and allow them to decompose for about 2 months before seeds are removed (NBV 1946). Collected fruits should be transported and stored in cool, aerated conditions to minimize molding and fermentation.

Prompt extraction of seeds from ripe mountain-ash fruits is recommended for best results (Flemion 1931; Heit 1967a); however, extended storage of fruits at low temperature before cleaning resulted in good germination of seeds in comparison tests of European mountain-ash (Flemion 1931) or white mountain-ash (*S. glabrescens* Cardot.) (Taylor and Gerrie 1987). The fruits can be macerated by hand or by mechanical methods available for fleshy fruits (Stein and others 1974), taking care not to cause physical damage. Seeds can be separated from wet pulp by flotation, skimming, or screening; dried; and then fanned to remove debris and empty seeds. In an alternate process, the fruits can be pressed, the matted pulp broken up, and dried pulp and seeds sown together, or the seeds can be separated out by a blower. The weight of cleaned seeds varies less among species in North America than among lots within the same species (table 4.)

Cleaned seeds of mountain-ash retain viability for an extended period if dried to a low moisture content and stored dry in cold, cool, or moderate temperatures. The length of time that seeds remain viable under different storage conditions has not been adequately determined. Seeds of American mountain-ash stored in a tightly closed metal container at –1 to 10 °C lost no viability in 8 years (USDA FS 1948). Seeds or intact fruits of European mountain-ash stored at temperatures ranging from –8 °C to room temperature in sealed or unsealed storage retained high viability for 1 to 2 years, but viability was much reduced at humidity levels above 25% or temperatures of 25 °C (Flemion 1931). Seeds can be stored over-winter under stratification conditions in outdoor pits or flats (Flemion 1931; Shoemaker and Hargrave 1936). Seeds of European mountain-ash retained some viability for 5 years when fruits were buried in the mor layer (acid humus in cold, wet soils) in northern Sweden (Granstrom 1987).

Low-temperature storage of cleaned mountain-ash seeds in sealed containers at 6 to 8% moisture content has been recommended (Heit 1967b). Considering their performance after storage under various conditions, seeds of this genus are likely to store well for extended periods under conditions best for many tree species—at low moisture content in closed containers at subfreezing temperatures.

Pregermination treatments and germination tests. Fresh mountain-ash seeds will not germinate readily; they require lengthy after-ripening, including cold stratification (Barclay and Crawford 1984; Flemion 1931; Taylor and Gerrie 1987; Zentsch 1970). The stratification requirements for European mountain-ash seeds vary somewhat by tree and year (Zentsch 1970). Seeds of this species require less cold stratification at 1 °C if they are first stored dry at room temperature for 6 months (Flemion 1931). They will enter into secondary dormancy if subjected to warm germination conditions when incompletely stratified or if stored dry after cold, moist stratification (Flemion 1931). To shorten the stratification period, Zentsch (1970) tested warm stratification at 20 °C for 1 to 6 months before cold stratification and germination at 3 °C; warm stratification generally prolonged

Table 4—*Sorbus,* mountain-ash: fruit weight and seed yield data

Species	Fruit wt/ fruit vol		Seed yield/ fruit vol		Cleaned seeds				Samples
					Range		Average		
	kg/hl	lb/bu	kg/hl	lb/bu	/kg	/lb	/kg	/lb	
S. americana	—	—	1.3–2.6	1–2	183,000–521,000	83,000–236,300	319,400	144,900	9
*S. aucuparia**	—	—	—	—	229,300–374,800	104,000–170,000	286,200	129,800	10
S. decora	—	—	—	—	—	—	280,400	127,200	1
S. sitchensis†	52	40	1.3	1	146,400–385,000	66,400–174,600	290,800	131,900	8

Sources: Harris and Stein (1974), King (1947), McKeever (1938), Mirov and Kraebel (1939), Swingle (1939), Van Dersal (1938).
* Data represent seeds only from North American sources.
† The number of dry fruits in one sample was 13,690/kg (6,210/lb) (Mirov and Kraebel 1939).

the total time required, but did not improve the high total germination. Lenartowicz (1988) reached a similar conclusion but recommended that European mountain-ash seeds be stratified at 20 °C for 6 weeks and then germinated at 3 °C to gain the benefits of a shortened period during which most germination occurs. Mechanical or chemical scarification of the seeds has not shortened the stratification or germination period (Flemion 1931; Harris and Hilton and others 1965; Stein 1974) but sulfuric acid treatment increased total germination in one instance (Hilton and others 1965).

The standard germination test procedure for mountain-ash species requires pre-chilling the seeds for 4 months at 3 to 5 °C followed by germination for 28 days at alternating temperatures of 20 and 30 °C (ISTA 1996). It is noteworthy that the highest germination (90% or higher) for mountain-ash seeds was obtained in various lengthy comparison tests at markedly lower germination temperatures than those prescribed in the standard test—at 1 to 3 °C (table 5). In fact, the same substrate and temperature were used during many tests for both stratification and germination. Given enough time, seeds of American and European mountain-ashes completed germination under moist low-temperature conditions (Flemion 1931; Harris and Stein 1974; Lenartowicz 1988; Zentsch 1970), a capability also demonstrated by other species of mountain-ash (Nikolaeva 1967).

Review of the methods employed and results obtained in comparison studies leads to the conclusion that the standard germination test for mountain-ash needs a firmer foundation. Hints among published results point to 2 aspects that deserve further investigation—after-ripening and germination temperature. After-ripening requirements may vary, depending on when and where fruits are collected, as indicated by collections made over an altitudinal gradient (Barclay and Crawford 1984). As early as 1931, Flemion reported that dry storage at room temperature shortened the time needed for cold stratification and that germination temperatures above 20 °C caused secondary dormancy. Warm stratification at 20 °C (Lenartowicz 1988; Zentsch 1970) may be too high and moist conditions may not be necessary. Likewise, germination at alternating 20 and 30 °C may approach or cause secondary dormancy; lower germination temperatures may prove more satisfactory as indicated by Taylor and Gerrie (1987) for white mountain-ash.

Viability of mountain-ash seeds is most easily and rapidly determined by a tetrazolium (TZ) test on excised embryos. It is the first choice among methods recognized by the International Seed Testing Association (ISTA 1996). Preparation and evaluation procedures to use are listed in the TZ testing handbook (AOSA 2000). Test procedures include soaking the seeds in water for 6 hours or more at 20 °C, exposing or excising the embryos, then soaking them in a 1% TZ solution for 18 to 24 hours at 30 to 35 °C, and evaluating the resulting staining. A fully viable embryo is uniformly stained red to pink, with even borders and shape. Growing excised embryos is a slightly longer yet also a quick means of determining seed viability. The excised embryos are incubated at 20 °C for about 6 days and their development evaluated. Those that retain their freshly excised appearance or whose cotyledons have enlarged and become deep green are viable; those that deteriorate or turn pale yellow-green are not (Flemion 1938; Heit 1955). Comparable estimates of the viability of mountain-ash seeds have been obtained by these 2 quick tests (Hilton and others 1965), but viability values determined by such tests are often higher than that obtained by germination test (Flemion 1938).

Nursery practice. Mountain-ash species can be propagated from seeds, cuttings, suckers, grafts, and small plant parts. Reproduction from seeds is most common but other methods also serve production objectives.

Untreated mountain-ash seeds can be sown in late summer and early fall or pretreated seeds can be sown in the fol-

Table 5—*Sorbus,* mountain-ash: stratification and germination test conditions and results*

Species	Stratification†			Germination test		Germination		Total germination	
	Days	Temp (°C)	Moist medium	Temp (°C)	Days	(%)	Days	(%)	Samples
S. americana	60	5	Sand	20–30	14	13	8	13	4
	90	5	Sand	10	60	11	22	12	4
	CSG	5	—	5	150	15	132	16‡	4
S. aucuparia	CSG	1	Peat moss	1	127	70	99	94	1
	CSG	1	Peat moss	1	82	69	61	96	1
	CSG	1	Peat moss	1	120	58	90	93	6
	CSG	1	Peat moss	1	120	57	90	90	4
	120	2	Paper	20	—	68	90	76	1
	CSG	3	Sand	3	150–210	—	—	95+	26
	30–180	20	Sand	3	150–210	—	—	90+	52
	CSG	3	Peat & sand	3	560	60	420	88	1
	70	20	Peat & sand	3	350	86	300	93	1
	126	2	Peat	20	42	—	—	30	3
S. decora	—	—	—	20–30	60	—	—	10	4
S. scopulina	115	3–5	Peat–verm	20	38	61	17	61	1
S. sitchensis	90§	3	Paper	20–30	53	30	10	30	1
	120	0	—	—	50	—	—	21	1
	140	5	Sand	21	17	15	11	15	1

Sources: Barclay and Crawford (1984), Flemion (1931), Harris and Stein (1974), Hilton and others (1965), Lenartowicz (1988), McKeever (1938), Mirov and Kraebel (1939), Trindle (1996), Zentsch (1970).

CSG = stratification and germination as a continuum under the same conditions; verm = vermiculite.

* Only the better test results for each species are listed.

† Stratification in moist sand, peat moss, soil, or petri dish.

‡ Reached 33% germination in 330 days (USDA FS 1948).

§ Ten-minute soak in H_2SO_4 before stratification.

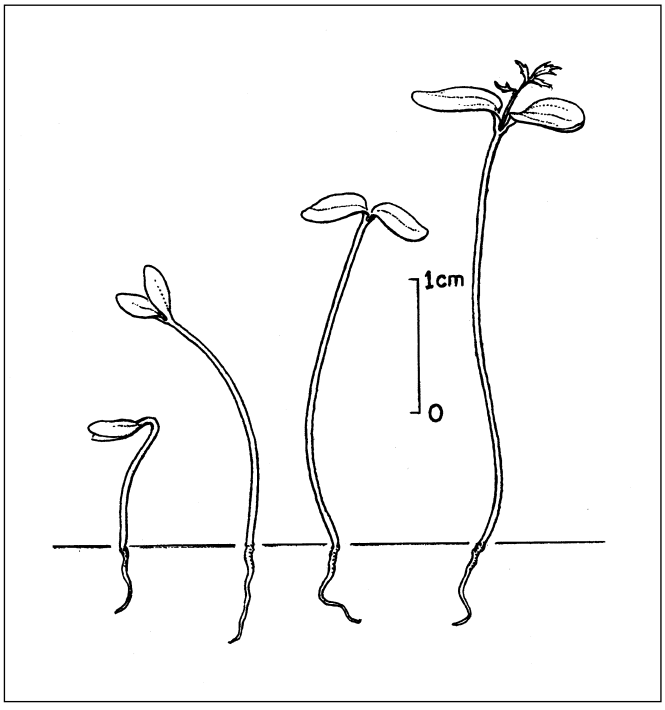
lowing spring for production of seedlings in the same growing season. Fall-sowing involves the following considerations: (1) sowing should perhaps be done as early as midsummer, because some seedlots or species benefit from moist warm conditioning prior to the moist chilling that is supplied by winter weather (Heit 1968); (2) the seeds are subject to predation by rodents, insects, and birds for a long time and may need protection; and (3) stored seeds must be available because time for after-ripening may not be sufficient for freshly collected seeds. Sowing outdoors in late winter or spring requires use of cold-stratified seeds or sowing early enough that natural cold stratification can still occur. Cold stratification at or near 1 °C for 60 to 120 days is needed for best results (Barclay and Crawford 1984; Flemion 1931; Hilton and others 1965; Taylor and Gerrie 1987). If seeds are sown late or are not sufficiently preconditioned, or conditions are too warm, germination will be delayed until the second or even third year (Fabricius 1931; Flemion 1931; Harris and Stein 1974). Mountain-ash seedlings can also be container-grown in greenhouses where good germination and growth conditions are readily maintained (McDonald 1989).

Cleaned seeds can be sown in drills; berries or dried macerated pulp with seeds must necessarily be broadcast. When seeds are sown without removal from berries or pulp, germination is slower and generally not as satisfactory (Fabricius 1931; Flemion 1931; Heit 1967a). Seeds should be lightly covered with sand, sawdust, sandy soil, or peat moss and the beds mulched heavily with pine needles, peat moss, wood chips, straw, or hardwood leaves to protect them from exposure and freezing (Heit 1967a). Late fall- or winter-sowing of untreated seeds in board-covered but unmulched coldframes and on snow has also produced satisfactory results (Fabricius 1931; Flemion 1931). Germination is epigeal (figure 4).

Cuttings of several mountain-ash species taken in early summer rooted readily and quickly developed into sturdy plants (McAllister 1985). Micropropagation of European mountain-ash has been successful by grafting, softwood cuttings, and in vitro culture (Chalupa 1992). Trees produced by shoot tip and axillary bud culture have been planted, survived well, and grew at about the same rate as trees grown from seeds—3.5 to 4 m (11 to 13 ft) in 5 years (Chalupa 1992). Tree production from excised embryos also appears feasible.

Mountain-ash seedlings are hardy and not very susceptible to insects or disease; however, they are subject to nipping by deer and moose (Fabricius 1931; Van Dersal 1938). For field planting, 1+1 transplants are best, but 2+0 seedlings are also suitable (Harris and Stein 1974).

Figure 4—*Sorbus americana*, American mountain-ash: seedling appearance at 1, 3, 7, and 24 days after germination



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Bignoniaceae—Trumpet-creeper family

Spathodea campanulata Beauv.

African tuliptree

Kristina F. Connor and John K. Francis

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Other common names. fountain tree, *tulipan Africano*

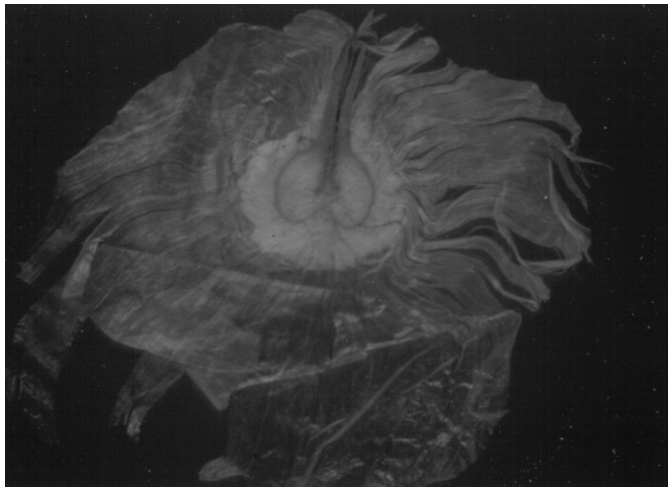
Growth habit, occurrence, and use. The African tuliptree—*Spathodea campanulata* Beauv.—is a medium-sized tree that commonly reaches a height of 21 m (Neal 1948) but may reach 30 m in some parts of West Africa (Unwin 1920). In Puerto Rico, the largest African tuliptree measures 35 m tall and 1.75 m in dbh (Francis 1990); heart and butt rots are common in trees older than 20 to 25 years that have suffered mechanical or fire damage.

African tuliptree grows naturally in the secondary forests in the high forest zone and in the deciduous, transition, and savanna forests of equatorial Africa. Its native range extends along the western coast of Africa from Ghana to Angola and inland across the humid center of the continent to southern Sudan and Uganda (Irvine 1961). It develops best in fertile, deep, well-drained loams but will also colonize heavily eroded sites (Francis 1990). The African tuliptree has been successfully planted outside its natural range (Little and Wadsworth 1964; Mahecha Vega and Echeverri Restrepo 1983). Throughout the humid tropics, its large brilliant flame-orange flowers have made it one of the most popular flowering ornamentals. The species has naturalized in at least Colombia (Mahecha Vega and Echeverri Restrepo 1983), Costa Rica (Holdridge 1942), Puerto Rico (Liogier and Martorell 1982), Cuba (White 1951), Jamaica (Streets 1962), Sri Lanka (Worthington 1959), and Guam (McConnell and Muniappan 1991). The wood of this fast-growing species is light and little used.

Flowering and fruiting. The 10-cm-long, bright red-orange flowers occur in terminal racemes on trees as young as 3 to 4 years of age (Francis 1990). Yellow-flowering trees have also been reported (Francis 1990; Menninger and others 1976). Flowering time varies, depending on location. Nalawadi and others (1980) report flowering of African tuliptree in India from early January until early March, with peak flowering in mid-February. However, in southern Africa, flowers occur in fall and winter and, in the Caribbean, trees bloom from late winter to early summer (Francis 1990). The 1 to 4 boat-shaped brown pods are 15 to 25 cm long and usually develop from each flower cluster (Eggeling 1947; Little and Wadsworth 1964); seeds mature 5 months after flowering (Francis 1990). The wind-dispersed seeds are lightweight and surrounded by a membranous wing (figure 1) (Vozzo 2002).

Collection, storage, and germination. The seeds should be collected from undehisced, brown pods and air-dried until they split open (Francis 1990). Seeds of most species in this genus are orthodox and should store well. The reported number of seeds per weight varies from 125,000/kg (57,000/lb) (Holdridge 1942) to 290,000/kg (132,000/lb) (Francis and Rodrıguez 1993). Francis and Rodrıguez (1993) report germination of 38% of the African tuliptree seeds sown on the surface of wet potting soil in a covered tray and kept at ambient (24 to 30 °C) temperatures. Germination is epigeous and may begin in as little as 2 days.

Figure 1—*Spathodea campanulata*, African tuliptree: winged seeds.



Nursery practices. Germinating seeds are fragile and should not be covered by more than a dusting of peat or fine sand. Francis (1990) reports that, under 50% shade, African tuliptree seedlings took 2 months after germination to develop the first true leaves; when transplanted into nurserybeds at 25% shade, the seedlings attained plantable size—that is, 35 cm (14 in) tall—in 5 months. He concluded that a regimen with more sunlight would probably have reduced the time needed to reach plantable size.

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Rosaceae—Rose family

Spiraea L.

spirea

John C. Zasada and Peter F. Stickney

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Growth habit, occurrence, and uses. There are about 80 species of the genus *Spiraea* throughout the world. The genus is subdivided into subgenera and sections in several ways depending upon the author—all classifications are based primarily on the structure of the inflorescence. In the system followed here (Batta 1977), the genus has 3 sections: Chamaedryon, Calospira, and Spiraria. In the United States and Canada, the taxa listed in table 1 are fairly common (Curtis 1959; Esser 1995; Fernald 1950; Habeck 1991; MacKinnon and others 1992; Ogle 1991b; Viereck and Little 1972). Virginia spirea occurs primarily in the southeastern United States and has been listed as a threatened species (Ogle 1991a).

Spireas are important ornamental shrubs—Dirr (1990) lists 13 species used as ornamentals. Within a species, as many as 15 to 20 cultivars may have been recognized. Most of the important ornamentals have been introduced from China and Japan; many of the original introductions occurred in the early to mid-1800s (Dirr 1990). Some introduced species, for example, Japanese spirea (*Spiraea japonica* L.f.), have become naturalized and occupy habitats similar to those of native spireas (Batta 1977; Fernald 1950; Ogle 1991a).

A common habitat for the genus in general seems to be in riparian areas, bogs, or other wetland habitats (Curtis 1959; Esser 1995; Klinka and others 1985; MacKinnon and others 1992; Ogle 1991a&b; Viereck and Little 1972). However, the eastern and western forms of birchleaf spirea and the hybrid *S.* × *pyrimidata* Greene (pro sp.) occur on drier upland sites than do other species (Corns and Annas 1986; Stickney 1986). These species can be found at all stages of succession, but they seem to achieve their greatest stature and best growth following disturbances—such as fire or flooding—that remove the overtopping trees and thus

Table 1—*Spiraea,* spirea: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***S. alba* Du Roi**	**meadowsweet**	Newfoundland, Quebec to Alberta S to North Carolina, Missouri, & South Dakota
***S. alba* var. *latifolia* (Ait.) Dippel** *S. latifolia* (Ait.) Borkh.	**meadowsweet**	SE Canada & NE US
***S. betulifolia* var. *corymbosum* (Raf.) Maxim.**	**birchleaf spirea**	Maryland, Virginia, West Virginia S to Alabama
***S. betulifolia* var. *lucida* (Dougl. ex Greene) C.L. Hitchc.**	**birchleaf spirea**	South Dakota, Montana, Idaho, Washington, Oregon, Wyoming, British Columbia, Alberta, & Saskatchewan
***S. douglasii* Hook.**	**Douglas spirea**	Alaska S to N California, British Columbia, Montana, Oregon
***S. stevenii* (Schneid.) Rydb.** *S. beauverdiana* (Schneid.)	**Beauverd spirea,** Alaska spirea	Alaska & NW Canada
***S. tomentosa* L.**	**hardhack,** steeplebush	Nova Scotia, New Brunswick, & Quebec to Minnesota & S to North Carolina, Tennessee, & Arkansas
***S. virginiana* Britt.**	**Virginia spirea,** Appalachian spirea	West Virginia, Virginia, Tennessee, North Carolina, & Georgia

Sources: Curtis (1959), Habeck (1991), MacKinnon and others (1992), Ogle (1991a&b), Viereck and Little (1972).

make light and other resources more available (Ogle 1991b; Stickney 1974, 1986, 1989, 1990).

Native spireas are generally 1 to 2 m tall. Plants growing at higher elevations tend to be shorter in stature than those at low elevations. Individual plant form tends to be a multi-stemmed clump arising from basal sprouting. Many species are rhizomatous and capable of forming dense stands (clones). Beauverd spirea does not appear to be rhizomatous. Layering occurs in some species when aerial stems come in contact with a suitable substrate long enough for rooting to occur (Calmes and Zasada 1982; Esser 1995; Fowler and Tiedemann 1980; Habeck 1991; Ogle 1991b; Stickney 1974, 1986, 1990).

Planting as an ornamental seems to be the major use of plants in the genus. Native species occurring in riparian and wetland areas can be used in rehabilitation projects on these sites. Some species were used to a limited extent for medicinal purposes by Native Americans (Dirr 1990; Esser 1995; Habeck 1991; Meeker and others 1993; Ogle 1991b).

Flowering and fruiting. Batta (1977) found that the various species and varieties of spirea growing in a common garden in Norway exhibited marked differences in phenology and the timing of floral bud differentiation. Differences in timing of floral bud initiation are determined in part by the type of shoot on which the buds form. Species in section Chamaedryon form buds on the previous year's growth; species in section Spiraria, on the current year's growth; and species in Calospira, on both types of shoots (Batta 1977). Goi and others (1974, 1975) demonstrated that species differ in their temperature requirements for initiation of flower buds. In the species they studied, one initiated flower bud development at temperatures below 20 °C and the other below 25 °C.

Within a species, microclimate significantly influenced the timing of flowering and fruit maturation. Birchleaf spirea flowered at about 16,000 degree-hours (threshold temperature 0 °C) at elevations of 590, 1,105, and 1,635 m, but the heat sums were attained over a period of 30 to 40 days, with earliest flowering in mid-to late May at the lowest elevation (Fowler and Tiedeman 1980). At elevations around 985 m in the northern Rocky Mountains, flowering may occur from early June to early July (Drew 1967; Stickney 1974). Fruits ripen from mid-July to early September (Drew 1967; Stickney 1974),and seeds disseminate in October (Drew 1967). Flowering in Beauverd spirea in Alaska occurs in June–August and fruit maturation from July–September. Timing, as in birchleaf spirea varies significantly with elevation and between boreal forest and tundra populations (Viereck and Little 1972). In the southern Appalachian Mountains, follicles of Virginia spirea begin to dehisce in late August–September and the process continues through late winter (Ogle 1991a&b).

Individual flowers are very small (1.5 mm) and perfect; they are borne in terminal clusters of various sizes shapes and colors (white and pink–deep rose) (Hitchcock and others 1961; MacKinnon and others 1992; Stickney 1974). Seeds are borne in a follicle and measure 2 to 3 mm in length (figures 1 and 2). Dispersal begins when the fruit

Figure 1—*Spiraea betulifolia* var. *lucida*, birchleaf spirea: seed.

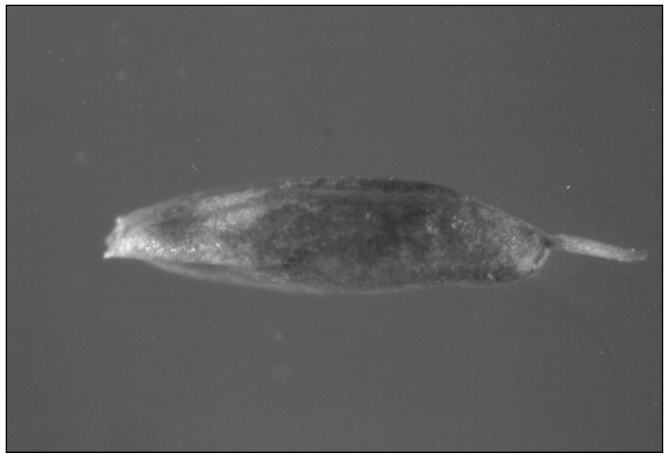
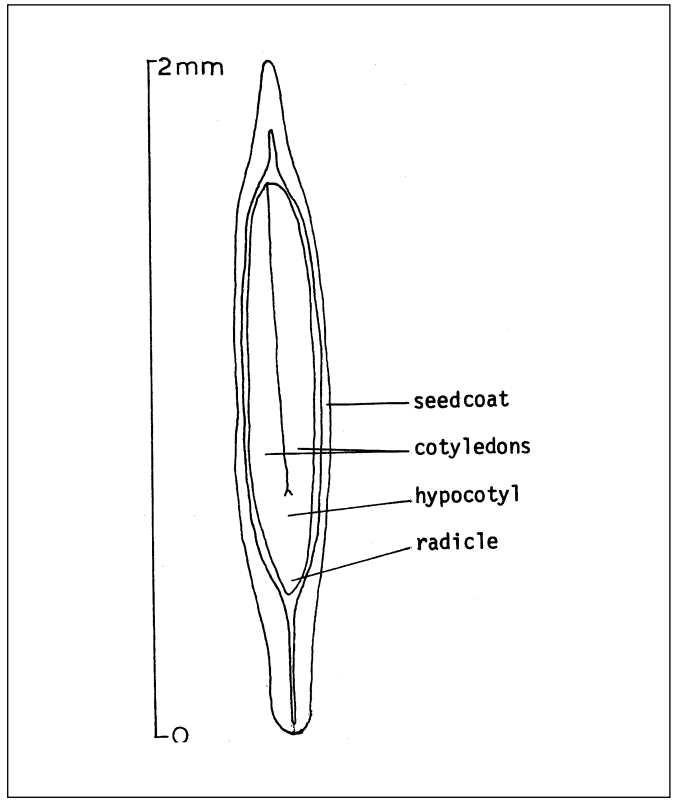


Figure 2—*Spiraea betulifolia* var. *lucida*, birchleaf spirea: longitudinal section through a seed.



becomes straw-colored or light brown and splits down one side. Although there are no estimates of the number of seeds per weight, the number is probably in the millions per kilogram (500,000+ per pound), due to the extremely small size of the seeds, usually 2 mm or less × 0.05 mm (0.8 × 0.02 in).

Annual variation in the quantity and quality of the seedcrop will depend on microclimate and its effect on pollination, flowering, seed maturation, time since disturbance, and other variables. Fowler and Tiedemann (1980) reported frost damage to birchleaf spirea flowers in early-flowering lower-elevation populations but not in later-flowering higher-elevation plants. Abortion of flowers and fruits is high in Virginia spirea growing in the southern Appalachian Mountains, particularly in years of low water availability (Ogle 1991b). Factors regulating flower bud differentiation, and thus flowering potential, vary for those species that differentiate flower buds in late summer–fall compared to those that differentiate in the spring shortly before flowering (Batta 1977).

Birchleaf spirea exhibits the phenomena of mass flowering after fire (Stickney 1986, 1989, 1990). In studies of succession following fire over a 20-year period, this species flowered profusely in the first postfire growing season, but only occasionally in scattered individuals during the subsequent 19 years. As tree canopies develop and light intensity declines, flowering is rare and the species maintains itself through vegetative reproduction.

Collection of fruits, seed extraction and storage. Seeds can be collected when the fruits turn brown. Fruits can be dried at room temperature so that they open fully; seeds are removed by tumbling or shaking the dried fruits. Seeds can be stored for several months to at least a year. In birchleaf spirea, mass flowerings in 1-year-old burns provides the best opportunity for seed collection.

Seeds have been recovered from studies of forest seedbanks in both the eastern and western United States. However, there is no good evidence that buried seeds are a significant source of regeneration after disturbance (Graber and Thompson 1978; Morgan and Neuenschwander 1988). These studies did not provide information on the length of time seeds remain viable in the forest floor or mineral soil.

Germination. Seeds germinate readily with no pretreatment, particularly if sown before there has been any significant drying (Dirr and Haeuser 1987). Birchleaf spirea seeds germinate at 0 to 2 °C when kept under such conditions for more than 120 days (McLean 1967). This suggests that seeds sown in the fall and overwintering under the snow will germinate at about the time of snowmelt to take best advantage of conditions favorable for seedling development. Unstratified seeds of Beauverd spirea germinated only at 25 °C. Germination of stratified seeds (30 days at 2 °C) was greater than 95% between 10 to 25 °C and 40% at 5 °C. Neither stratified nor unstratified seeds germinated to any degree in the dark (Calmes and Zasada 1982). Filled seeds made up 68 and 85% of seedlots of birchleaf and Beauverd spireas, respectively (Calmes and Zasada 1982; McLean 1967).

Nursery practice and natural regeneration. Natural regeneration following disturbance appears to be mostly by basal sprouting or from rhizomes. Only very severe fires or soil disturbances can eliminate vegetative reproduction (Calmes and Zasada 1982; Morgan and Neuenschwander 1988; Ogle 1991; Stickney 1986, 1989).

Seed regeneration of birchleaf spirea occurs 2 to 3 years after fire, when seeds are abundant following the mass flowering in the first post-fire growing season (Stickney 1989). This appears to be the main window for seed regeneration, as seed availability and seedbed conditions are best at this time (Stickney 1986, 1989, 1990). However, recent germinants and 1- to 2-year-old seedlings are not common (Miller 1996; Morgan and Neuenschwander 1988; Stickney 1990).

Plants can be produced from seeds or by vegetative propagation. Seeds should be sown immediately after collection for the most rapid germination. Stored seeds may require some stratification for best germination, but unstratified seeds germinate well. Softwood or hardwood cuttings of horticultural varieties can be rooted and grow fairly rapidly, filling a 3.8-liter (1-gal) container in a single growing season. Softwood cuttings appear to be used most commonly (Dirr and Heuser 1985). Shoot explants and micropropagation can be used to increase desirable clones; performance and vigor of plants produced in this way varies with season of the year and the number of times vegetative material is subcultured (Norton and Norton 1988 a&b).

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Styracaceae—Storax family

Styrax L.

snowbell

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Growth habit, occurrence and use. The genus *Styrax*—the snowbells—comprises about 100 species of trees and shrubs in the warm temperate and tropical regions of the Northern Hemisphere (LHBH 1976). The snowbells in the United States are shrubs or small trees planted for their showy flowers (table 1). Southeastern Asian species are the source of the balsamic resin benzoin (LHBH 1976).

American snowbell grows to 5 m and 9 cm dbh, with 9-cm-long pubescent leaves. Even though American snowbell is common, it rarely grows large enough to be considered a tree. It grows under 200 m of elevation in moist to wet places, such as bottomland woods, flood plains, swamps, and stream banks (Duncan and Duncan 1988; LHBH 1976).

Bigleaf snowbell reaches 8 m and 10 cm dbh, with 18-cm-long gray pubescent leaves. It grows to 1,000 m elevation in deciduous or mixed woods, usually in well-drained areas. Bigleaf snowbell rarely reaches tree size (Duncan and Duncan 1988; LHBH 1976). The USDI Fish and Wildlife Service has designated Texas snowbell as an endangered species.

Several Asian snowbells are grown in the United States. Japanese snowbell grows to 9 to 10 m with 8-cm-long glabrous leaves. Fragrant snowbell also reaches 9 to 10 m but has 25-cm-long tomentose or densely pubescent leaves (LHBH 1976).

Flowering and fruiting. Snowbells have bell-shaped, showy white flowers that are deeply lobed (5 to 8 lobes), with 10 to 16 stamens and a superior ovary 3-celled below and 1-celled above (LHBH 1976). The fruit, although often referred to as a drupe, is a berry—or a capsule in dehiscent species such as drug snowbell or keminyan (*Styrax officinalis* L.)—because the stony layer is really the seedcoat instead of endocarp (Ng 1976). The American snowbell berry is about 7 mm across, grayish, with dense, short hairs (Dirr and Heuser 1987; Duncan and Duncan 1988). It matures in August and drops by November (Dirr and Heuser 1987).

Collection of fruit, extraction, and storage. The single, hard, shiny brown seed separates from the fruit at maturity (Dirr and Heuser 1987) and is easily collected. The fruits may also be collected while they are still green in September (in Louisiana) or should be collected at least 14 weeks after flowering for Japanese snowbell, and air-dried in a well-ventilated place until the drupe walls turn brown

Table 1—*Styrax,* snowbell: nomenclature and occurrence

Scientific name & synonyms(s)	Common name(s)	Occurrence
***S. americanus* Lam.** *S. americanus* var. *pulverulentur* (Michx.) Perkins ex Rehd. *S. pulverulentus* Michx.	**American snowbell,** mock-orange*	Virginia to Florida & Louisiana
***S. grandifolius* Ait.**	**bigleaf snowbell**	Virginia to Florida & Louisiana
***S. japonicus* Sieb. & Zucc.**	**Japanese snowbell,** Japanese snowdrop tree, snowbell tree	Japan, Korea, & China
***S. obassia* Sieb. & Zucc.**	**fragrant snowbell,** bigleaf snowbell	China, Japan, & Korea
***S. platanifolius* Engelm. ex Torr. ssp. *texanus* (Cory) P.W. Fritsch**	**Texas snowbell**	Texas

Sources: Duncan and Duncan (1988), LHBH (1976), Wasson (2001).

* Although this common name is in use, it is more correctly applied to members of the genus *Philadelphus.*

and seeds become loose. The dried seeds can be separated from the fruit fragments by running them through a debearder or macerator (Delaney (2002). Small amounts may be separated by rubbing the lot between the hands. Seed weight data are listed in table 2.

There have been no storage data reported for the snowbells, but the nature of the seeds suggests that they are orthodox in storage behavior and should store well in cold, dry conditions. Seeds stored dry at room temperature (20 to 21 °C) for a year germinated well after a proper warm and cold stratification treatment.

Seed germination as influenced by seed maturity. In 1999, when Japanese snowbell seeds were harvested on August 25 and September 8, there were 67 and 80% of seeds germinated in 6 and 7 weeks, respectively (table 3) (Roh and others 2003). More than 80% of the seeds germinated in less than 4.5 weeks when seeds were harvested after September 8. Based on the final seed germination rate, seeds were considered to be mature when harvested on or after August 25, which is 12 weeks after flowering. In 2000, more than 73% of seeds germinated in a period of 6 weeks or less when seeds were harvested on or after October 4 (table 3), and seeds were considered to be mature when harvested on September 13, about 14 weeks after flowering. For both years, the mean peak germination, and the mean number of weeks for germination peak were significantly influenced by harvest date, that is, seed maturity.

Pregermination treatments and germination tests. American snowbell germinates successfully after 3 months of cold stratification. Fall-sowing of fresh, cleaned seeds in Alabama also yielded excellent spring germination (Dirr and Heuser 1987). Bigleaf snowbell, another snowbell from the southeastern United States, is believed to have the same germination requirements as American snowbell (Dirr and Heuser 1987). Japanese snowbell seeds that are sown in the fall without a sequential warm stratification and cold stratification may germinate the second spring (Dirr 1990; Kwon 1995). Kwon (1995) suggested that the radicle might emerge after 3 months of warm stratification and then enter a dormancy. Stratification of seeds using warm and cold temperatures is required to break seed dormancy for many woody plants to improve seed germination (Young and Young 1992). It has been recommended that snowbell seeds should be stored in a moist, warm environment for 3 (Kwon 1995) or 5 (Dirr 1990) months , and then stored at low temperatures for 3 or 4 months (Dirr 1990; Kwon 1995). Seeds that are sown immediately after collection may germinate by the following spring, suggesting that non-fresh seeds may take longer to germinate (Dirr 1990).

Japanese snowbell has been reported to need 3 to 5 months of warm stratification followed by 3 months of cold stratification to germinate (Dirr and Heuser 1987). Seedlots in one study germinated at 64% after 3 months of warm and 3 months of cold stratification and at 76% after 3 months of warm and 4 months of cold stratification. Seeds with 3 or 4 months of cold stratification did not germinate (Dirr and Heuser 1987).

Fragrant snowbell germinated 88% after 3 months of warm stratification and 3 months of cold stratification (Dirr and Heuser 1987). Benzoin tree—*Styrax benzoin* Dryander, a species from Southeast Asia—is one of the few trees in Malaysia with dormant seeds. They germinate when the stony layer cracks open about 7 months after fruit fall. Fresh seeds will germinate if the stony layer is removed (Kiew 1982).

Table 2—*Styrax,* snowbell: seed data (average cleaned seeds per weight)

Species	Seeds/weight /kg	/lb	Samples
S. americanus	11,200	5,090	1
S. japonicus	8,000	3,630	2
S. obassia	2,950	1,340	2

Table 3—*Styrax japonicus,* Japanese snowbell: effect of seed maturity on seed germination

Harvest date	Mean peak germination* (%)		Mean no. of weeks until peak germ.
1999			
23 June	0		—
14 July	0		—
27 July	0		—
10 Aug	7	d	3.0 b
25 Aug	67	c	6.0 a
8 Sept	80	b	7.0 a
22 Sept	83	ab	4.0 b
5 Oct	84	a	4.5 ab
26 Oct	80	b	3.0 b
2000			
19 July	0		—
2 Aug	0		—
16 Aug	5	e	2.3 c
30 Aug	16	d	7.0 a
13 Sept	65	c	8.0 a
4 Oct	73	b	4.7 b
19 Oct	88	a	6.0 ab

Source: Roh and others (2003).
Note: For each year, means within each column followed by the same letters are not significantly different from each other.
* For mean peak germination, 1999: F = 80.20; df = 5, 11; P < 0.0001; and N = 12. For 2000: F = 254.17; df = 4, 14; P < 0.0001; and N = 15.
† For mean number of weeks until peak germination, 1999: F = 4.88; df = 5, 11; P < 0.0398; and N = 12. For 2000: F = 15.61; df = 4, 14; P < 0.003; and N = 15.

However, recent research results indicate that 3 months of warm stratification is not required for high germination of mature seeds (Roh and Bentz 2003; Roh and others 2003). Japanese snowbell seeds need warm moist stratification for at least 1 month followed by cold stratification for 3 months to improve germination. Without any warm stratification, seeds would not germinate. Control seeds that were kept dry in a 18.5 °C greenhouse did not germinate by the time the completion of the experiment (table 4). Examination of non-germinated seeds revealed that the seedcoat was intact in most of the seeds, but a radicle was visible through the seedcoat in less than 10% of the non-emerged seeds (figure 1). After 1 month of dry warm stratification, more than 70% of the seeds had germinated. For example, seeds that were sown in the fall germinated in the second spring in the field. If seeds were on the ground dry, warm stratification requirements could not be fulfilled, and thus seeds may not be able to respond to cold stratification. When seeds become dried after experiencing the moist conditions, germination percentage will be low (table 5). The low germination of seeds that were harvested in 2000 and stored dried for 4 months could be due to an unknown physiological process in the seeds, because seeds that were harvested in 1999 showed higher than 80.8% germination while seeds harvested in 2000 showed less than 53.5% (table 3).

Nursery practice and seedling care. American snowbell seeds should be planted in the fall or stratified and planted in the spring. Fragrant and Japanese snowbell seeds should be planted in summer or given warm stratification before cold stratification. Seeds should be sown immediately upon harvest to avoid any possible reduction in the germination percentage by dry storage. At least 1 month of warm stratification is required, followed by 3 months of cold stratification to improve germination. Japanese snowbell seeds harvested 12 to 14 weeks after flowering are mature and respond to germination-promoting treatments. One month of warm stratification at 18.5/18 °C followed by 2 months of cold stratification at 5.5 °C resulted in germination higher than 73%, while the maximum germination percentage was 98% after 2 months of warm stratification, followed by 3 months of cold stratification (figure 2).

Table 4—*Styrax japonicus*, Japanese snowbell: effect of seed harvest year and months in moist storage on seed germination

Seed harvest year	Moist storage at 18.5 °C	Germination %
1999		
	0	0
	1	70.8 ± 2.4 b
	2	85.0 ± 2.4 a
	3	80.8 ± 2.4 a
	4	85.0 ± 2.4 a
2000		
	0	0
	1	72.5 ± 2.4 b
	2	75.8 ± 2.4 b
	3	52.5 ± 2.4 c
	4	53.3 ± 2.4 c

Sources: Roh and Bentz (2003), Roh and others (2003).
Note: Germination values are means ± standard error of the means; means within each column, followed by the same letters, do not differ significantly from each other.

Figure 1—*Styrax japonicus*, Japanese snowbell: seeds, with only a few showing an emergent radicle (courtesy of Roh and Bentz 2003).

Figure 2—*Styrax japonicus*, Japanese snowbell: uniform and well-germinated seedlings from seeds that received 2 months of warm stratification followed by 3 months of cold stratification (courtesy of Roh and Bentz 2003).

Table 5—*Styrax japonicus*, Japanese snowbell: effect of storage duration and moisture on seed germination, as evidenced by the number of weeks to reach peak germination

Months in storage	Moisture during storage	Germination peak (%)	Weeks to peak germination
0	Dry	0	—
	Moist	0	—
1	Dry	70.8 ± 2.2 a	6.3 ± 0.45
	Moist	53.3 ± 2.2 c	6.3 ± 0.45
2	Dry	59.2 ± 2.2 bc	7.0 ± 0.45
	Moist	65.0 ± 2.2 ab	5.0 ± 0.45
3	Dry	41.7 ± 2.2 d	6.7 ± 0.45
	Moist	61.7 ± 2.2 b	5.3 ± 0.45
4	Dry	28.3 ± 2.2 e	5.3 ± 0.45
	Moist	66.7 ± 2.2 a	5.7 ± 0.45

Sources: Roh and Bentz (2003).

Note: Values are means ± standard error; means within each column followed by the same letters do not differ significantly from each other at $P < 0.05$.

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Meliaceae—Mahogany family

Swietenia Jacq.

mahogany

John K. Francis

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Growth habit, occurrence and use. There are 3 species of mahogany and 1 important hybrid, all of which grow in dry or moist, tropical or subtropical forests of the New World (table 1). All are large trees capable of reaching to 20 to 40 m of height (depending on site) and more than 2 m in diameter. Mahogany species are medium- to long-lived, mid-successional species. Their wood is used for furniture, trim, cabinets, carving, boat building, timbers, posts, and fuel (Chudnoff 1984; Francis 1991). Mahogany wood is particularly desirable because it is dimensionally stable, easily worked with hand and power tools, and very attractive. The mahoganies are also extensively planted as shade and ornamental trees.

Flowering and fruiting. The small greenish white flowers are borne in panicles attached at leaf axials near the ends of branches. The flowers are pollinated by insects and usually produce only 1 fruit (a capsule) per inflorescence. Flowering generally takes place during the spring, with fruits ripening 9 months later. Season of fruiting varies between portions of the range and individual trees. Occasional trees can be found with fruits at any season of the year in Puerto Rico. Fruiting begins when trees are between 10 and 25 years old for open-grown and dominant or codominant trees. A few to more than a hundred capsules may be produced, depending on the size and vigor of the tree. Mahogany species produce good seedcrops nearly every year. Table 2 lists the fruit sizes, seeds per fruit, and seeds per weight for members the genus.

Collection, cleaning, and storage. As the fruits mature, they turn from gray-green to reddish brown. At maturity, the capsule walls split into 5 carpels from the bottom upwards and then fall off. The exposed seeds (samaras)

Table 1—*Swietenia,* mahogany: nomenclature and occurrence

Scientific name & synonym	Common name(s)	Occurrence—native (& planted)
***S. humilis* Zucc.**	**Pacific Coast mahogany**	Mexico to Costa Rica
***S. macrophylla* King** *S. candollei* Pittier	**bigleaf mahogany,** Honduras mahogany	Mexico to Bolivia (Puerto Rico & Hawaii)
***S. mahagoni* (L.) Jacq.**	**West Indies mahogany,** littleleaf mahogany	Florida, Cuba, Bahamas, Jamaica, & Hispaniola (Puerto Rico, US Virgin Islands, & Hawaii)
S. macrophylla x mahagoni	**hybrid mahogany**	St. Croix, Puerto Rico*

Sources: Blake (1920), Francis (1991), Lamb (1966), Whitmore and Hinjosa (1977).
* Arose spontaneously from the introduced parent species.

Table 2—*Swietenia,* mahogany: seed yield data

Species	Median fruit dimensions (cm)	Seeds/fruit	Seeds/weight /kg	Seeds/weight /lb
S. humilis	17 x 11	50 +	1,500	680
S. macrophylla	15 x 8	50–70	1,400–2,400	640–1,100
S. mahagoni	7 x 4	35–60	5,400–7,800	2,500–3,500
S. macrophylla x mahagoni	12 x 7	45–65	1,900–3,000	860–1,400

Sources: Blake (1920), Francis and Rodrıguez (1993), Marraro (1949), Montalvo and others (1991), Whitmore and Hinojosa (1977).

dry quickly and are released a few at a time, usually in the afternoon. Borne on papery wings (figures 1 and 2), they spiral downward and outward and usually land within 1 or 2 tree lengths of the mother tree.

Small quantities of seeds can be picked up from the ground near seed-bearing trees. Seeds can be collected in quantity by clipping the capsules from short-statured trees with pruning poles after the first few capsules on a tree have opened. Large trees must be climbed or collections must be made at logging sites. When spread on trays in ventilated rooms or in the sun, the capsules open in a few days and the seeds can be separated by hand. Two or three days of further drying at mild temperatures is recommended before storage, but no precise guideline for storage moisture content is available. Considerable volume, but little weight, can be saved by de-winging the seeds. Room temperature is adequate for short-term storage (up to 4 months); for longer periods, 4 °C is recommended. Perhaps because of their high oil content, mahogany seeds lose their ability to germinate during storage. Storage at temperatures ranging from 0 to 30 °C resulted in significant losses in germinative capacity after 3 or 4 months. Reductions in germinative capacity were more severe for seedlots having high initial germination than those with moderate germinative capacity (Vivekanandan 1978). Bigleaf mahogany in Puerto Rico stored at room temperature also began to lose germinative capacity rapidly after 3 to 4 months and finally approached 0% between 1 and 2 years (Marrero 1943). Seeds of bigleaf mahogany from Cuba that were stored at 5 °C with an initial germination percentage of 39% had 13% germination after 2 years and 4% germination after 3 years (Montalvo and others 1991).

Figure 1—*Swietenia*, mahogany: seeds, showing the papery wings.

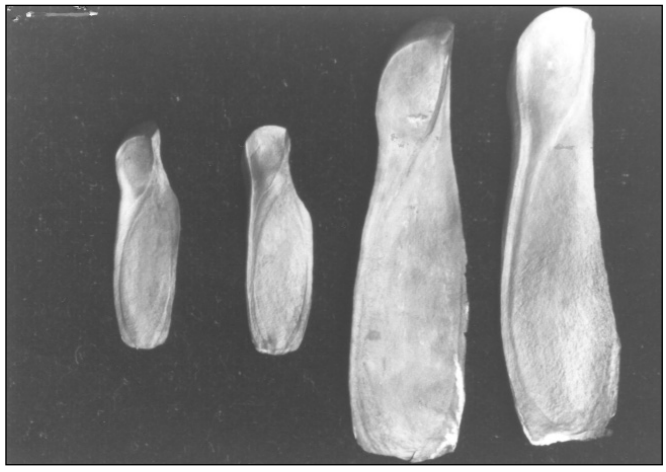
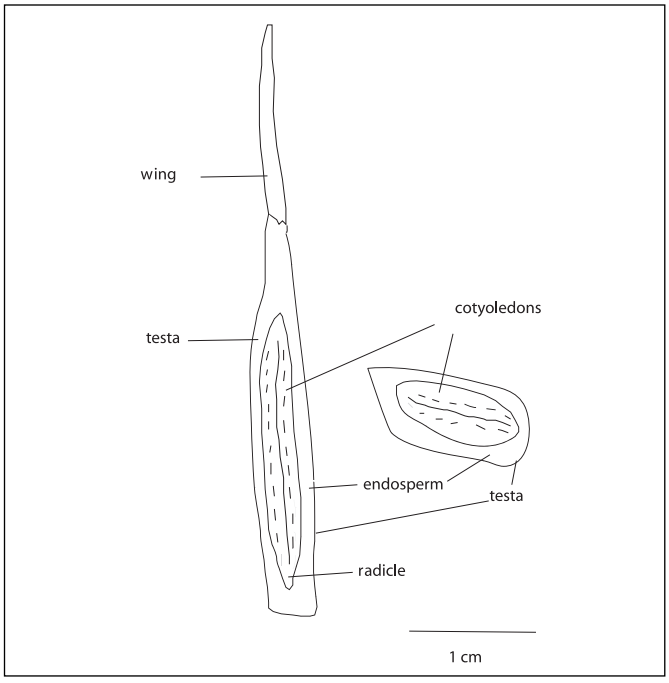


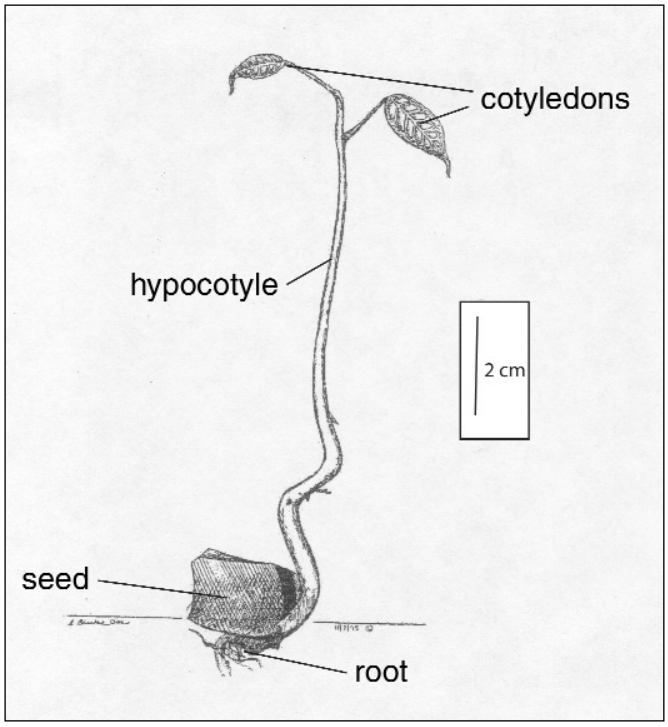
Figure 2—*Swietenia macrophylla*, bigleaf mahogany: longitudinal and cross sections of seed.



Germination. Seeds from 14 provenances of bigleaf mahogany in Cuba were subjected to cutting tests. Ninety-eight percent were sound, 1.2% were empty, and 0.9% were diseased (Montalvo and others 1991). However, sound endosperm is not a reliable indicator of germinative capacity. Seedlots of fresh mahogany seeds normally give 39 to 98% germination (Campbell de Araujo 1971; Francis and Rodrıguez 1993; Marrero 1949; Montalvo and others 1991; Ricardi and others 1977). Conditions during the seed year appear to affect the ability of fresh seeds to germinate. Mahogany seeds usually began to germinate (figure 3) 12 to 18 days after sowing, with complete germination within about 30 days of sowing (Campbell de Araujo 1971; Francis and Rodrıguez 1993; Marrero 1949; Ricardi and others 1977). No pretreatments are necessary. Germination is hypogeal.

Nursery practice. A common method of sowing mahogany seeds is to insert them edge-wise by hand, leaving half of the seed's width exposed and keeping the medium moist until germination. Orientation of the seeds is for convenience only, as it has no significant effect on germination or growth (Mondala 1977). Seeds may also be sown and covered with about 1 cm ($^1/_2$ in) of sand, sawdust, or loose soil. In a test of depth of sowing on bigleaf mahogany seeds, depth did not affect germination, but deep sowing adversely affected early seedling growth (Schmidt 1974). In a Brazilian test of deep sowing at 6 cm (2.4 in), germinants failed to reach the soil surface (Campbell de Araujo 1971). In nurserybeds, seeds are sown 5 to 10 cm (2 to 4 in) apart

Figure 3—*Swietenia,* mahogany: germinating seedling.



in rows spaced 20 to 30 cm (8 to 12 in) apart. Seeds are spaced at about 2.5 cm (1 in) in germination trays and pricked-out after they develop 1 or 2 true leaves. Another approach is to sow directly into nursery containers (usually 2 seeds per container) and thin the plants to 1 seedling per container.

Mahogany species are easy to grow in the nursery and transplant well. They may be grown in full sun or light shade. The most common method today is to grow mahogany seedlings in plastic nursery bags. Bareroot seedlings with the leaves removed (striplings), stump plants (Jacalne and others 1957), and top- and bottom-pruned large seedlings about 1 m (3 ft) tall—all have performed well. Bigleaf and hybrid mahogany seedlings are ready to outplant in 6 to 9 months and West Indies mahogany seedlings are ready in 1 year. Bigleaf mahogany seedlings in a Brazilian nursery were reported to reach a maximum of 30 cm (12 in) in 3 months and 60 cm (24 in) in 6 months (Campbell de Araujo 1971). Direct seeding, which is best done with prepared seed spots, has been successful on several occasions (Lamb 1966). Bigleaf mahogany can be reproduced with cuttings (Burgos 1954; Zanoni-Mendiburu 1975).

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Caprifoliaceae—Honeysuckle family

Symphoricarpos Duham.

snowberry

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Growth habit, occurrence, and use. Species of the genus *Symphoricarpos* occur in North America from Alaska to Mexico (with 1 additional species native to China). There are over a dozen species and varieties (Evans 1974; SCS 1982); 7 are presented here (table 1). Common names include buckbrush, wolfberry, and other vernacular names. The white-berried species are most commonly known as snowberries and the red-berried species as coralberry (Evans 1974; Grimm 1957; Shiell 1992). Snowberry species are usually 40 to 150 cm tall, erect to spreading, densely opposite-branched, thicket-forming, deciduous shrubs. Leaves are 1 to 8 cm long by 0.3 to 4 cm wide, oval or ovate to roundish, opposite, simple, with entire leaf margins (Welsh and others 1987; Grimm 1957). Snowberry species form distinct colonies by underground rhizomes, except for Parish snowberry, which layers by rooting at above-ground stem nodes that touch the ground (Mozingo 1987). This dense colony stand pattern results in grazing resistance and fire tolerance, making them suitable for stabilizing disturbed lands. Western snowberry and coralberry have been used to some extent for erosion control (Evans 1974). Snowberry can be quite adaptable to site conditions and can grow on a variety of soil types from sandy to heavy clays and on both alkaline and acidic soils (Plummer 1968; Thames 1977). Most species within the genus are generally quite drought tolerant (Shiell 1992).

The snowberries have considerable value for wildlife, for they produce high-quality forage and good cover for game birds and small animals. The foliage provides considerable forage for big game and livestock, and the berries are

Table 1—*Symphoricarpos,* snowberry: nomenclature and occurrence

Scientific name & synonyms	Common name(s)	Natural occurrence*
***S. albus* var. *albus* (L.) Blake** *S. racemosus* Michx.	**common snowberry**	Hudson Bay to Alaska, S to California, & E to North Carolina
***S. albus* var. *laevigatus* (Fern.) Blake** *S. albus* ssp. *laevigatus* (Fern.) Hulten *S. rivularis* Suksdorf	**garden snowberry,** Columbia snowberry	S Alaska, S to California, Montana, & Colorado
S. occidentalis Hook.	**western snowberry,** buckbrush	Saskatchewan to British Columbia, wolfberry, N Washington, Utah, New Mexico, to Minnesota, Missouri, & Illinois
S. orbiculatus Moench	**coralberry,** Indian currant, snowberry	New York to North Dakota, S to E Texas & Georgia
***S. oreophilus* var. *oreophilus* Gray**	**mountain snowberry,**	Southeast variety, Colorado, Arizona, New Mexico, N Sonora, occasionally in Utah
***S. oreophilus* var. *utahensis* (Rydb.) A. Nels.** *S. utahensis* Rydb. *S. vaccinoides* Rydb.	**Utah snowberry**	Northern variety, British Columbia to Montana, S to California, central Nevada, Utah, & Colorado
***S. rotundifolia* var. *parishii* (Rydb.) Dempster** *S. parishii* Rydb.	**Parish snowberry**	Southern variety, from S California to Arizona & central Nevada, & barely entering the W edge of Utah

Sources: Conquist and others (1984), Evans (1974).

* Distribution of *Symphoricarpos* species used in cultivation can vary.

used by birds and black bear (*Ursus americanus*) (Auger 1994; Banister 1991; Evans 1974; Mozingo 1987). Coralberry, common snowberry, and garden snowberry make desirable ornamental plantings because of their attractive fruits (Evans 1974; Shiell 1992).

Flowering and fruiting. Flowers of coralberry are inconspicuous green and purple, whereas the flowers of other species of snowberry are pinkish to yellowish white. All are bell-shaped with 5 rounded lobes, perfect, and borne in dense axillary or terminal clusters (table 2). The fruit is a 2-seeded berrylike drupe that is 5 to 10 mm long (Mozingo 1987; Shiell 1992; Vories 1981; Welsh and others 1987). Fruit color is white in the snowberry species but dark red, pink, or bluish black in coralberry. Fruits mature mid- to late summer or early fall (mid-June through September) (Evans 1974; Link 1993; Shaw 1984; Shiell 1992; Vories 1981). Each fruit contains 2 nutlets (pyrenes). These are flattened on 1 side and are composed of a tough, bony endocarp, a seedcoat, a fleshy endosperm, and a small embryo (figures 1 and 2). The nutlets are used as seeds. They are dispersed from late fall to the following spring, largely by birds and mammals. Normally, a good seedcrop is produced each year (Evans 1974).

Collection of fruits. Fruits persist on the plants until the following spring, except for those consumed by birds and mammals, making collection of fruit relatively easy (Evans 1974; Link 1993). Collection is done by stripping or flailing the fruit into a hopper or container, or the fruits may be picked by hand. Those collected in early fall contain considerable moisture and therefore require careful handling to prevent heating (Evans 1974; Vories 1981). Weight of fruits per volume for western snowberry (fresh weight) are 3.6 kg/liter (58 lb/bu) and for coralberry (dry weight) are 0.81 kg/liter (13 lb/bu) (Evans 1974).

Figure 1—*Symphoricarpos*, snowberry: nutlets of *S. albus* var. *laevigatus*, garden snowberry (**top**); *S. occidentalis*, western snowberry (**center**); and *S. orbiculatus*, coralberry (**bottom**).

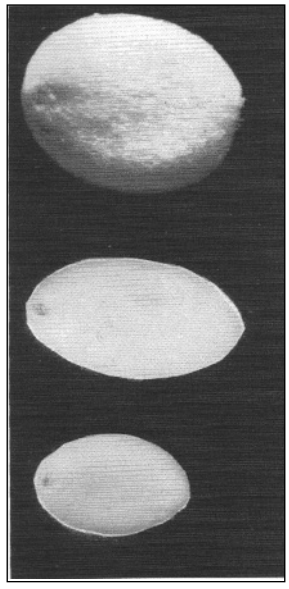


Table 2—*Symphoricarpos,* snowberry: phenology of flowering and fruiting.

Species	Location (& elevation)	Flowering	Fruit ripening
S. albus			
var. *albus*	Michigan	June 1–July 31	Sept 1–Oct 31
	Michigan	May 1–Sept 30	Aug 1–Oct 31
	Idaho		
	700 m	June 5–Aug 5	Aug 1– Sept 5
var. *laevigatus*	Missoula Co., Montana		
	1,000 m	June 20–Aug 15	Aug 15–Sept 30
	1,300 m	July 1–July 30	Aug 25–Sept 20
	1,650 m	July 15–Aug 30	Sept 10–Oct 5
	2,000 m	July 25–Sept 5	Sept 25–Oct 25
S. occidentalis	Pennington Co., South Dakota		
	750 m	June 1–July 31	Sept 1–Oct 31
S. orbiculatus	—	July 1–Aug 31	Sept 1–heavy frost
S. oreophilus	Wasatch Plateau, Utah		
	2,230 m	June 17–June 26	Aug 20–Sept 18
	2,576 m	June 22–June 30	Aug 17–Sept 12
	2,698 m	July 2–July 8	Aug 21–Sept 26
	Northern Utah		
	2,080 m	June 5–June 10	July 15–Aug 3

Sources: Billington (1943), Costello and others (1939), Evans (1974), Willard (1971).

Extraction and storage of seeds. Twigs, leaves, and other non-fruit debris should first be screened out. Seeds can then be readily extracted by running the fruits through a macerator with water, floating off pulp and empty seeds. Dried fruits should be soaked for several hours before maceration. Remaining seeds and pulp should be dried and then cleaned on an air-screen cleaner (Evans 1974; Link 1993; Shaw 1984; Vories 1981; Wasser 1982). After being dried and cleaned, the seeds are ready for storage. Numbers of cleaned seeds per weight are listed in table 3.

Stored snowberry seeds have been reported to retain good viability when stored dry at low temperature near 5 °C (Vories 1981; Evans 1974). Seeds of coralberry are reported by Vories (1981) to maintain good viability for over 5 years.

Figure 2— *Symphoricarpos albus* var. *albus*, common snowberry: longitudinal section through a nutlet.

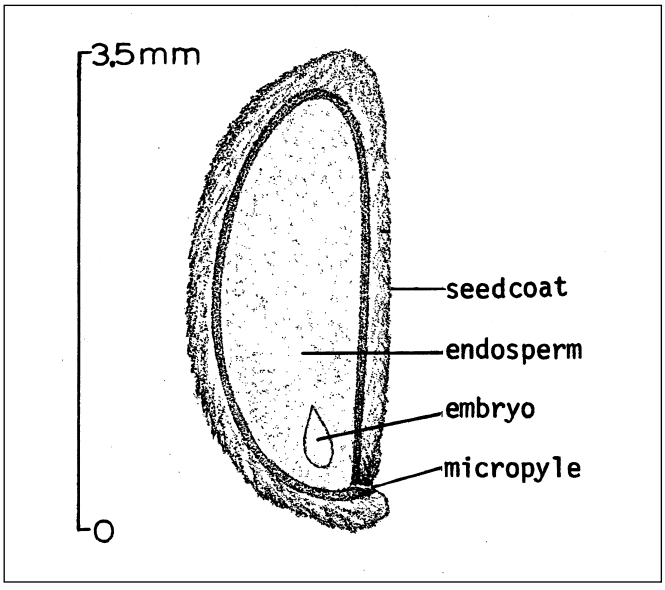
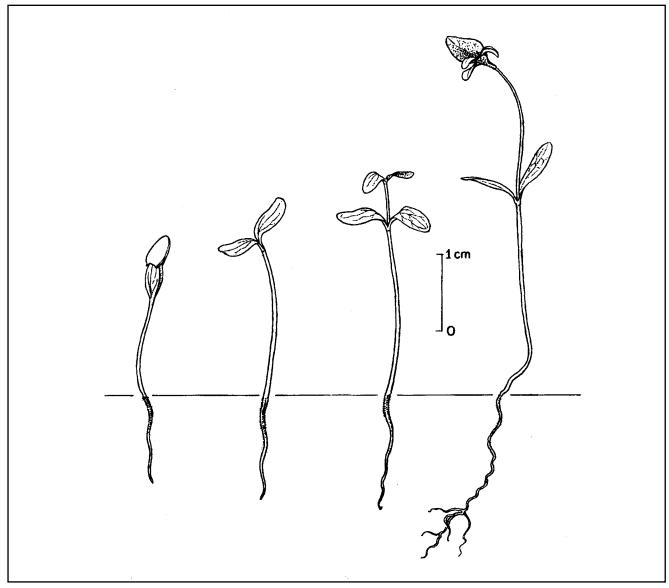


Figure 3—*Symphoricarpos albus* var. *albus*, common snowberry: seedling development at 5, 7, 13, and 20 days after germination.



Mountain snowberry germinated to 80% after 7 years, 44% after 10 years, and 8% after 25 years of dry storage in an open warehouse (Stevens and Jorgensen 1994). Dried seedlots of common snowberry stored in a sealed container at 5 °C yielded 45% germination after 2 years, with an additional 35% still sound at the conclusion of the test (Evans 1974). Acceptable purity is 95%, with 80% germination (Shaw 1984).

Pregermination treatments. The nutlet-like seeds of snowberries have a hard endocarp and an undeveloped embryo (Evans 1974; Plummer 1968). Hidayati and others (2001) reported that the endocarp and seedcoat of coralberry are permeable to water; thus the seeds do not have physical dormancy. Warm stratification at room temperature between

Table 3—*Symphoricarpos,* snowberry: seed yield data

Species	Seed wt/ fresh fruit wt	Seeds (1,000s)/weight Range /kg	Range /lb	Average /kg	Average /lb	Samples
S. albus						
var. *albus**	3	119–250	54–113	167.5	76	10
var. *laevigatus*	—	86–144	39–65.2	122	55.4	5+
S. occidentalis	5–10	114–217	52–98.7	164	74.4	6+
S. orbiculatus†	7	298–317	135–144	308	140	2
S. oreophilus						
var. *oreophilus*	—	117–165	53-75	141	53.9	1

Source: Evans (1974).
* Number of dried fruits per weight was 39,600/kg (18,000/lb).
† Seed yield per weight of dried fruit was 18 to 33 kg/100 kg (18 to 33lb/100lb).

22 to 30 °C for 3 to 4 months has been used to soften the endocarp and is reported to be an adequate treatment for fall-planting where cold stratification will occur naturally (Wasser 1982; Evans 1974). For spring-planting or situations where natural stratification will not occur, a subsequent period of cold stratification at 5 °C for 4 to 6 months is necessary to induce full development of the embryo. Sulfuric acid scarification (soaking for 30 to 60 minutes) can be used in place of warm stratification to soften the endocarp. However, warm stratification has been shown to be more effective than the acid treatment (table 4), possibly because it is necessary for embryo maturation (Evans 1974; Shaw 1984).

In seedlots collected from the Book Cliffs of northeastern Utah, 72.5% of viable seeds germinated after 20 weeks of wet chill at 2 °C; 5 weeks of warm stratification at 10/30 °C did not increase germination substantially. Scarification in the form of passage through a black bear's digestive system actually lowered germination to 51.6% (Auger 1994).

Germination. Results of germination tests of nonstratified seedlots showed 0 to 46% germination at 4 °C for over 12 months, and 55% after 24 months. Under moist warehouse storage conditions, germination ranged from 0% after 1 year to 37% after 24 months, for mountain snowberry (GBRC 1985). Once seedlots have been adequately pretreated, they can be germinated at diurnally alternating temperatures of 20 and 30 °C for 30 days in the light (Akagi 1996; Evans 1974). Germination could be expected to be between 40 to 90% in 28 days (Akagi 1996; Evans 1974). Germination is epigeal (figure 3). Weber and Wiesner (1980) showed that, for common snowberry, tetrazolium chloride (TZ) testing did not distinguish between dormant and nondormant seeds, but was adequate for viability evaluation.

Nursery practice. Effective propagation from seeds is possible if they are properly treated and given sufficient cold stratification. Desired seedling density in nursery beds is about 325/m^2 (30 seedlings/ft^2). Seeds should be covered with about 6 mm ($^1/_4$ in) of soil and 2 cm ($^3/_4$ in) of mulch. Early shade has been beneficial for seedlings of Indian currant (Evans 1974).

Cuttings and transplanting of pulled-up wildlings and pieces of stem with roots can be especially successful when planted in early spring (Plummer 1968; Vories 1981;Wasser 1982). Expected transplanting establishment success is nearly 90% when proper transplanting techniques are used for both bareroot and container stock (Stevens 1994). Cuttings should be irrigated when set out and as needed afterward until they are well established. Mountain snowberry has been shown to do poorly when planted as 1+0 stock but to perform much better when planted as 2+0 or larger stock (Monsen 1984). Plant competition needs to be reduced to a minimum during the first season. When seeding in rangeland conditions, species should be mixed with other adapted browse and forage plants and preferably planted in rows, strips, or blocks separate from grasses (Wasser 1982).

Table 4—*Symphoricarpos,* snowberry: effect of pregermination treatments on germination percentage

Species	Immersion in H_2SO_4 (min)	Stratification (days)		Germination (%)
		Warm*	Cold†	
S. albus				
var. *albus*	60	60	180	35
	75	20	180	74
var. *laevigatus*	20	0	60	1
	0	112	182	45
	60	84	168	69
	0	91	182	87
	60	0	140	32
S. orbiculatus	0	120	120	72
	30	20	120	58
	30	120	180	81

Sources: Evans (1974), Flemion (1934), Flemion and Parker (1942).
* Room temperature.
† 5 to 10 °C.

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Oleaceae—Olive family

Syringa L.

lilac

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Growth habit, occurrence, and use. The lilac genus comprises about 30 species of deciduous shrubs or small trees with opposite, usually undivided leaves. The genus name—*Syringa*—is derived from the Greek word *syrinx,* a "pipe," and refers to the hollow shoots. Lilacs are native to temperate Asia and southeastern Europe (Everett 1982) and were probably introduced to America before 1700 (Heriteau 1990; Wyman 1986). They are grown primarily as ornamentals because of their large, showy, and often fragrant inflorescences (Rehder 1940). Lilacs are generally hardy and long lived (Everett 1982). At least 3 species are used in shelterbelts and windbreaks. Four species or varieties grown for conservation purposes in the United States are discussed in this chapter (table 1); their heights at maturity and years of first cultivation are also listed (Hoag 1965; Rehder 1940).

Hybrids and cultivars. Numerous lilac hybrids and cultivars have been developed for horticultural use. These selections exhibit variation in such characteristics as flower color, period of flowering, and growth habit. Krüssmann (1986) reported that more than 900 cultivars are grown, including more than 800 developed from common lilac (*S. vulgaris* L.). The largest collections and numbers of varieties are found in the United States. Persian lilac (*S.* × *persica* L.), previously considered a separate species, is now thought to be a hybrid of *S. laciniata* Mill. (*S. afghanica* C.K. Schneid.) (Everett 1982; LHBH 1976; Wyman 1986); a fixed juvenile form of *S. laciniata* (Krüssmann 1986); or a backcross between *S.* × *laciniata* and *S. vulgaris* with *S.* × *laciniata* = *S. protolaciniata* P.S. Green & M.C. Chang × *S. vulgaris* L. (Griffiths 1994).

Flowering and fruiting. Flowers are borne in panicles that develop on the previous year's shoots. The small, perfect flowers have 4-lobed, funnel-shaped to cylindrical corollas and colors ranging from white to violet, purple, and deep reddish purple. Flowers bloom in spring or early summer after development of the foliage (table 2). Seedcrops are produced annually on cultivated plants. The fruit, a 2-celled capsule, is smooth, brown, woody, oblong, and terete or compressed (figure 1). It ripens in late summer or fall. Each capsule contains 4 shiny, brown, lozenge-shaped seeds that are about 13 mm long, 5 mm wide, and more or less obliquely winged at the base (figure 2). Seeds are covered by a thin, brown seedcoat and a thick layer of living endosperm. Cotyledons are large and well developed.

Table 1—*Syringa,* lilac: nomenclature and original occurrence

Scientific name & synonyms	Common name(s)	Occurrence	Height at maturity (m)	Year first cultivated
***S.* × *persica* L.**	**Persian lilac**	Iran to NW China	1.5–3.0	1614
***S. reticulata ssp. amurensis* (*Rupr.*) P.S. Greene & M.C. Chang** *S. amurensis* Rupr. S.reticulata var. *mandschuria* (Maxim.) Hara	**Amur lilac,** Manchurian lilac	SE Siberia in Amur River region		
***S. villosa* Vahl.** *S. bretschneideri* Lemoine	**late lilac,** villous lilac	N China to Himalayas	3.0–3.9	1882
***S. vulgaris* L.**	**common lilac**	SE Europe	3.0–7.0	1563

Source: Rudolf and Slabaugh (1974).

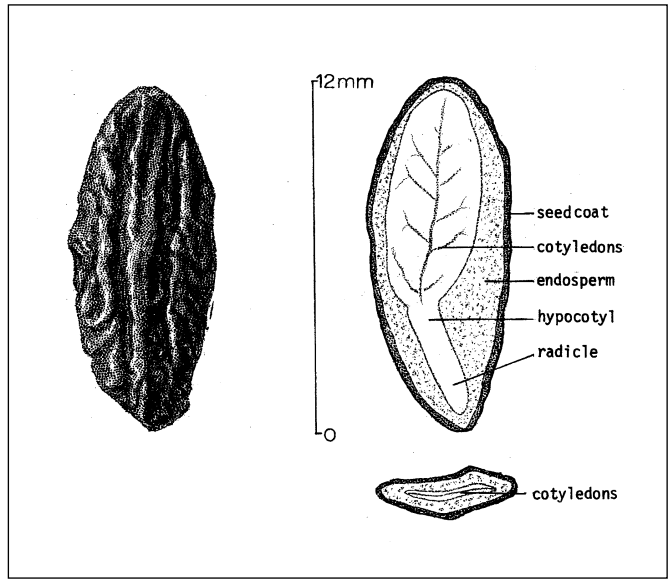
Table 2—*Syringa,* lilac: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
S. × *persica*	NE US, Kansas	May–June	Late Mar–Apr
S. reticulata var. *amurensis*	North Dakota	Early June	—
	Manitoba	June–July	Sept–Oct
S. vulgaris	NE US & Europe	Apr–June	Aug–Oct
	Kansas	Late Mar–early May	—
	W US	Late Mar–mid-May*	—

Sources: Caprio and Snyder (1989), Cummings (1963), Hoag (1965), Hulbert (1963), LHBH (1976), NBV (1946), Rehder (1940), Walker (1968).
*First flowering.

Figure 1—*Syringa amurense*, Amur lilac: fruits (capsules).

Figure 2—*Syringa vulgaris*, common lilac: exterior view of seed (**left**), longitudinal section through a seed (**top right**), and transverse section (**bottom right**).



Collection of fruits and extraction and storage of seeds. Mature capsules are hand-harvested in fall. A late (October 9) collection of Amur lilac capsules yielded seeds with greater germinability than an early (September 10) collection (Walker 1968). Harvested fruits should be spread to dry in a well-aerated room (NBV 1946). Air-dried fruits may be crushed in a macerator. A fanning mill is used to remove impurities, but fanning must be done carefully or good seeds will be lost (NBV 1946). Air-dried fruits may also be stored over winter in paper bags. By spring, many seeds will have fallen from the capsules and can be separated by fanning or sieving.

Data on seed yields are available for only 2 species. For common lilac, 45 kg (100 lb) of capsules yielded 0.9 to 3.2 kg (2 to 7 lb) of cleaned seeds (Swingle 1939). The number of cleaned seeds per weight in 16 samples ranged from 74,956 to 286,598/kg (34,000 to 130,000/lb), averaging 189,630/kg (86,000/lb) (Rafn and Son 1928; Rudolf and Slabaugh 1974; Swingle 1939). Average purity of cleaned lots of common lilac seeds is 60% and sound seeds made up 85% (Rudolf and Slabaugh 1974; Swingle 1939). For late lilac, purity of a cleaned seed sample was 91% and number of seeds per weight was 90,830/kg (41,200/lb).

Lilac seeds will remain viable for up to 2 years if stored in bags or sacks in a dry, well-aerated place (NBV 1946). For longer storage, air-dried seeds should be kept in sealed containers or polyethylene bags at 1 to 3 °C (Heit 1967; Walker 1968).

Pregermination treatments. Dormancy varies among species and seed collections, but is usually not very strong (Junttila 1973a). It may be induced by high temperatures during seed development (Junttila 1971).

In common, nodding (*S. reflexa* C.K. Schneid.), and Hungarian lilacs (*S. josikaea* Jacq. F. ex Reichenb.), the mechanical restraint imposed by the endosperm surrounding the radicle imposes an embryo dormancy at low incubation temperatures (9 to 15 °C). This dormancy is generally relieved by embryo excision, wet prechilling at 1 to 9 °C for periods of 30 to 90 days, or application of gibberellic acid (which increases the growth potential of the embryo) (Junttila 1970a&b, 1971; Walker 1968; Wyman 1986). Mechanical resistance of the endosperm decreases prior to germination. At high incubation temperatures (27 to 30 °C), dormancy is imposed by seedcoat and endosperm restriction of oxygen uptake (Junttila 1970b, 1973a, 1974a).

Embryos are generally nondormant. Some nodding lilac embryos, however, may be dormant at high incubation temperatures during the early stages of maturation, whereas some mature embryos are dormant at low incubation temperatures (Junttila 1973b).

Germination tests. Official rules for testing germination of common lilac seeds prescribe a 21-day incubation at 20 °C (ISTA 1966; Isely and Everson 1965). Junttila (1974b) recommends germinating excised common lilac embryos at 24 °C and seeds at 18 °C. Light is not required (Heit 1968b). Maximum germination of late lilac may be obtained by incubating seeds at 30/20 °C in artificial light with a good supply of water (Heit 1974). Test results for 3 lilac species are shown in table 3. Germination is epigeal.

Nursery practice. Rudolf and Slabaugh (1974) recommend that lilac seeds be sown at a rate adjusted to produce 270 to 430 seedlings/m^2 (25 to 40/ft^2). Macdonald (1993) recommends densities of 150 to 200 seedlings/m^2 (14 to 19/ft^2) for lining-out stock and 250 to 300/m^2 (23 to 28/ft^2) for rootstocks. For some lots of common lilac seeds, yield of usable 1+0 seedlings has been as low as 12% of viable seeds planted. Seeds may be planted in fall without pretreatment (Cram and others 1960; Heit 1968a), or untreated or wet-prechilled seeds may be planted in spring (LHBH 1976; NBV 1946; Rudolf and Slabaugh 1974). Seeds should be covered with 6 to 9 mm (0.2 to 0.4 in) of soil. A mulch may be helpful on fall-sown beds (Heit 1968a;, Walker 1968). Nursery beds should be given half-shade, kept moist, and protected from late spring frosts (NBV 1946). Field plantings can be made using 1+1 stock (LHBH 1976).

Table 3—*Syringa,* lilac: germination test results

Species	% germination		Tests
	Average	Range	
S. reticulata var. *amurensis*	72	64–80	5
S. villosa	77	70–84	2
S. vulgaris	61	33–85	13
	44	—	61

Sources: Heit (1968a&b, 1974), Junttila (1974b), Rafn and Son (nd), Rudolf and

Lilac cultivars are generally propagated vegetatively to maintain genetic constancy (Hartmann and others 1990). Plants are commonly obtained by rooting softwood cuttings under mist. The time-frame for making softwood cuttings, however, is limited to the spring flush of active growth, which extends from slightly before to slightly after flowering, usually a 4- to 6-week period (Macdonald 1993; Wyman 1986). Grafting is often used as an alternative to propagating cuttings, because grafting can be done at any time during the winter. Lilac, privet (*Ligustrum* spp.), and green ash (*Fraxinus pennsylvanica* Marsh.) seedlings are used as rootstocks. Scions cut from vigorous 1-year-old wood should be planted deeply to improve the rooting. Understock can be removed later, thus creating "own-root" plants (Fordham 1959; Hartmann and others 1990).

Root cuttings, budding, layers, divisions, hardwood cuttings, t-budding, and micropropagation are also used for propagation if only small numbers of plants are needed (Everett 1982; LHBH 1976; Macdonald 1993). If vegetative material for propagation is harvested from grafted plants not growing on their own rootstocks, shoots produced by the understock must be avoided.

Lilacs grow on a variety of soils having a pH of 6.0 to 7.5 (Fordham 1959). They do best on moderately rich, moist soils with good drainage and aeration and exposure to full sun (LHBH 1976). Though persistent without care, flowering is enhanced by removal of inflorescences after flowering (deadheading), proper pruning, and periodic fertilization (Macdonald 1993; Wyman 1986).

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Tamaricaceae—Tamarix family

Tamarix chinensis Lour.

saltcedar or five-stamen tamarisk

Wayne D. Shepperd

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Synonym. *T. pentrandra* Pall.

Growth habit, occurrence, and use. Saltcedar (*Tamarix chinensis* (Lour.)) and smallflower tamarisk (*T. parviflora* DC.) hybridize in the Southwest (Baum 1967; Horton and Campbell 1974) and are deciduous, pentamerous tamarisks that are both commonly referred to as saltcedar. Saltcedar is a native of Eurasia that has naturalized in the southwestern United States within the last century. It was introduced into the eastern United States in the 1820s (Horton 1964) and was once widely cultivated as an ornamental, chiefly because of its showy flowers and fine, graceful foliage. However, saltcedar has been an aggressive invader of riparian ecosystems in the Southwest (Reynolds and Alexander 1974) and is the subject of aggressive eradication campaigns. It achieves heights of 12 m and trunk diameters of 0.5 m in southern New Mexico and trans-Pecos Texas (Everitt 1980). Although considered a threat to native vegetation, saltcedar has been utilized for browse, firewood, and lumber and also to produce premium honey (Everitt 1980). Saltcedar is halophytic and tolerates an extreme range of environments from below sea level to above 2,100 m (Everitt 1980). Though a riparian plant, it is also drought tolerant and can survive indefinitely in non-saturated soils, making it a "facultative phreatophyte" (Turner 1947). In some areas, saltcedar thickets are valued nesting habitat for white-winged doves (Reynolds and Alexander 1974). Saltcedar can naturally reproduce vegetatively from roots and can layer when foliage is buried by sediment (Everitt 1980). These prodigious reproductive capabilities are well suited to colonizing riverbanks and disturbed areas (Horton and others 1960). Because saltcedar is a heavy water user, its spreads rapidly along drainages and flood plains—for example, the infested area increased from 4,000 to 364,000 ha in 41 years (1920 to 1961), (Robinson 1965)—and has required extensive eradication or control efforts.

Flowering and fruiting. The pink to white flowers, borne in terminal panicles, bloom from March through September. A succession of small capsular fruits ripen and split open during the period from late April through October in Arizona (Horton and others 1960). Seeds are minute and have an apical tuft of hairs (figures 1 and 2) that facilitates dissemination by wind. Large numbers of small short-lived seeds are produced that can germinate while floating on water, or within 24 hours after wetting (Everitt 1980).

Collection, extraction, and storage. Fruits can be collected by hand in the spring, summer, or early fall. It is not practical to extract the seeds from the small fruits. At least half of the seeds in a lot still retained their viability after 95 weeks in storage at 4.4 °C, but seeds stored at room temperature retained their viability for only a short time (Horton and others 1960).

Figure 1—*Tamarix chinensis*, saltcedar: longitudinal section through a seed.

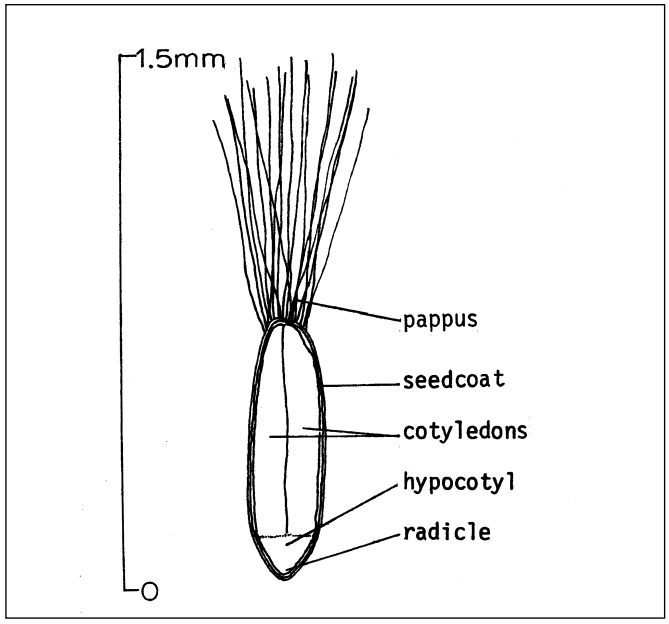
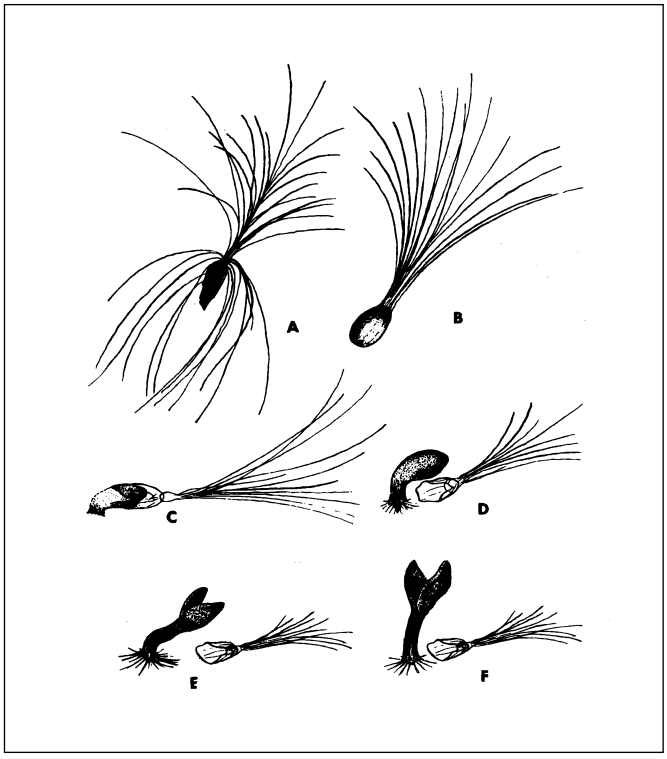


Figure 2—*Tamarix chinensis*, saltcedar: dry seed (**A**) and seedling development at the following intervals after moistening the seed—several hours (**B**), 8 hours (**C**), 24 hours (**D**), 40 hours (**E**), 48 hours (**F**) (drawings by Dennis C. Jackson, from Horton and others 1960).



Germination tests. Fresh seeds usually germinate within 24 hours after imbibing water (figure 2). No pretreatment is necessary. Germination tests have been run in moist soil in covered petri dishes at room temperature. The germination rate after 24 hours averaged 78% and the percentage germination after 6 days was 88% (Horton and others 1960). Seed can survive up to a year in cold storage (Merkel and Hopkins 1957).

Nursery practice. Germination and survival is favored by fine-grain sediment. Bare, sunny, saturated soil is ideal for the first 2 to 4 weeks of life, but survival is limited because of slow early seedling growth (Everitt 1980). Top height averages about 2.5 cm (1.0 in) 30 days after emergence, and seedlings average only 10 cm (4 in) tall after 60 days. At this time, roots are about 15 cm (6 in) long. Soil must be kept continuously moist during this establishment period; 1 day of drought can kill most seedlings (Reynolds and Alexander 1974).

Saltcedar is also readily propagated from cuttings. Cuttings will root during any season, if planted in moist soil at 16 °C (Gary and Horton 1965). Hardwood cuttings should be at least 2 cm ($^3/_4$ in) thick. A peat and perlite medium under mist works well with softwood cuttings, but root systems may be sparse and difficult to handle (Dirr and Heuser 1987). Seedlings are hearty after they become established and can withstand severe drought (Horton and others 1960). Softwood cuttings should be weaned from mist as soon as rooting begins to avoid decline from excessive moisture (Dirr and Heuser 1987).

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Taxodiaceae—Redwood family

Taxodium L.C. Rich.

baldcypress

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Growth habit, occurrence, and use. Baldcypresses are large deciduous conifers that occur naturally in wetlands of the Southeastern and Gulf Coastal Plains. Two species, once classified as varieties of a single species, are now recognized (table 1). The ranges of these species overlap in the Southeast and Gulf South; baldcypress extends much further north and west, however. They are often difficult to identify where mixed (Wilhite and Toliver 1990). Baldcypress may be encountered in almost all temperate regions of the world, as it has been planted extensively as an ornamental. It was introduced in Europe as early as 1640 (Bonner 1974). Baldcypress wood is well-known for its use in boat construction, pilings, interior trim, flooring, paneling, and many other items. It is an important source of wildlife food and habitat and a valuable component of wetland hydrology (Wilhite and Toliver 1990).

Flowering and fruiting. The monoecious flowers of baldcypress appear in March to April, before the leaves. The male catkins are about 2 mm in diameter and are borne at the end of the previous year's growth in slender, purplish, tassel-like clusters 7 to 13 cm long. Female conelets are found singly or in clusters of 2 or 3 in leaf axils near the ends of the branchlets (Vines 1960; Wilhite and Toliver 1990). The globose cones turn from green to brownish purple as they mature in October to December. Flowering and fruiting of pondcypress is essentially the same as for baldcypress (Wilhite and Toliver 1990). Baldcypress cones are 13 to 36 mm in diameter (figure 1), and consist of a few 4-sided scales that break away irregularly after maturity. Each scale bears 2 irregularly shaped seeds that have thick, horny, warty

Figure 1—*Taxodium, baldcypress*: cones of *T. distichum*, baldcypress (**top**) and *T. ascendens*, pondcypress (**bottom**).

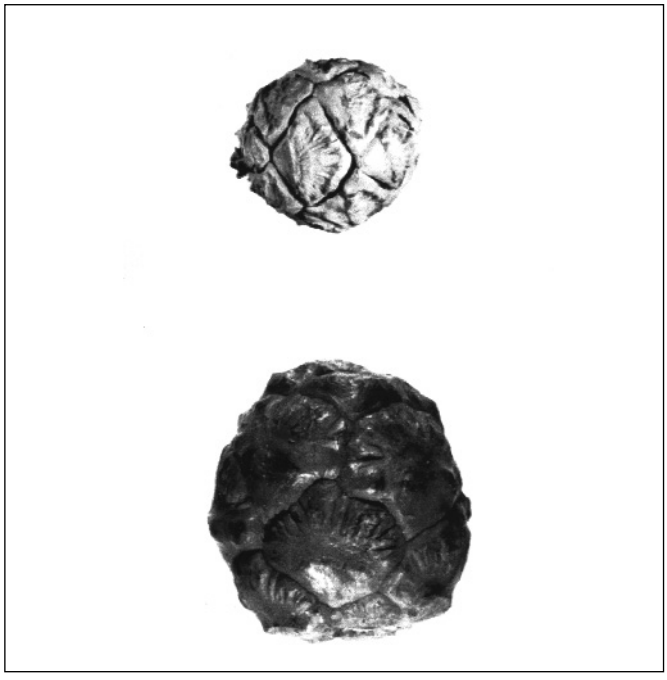


Table 1—*Taxodium,* baldcypress: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***T. ascendens* Brongn.** *T. distichum* var. *imbricarium* (Nutt.) Croom *T. distichum* var. *nutans* (Ait.) Sweet	**pondcypress**, pond baldcypress, cypress	Coastal plain from Virginia to Florida & Louisiana
***T. distichum* (L.) Rich.**	**baldcypress,** common bald cypress, gulf cypress, red cypress, tidewater red cypress, white cypress, yellow cypress, cypress	Coastal plain from Delaware & Florida W to Texas & N to Illinois in Mississippi River Valley; planted from Michigan to Massachusetts

Sources: Little (1979), Wilhite and Toliver (1990).

coats and projecting flanges (figures 2 and 3). Collections from 45 families of baldcypress from Mississippi to Texas found that cones contained anywhere from 2 to 34 seeds, with an average of 16 (Faulkner and Toliver 1983). The proportion of seeds with embryos is frequently less than 50%, however. Some seeds are borne every year, and good crops occur at 3- to 5-year intervals.

Figure 2—*Taxodium*, baldcypress: seeds of *T. distichum,* baldcypress (**top**) and *T. ascendens*, pondcypress (**bottom**).

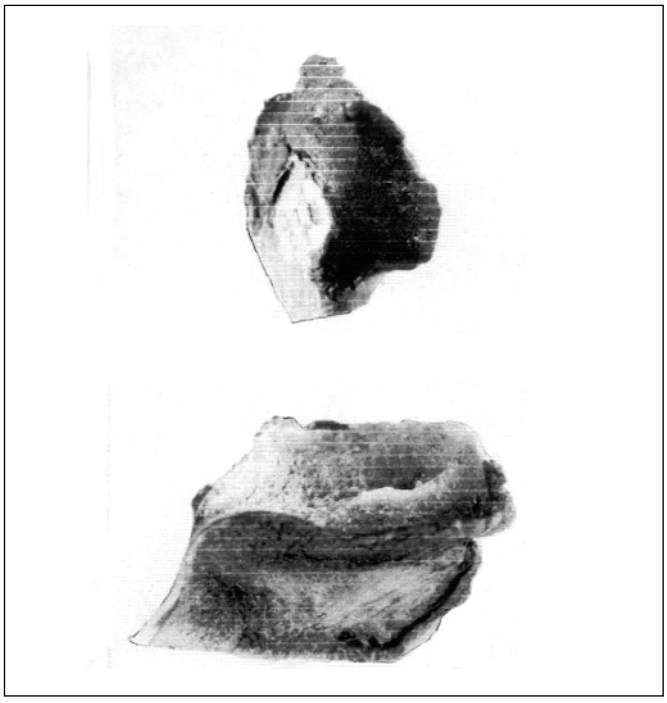
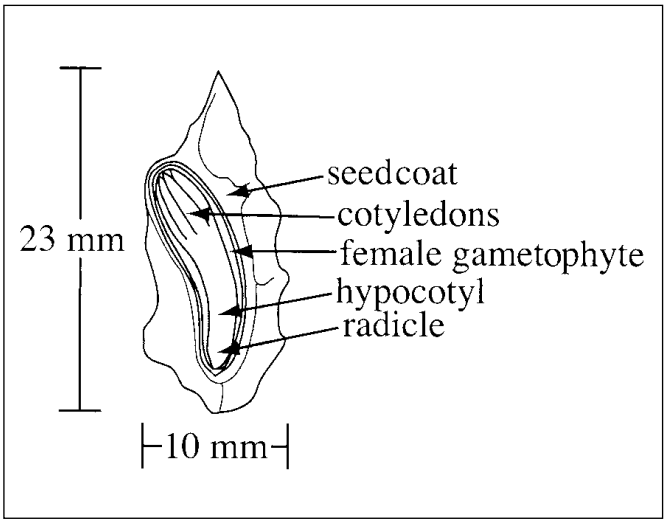


Figure 3—*Taxodium distichum*, baldcypress: longitudinal section through a seed.



Two insect pests destroy significant amounts of baldcypress and pondcypress seeds—southern pine coneworm (*Dioryctria amatella* (Hulst)) and baldcypress coneworm (*D. pygmaeella* Ragonot). The baldcypress seed midge (*Taxodiomyia cupressi* Schweinitz) forms small round galls inside the cones of baldcypress (Hedlin and others 1980; Merkel 1984). The seed midge apparently does little damage to seeds, but the galls are difficult to separate from the seeds and become a quarantine problem for seed exporters.

Collection, extraction, and storage. Mature, dry cones can be picked by hand from standing or felled trees and spread in a thin layer for air-drying. The dried cones should be broken apart by flailing or dry maceration. The resin in the cones presents a major problem in separation and cleaning because it causes seeds and cone fragments to stick together. The resin also gums up mechanical macerators. One possible solution is to place the dried seeds and cone fragments in a freezer to harden the resin, then run them through a macerator again while the resin is still in a solid state. Resin can be cleaned from equipment with alcohol or other organic solvents.

The number of seeds per cone volume for baldcypress averages about 58 kg/hl (45 lb/bu) of fresh cones. About 50 kg of seeds can be obtained from 100 kg (110 lb/220 lb) of fresh cones, and there are 7,300 to 10,000 cones/hl (2,600 to 3,550 cones/bu) (Bonner 1974). For baldcypress, the average number of cleaned seeds per weight determined from 26 samples was 11,500/kg (5,200/lb) with a range of 5,600 to 18,500/kb (2,540 to 8,400/lb). One sample of pondcypress from Florida contained about 9,000 seeds/kg 4,100 seeds/lb) (Bonner 1974). Baldcypress seeds keep well in dry storage at 2 to 5 °C for at least 3 years. Because they appear to be orthodox in storage behavior, longer storage under the same conditions will probably succeed.

Germination. Baldcypress seeds exhibit a moderate amount of dormancy that can be overcome by cold stratification (table 2). For germination testing, moist stratification for 30 days at 3 to 5 °C is recommended, followed by 28 days of testing at alternating temperatures of 20 °C for 16 hours (dark) and 30 °C for 8 hours (light) (ISTA 1993). Studies with collections from the Gulf Coast region suggested that dormancy in both species is regulated by the seedcoat, and any treatment that softens or weakens the coats will increase rate of germination. Soaking for 4 hours in concentrated sulfuric acid was recommended as the easiest treatment (Murphy and Stanley 1975). An alternative method for nursery use has been to soak the seeds in water

at 4 °C for 90 days or until ready to plant in the spring. Pondcypress seeds respond well to 60 to 90 days of stratification at 4 °C in peat moss, preceded by a 24- to 48-hour soak in 0.01% citric acid (Bonner 1974). In addition to the test conditions recommended in table 2, tetrazolium staining can be used to determine viability (ISTA 1993).

Nursery practice. Spring-sowing of pretreated seeds and fall-sowing (December) of untreated seeds are both practiced. The latter method has proved successful in northern nurseries. Seeds and cone scales can be broadcast or drilled together and should be covered 6 to 12 mm ($^1/_2$ to $^3/_4$ in) deep with sand, soil, or peat moss. Beds should then be mulched with leaves or other material, especially when fall sowing is used. Shade may be needed in the South from June to September, and beds must always be well watered. The resinous seeds are not eaten to any extent by rodents or birds (Bonner 1974). Germination is epigeal (figure 4). Rooting of cuttings is difficult but possible, as is grafting (Dirr and Heuser 1987).

Figure 4—*Taxodium distichum*, baldcypress: seedling development at 3 and 8 days after germination.

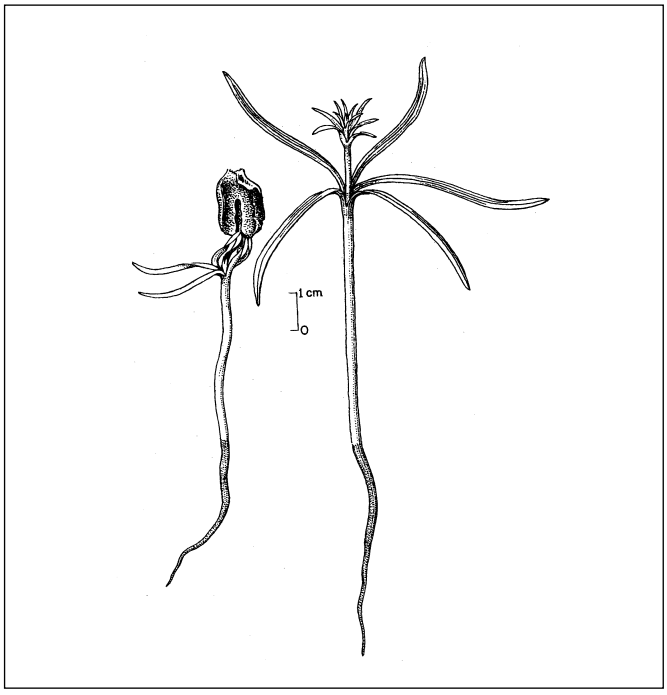


Table 2—*Taxodium,* baldcypress: germination test conditions and results on stratified seedlots

	Germination test conditions				Germinative energy		Germinitive capacity		
	Daily		Temp (°C)						
Species	light (hr)	Medium	Day	Night	Days	(%)	Days	(%)	Samples
T. ascendens	8	Kimpak	30	20	30	76	8	93	4
T. distichum	8	Kimpak	30	20	30	67	17	74	7

Sources: Bonner (1974), ISTA (1996).

Germ = germinitive; percentages are based on full seeds only.

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Taxaceae—Yew family

Taxus L.

yew

Nan C. Vance and Paul O. Rudolf

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Growth habit. The yews—members of the genus *Taxus* of the family Taxaceae—are non-resinous evergreen gymnosperms that are widely distributed throughout the moderate zone of the Northern Hemisphere (table 1). They grow primarily in the understory of moist, forested habitats in cool, temperate to subtropical climates (Price 1990). The growth form may be a tree or a shrub. In the understory, the yew's sprawling branchiness and spreading crown enable it to capture light gaps in the canopy. The tree may convert to shrub form if the main shoot is injured or declines and is replaced by lateral branches or new growth. Shrubbiness may also be sustained by frequent browsing. Crowns of these shrubby forms may attain as much as 24 m in diameter (Bugala 1978). The main stem of the yew tree can become quite stout in proportion to its height. Often the large diameter is attained by multiple stems that have fused over time. English yew has reached great age (1,000+ years) and girth, especially those planted in country churchyards (Lewington and Parker 1999).

Cultivated for centuries, the many English yew cultivars show distinct morphological differences in growth form and habit and in needle form and color (Krüssmann 1983). Since the 1920s, cultivars of *T.* × *media* Rehder (a hybrid of English and Japanese yews) have increased the number and variety of these commercially important ornamental shrubs (Chadwick and Keen 1976). The height of most yew species ranges from 6 to 12 m, although open-grown English yew may reach heights of 12 to 25 m and grow extremely thick trunks up to 17 m in girth (Krüssmann 1983; Lewington and Parker 1999). Florida yew is a small, broad tree, about 1 to 5 m in height at maturity (Redmond 1984). Pacific yew trees growing in the wild may reach diameters as large as 6 m and heights up to 18 m under favorable conditions (Bolsinger and Jaramillo 1990). A shrubby form of the

Table 1—*Taxus*, yew: nomenclature and occurrence

Scientific name & synonym(s)	Common name	Occurrence
***T. baccata* L.** *T. baccata* ssp. *eubaccata* Pilger.	**English yew,** common yew	Throughout Europe & Algeria, N Iran & the Himalayas
***T. brevifolia* Nutt.** *T. baccata* ssp. *brevifolia* Pilger.	**Pacific yew**	From SE Alaska S to N California & central Nevada; E to coastal Oregon & Washington to W Montana
***T. canadensis* Marsh.** *T. baccata* ssp. *canadensis* Pilger.	**Canada yew,** eastern yew, ground hemlock	E from Ontario into E Canada, S to Virginia & Tennessee
***T. chinensis* (Pilger.) Rehder** *T. celebica* (Warburg) Li. *T. mairei* S.Y. Hu ex Liu. *T. yunnanensis* Cheng & L.K.Fu.	**Chinese yew,** Maire yew, Yunnan yew	Central & W China from Yunnan to Guangxi
***T. cuspidata* Sieb. & Zucc.** *T. baccata* ssp. *cuspidata* Pilger.	**Japanese yew**	Throughout Japan & in E China
***T. floridana* Nutt. ex Chapman** *T. baccata* ssp. *floridana* Pilger.	**Florida yew**	Along Appalachicola River bluffs in N Florida
***T. globosa* Schltdl.** *T. baccata* ssp. *globosa* Pilger.	**Honduran yew,** Guatemalan yew, Mexican yew	From NE Mexico to Guatemala & El Salvador
***T. wallichiana* Zucc.** *T. baccata* ssp. *wallichiana* Pilger.	**Himalayan yew**	Himalayan Mtns from E Afghanistan & N India, E to Tibet, Burma & the Philippines

Sources: Krüssmann (1983), Rehder (1971), Rudolf (1974), Voliotis (1986).

Pacific yew is common east of the Cascade Divide (Arno and Hammerly 1977).

Occurrence. Eight of the recognized species of yews grow in the United States (Krüssmann 1983; Rehder 1951) (table1). English, Japanese, and Himalayan yews occur in Europe and Asia (Bugala 1978; Voliotis 1986) and Honduran, Florida, Canada, and Pacific yews occur in North America (Little 1971) (table 1). Chinese yew, considered a separate species in Chinese flora, is found in the mountainous regions of China up to about 3,000 m (Lee 1973; Zhang and Jia 1991). *Taxus mairei* (Lemee et Level.) S.Y. Hu & Liu; *T. yunnanensis* Cheng and L.K. Fu; and *T. celebica* (Warburg) Li may also be identified as sub-species or varieties of *T. chinensis* (Krüssmann 1983). Species classification within the genus is disputed and its phylogeny is not well understood (Bugala 1978; Voliotis 1986).

Of the 4 species native to the North American continent, 3 of them—Pacific, Canada, and Florida yews—occur in the United States. Honduran yew ranges from Honduras to southern Mexico. Of the species growing in the United States, Pacific yew has the most widespread range (table 1), and Florida yew, which is confined to the Appalachicola River bluffs in northwest Florida, the most restricted. Although distinct geographic races have not been fully established, allozyme evaluation of 54 Pacific yew populations from 174 geographic areas indicate that Sierra Nevada populations were genetically distinct from Idaho, Montana, and northeast Oregon populations (Doede and others 1993). Six geographic seed zones established by the Oregon State Department of Forestry divide Oregon into north coast, south coast, Willamette valley, south valley, north Cascades, south Cascades; and an elevation band in the Cascades separated at 762 m (Randall 1996).

Use. *Taxus* is the only genus of the yew family of economic importance (Price 1990). For centuries, indigenous people have used yew species in traditional utensils and medicines (Hartzell 1991). North American indigenous people used yew for implements, including bows and dip-net and drum frames, as well as for medicines (Alaback and others 1994). In Europe and Asia, the wood of the tree was once prized for making bows and is still valued for its quality in making fine musical instruments, cabinets, and utensils (Ambasta 1986; Hartzell 1991). Yew has gained additional importance in recent years for a unique class of diterpenoid alkaloids, or taxanes, contained in its needles, bark and seeds (Miller 1980). These taxanes are the source of a chemotherapeutic drug (taxol) used to treat cancer (Rowinsky and others 1990). The fruit-like arils are eaten by birds, and birds and small mammals eat the seeds. Although rabbits (*Sylvilagus* spp.), deer (*Odocoileus* spp.), and elk (*Cervus elaphus*) feed on foliage, leaves, and shoots of the Pacific yew, the European yew is reportedly toxic to horses and cattle but apparently not to white-tailed deer (*O. virginianus*) (Nisley 2002; Smith 1989; Veatch and others 1988).

Flowering and fruiting. Almost all yew species are dioecious; however, Canada yew is monoecious. Nevertheless, a small percentage of unisexual plants have been observed in this species (Allison 1991). Co-sexuality has been reported in Pacific yew—fruits and seeds have been observed on branches of male trees (DiFazio and others 1996; Owens and Simpson 1986). Co-sexuality and sex reversion have also been reported in other taxa (Chadwick and Keen 1976).

Yew flowers are small and solitary and arise from axillary buds. Female buds consist of single ovules surrounded by bracts. Anthesis is indicated by the appearance of the micropylar opening in the exposed ovule, which eventually develops into a seed. Male buds usually cluster along the underside of the previous season's branches. The male flower at anthesis is a stalked, globose head on which are 14 stamens, each with 5 to 9 microsporangia or pollen sacs. The pollen is shed between February and May (table 2). Dry pollen grains are yellow, indented spheroids, lacking sacci; diameters range from 19 to 26 μm (Owens and Simpson 1986).

The fruit, which ripens from late summer through autumn, consists of a scarlet fleshy, cup-like aril (figure 1)

Figure 1—*Taxus canadensis*, Canada yew: fruits.

bearing a single, hard, ovate seed up to 6 mm long (figures 2 and 3). The mature seed has a greenish brown to brown seedcoat and is filled with white megagametaphyte tissue (rich in lipids) that surrounds a small embryo 1 to 2 mm long. Times of flowering, fruit ripening, and seed dispersal for each species are listed in table 2.

Little information is available on the frequency of good seedcrops among the yews, but most species produce some seeds almost every year (Chadwick and Keen 1976; Harlow and Harrar 1958). Flowering and seed production was found for Pacific yew in western Oregon to be related to overstory openness and tree vigor (DiFazio and others 1997; Pilz 1996a). However, predation of fruit on trees in the open was higher, limiting seed production (DiFazio and others 1998). For Japanese yew, good crops are reported every 6 to 7 years (Rudolf 1974). English yew begins to produce seeds at about 30 years of age (Dallimore and Jackson 1967).

Figure 2—*Taxus*, yew: seeds of *T. baccata*, English yew (**left**); *T. brevifolia*, Pacific yew (**middle**); *T. canadensis*, Canada yew (**right**).

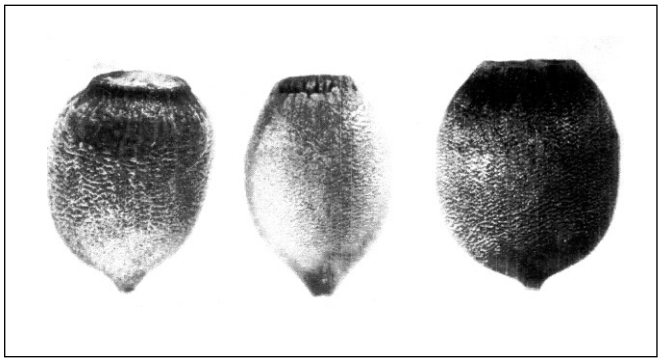
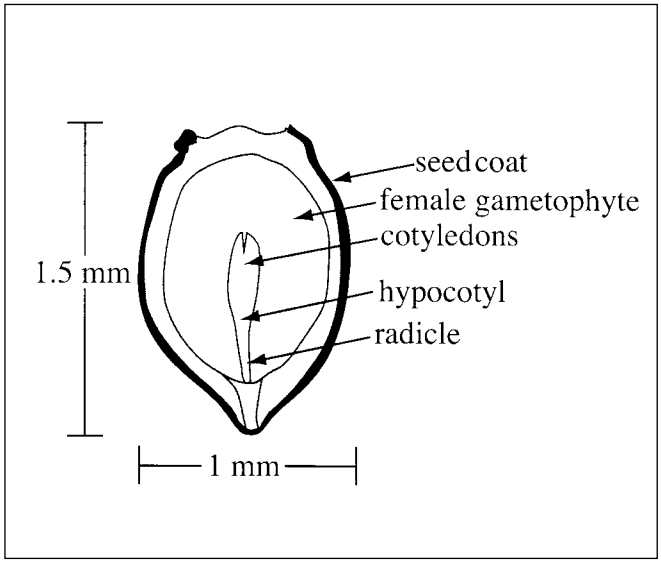


Figure 3—*Taxus canadensis*, Canada yew: longitudinal section through a seed.



Comparable information for the other species is lacking. For dioecious species, good seedcrops are produced where there is a good intermixture of male and female trees. Pollen may limit seed production in some populations of Canada yew where deer browsing has created widely spaced plants that produce little pollen (Allison 1990). Although pollination was found to be limiting, it was not the primary factor limiting seed production in Pacific yew trees examined in western Oregon (DiFazio and others 1998). Yew seeds have been found to survive in a soil seedbank for several years (Minore and others 1996). Although seeds will germinate under mature overstories in canopy gaps, seedlings may be abundant following disturbance such as burning and overstory removal. However, Crawford (1983) noted that, in Idaho, most abundant yew seedlings were found growing in forest litter and decaying wood.

Collection of fruits. The maturation of seeds and ripening of arils (full expansion and orange-red coloration) may occur over a span of months. Over this time, losses to birds and small mammals such as chipmunks (*Eutamia*s spp.) can be considerable (DiFazio 1995). To prevent losses to predation, yew fruits should be picked frequently from the branches, beginning when individual fruits first ripen. To ensure that adequate amounts of seeds are collected in specific seed collection areas, bagging branches of desirable trees well before fruit ripens is recommended so that fruits are not lost or destroyed by squirrels (*Citellus* spp.) and other predators (DiFazio and others 1998). If returning repeatedly to individual trees is impractical, harvesters can bag branches in July with light-weight mesh bags and then collect the fruits in late fall.

Randall (1996), when collecting seeds in Oregon and Washington, noted differences in phenology in nursery-grown yews from seeds collected in the coastal range and the Cascades. Seed zones that have been identified should be used for collecting; ideally seeds should be collected from the approximate area where the yew trees will be grown.

Extraction and cleaning. Seeds should be extracted from the fruit shortly after harvest (storage with fruit promotes mold) by macerating the fleshy arils in water. A blender with the blades covered by rubber tubing (Munson 1986) and set at low speed will efficiently and quickly separate seeds from arils without damaging seeds. Light, unfilled seeds float to the top and can be easily removed. In some species, the membranous outer seedcoat is partially destroyed during extraction; in others, it remains tightly fixed to the bony inner coat. After extraction, excess moisture should be dried from seeds. Seeds can then be weighed, sown, cold-stored, or stratified as soon as possible. The

number of cleaned seeds per weight is listed in table 3. Purity of seedlots generally ranges from 96 to 100%, and soundness, from 78 to 99% (Rudolf 1974).

Storage. Yew seeds are orthodox in storage characteristics and, if kept at low moisture content, may be successfully stored frozen for years without losing viability. The viability of yew seeds can be maintained for 5 or 6 years if they are dried just after extraction at room temperature for 1 or 2 weeks and then stored in sealed containers at 1 to 2 °C (Heit 1967). If seeds are dried to 15 to 25% relative humidity (moisture content of 2 to 3%), seedlot viability of greater than 90% can be maintained for weeks at 25 °C. Pacific yew seeds have a high lipid content (mega gametophyte lipid content is about 71% of the dry mass); therefore, long-term storage conditions should maintain seeds at 14% relative humidity and subzero temperatures (Walters-Vertucci and others 1996). Analysis of seeds for cryopreservation indicates that they can be stored at –18 to –20 °C without losing viability, provided that they have reached sufficient maturity, and that they probably will remain viable for decades under these conditions (Walters-Vertucci and others 1996). Yew seeds can be held for several months in cold stratification without losing viability. Reasonably good viability of English yew seeds was maintained for up to 4 years by storing them in moist sand or acid peat at low temperatures (Rudolf 1974).

Pregermination treatments. Yew seeds are slow to germinate; natural germination usually does not take place until the second spring after seedfall (Suszka 1978). Viable seeds of Pacific yew have been found in soil seedbanks for several years (Minore 1994). Although a variety of birds and small mammals eat, digest, and disperse yew seeds (Bartkowiak 1978), germination does not appear to be hastened by their passing through the alimentary canal of birds. Yew seeds have a strong but variable dormancy that can be broken by warm-plus-cold stratification (Suszka 1978). One recommendation is to hold the seeds for 150 to 210 days at 16 to 18 °C, then for 60 to 120 days at 2 to 5 °C (Heit 1967, 1969). The ISTA rules specify prechilling yew seeds for 270 days at 3 to 5 °C. Steinfeld (1993a) reported on 2 groups of seeds collected in the fall in Oregon that were stratified during the fall and winter. One group was chilled for 1 month and the other was kept at warm temperatures for 5 months and then chilled for 2 months. The seeds were sown in bareroot beds covered with mulch the following spring.

Table 2—*Taxus*, yew: phenology of flowering and fruiting

Species	Location	Flowering	Fruit & seed ripening	Seed dispersal
T. baccata	W Europe	Mar–May	Aug–Oct	Aug–Oct
T. brevifolia	Washington & Oregon	Mar–May	July–Oct	July–Oct
T. canadensis	Minnesota & Wisconsin	Apr	Aug–Sept	Aug–Sept
T. cuspidata	Japan	Apr–June	Sept–Oct	Oct
T. floridana	NW Florida	Jan–Mar	Aug–Oct	Aug–Oct

Sources: Allison (1990), Chadwick and Keen (1976), Redmond (1984).

Table 3—*Taxus*, yew: seed yield data

		Cleaned seeds/weight				
		Range		Average		
Species	Place collected	/kg	/lb	/kg	/lb	Samples
T. baccata	Western Europe	13,900–18,000	6,300–8,200	17,000	7,700	14
	NE US	13,200–15,000	6,000–6,800	14,100	6,400	3
T. brevifolia	Carson & Skamania Cos., Washington	32,400–36,200	14,700–16,500	33,100	15,000	2
	S Cascades, Oregon	23,800–25,900	10,800–11,800	24,950	11,300	10
	Central Cascades, Oregon	26,330–39,950	12,000–18,200	31,077	14,100	4
T. canadensis	Upper mid-West	33,000–62,400	15,000–28,400	46,300	21,000	4
	Minnesota & Wisconsin	35,700–38,460	16,200–17,500	37,000	16,800	
T. cuspidata	Japan	24,700–43,000	11,200–19,500	31,300	14,200	7
	NE US	14,840–19,300	6,700–8,800	16,300	7,400	3

Sources: Allison (1995), Heit (1969), Rudolf (1974), Vance (1993), Yatoh (1957).

Germination was negligible for the cold-treated seeds and about 5% for the warm/cold-treated seeds; however, in the following spring, the germination rate of the remaining seeds combined with that of the previous spring exceeded 95%. No difference in total germination between the 2 treatment groups was detected by the second year.

Germination and seed viability tests. Germination of yew seeds is epigeal (figure 4). Because of the deep dormancy of the seeds, germination will be sporadic over the course of several years. Germination percentages after the first year do not indicate the potential of the seeds to germinate, for germination will continue in the following year (Heit 1969; Pilz 1996b). Official testing rules recommend tetrazolium staining as the first choice in testing, followed by germination in sand at 30 °C for 28 days after 270 days of stratification (ISTA 1993). Cutting tests are also recommended for rapid viability checks. After a seed is carefully split in half with sharp knife or scalpel, the embryo and megagametophyte tissue can be examined. If an embryo is opaque and developed, with visible cotyledon buds, and gametophyte tissue is white and fills the seed cavity, the seed should be considered mature and viable. A tetrazolium test for viability requires cutting seeds to expose tissue, staining for about 24 to 48 hours, then cutting out the embryos. A seed is considered viable if all of the embryo and endosperm is stained (Edwards 1987). Removing embryos from Pacific yew seeds and culturing them on nutrient medium with an energy source such as 2% sucrose has resulted in germination of 70 to 100%. Cleaned, mature seeds showed high germination whether seeds were fresh, cold stored, or stratified (Vance 1995). Embryo germination was shown to improve with a 14-hour photoperiod and up to 50 days of cold treatment in *in vitro* germination tests of embryos from English and Japanese yews (Flores and others 1993). Test results for 3 species are given in table 4.

Nursery practices. Freshly collected yew seeds can be sown in late summer or early fall of the year of collection, whereas stratified seeds can be sown in the spring of the year following collection. The seeds should be covered with about 1 to 2 cm (.4 to .8 in) of soil, and mulching the seedbed is beneficial (Steinfeld 1993a). Beds should be shaded during the summer. Even with these treatments many seeds often will not germinate until the second spring (Heit 1969; Steinfeld 1993a). Seedlings should be shaded after they emerge the first spring and summer. Rabbits have been observed feeding on Pacific yew seedlings in the bareroot beds at the USDA Forest Service's J. Herbert Stone Nursery at Central Point, Oregon (Steinfeld 1993b). Birds eat seeds, and germinants may be susceptible to damping-off fungi (*Fusarium* spp.). Although most ornamental yews are propagated by cuttings, seedlings of the Japanese yew cultivar 'Capitata' are germinated from seeds after 3 months of warm stratification (20 °C) followed by 4 months at 5 °C (Hartmann and others 1990). Seedlings are grown 2 to 3 years in seedbeds in a poly house, followed by 2 to 3 more years in liner beds, then 3 or 4 years in a nursery field

Figure 4—*Taxus baccata*, English yew: seedling development 1, 8, 12, 22, and 39 days after germination.

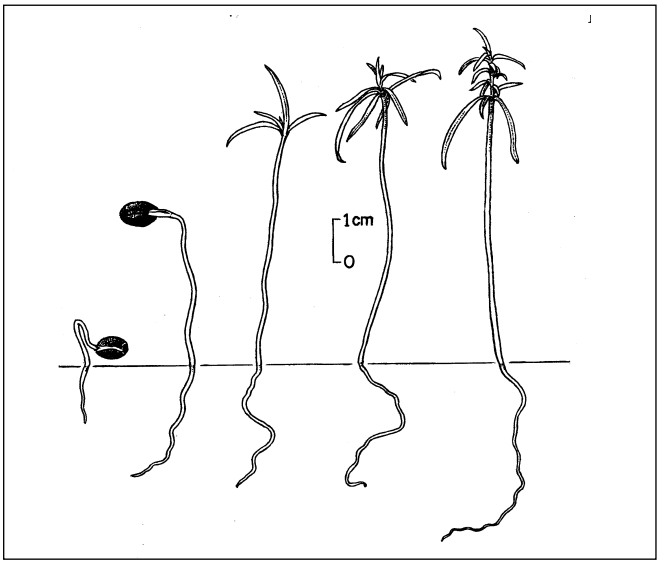


Table 4—*Taxus*, yew: stratification periods, germination test conditions, and results

Species	Germination test conditions: Stratification (days) Warm	Stratification (days) Cold	Temp (°C) Day	Temp (°C) Night	Days	Germinative capacity Avg (%)	Germinative capacity Range (%)	Samples
T. baccata	—	—	16	10	—	67	47–70	12
	120	365	10–16	10–16	60	47	—	1
T. brevifolia	—	—	30	20	60	55	50–99	3
T. cuspidata	120	365	10–16	10–16	60	68	—	1

Source: Rudolf (1974).

before they are of salable size (Hartmann and others 1990; Shugert 1994). In the first 3 years, 55% shade is used from mid-June until November to reduce stress (Shugert 1994). Young yew plants are susceptible to root weevils. Commercial preparation of nematodes that are effective against weevil larvae can be applied in early spring when soil temperatures reach 7 °C.

All yew species can be successfully propagated by rooting cuttings, and most commercial cultivars are produced this way. Successful stecklings from Pacific, Canada, Florida, and Honduran yews were obtained by rooting cuttings in a greenhouse under shaded conditions, on benches that had bottom heat of about 21 °C, an overhead mist system to maintain high humidity, and cool air temperatures (Hartmann and others 1990; Suszka 1978). On 1- to 2-year-old stems, from healthy branch tips, cuttings should be clipped at an angle and needles removed from the clipped end. Cutting length varies depending on the branch but may range from 10 to 20 cm (Chadwick and Keen 1976). The clipped tip should be dipped in a solution containing a root-promoting compound such as indole B-indolebutyric acid (IBA) or a-naphthalenacetic acid (NAA) and a fungicide, then stuck to a depth of about 3 cm (1.2 in) in rooting medium. Using 5,000 to 10,000 ppm of IBA dissolved in 50% ethanol and dipping cuttings quickly achieves satisfactory rooting (Hartmann and others 1990). The medium should hold the cuttings, maintain a high moisture content, and be well drained. A mixture of sphagnum peat moss, coarse vermiculite, and perlite or sand will enhance rootability and promote a desirable root system (Copes 1977). If Pacific yew cuttings are stuck in the winter, rooting may begin to occur within 4 to 6 weeks, depending upon species and cultivar but may also take up to 3 or more months. Rooting ability varies widely by clone or cultivar and by the time of year that yews are propagated. Clonally propagated plants should only be used where genetic selection for desired traits is needed in a cultivated setting. Seedlings are preferred over rooted cuttings for reforestation because they have genetic variation that more nearly approximates that of wild populations.

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Verbenaceae—Verbena family

Tectona grandis L. f.

teak

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Growth habit, occurrence, and use. Native to Southeast Asia in India, Myamar (Burma), Thailand, and Indochina, teak is the only important species of the 3 in the genus *Tectona* (Schubert 1974). It is a large deciduous tree that reaches maximum heights of 30 to 40 m. It grows best in warm, moist tropical climates with 1,250 to 3,000 mm of mean annual precipitation and a marked dry season of 3 to 6 months (Webb and others 1984). Teak has probably been cultivated for centuries in Asia and has been planted for timber production in India and Burma since at least 1840 (Troup 1921). In the Western Hemisphere, teak has been planted since about 1900, beginning in the Caribbean region (Marshall 1929; Moldenke 1935). Because it is a tropical species, in the continental United States, it grows successfully only in southern Florida. Adaptability trials have been successful in Hawaii (Whitesell and Walters 1976). About 130 ha of teak plantations have been established in Puerto Rico and the U.S. Virgin Islands (Weaver 1993). Teak wood is famous the world over for its strength, durability, dimensional stability, working qualities, and the fact that it does not cause corrosion when in contact with metal (Kukachka 1970; Troup 1921). It is currently used for shipbuilding, fine furniture, trim, decorative objects, veneer for decorative plywood, posts, poles, and fuel (Kukachka 1970; Webb and others 1984).

Geographical races of teak have been distinguished by differences in stem form and rate of growth (Champion 1933). These are not recognized botanically even as varieties, but it is most important when establishing plantations to use seeds from a race that will grow well under local conditions (Beard 1943; Champion 1933; Laurie 1938). In Trinidad, trees grown from seeds of Burmese origin have been more satisfactory than those grown from seeds of Indian origin (Beard 1943).

Flowering and fruiting. The small white, perfect flowers of teak are borne on short pedicels, in large erect terminal panicles, about 2 months after the dry season has ended and the large obovate leaves have emerged. The dates vary somewhat depending on the climatic regime, but flowering generally takes place for several months between June and September, and the fruits ripen 2 $^1/_2$ to 3 months later (Chable 1969; Mahapol 1954; Troup 1921; White and Cameron nd). The fruits gradually fall to the ground during the following dry season. The fruit consists of a subglobose, 4-lobed, hard bony stone about 1.2 cm in diameter, surrounded by a thick felty, light brown covering (figure 1), the whole enclosed in an inflated bladder-like papery involucre. The stone (often called a nut) contains 1 to 3, rarely 4, seeds (figure 2) and has a central cavity, giving the appearance of a fifth cell. Schubert (1974) found that the average number of seeds per stone was 1.7. In a survey of the fruits from 23 provenances in India, an average of 51% of the fruits were found to have no seeds, 35% had 1 seed, 12% had 2 seeds, 2% had 3 seeds, and 0.4% had 4 seeds per fruit (Gupta and Kumar 1976).

Figure 1—*Tectona grandis*, teak: (**top**) and side (**bottom**) views of fruits with their bladder-like involucres removed.

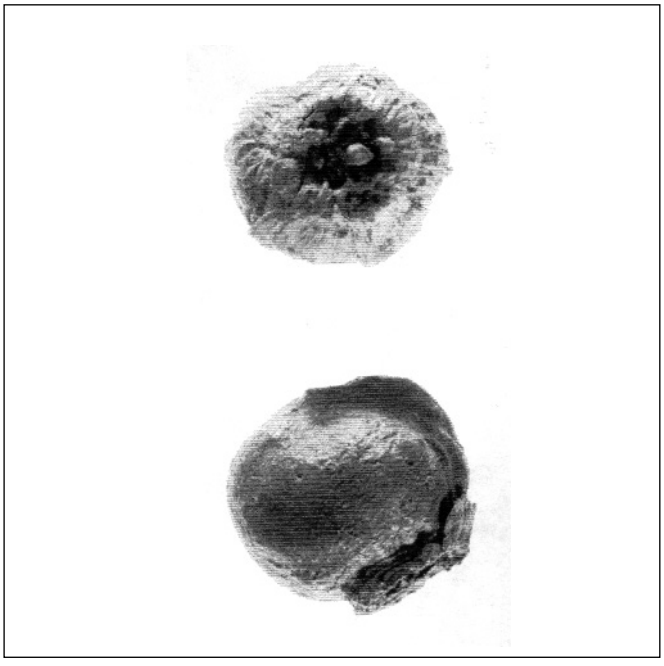
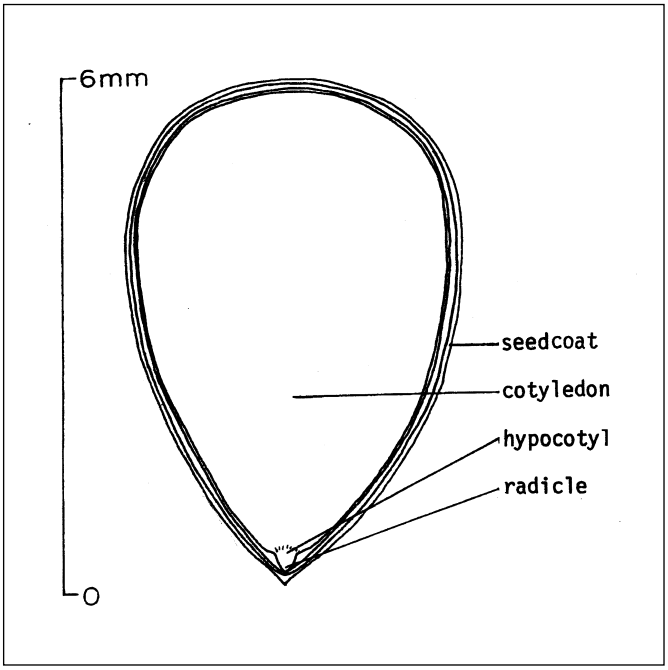


Figure 2—*Tectona grandis*, teak: longitudinal section through a seed.



Collection, extraction, and storage. Teak has borne viable seeds when only 3 years old (Schubert 1974), and good seedcrops are produced by plantations less than 20 years old (Troup 1921). The bladder-like involucre turns from green to brown when the seeds are ripe. The fruits can be swept up from the ground beneath the trees as they fall or else clipped with pruning poles or shaken from the branches. Drying can be completed by spreading the fruits on racks in the sun. For convenience in handling and storage, the involucre can be removed in a mechanical dehusker or by working a cloth bag half-filled with dried fruits against the ground with a foot and then winnowing to separate the fruits from the chaff. Teak fruits in Honduras average 705/kg (320/lb) with the involucres intact and 880/kg (400/lb) with the involucres removed (Chable 1969). In other parts of the world, the number of clean fruits per weight varies from a low of 880 to a high of 3,070/kg (400 to 1,400/lb) (Champion and Brasnett 1958; Parry 1956). The seeds make up about 3% of the weight of the cleaned fruits (Dabral 1976). Teak seeds are true orthodox in storage behavior and keep best at low temperatures and moisture contents. Keiding (1985) reported that seeds stored at 0 to 4 °C and about 12% moisture for 7 years lost no viability. Seeds from fruits stored in sacks in dry warehouses retained their viability for about 2 years (Kushalappa 1977). Longer periods of storage have not been needed in most areas because teak produces good seedcrops almost every year (Mahapol 1954; Troup 1921).

Germination tests. Cut tests of fruits on 56 collections from across the range of teak revealed a potential mean viability of 71% and ranged from 40 to 96% (Danish/FAO Forest Tree Seed Centre 1973). Laboratory germination tests should be carried out in sand at a constant 30 °C for 28 days. Pretreatment to stimulate germination should be 6 repetitions of soaking the fruits in water, followed by 3 days of drying (ISTA 1993). Germination in nursery beds in various parts of the world has varied from 0 to 96% in periods varying from 10 days to 3 months. Seeds extracted from the fruits and treated with fungicide gave a germination of 54% in 12 days (Dabral 1976). Because it is difficult to extract teak seeds from their fruits and untreated teak fruits give protracted, often low and unpredictable germination, some pre-treatment is usually applied to fruits. Various pretreatments to hasten or improve germination have been used. Soaking the fruits in water for several days, or alternate wetting and drying as in laboratory testing, have proven effective (Schubert 1959; Troup 1921; White and Cameron nd). In one test, clean fruits were pretreated by 5 cycles of alternate soaking in water for 24 hours and drying in the sun for 48 hours and then sown. Germination began 18 days after sowing and continued to increase for 15 days, after which it gradually decreased. Germination 68 days after sowing was 61% of the total number of fruits sown (Schubert 1974). Weathering of the epicarp and mesocarp aids germination. Seeds inoculated with *Scytalidium* sp. (a cellulolytic fungus isolated from teak litter), 0 and kept moist for 21 days had 96% germination compared to 20% for uninoculated control (Dadwal and Jamaluddin 1988). Increases in germination of 5 to 12% over controls (21% germination) were obtained with treatments of IAA and GA alone and in combination at various concentrations (Uanikrishnan and Rajeeve 1990). A novel method reported from Thailand is to expose the fruits to ants for 1 to 2 weeks: they attack and remove the felty covering and thus speed up germination without loss of viability (Bryndum 1966). Soaking fruits from 11 Indian provenances in a nutrient solution resulted in a higher seedling yield (34%) than control (18%), water soak (30%) or scarification (28%). It is felt that nutrient deficiencies in some of the sources resulted in lower germination or early seedling failure (Gupta and Pattanath 1975). A temperature of 30 °C appears to be optimal for germinating teak seeds (Dabral 1976). Some seeds that were stored for several months germinated better than fresh seeds (Champion and Brasnett 1958; Mahapol 1954; Troup 1921), probably because seeds need a period of after-ripening (Coster 1933). Because they tend to have a greater number of seeds per fruit, larger fruits yield a significantly higher number of seedlings per fruit. It is recommended that fruits smaller than 14 mm in diameter be culled (Banik 1977). Seeds from dry regions frequently

are more difficult to germinate (Troup 1921). Germination is epigeal (Troup 1921).

Nursery practice. Teak fruits are usually broadcast in nurserybeds and covered with 1.2 to 2.5 cm ($^1/_2$ to 1 in) of sand, soil, or sawdust (Schubert 1956; White and Cameron nd). A seedling yield of about 25% can be expected from good seedlots (White and Cameron nd). The beds should be watered just enough to keep them moist. Once the seedlings have become established, watering should gradually be reduced. Field planting is generally done with "stump" plants (seedlings with the tops removed) or potted plants grown in plastic nursery bags. The stump plants are grown in the nursery until they reach 1.2 to 2.5 cm ($^1/_2$ to 1 in) in diameter at the root collar; then they are top-pruned to about 2.5 cm (1 in) and root-pruned to 18 or 20 cm (7.0 to 7.9 in) in length (Schubert 1956; White and Cameron nd). Ideally, plants of suitable size can be grown in 6 to 9 months. In Thailand (Kushalappa 1977) and India (Gupta and Pattanath 1975) at least some nurseries undercut the beds and remove seedlings large enough for stump plants after 1 year and allow the rest to grow another year when the whole bed is harvested. Sowing of the nurserybeds should be timed so that the proper size is reached in time for planting at the start of the rainy season. Another approach is to harvest in the dry season and store the dormant stumps in beds of dry sand for 3 months before planting at the start of the wet season (Kushalappa 1977). Direct seeding into prepared seed spots is practiced, but early growth is slow and often high mortality results (Weaver 1993). Teak can also be reproduced by coppicing, because cut stumps produce very vigorous sprouts.

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Asteraceae—Aster family

Tetradymia DC.

horsebrush

Lee E. Eddleman

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Growth habit, occurrence and use. *Tetradymia* (horsebrush) is a rather low-growing, multi-branched unarmed or spiny shrub, found either as well-scattered individuals or as small colonies mixed in with other vegetation. Some species may reach heights of 2 to 2.5 m but they are more commonly 1 m or less. Reproduction is from wind-dispersed seeds and from sprouting of root crowns and rhizomes in longspine horsebrush, hairy horsebrush, spiny horsebrush, and cotton horsebrush (Hartman 1984; McArthur and others 1979; Mozingo 1987; Strother 1974). Eight species (table 1) are found, primarily in the intermountain region and its fringe areas, and 2 species are found in southern California and Baja California (McArthur and others 1979; Strother 1974). Elevational range is from 800 to 2,400 m, although the southern California species range downward to 300 m. Horsebrush is commonly associated with the sagebrush vegetation type, but the genus has widespread occurrence from barren slopes and alkaline plains upward into the piñyon–juniper and yellow pine types.

Horsebrush provides ground cover and soil stability. It is generally considered of low forage value, although buds and new leaders are consumed by cattle, sheep, goats, antelope (*Antilocapra americana*), and mule deer (*Odocoileus hemionus*) (McArthur and others 1979). Most species are

Table 1—*Tetradymia,* horsebrush: nomenclature and occurrence

Scientific name & synonym(s)	Common name	Occurrence
***T. argyraea* Munz & Roos**	**striped horsebrush,** striped cottonthorn	Mountains of E Riverside & San Bernadino Cos., California
***T. axillaris* A. Nels.** *T.a.* var. *axillaris* *T.a.* var. *longispina* (M. E. Jones) Strother	**longspine horsebrush**	S Nevada into Inyo Co., California; S California
***T. canescens* DC.** *T. inermis* Nutt.; *T. multicaulis* A. Nels. *T. linearis* Rydb.	**gray horsebrush,** spineless horsebrush, common horsebrush	S British Columbia to S California E of Cascades–Sierra Nevada and from S Saskatchewan to N Arizona
***T. comosa* Gray**	**hairy horsebrush**	SW California to N Baja California
***T. filifolia* Greene**	**threadleaf horsebrush**	Central New Mexico
***T. glabrata* Torr. & Gray**	**smooth horsebrush,** littleleaf horsebrush	Great Basin, SE Oregon & SW Idaho, Utah, Nevada, to S California, mostly E of Sierra Nevada
***T. nuttallii* Torr. & Gray** *T. spinosa* Nutt. x *T. permixta* Payson	**Nuttall horsebrush**	SE Wyoming across central & N Utah to NE Nevada
***T. spinosa* Hook. & Arn.** *Lagothamnus ambiguus* Nutt. *L. microphyllus* Nutt.	**spiny horsebrush,** cottonthorn horsebrush, catclaw horsebrush, shortspine horsebrush, thorny horsebrush	SE Oregon, S Idaho, SW Montana S across W Wyoming & and Colorado, NW Arizona, W to Sierra Nevada
***T. stenolepis* Greene**	**Mojave horsebrush**	S California to extreme S tip of Nevada
***T. tetrameres* (Blake) Strother** *T. comosa* Gray ssp. *tetrameres* Blake	**cotton horsebrush,** four-part horsebrush, dune horsebrush	Central N Nevada SW to Mono Co., California

Sources: Cronquest (1994), McArthur and others (1979), Mozingo (1987), Strother (1974).

poisonous to sheep, especially smooth horsebrush (Johnson 1974; Kingsbury 1964). Flowers are used by small moths, bees, flies, and beetles (McArthur and others 1979). Gelechiid moths form galls in leaves and stems (Hartman 1984). Smooth horsebrush is considered ideal for desert landscaping because its leaves develop early and are dropped by mid-summer (Mozingo 1987). Late-season flowering species of horsebrush provide an attractive contrast to the vegetation types of dry areas.

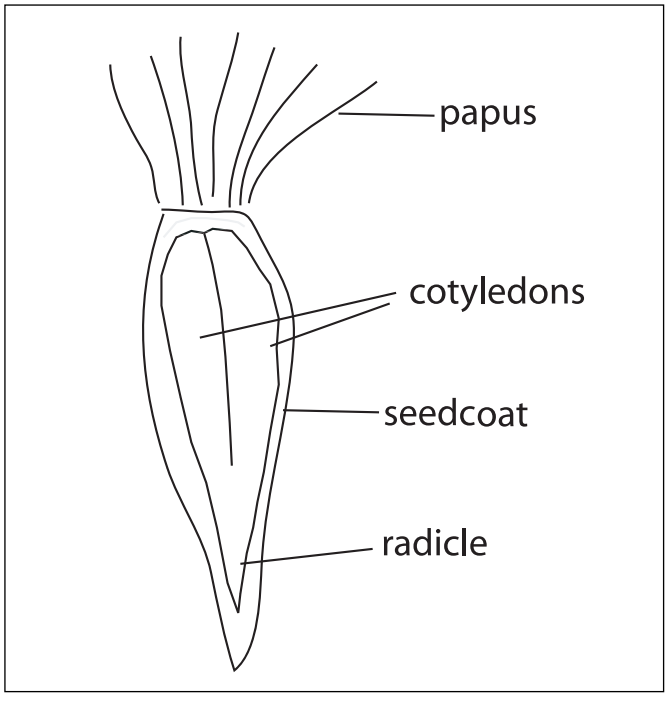
Flowering and fruiting. Horsebrush flowers are borne in heads of 4 to 8 florets each and are located either in the axil of primary leaves or are clustered as dense racemes or corymbs at the tips of branches. Flowering begins as early as April and may last into September. Horsebrush species flower at the following times: striped horsebrush, late June to early August; longspine horsebrush, April and May; gray horsebrush, late May through September; hairy horsebrush, June through mid-August; threadleaf horsebrush, July; smooth horsebrush, May through July; Nuttall horsebrush, late May and June; spiny horsebrush, April through August; Mojave horsebrush, late May through early August; and cotton horsebrush, June and July (Cronquist and others 1994; Mozingo 1987; Strother 1974). Longspine and smooth horsebrushes are the first to flower, where as gray horsebrush flowers from late May through mid-September and has the unique characteristic (among the horsebrush species) of flowering earliest in the north and progressively later southward (McArthur and others 1979; Strother 1974).

Collection, extraction, and cleaning. Horsebrush achenes (figures 1 and 2) are more or less hairy and sometimes glabrous; they possess a well-developed pappus of bristles. As in similar plant forms (Eddleman 1977), the seeds may be hand-stripped or knocked from the head onto a canvas. Mature achenes from which the hairs have been removed have a light to medium reddish brown cast and a parismatic to fusiform shape. Cleaned seeds per weight are reported at 309/g (140,000/lb) for gray horsebrush (McArthur and others 1979) and may be less for the larger seeded species—Nuttall, spiny, Mojave, and cotton horsebrushes.

Germination. Germination is poor for gray horsebrush (Stark 1966), and only 2% of spiny horsebrush seeds germinated in one test (Swingle 1939). Some germination may occur without pretreatment, but prechilling seeds for 4 to 6 weeks is reported to help germination (Young and Young 1992).

Figure 1—*Tetradymia* horsebrush: seeds. *T. comosa* **(left),** *T. spinosa* **(right)**.

Figure 2—*Tetradymia* horsebrush: *T. comosa* longitudinal section through achene.



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Malvaceae—Mallow family

Thespesia Soland. ex Correa

thespesia

John K. Francis

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Species, occurrence, and growth habit. There are 17 species of *Thespesia,* all trees or shrubs (Howard 1989). Two are of particular interest. *Thespesia populnea* (L.) Soland. ex Correa—with botanical synonyms *Hibiscus populneus* L. and *T. lampas* (Cav.) Dalz. ex. Dalz. & Gibson—is known locally as portiatree, seaside mahoe, *emajagüilla, milo*, and many other names (Little and Skolmen 1989; Parrotta 1994). Portiatree is native to tropical shores from East Africa to Polynesia. It has naturalized (and is sometimes considered invasive) and is planted in coastal areas throughout the tropics. Portiatree is a small tree in moist habitats, although it is often shrubby on dry or salty coastal soils.

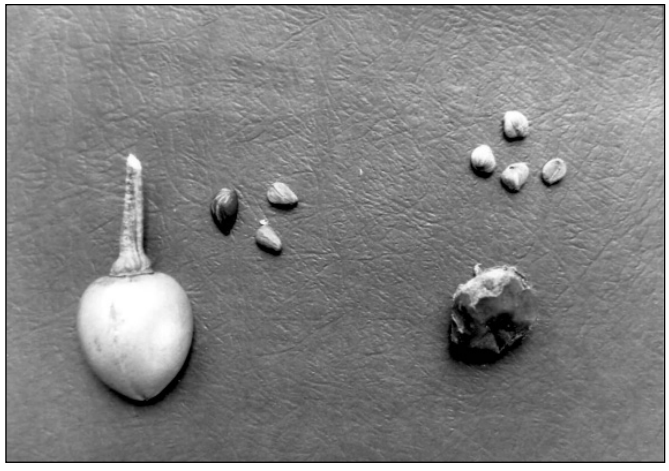
Thespesia grandiflora DC.—known as *maga*—is a small to medium-sized tree with a straight stem that is endemic to Puerto Rico (Francis 1989). This species has been referred to in the literature by the botanical synonyms *Montezuma speciocissima* Sessé & Moc., *M. grandiflora* DC., and *Maga grandiflora* (DC.) Urban (Francis 1989).

Use. Portiatree is planted as an ornamental throughout the tropics, especially in coastal areas. Its manageable size, heart-shaped, yellow-green leaves, and yellow flowers endear it to many. More than for any other reason, portiatree succeeds as an ornamental because it can grow on almost any soil. Maga is planted as an ornamental in Florida, Hawaii, Puerto Rico, and several other locations (Little and Wadsworth 1964; Neal 1965). Although its dark-green foliage is very attractive, its large (15 cm) dark pink flowers are its principal asset. Maga requires fertile soils and does not tolerate compaction. The wood of both species is dark reddish brown to chocolate brown, moderately heavy, and moderately hard, with excellent working properties. The small amounts of portiatree wood available fetch high prices and are used for carving, furniture, and posts. The small amounts of maga harvested are used for making musical instruments, furniture, and craft items. Seeds of portiatree are widely used for medicinal purposes (Little and Skolmen 1989; Parrotta 1994).

Flowering and fruiting. Open-grown maga are reported to begin flowering when 5 to 10 years old (Francis 1989); portiatree flowers even earlier. Except in dry areas and seasons of drought, flowering and fruiting of both species proceeds throughout the year (Francis 1989; Parrotta 1994). The fruits of portiatree are flattened, leathery 5-celled capsules 2.5 to 4.0 cm in diameter and 2 cm long (Rashid 1975). They may remain attached to the tree for some time. A sample of 50 fruits from Puerto Rico contained from 1 to 11 seeds/fruit with an average of 5.7 seeds/fruit (Parrotta 1994). The seeds are hairy, 1 cm long, and 0.6 cm broad (figure 1). Reported weights of air-dried seedlots range from 3,500 to 6,700/kg (1,600 to 3,000/lb) (Francis and Rodríguez 1993; Parrotta 1994; Rashid 1975; Von Carlowitz 1986). The fruit of maga is smooth and green, subglobose, and 3 to 5 cm in diameter. From 1 to 12 brown seeds are embedded within a white, fleshy matrix. Fresh seeds numbered 2,500/kg (1,100/ lb); air-dried seeds, 3,900 seeds/kg (1,800/lb) (Francis 1989). The seeds of portiatree are dispersed by wind and water (Parrotta 1994). Maga depends upon fruit bats and birds for dispersal (Francis 1989).

Collection, cleaning, and storage. Quantities of portiatree fruits can be easily picked off the ground under bear-

Figure 1—*Thespesia*, thespesia: fruits and seeds of *T. grandiflora*, maga (**left**), and *T. populnea*, portiatree (**right**).



ing trees, or they can be picked by hand or clipped with a pruning pole from the branches. The fruits are mature when they have turned black (Rashid 1975). Accumulating quantities of maga seeds is more difficult. Maga fruits can be clipped from the trees when they reach full size (no color change is observed). Fruits that are still hard should be left for 2 or 3 days and will continue to ripen. If not eaten by bats and birds, the fruits fall soon after ripening and can be picked up from the ground. Because bats and birds drop the seeds as they consume the fruits, seeds can be collected from the ground under bearing trees or beneath nearby perch trees. Good seeds have a cinnamon-brown color with a waxy luster and are free of fungal spots. Lighter or darker colors denote immaturity or overmaturity and loss of viability (Marrero 1949). Nursery workers normally clean the seeds by hand, a fairly rapid process. Cleaning with macerators may not be possible due to the fragile nature of the seeds, especially those of maga. Seeds of portiatree are apparently recalcitrant but somewhat resistant to drying and can be stored in sealed containers for weeks to months under refrigeration (4 °C). The seeds of maga are highly recalcitrant. The folded cotyledons (figure 2) are active and turn green within the seed as germination begins. The seeds begin germinating 5 to 7 days after the fruit ripens (Francis 1989). Many of the seeds picked up from the ground, either loose or within rotting fruits, already have the radicle exposed. It is best to place moist paper towels or other moistened material in the collection container and sow the seeds as soon as possible. Viability of maga seeds can be extended to nearly 4 months by drying to 62.5% moisture and storing at 2 to 4 °C (Marrero 1942).

Germination. No pregermination treatments are necessary. Seeds of portiatree should be sown in sandy media and lightly covered (Parrotta 1994). From 65 to 79% of fresh seeds germinate, beginning in 8 days and continuing over a 9-week period (Francis and Rodríguez 1993; Ricardi and others 1977; Parrotta 1994). Maga seeds may be sown and lightly covered in ordinary potting mix. Marrero (1942) reported that, although 70 to 80% of fresh seeds germinated, only 20% of seeds stored at room temperature for 2 weeks germinated. Francis and Rodríguez (1993) reported 80% germination beginning 6 days after sowing. Germination of both species is epigeal (figure 3) (Francis 1989; Parrotta 1994).

Nursery practice. Ordinary nursery practice is to germinate seeds in germination trays or beds and transplant seedlings into containers (pots or plastic nursery bags) after the first true leaves emerge. Portiatree seedlings reach 15 cm (6 in) in height about 3 months after sowing (Parrotta 1994). Moving portiatree seedlings into full sunlight after they are established in the pots is recommended. Rooted cuttings are also used to produce portiatree stock. Maga seedlings develop rapidly in partial shade, reaching 20 cm (8 in) in 3 months and 40 cm (16 in) in 6 months (Francis 1989). Maga seedlings should be moved into full sun a few weeks before outplanting. Seedling stock of either species from 15 to 50 cm (6 to 20 in) can be used to establish plantations. Trees destined to become ornamentals are often grown in pots until they attain 1 to 2 m (39 to 79 in) in height. Wildlings are sometimes collected, potted, and allowed to rebuild their root system before outplanting.

Figure 2—*Thespesia grandiflora*, maga: seed cut in longitudinal section.

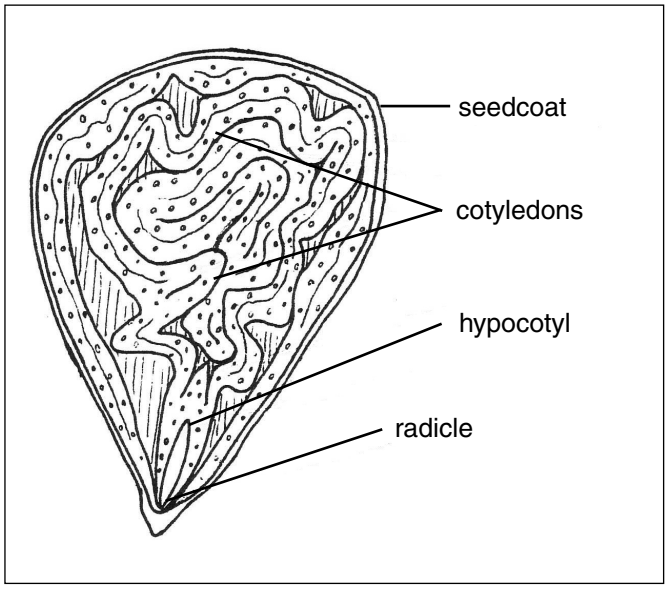
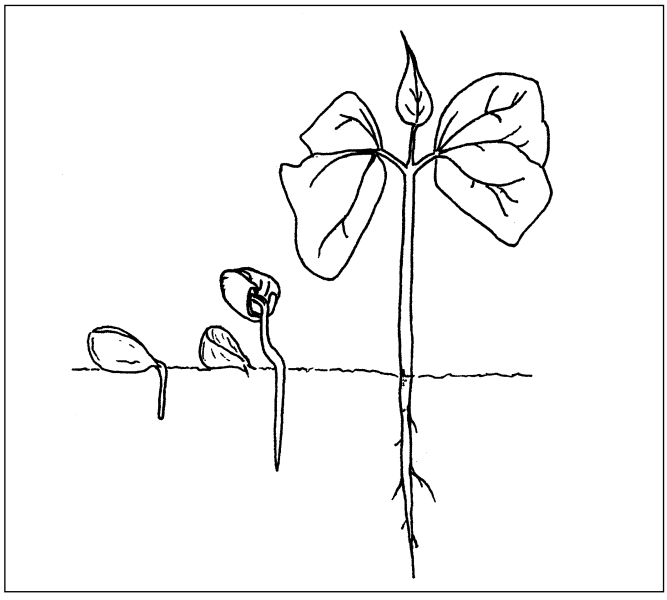


Figure 3—*Thespesia grandiflora*, maga: germination and seedling development.



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Cupressaceae—Cypress family

Thuja L.

arborvitae

Gary J. Brand and C. S. Schopmeyer

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Growth habit and occurrence. The arborvitae genus—*Thuja*—includes 2 species native to North America and 3 or 4 (depending on the authority consulted) Asian species (table 1). All individuals in the genus are aromatic, evergreen trees, but some species also have shrubby forms.

Mature northern white-cedars are medium-sized trees, usually 12 to 15 m tall and 60 to 90 cm in dbh (Harlow and others 1991). The rooting habit of mature trees is usually shallow and spreading. In addition to regeneration from seeds, vegetative reproduction by layering is common where there is sufficient moisture (Johnston 1990). Northern white-cedar grows on a wide variety of organic and mineral soils but does not develop as well on extremely wet or extremely dry sites (Johnston 1990). However, most commercial stands of northern white-cedar are in swamps. Geographical range for the species extends from Nova Scotia to Maine and westward to Manitoba and Minnesota. Isolated stands occur in west-central Manitoba, northern Ontario, southern Wisconsin, northern Illinois, Ohio, Massachusetts, Connecticut, and the Appalachian Mountains as far south as Tennessee (Little 1971).

Western redcedar can grow into large trees, especially in stream bottoms, moist flats, and gentle, north-facing slopes at low elevations (Curran and Dunsworth 1988; Schopmeyer 1974). It will grow to 45 to 60 m tall and 120 to 240 cm in dbh (Harlow and others 1991). Western redcedar develops extensive roots with a dense network of fine roots (Minore 1990). As in northern white-cedar, vegetative reproduction in western redcedar is common and provides the dominant means of regeneration in some stands. Branch layering, rooting of fallen branches, and rooting of branches attached to fallen trees have all been reported (Minore 1990). Western redcedar grows on many different soils and at a wide range of elevations. Its native range includes the Pacific Coast from northern California to southeastern Alaska; the Cascade Mountains in Oregon and Washington; and the Rocky Mountains in southeastern British Columbia, northeastern Washington, northern Idaho, and western Montana (Little 1971).

Table 1—*Thuja,* arborvitae: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***T. occidentalis* L.** *T. obtusa* Moench *T. odorata* Marshall	**northern white-cedar,** white-cedar, eastern arborvitae, swamp-cedar, arborvitae, eastern white-cedar	Nova Scotia to Maine & W to Minnesota & Manitoba; S in Illinois, Ohio, & New York; locally in Appalachian Mtns.
***T. plicata* Donn ex D. Don** *T. plicata* D. Don; *T. plicata* Donn *T. plicata* Donn ex D. Don in Lamb. *T. gigantea* Nutt. *T. menziesii* Dougl. ex Endl. *T. lobbii* Hort. ex Gord.	**western redcedar,** Pacific redcedar, giant-cedar, arborvitae, giant arborvitae, canoe-cedar, shinglewood	Pacific Coast region, from SE Alaska to N California, Cascade Mtns. in Washington & Oregon, Rocky Mtns in British Columbia, N Idaho, & W Montana
***T. standishii* (Gord.) Carr.** *T. japonica* Maxim. *Thujopsis standishii* Gord.	**Japanese thuja,** Japanese arborvitae	Japan
***T. koraiensis* Nakai** *T. kongoënsis* Nakai	**Korean thuja,** Korean arborvitae	Korea
***T. sutchuensis* Frachet**	**Sichuan thuja**	China

Sources: Cope (1986), Kartesz (1994a&b), Little (1979), Rushforth (1987), Vidakovic (1991).

The 3 Asian species listed (table 1) are only planted for ornamental purposes in the Untied States. Korean thuja reaches a height of 11 m, and Japanese thuja may grow as tall as 15 m (LHBH 1976).

Use. Both native species are valuable timber trees because their heartwood is light in weight and resists decay. The wood is used extensively for shingles, shakes, siding, and poles. Young northern white-cedar and the crowns of felled trees are browsed extensively by deer (Schopmeyer 1974). Many horticultural varieties of arborvitae with distinctive growth forms and foliage colors are propagated vegetatively for ornamental use (Cope 1986; Dirr 1990; Rushforth 1987; Vidakovic 1991). Northern white-cedar is commonly used as a root stock for horticultural grafts of *Thuja* spp. (LHBH 1976). Extractives from western redcedar inhibit the growth of numerous bacterial and fungal species (Minore 1983).

Geographic races and hybrids. Although no naturally occurring races or hybrids of northern white-cedar or western redcedar have been reported (Kartesz 1994a; Vidakovic 1991), a hybrid between western redcedar and Japanese thuja has been produced (Minore 1990; Vidakovic 1991).

The many horticultural varieties of northern white-cedar and western redcedar suggest that these 2 species have considerable genetic variability. However, variation in growth and survival has not been demonstrated by all provenance tests. Northern white-cedar provenance tests demonstrated some differences in height growth rates but not consistent differences in survival rates (Jeffers 1976; Jokela and Cyr 1979). Based on their provenance work, Bower and Dunsworth (1988) concluded that western redcedar has little genetic variability. In contrast, Sakai and Weiser reported differences in frost-tolerance for western redcedar (1973).

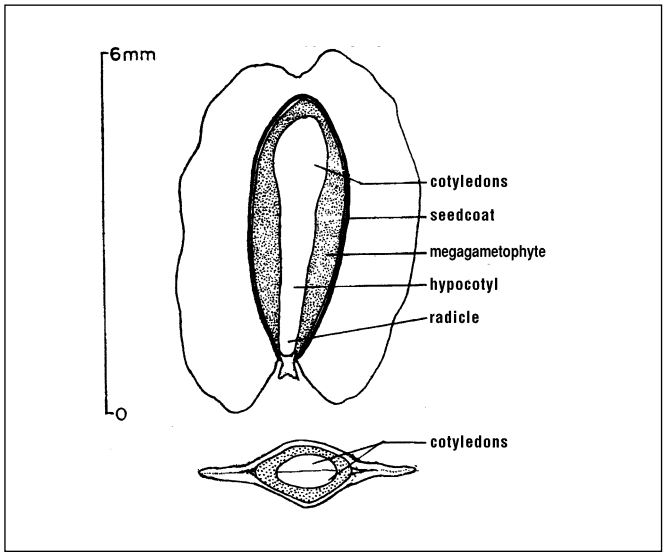
Flowering and fruiting. Male and female flowers are borne on the same tree but usually on separate twigs or branchlets (Schopmeyer 1974). Flower initiation begins in spring to early summer, development ceases in the fall, pollen is shed in late winter to early spring, and fertilized cones are mature by fall (Owens and Molder 1984). Female flowers form near the tips of vigorous lateral branches (figure 1) and are usually higher on the tree than the male flowers. The presence of low numbers of cone buds in the dormant season indicates that a poor cone crop will follow in the fall (Owens and Molder 1984). Cones of both native and Asian species are about 8 to 12 mm long (Little 1976; Schopmeyer 1974). Western redcedar cones have 5 to 6 pairs of scales. The 3 middle pairs are fertile and contain 2 to 3 seeds (Owens and Molder 1984). Cones of northern white-cedar have 4 to 5 pairs of scales with the middle 2 or 3 pairs fertile (Briand and others 1992). Each fertile scale contains 2 seeds. During the ripening period, cones change in color from green to yellow and finally to a pale cinnamon brown. Depending on location, cones are ripe in August or September (Schopmeyer 1974). Their light chestnut-brown seeds are 3 to 5 mm long and have lateral wings about as wide as the body (figures 2 and 3). Embryos of both species have 2 cotyledons.

Collection of cones. Trees as young as 10 years old have produced cones (Curtis 1946; Edwards and Leadem 1988), but heavy cone production usually occurs only on older trees. Cones may be picked by hand from standing or recently felled trees, or the cones maybe flailed or stripped onto a sheet of canvas, burlap, or plastic. Cones of western

Figure 1—*Thuja*, arborvitae: mature cones of *T. occidentalis*, northern white-cedar, with female cone buds on branch tips above the brown mature cones.

Figure 2—*Thuja*, arborvitae: mature cones and seeds of *T. occidentalis*, northern white-cedar.

Figure 3—*Thuja occidentalis*, northern white-cedar: longitudinal section **(top)**, and transverse section showing 2 cotyledons **(bottom)**.



redcedar have been harvested with aerial rakes attached to helicopters (Edwards 1986; Wallinger 1986). A good time for collection is when seeds have become firm and most of the cones have turned from yellow to brown. For northern white-cedar, the period between cone ripening and start of cone opening is only 7 to 10 days (Schopmeyer 1974). Cones of western redcedar also start to open soon after they ripen. Owens and Molder (1984) recommend collecting cones in late August to early September. Peak rate of seedfall from both species occurs about 4 to 6 weeks after the first cones have opened (Schopmeyer 1974). Mature trees of both species produce cones prolifically every 3 to 5 years, but all cones do not open at the same time. Seed release therefore progresses slowly. Substantial seed yields probably can be obtained from cones collected as late as 1 month after the first cones have opened.

Extraction, cleaning, and storage of seeds. Seeds can be extracted from cones by air-drying for 1 to 3 weeks (VanSickle 1994) or cones may also be spread out to sun-dry. Kiln-drying is more efficient for large quantities of cones. Cones of northern white-cedar have been opened by exposing them for 4 hours in an internal-fan-type kiln at a temperature of 54 °C and a relative humidity of 38% (Schopmeyer 1974). Kiln temperatures below 43 °C are preferred, however, to prevent damage to the seeds (Schopmeyer 1974). Western redcedar cones were opened in 24 to 36 hours at a temperature of 33 °C (Edwards 1986), 18 to 20 hours at 41 °C (Owens and Molder 1984), or 27 °C for 12 hours (Henchell 1994). Higher temperatures increase the probability that seeds will be damaged. After cones have opened, seeds are extracted in a mechanical cone shaker or tumbler and separated from the cone scales by fanning or gravity separation. Seeds should not be de-winged (Edwards and Leadem 1988; Gordon and others 1991).

The number of fully developed seeds in each cone can vary dramatically. As few as 2 to as many as 12 (average 7.7) fully developed seeds were counted in northern white-cedar cones (Briand and others 1992). For western redcedar, cones from natural stands contained an average of 2.6 filled seeds/cone, whereas cones from seed orchards contained an average of 6 fully developed seeds per cone (Colangeli and Owens 1990). One kilogram of cleaned northern white-cedar seeds contains an average of 763,000 seeds (346,000/lb) (Schopmeyer 1974). The average number of cleaned western redcedar seeds reported is 913,000/kg (414,000/lb) (Schopmeyer 1974). Empty seeds can be readily separated from full seeds in a seed aspirator or blower.

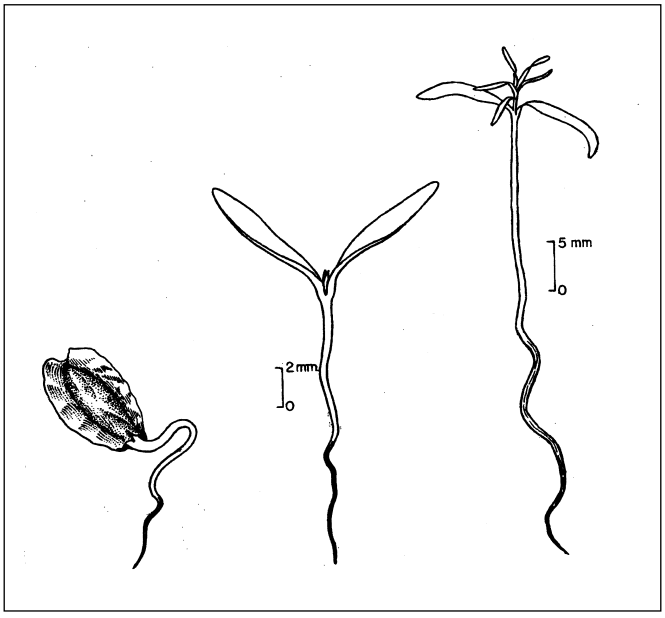
Arborvitae seeds are orthodox in storage behavior. Seeds should be stored in fiber containers with plastic or foil liners (Gordon and others 1991). Seeds stored at a moisture content of 5 to 10% in sealed containers at 0 to 5 °C should remain viable for up to 5 years (Gordon and others 1991). For longer periods, storage at –18 °C is recommended.

Pregermination treatments. The need for stratification to ensure that a high percentage of seeds germinate uniformly is not clear. Some authors state that stratification is not needed. Others recommend stratification for 30 to 60 days in moist medium at 1 to 5 °C (Henchell 1994; Schopmeyer 1974). Dirr and Heuser (1987) report that 2 weeks of stratification will improve germination of Japanese thuja. Germination of northern white-cedar and western redcedar seeds is tested by placing seeds on top of moist germination paper kept at 20 to 30 °C; no pretreatment is recommended. Germination is epigeal (figure 4). The first count of germinated seeds is made after 7 days and the last count after 21 days (ISTA 1993).

Nursery practice and seedling care. Northern white-cedar and western redcedar seedlings are not produced in large numbers but can be grown in both bareroot nurserybeds and in containers. Many ornamental varieties of arborvitae, both native and Asian, are propagated from cuttings or by layering (Dirr and Heuser 1987). Cultural practices vary by nursery.

The irregular shape and small size of western redcedar seeds make it difficult to sow the seeds mechanically. Coating seeds with fine-textured materials such as clay, sand, charcoal, or peat has been attempted to make the seeds more uniform in size and shape (Edwards and Leadem 1988). This process should be done just before sowing,

Figure 4—*Thuja occidentalis*, northern white-cedar: seedling development at 1, 5, and 25 days after germination.



because seed viability is reduced if seeds are stored after being coated (Edwards and Leadem 1988).

In bareroot nurseries, seedlings are grown as 1+1, 2+0, 2+1, and 3+0 stock. Fall-sowing is preferred for northern white-cedar and spring-sowing for western redcedar. Some nurseries soak seeds in water for 24 to 48 hours and then stratify them for 7 to 60 days at 2 °C before sowing. Because of better mycorrhizal colonization, planting western redcedar seeds in nurserybeds that have not been fumigated for 1 year seems beneficial (Henchell 1994). Average seedbed density for western redcedar is about 500 seedlings/m^2 (46/ft^2) but varies from 240 to 1000/m^2 (22 to 93/ft^2) (Edwards and Leadem 1988; Henchell 1994). The wider spacings may produce higher quality seedlings (van den Driessche 1984). Sowing depth varies from 0.3 to 1.0 cm ($^1/_8$ to $^3/_8$ in) (Schopmeyer 1974). In another approach used in Minnesota, VanSickle (1994) sowed northern white-cedar seeds at 0.15 cm ($^1/_{16}$ in) and covered them with a double layer of hydromulch. Western redcedar seeds have also been sown on the surface, pressed into the soil by the packing roller of a seed drill, and covered immediately with shade material (Henchell 1994). First-year northern white-cedar seedlings are grown both with half-shade (Jones 1994) and without shading (VanSickle 1994). Shading (50 to 70%) is recommended for first-year western redcedar seedlings. Soil moisture needs to be monitored closely because seeds and seedlings of western redcedar are sensitive to drying (Henchell 1994).

Container seedlings have become more common in the last decade and can be produced in 1 or 2 years. Various container sizes are used, depending on the desired size of the outplanted stock. Common container volumes used are 66 to 164 ml (4 to 10 in^3) (Olson 1994; Schaefer 1994). Seedlings of northern white-cedar grown from fall-planted seeds are ready for outplanting in May, unless the larger containers are used. Seedlings of western redcedar grown from spring-planted seeds are ready for outplanting in the fall or following spring. Seedlings in larger containers are grown in the greenhouse for 10 to 18 months before outplanting. Seeds sown in the containers are covered with a thin layer (about 0.3 cm, or $^1/_8$ in) of crushed granite (Olson 1994) or quartz (Schaefer 1994). Western redcedar seedlings grown in containers and chemically root pruned by painting the inside of the container with latex paint containing copper carbonate showed good height and volume growth when outplanted (Curran and Dunsworth 1988). In container-grown western redcedar, a mild nitrogen and moisture stress after the seedlings reach 8 to 10 cm (3 to 4 in) produces hardened stock with a balanced root to shoot ratio (Schaefer 1994). Seedlings grown for 1 year in containers and then transplanted to the nursery bed (plug+1 transplants) are well-balanced and have been successful when outplanted (Ramirez 1993).

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Tiliaceae—Linden family

Tilia L.

linden or basswood

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Growth habit, occurrence, and uses. The genus *Tilia* L.—linden or basswood—consists of about 40 species of large or medium-sized, deciduous trees that are indigenous to the temperate Northern Hemisphere. *Tilia* is the only genus of its family, Tiliaceae. Species reach their maximum size in loamy, moist, fertile soil, but they tolerate poor soils, pollution, windy conditions, and transplanting and can be grown in full sun or partial shade (Dirr 1990; Haller 1995; Kunneman and Albers 1991). Lindens possess a well-developed root system and are long lived, with some species living between 500 to 1,000 years (Haller 1995; Kunneman and Albers 1991). Table 1 lists species native to North America as well as widely grown non-native species.

Few shade trees vary so greatly in shape, leaf size, and growth rate as do the lindens (Flemer 1980). They generally possess a uniform globular crown and smooth, silver-gray bark that becomes fissured on old trees (table 2). The winter form is striking, with stiff, erect branches growing upward at 30° angles from a thick trunk (Burgess 1991). Considerable differences in growth habit exist among cultivars of littleleaf linden, ranging from the very dense, formal pyramidal habit of 'Greenspire', the dense upright oval shape of 'Chancellor', to the more open, informal oval habit of 'Fairview' (Pellett and others 1988).

There is much disagreement among taxonomists as to correct identification of species, and there are numerous names in the literature that are no longer recognized by many botanists. For example, *T. monticola* Sarg. and *T. michauxii* (Nutt.) Sarg. are sometimes seen in the literature or listed as specimens in botanical gardens, but they are now considered to be varieties of white basswood—*T. americana* var. *heterophylla* (Venten.) Loud.—recognized previously as *T. heterophylla* Venten. (Ayers 1993; Rehder 1990).

Table 1—*Tilia,* linden: nomenclature, and occurrences

Scientific name & synonym(s)	Common name(s)	Occurrence
***T. americana* L.** *T. glabra* Venten.	**American linden,** basswood, whitewood, American lime, bee-tree	New Brunswick S to Virginia & Texas
***T. americana* var. *caroliniana* (P. Mill.) Castigl.**	**Carolina basswood**	SE US
***T. americana* var. *heterophylla* (Venten.) Loud.**	**white basswood**	West Virginia to Florida, W to Indiana & Alabama
***T. cordata* P. Mill.** *T. parviflora* J. F. Ehrh. ex Hoffm.)	**littleleaf linden,** small-leaved lime, European linden	Europe
***T. euchlora* K. Koch** *T. cordata* x *T. dasystyla*	**Crimean linden,** Caucasian lime	SE Europe & SW Asia
***T. europaea* L.** *T. cordata* x *T. platyphyllos* *T. intermedia* DC. *T. vulgaris* Hayne	**European linden,** common linden, lime	Europe
***T. mexicana* Schldl.**	**Mexican basswood**	Mexico
***T. petiolaris* DC.**	**pendent silver linden,** pendent white lime, weeping lime	SE Europe & W Asia
***T. platyphyllos* Scop.** *T. europaea* var. *grandiflora* Hort.	**bigleaf linden,** large-leaved lime, largeleaf linden	Europe to SW Asia
***T. tomentosa* Moench** *T. argentea* DC.	**silver linden,** European white linden	SW Europe & Asia

Sources: Dirr (1990), LHBH (1976), Plotnik (2000), Rehder (1990), RHS (1994).

Table 2—*Tilia,* linden: growth habit and general comments

Species	Growth habit & maximum height	General comments
T. americana	Tree to 40 m with numerous, slender, low-hung spreading branches; pyramidal when young, crown somewhat rounded at maturity	Flowers pale yellow in summer; bee plant; wood used for making expensive furniture & excelsior, inner bark used for fabric
T. a. var. *caroliniana*	Tree to 20 m; close to habit of *T. americana*	—
T. a. var. *heterophylla*	Tree to 30 m; crown conical	—
T. cordata	Tree to 30 m; pyramidal when young; upright-oval to pyramidal-rounded & densely branched in old age; crown outspread	Widely planted as a street tree; pollution-tolerant; excellent shade tree
T. euchlora	Tree to 20 m	Similar to *T. cordata*
T. europaea	Tree to 37 m	—
T. mexicana	Tree to 20 m	—
T. petiolaris	Tree to 23 m	Sometimes considered as a pendulous selection of *T. tomentosa*
T. platyphyllos	Tree to 40 m; crown conical to broadly conical	Not widely planted in the US
T. tomentosa	Tree to 27 m; pyramidal when young; upright-oval to pyramidal-oval in later years; crown dense	Can be grown effectively as a multi-stemmed specimen to highlight light gray, smooth bark; good street tree, tolerating heat & drought better than other lindens

Sources: Dirr (1990), LHBH (1976), Plotnik (2000), Rehder (1990), RHS (1994).

Lindens are generally not suitable for lumber because the wood is soft and rots easily. However, the soft, straight-grained and even-textured wood is ideal for woodcarving and is utilized to make musical instruments, piano keys, Venetian blinds, and veneer and can serve as a source of fiber (Haller 1995; Kunneman and Albers 1991). The wood does not produce splinters, thus making it ideal for tool handles. The inner bark (or "bast") consists of long, tough fibers that once were used in the production of cordage, mats, and clothing. The common names for the species—basswood, linden, and lime—are derived from this characteristic: *bast* gives us the name bastwood or basswood; *linden* and *lime* are thought to be derived from the Latin word for linen (Haller 1995). In addition, flowers of linden are quite fragrant and produce large quantities of nectar that is very attractive to bees. The flowers of European, bigleaf, and littleleaf lindens are brewed for tea (Bremness 1994). The nectar of some species is so overpowering that bees can be found inebriated on the ground beneath the tree (Haller 1995). The light-colored honey produced is world famous.

Lindens are used primarily as ornamental shade and street trees (table 2), more so in Europe than in the United States. For example, Berlin's most famous boulevard is named *"Unter den Linden"*. They are well-adapted to a broad range of soil and climatic conditions and are relatively free of major disease problems that may threaten the survival or landscape value of established trees (Pellett and others 1988). The European lindens—littleleaf, European, bigleaf, and silver lindens—have greater importance in landscape plantings in the United States because they are more tolerant and ornamental than American species such as American linden (Dirr 1990; Heit 1977). In addition, American linden becomes too large for the average home property and is better left in the forest (Dirr 1990). However, silver linden possesses a shallow root system and its canopy casts dense shade, making it unsuitable for underplanting (Burgess 1991).

Geographic races and hybrids. As mentioned previously, there is much disagreement among taxonomists as to correct identification of species. For example, there is debate whether white basswood is a southern race of American linden or a separate species. Also, hybridization between species occurs naturally and has given rise to variability among seedlings (Kunneman and Albers 1991). Of the more common hybrids, Crimean and European lindens are not considered superior landscape trees relative to littleleaf linden (Dirr 1990).

Flowering and fruiting. Perfect, fragrant, yellowish or whitish flowers that bloom in June or July are borne in short, pendulous cymes with stalks attached to a large thin-textured oblong bract. Trees and clonal groups of trees flower almost simultaneously over the exposed parts of their crowns. In each inflorescence, the terminal flower of the dichasium opens first and in warm weather is followed at intervals of a day by flowers on the branches of successive orders (Pigott and Huntley 1981). Trees usually flower within 5 to 15 years when grown from seed. Shortness of blooming period (several days to 2 weeks, depending on

weather conditions) and lack of consistent flowering from year to year are problems for beekeepers harvesting honey (Ayers 1993). In particular, the American lindens have a reputation for not flowering every year. Some of the introduced species are more consistent (Ayers 1993).

Following pollination, temperatures must be > 15 °C for growth of the pollen tube and for fertilization to occur so that fruits will be produced (Pigott and Huntley 1981). Fruits are grayish, nut-like, round to egg-shaped capsules that mature in autumn but may persist on the tree into the winter. Each consists of a woody pericarp enclosing a single seed (but sometimes 2 to 4 seeds) (figures 1 and 2) (Brinkman 1974; Pigott and Huntley 1981). The pericarp consists of an outer layer of loose fibers forming a mat (or tomentum) and a broad region of thick-walled lignified fibers that are responsible for its hard, tough, woody character (Spaeth 1934). Fruits of American linden are tough and leathery, whereas those of littleleaf linden tend to be thinner and rather brittle (Heit 1967). Seeds possess a crustaceous seedcoat; a fleshy, yellowish endosperm; and a well-developed embryo (figures 2 and 3). Natural dispersion is primarily by wind and animals (Brinkman 1974).

Collection of fruits, seed extraction and cleaning. The ideal time to harvest fruits is early fall, when seed moisture content is approximately 16% (Vanstone 1982). During fruit ripening, moisture is lost from the seeds at a rate of 1 to 2% per day, so that seeds must be monitored closely. Pericarp color is a reliable indicator of moisture content in relation to germination. Fruits should be picked when the pericarp is turning from green to grayish-brown and before the pericarp becomes tough and leathery. Otherwise, seeds will require greater efforts during extraction and scarification. There is generally uniform ripening on any individual tree, but the exact date of ripening may vary by several weeks among trees (Vanstone 1978). Because fruits of lin-

Figure 1—*Tilia*, linden: fruits of *T. americana*, American linden (**top**) and *T. cordata*, littleleaf linden (**bottom**).

Figure 2—*Tilia cordata*, littleleaf linden: seed.

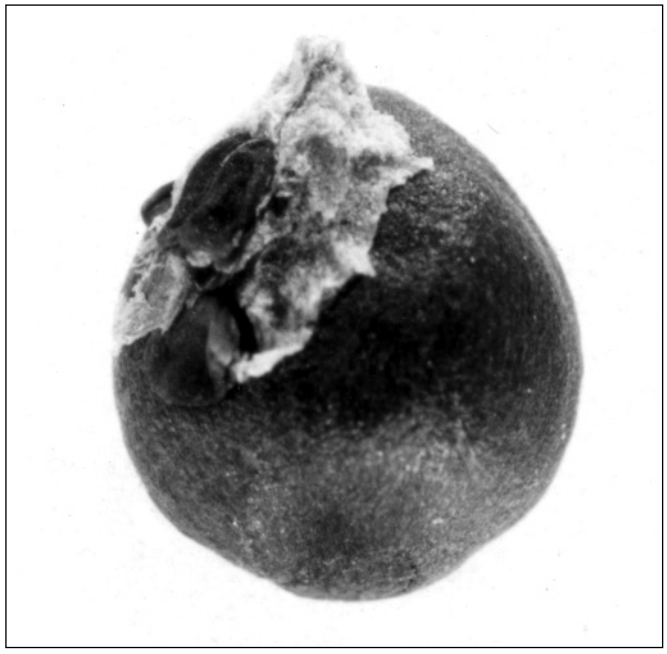
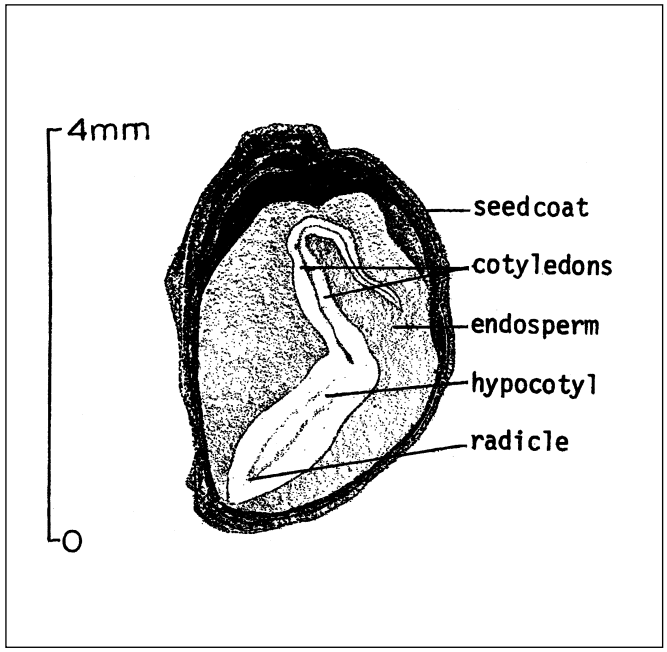


Figure 3—*Tilia americana*, American linden: longitudinal section of a seed.



den persist on the tree, fruit collection is often postponed until after maturity. After a heavy frost, fruits can be shaken from branches onto a canvas tarp and spread out to dry (Brinkman 1974).

Once fruits have been collected, bracts can be removed by flailing or passing the fruits through a de-winging machine. The hard pericarp must then be removed. Fruits of littleleaf and bigleaf lindens have prominent sutures that are helpful in the extraction process by serving as a breaking point for both mechanical and rubbing techniques (Heit 1977). Fruits of European and silver lindens can be handled similarly, and a combination of sieving, screening, and blowing can readily remove debris (Heit 1977). However, fruits of American linden have a hard, tough, leathery pericarp and must be run through a coffee grinder or a similar device or treated with acid to accomplish its removal (Heit 1977). Mechanical extraction of seeds is often difficult. Any crushing force sufficient to fracture the tough pericarp is likely to exert a shattering pressure on the brittle seedcoat (Spaeth 1934). Seed yields and size vary by species (table 3)

Storage. Seeds of the lindens are orthodox in storage behavior and should be stored in sealed containers at a moisture content of 8 to 12%. Seeds of American linden have retained their viability for 2 years when stored under dry conditions at room temperature and for 5 to 6 years when stored at 1 to 4 °C (Heit 1977).

Pregermination treatments. In addition to their tough pericarps, seeds of linden exhibit double dormancy and thus require both scarification and stratification (moist-prechilling) because of their impermeable seedcoat and dormant embryo, respectively. For seeds of littleleaf linden, Heit (1977) recommended a sulfuric acid treatment of 10 to 50 minutes at a temperature ranging from 23 to 27 °C. Colder temperatures required a longer duration of acid treatment. Because all species of linden and individual seedlots within the same species are variable in their percentage and degree of hardseededness, it is advisable to soak some seeds in water for 1 or 2 days to determine the degree of hardseededness before treating with acid. Ten to 20 minutes of acid treatment may be ideal for some seedlots, but 20 to 50 minutes would produce the best results for others. The degree of hardseededness depends on factors such as seed source, time of collection, and storage conditions, including temperature and relative humidity (Heit 1967, 1977). Other scarification treatments include mechanical scarification and hot water treatments, but neither are as good as acid scarification (Heit 1977). Freezing to –80 and –185 °C had little effect on the permeability of the seedcoat (Spaeth 1934). Surface sterilization with sodium hypochlorite (NaOCl) and ethanol proved to control seed pathogens but lowered germination percentages of littleleaf, bigleaf, and silver lindens (Magherini and Nin 1993).

In addition to scarification, stratification is essential for maximum germination and seedling production. Following scarification, seeds must be either fall-sown immediately or stratified at 1 to 3 °C for about 3 months before spring-sowing. Vanstone (1978) recommends stratification in a 1:1 mixture (by volume) of peat and sand containing 30% moisture by weight. Enzyme activity and levels of soluble proteins and amino acids in the seeds increase gradually during stratification at 4 °C (Pitel and others 1989). Nontreated seeds have been known to lie in the ground for over 5 years without germinating while still maintaining viability (Heit 1967). Bigleaf linden requires 3 to 5 months of warm stratification followed by 3 months of cold, and even this treatment does not guarantee high germination (Dirr and Heuser 1987). Flemer (1980) recommends burying seeds in a wooden box filled with damp sand and leaving the box outdoors during the winter. Boxes are then dug up the following fall and the seeds are sown. Seed treatments that consistently result in

Table 3—*Tilia,* linden: seed yield data

Species	Seed wt/fruit wt		Cleaned seeds/weight (x1,000)				Samples
			Range		Average		
	kg/45.4 kg	lb/100 lb	/kg	/lb	/kg	/lb	
T. americana	—	—	—	—	6.6	3	2
	34.1	75	6.6–17.6	3.0–8.0	11	5	15+
	—	—	20–32.1	9.1–14.6	—	—	—
T. cordata	36.3	80	24.9–38.3	11.3–17.4	30.4	13.8	57+
	—	—	48.8–65.1	22.2–29.6	—	—	—
T. x europaea	—	—	23.3–29.7	10.6–13.5	—	—	—
T. platyphyllos	—	—	25.1–30.6	11.4–13.9	—	—	—
T. tomentosa	—	—	20.0–25.1	9.1–11.4	—	—	—

Sources: Brinkman (1974), Heit (1977).

good germination for all species and seedlots have not been developed. Much variability exists among species and seedlots in regards to permeability of the pericarp and seedcoat, as well as stratification requirements.

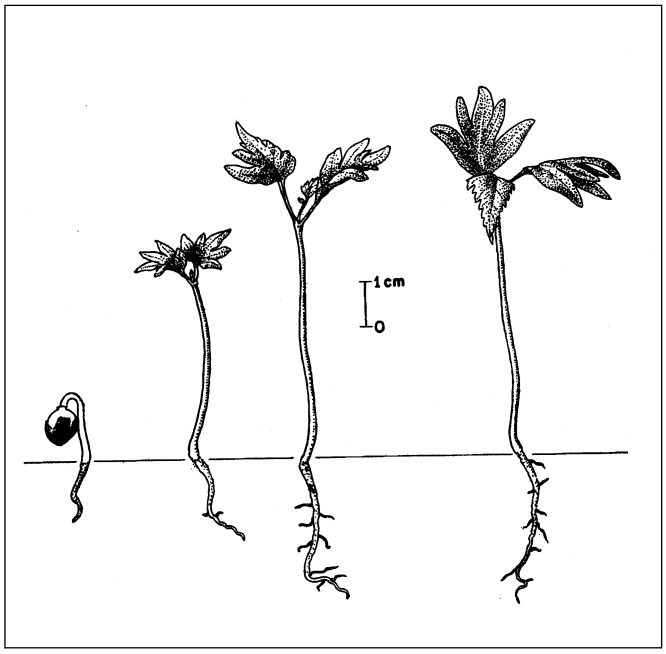
In Europe, dormancy in littleleaf linden is overcome by the use of warm incubation or acid scarification, followed by stratification (Suszka and others 1996). Fully imbibed seeds are first stored for 4 months at 20 to 25 °C (or scarified with concentrated sulfuric acid for 12 minutes), then stratified at 3 °C for 14 to 18 weeks. Stratification should be stopped when the first seeds start to germinate.This complete process may take 8 or 9 months.

Germination tests. Germination is epigeal (figure 4). Optimum germination occurs at temperatures above 20 °C (68 °F), but seeds will germinate at temperatures as low as 2 °C once stratification requirements have been satisfied (Spaeth 1934). Thus, seeds should be checked periodically for radicle emergence during stratification. Light is not required for germination (Heit 1967). The use of any stratification procedure requires far too much time to be used in routine germination testing, however, so rapid estimates of viability are recommended for this purpose. This can be done with tetrazolium staining, indigo-carmine staining, or excised embryo tests (ISTA 1996; Suszka and others 1996). However, these tests require removal of the pericarp and the seedcoat without damaging the embryo. Tetrazolium staining is the most common test. It requires soaking seeds in water for 18 to 24 hours, removing all or a large part of the seedcoat, and soaking the seeds in a 1% tetrazolium solution for 24 to 48 hours at 30 °C.

Pitel and Wang (1988) found that both the rate and percentage of germination of seeds of American linden were increased by treating scarified seeds with a solution of kinetin (1 mg/liter) and gibberellic acid (GA_3, 500 mg/liter. Over 90% germination was obtained after 60 to 80 days at 4 °C. However, GA did not improve germination percentage of seedlots of littleleaf, bigleaf, and silver linden (Magherini and Nin 1993). The conflicting results are likely due to the level of gibberellin present. Natural levels of GA exist in dormant, nonstratified seeds and a sudden increase in the quantity of gibberellin is observed from the sixth week of stratification (Nagy 1980). It is likely that a specific quantity, rather than just the presence of free gibberellins, is required to break dormancy and stimulate germination.

Traditionally, for an accurate germination test, the outer pericarp must be removed and the hard seeds must undergo scarification and stratification. However, excised embryos of American linden that were separated from the seedcoat and endosperm were able to germinate and grow when placed on an agar medium without any pretreatment (Vanstone 1982). If any of the endosperm was retained around the embryo, no growth took place, indicating an apparent lack of embryo dormancy, for the naked embryo will grow when it is separated from other parts of the seed. Some factor that restricts germination seems to be present in the endosperm and must be overcome before an intact seed can germinate. That factor would normally be overcome by stratification. The same result was obtained with bigleaf linden, for germination was induced by removing the endosperm tissue around the radicle (Nagy and Keri 1984).

Figure 4—*Tilia americana*, American linden: seedling development at 1 day and 3, 16, and 19 days after germination.



Nursery practice and seedling care. Most trees in culture are of seedling origin (Kunneman and Albers 1991). However, some are propagated by grafting, chip budding, layering, rooting winter hardwood or leafy softwood cuttings, or tissue culture (Flemer 1980; Howard 1995; Kunneman and Albers 1991). For grafting, seedling rootstocks are used, preferably of the same species as the scion, as incompatibility is a common phenomenon (Kunneman and Albers 1991). Named cultivars are grafted commonly in spring or budded in summer (LHBH 1976). Plants of littleleaf linden have been propagated by somatic embryogenesis initiated from immature zygotic embryos and then established successfully in soil (Chalupa 1990). Except for hybrids such as Crimean and European linden, all can be seed-propagated (Dirr and Heuser 1987).

Production by seed at a specified time is often relatively difficult (Dirr and Heuser 1987; Heit 1967). As described

previously, seeds show delayed germination because of a tough pericarp, an impermeable seedcoat, and a dormant embryo. Seeds may remain in the ground for several years and never produce a good stand of seedlings. The degree of seedcoat hardness and embryo dormancy varies within and among seedlots for most species (Hartmann and others 2002). Also, germination is irregular, and unknown seed sources and hybridization between species have given rise to variability among seedlings (Kunneman and Albers 1991). In addition, Heit (1977) found that several lots of seeds of bigleaf and silver lindens from Europe contained high percentages of empty seeds, from 20 to 72% (Heit 1977). This condition should always be checked before sowing or treating seeds.

Mature fall-collected seeds may be sown in spring following scarification and stratification (see Pregermination treatments). An alternate method is to collect seeds early, before the pericarp turns brown and sow in the fall. Early seed collections may result in seeds that have soft seedcoats that do not require scarification (Heit 1977). However, some propagators have harvested early and obtained inconsistent results, with the seeds sometimes decaying. Late-harvested seeds may also be germinated the first season but require more treatment than seeds harvested at the ideal stage of maturity (Vanstone 1978).

Seeds are sown in shallow rows—6 to 13 mm ($^1/_4$ to $^1/_2$ in)—in beds and covered with sand to aid in seedling emergence. The emerging seedlings are very delicate and subject to sun scald, so lathe screens or shade netting over the seedbeds greatly improves seedling stands (Flemer 1980). Fall-sown seedbeds should be mulched, protected from rodent damage, and kept moist until germination begins in the spring (Vanstone 1978). Good stands of littleleaf, bigleaf, and silver lindens are normal, but seeds of American linden exhibit great variation in germination from year to year (Flemer 1980). When poor stands result, seedlings should be removed carefully so as not to disturb the bed, for additional germination often occurs the second year after planting. Seedlings are usually outplanted as 1+0 or 2+0 stock.

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Meliaceae—Mahogany family

Toona ciliata Roemer

Australian toon

Gerald A. Walters and John K. Francis

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Synonyms. *Toona australis* Harms, *Cedrela toona* var. *australis* (Roxb.) C. DC.

Other common names. toona, Australian redcedar, Burma-cedar.

Growth habit, occurrence, and use. Distributed in a natural range from India to Queensland, Australia (Francis 1951; Webb and others 1984), Australian toon—*Toona ciliata* Roemer—is the only species of *Toona* important in Hawaii and Puerto Rico. It was introduced into Hawaii from coastal rain forest areas of Australia in 1914 (Carlson and Bryan 1959; Streets 1962). Several small plantings of toon of an Indian provenance have reached sawlog size in Puerto Rico. Australian toon is a deciduous timber tree that attains heights of 30 to 43 m. It keeps its leaves longer on moist sites than on drier sites, and sometimes trees are said to be evergreen. Toon has been widely planted because the wood is valued for cabinets, furniture, decorative veneer, boats, and musical instruments (Chudnoff 1984). The red, often highly figured, wood is durable and seasons rapidly (Carlson and Bryan 1959; Francis 1951).

Flowering and fruiting. In Hawaii, Australian toon flowers from April to June. The flowers are bisexual. The 5-valved, teardrop-shaped capsules are 18 to 25 mm long (figures 1 and 2), in pendulous clusters, ripening during July to September. Seeds are disbursed during August to October (Walters 1974). Trees begin to produce seeds as early as 5 years of age, but generally do not do so with regularity or in quantity until they are 10 to 15 years old (Carlson and Bryan 1959).

Collection, extraction, and storage. The capsule turns from green to brown or reddish brown when ripe. When the first capsule in a cluster dehisces, the whole cluster should be picked. Clipping fruited branches using a pruning pole or cherry picker is recommended for seed orchards or open-grown trees. Climbing or felling will be necessary to collect capsules from mature trees in stands. The harvested fruit should be spread on trays in the sun to dry. The light

Figure 1—*Toona ciliata*, Australian toon: seed.

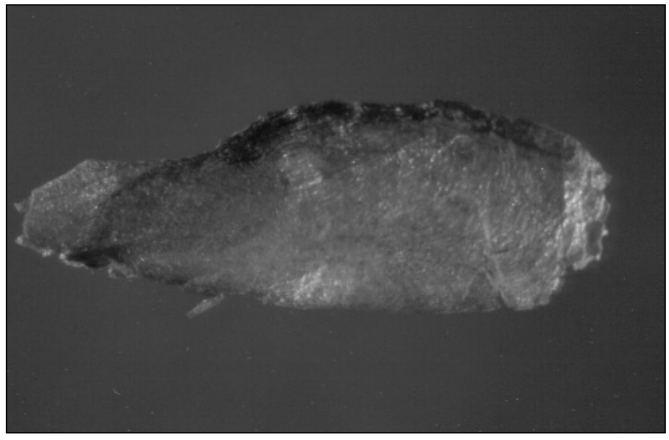
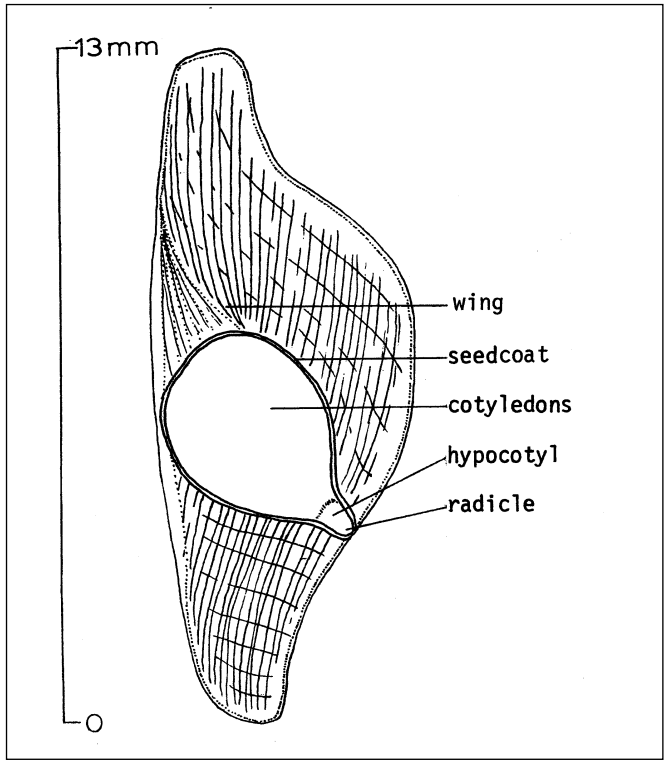


Figure 2—*Toona ciliata*, Australian toon: longitudinal section through a seed with wing attached.



brown, membranous winged seeds (figures 1 and 2) fall from the capsule as the fruit dehisces. Agitation aids the separation of seeds from the fruits. Various seed cleaners can be used to separate the seeds from chaff. Ten samples showed from 293,000 to 375,000 cleaned seeds/kg (133,000 to 174,000/lb) (Walters 1974). Seed purity was about 84% (Walters 1974). Toon seeds can be stored dry in sealed polyethylene bags at about 1 °C (Walters 1974). Even with this apparent orthodox storage behavior, however, storage life is reported to be only from 6 to 12 months (Webb and others 1984).

Germination. Australian toon seeds germinate without special treatment, but stratification for 30 days at 3 °C in plastic bags greatly increases the speed of germination. A water soak also may speed up germination (Walters 1974). Full germination of 90% of unstratified seedlots occurred in 2 weeks; full germination of 96% of stratified seedlots occurred in 1 week (Walters 1974). Another source (Webb and others 1984) cites 40 to 60% germination of fresh seeds. Germination is epigeal.

Nursery practice. Australian toon seeds can be sown in Hawaii and Puerto Rico during any month of the year, but best results in Hawaii are obtained from March to November sowings and in Puerto Rico from April and May sowings. Seeds for bareroot seedling production are broadcast into precut lines. The lines are about 12 mm deep and about 15 cm apart. Most of the seeds that fall away from the lines are put in place as the lines are covered with soil. The beds are made level to prevent washing. The soil is kept moist by frequent watering. No mulch or shade is used. Seedling density in the beds is about 160 to 270 seedlings/m^2 (15 to 25/ft^2). Seedlings are outplanted as 1+0 or $1^1/_2$+0 stock (Walters 1974). Seedlings are now more frequently grown containerized in plastic nursery bags. Seeds are germinated in germination trays or beds and transplanted to the containers after they have developed 2 or 3 leaves. Seedlings can also be planted as striplings or stumps (Webb and others 1984). Australian toon seedlings grow slowly at first and should be given shade for 2 months. Potted stock reaches plantable size in 18 to 24 months (Webb and others 1984). Attacks of the shootborer *Hypsipyla grandella* (Zeller), which usually prohibits planting *Cedrela* species in the Neotropics, are absent or unimportant in toon plantations (Viga 1976; Whitmore and Medina Gaud 1974).

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Taxaceae—Yew family

Torreya Arn.

torreya

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Growth habit, occurrence, and uses. The genus *Torreya* includes 7 species of conifer trees found in North America and eastern Asia (Little 1979; Price 1990). These species of limited distribution represent a genus that in earlier geologic times was widespread in the Northern Hemisphere—Europe, Greenland, Alaska, British Columbia, Oregon, Colorado, Virginia, and North Carolina (Abrams 1955; Boeshore and Gray 1936; Florin 1963; Schwartz and Hermann 1993a). Two species are native in the United States: Florida torreya is endemic to a small area in Florida and Georgia, and California torreya to central California (table 1). Little genetic variability has been found among populations of Florida torreya in contrast to those of California torreya (Schwartz 1993). Although growing in markedly different climates, the 2 species responded similarly in water stress tests (Schwartz and others 1995).

California torreya is a slow-growing, medium-sized tree found along streams and in canyon bottoms and other moist locations (Griffin and Critchfield 1976; Storer and Usinger 1963; Sudworth 1908). In its shrub form, it is found on serpentine soils and in chaparral. In elevation, California torreya ranges from coastal lowlands to almost 2,130 m in the southern Sierra Nevada. Under very favorable conditions, trees may grow to 23 m or more in height and 60 to 90 cm in diameter (Sudworth 1908). The tallest tree now on record is 29.3 m tall and 638 cm in circumference at 137 cm above ground (AFA 2000).

Florida torreya, also a slow-growing tree, is an endangered species found only at low elevations on ravine slopes 12 to 45 m above constant running streams on the east bank of the Apalachicola River and tributaries in Florida and Georgia and in a colony on low flat land that is 10 km west of the river (Kurz 1938; Nicholson 1990; Schwartz and Hermann 1993a&b). Florida torreya is commonly associated with seepage locations on soils ranging from coarse or fine sand to clay with limestone pebbles (Kurz 1938; USFWS 1986). In their native habitat, mature trees have reached 15 to 20 m in height and 30 to 60 cm in diameter (Harrar and Harrar 1962; Nicholson 1990; Schwartz and others 1995). However, due to severe population decline since the 1950s (the primary cause of this decline is unknown), the 1,500 or fewer immature survivors are generally less than 2 m tall (Bronaugh 1996; Schwartz and Herman 1999; Schwartz and others 1995). The tallest existing trees are found in several plantings outside of the species' endemic habitat; the largest, in North Carolina, measures 13.7 m tall and 277 cm in circumference (AFA 2000).

Because of their low availability, uses of both species of torreya are limited. Their wood is aromatic, rot-resistant, fine-grained, and excellent for cabinet-making (Burke 1975;

Table 1—*Torreya,* torreya: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***T. californica* Torr.** *T. myristica* Hook. *Tumion californicum* (Torr.) Greene	**California torreya,** California-nutmeg, stinking-yew, stinking-cedar	Central California—scattered in the Coast Ranges and on western slopes of the Cascades & Sierra Nevada
***T. taxifolia* Arn.** *Tumion taxifolium* (Arn.) Greene	**Florida torreya,** Florida-nutmeg, stinking-cedar	E bank of Apalachicola River & tributaries from Decatur Co., Georgia, to Liberty Co., Florida, & an outlying population in Jackson Co., Florida

Sources: Griffin and Critchfield (1976), Kurz (1938), Little (1979), Stalter (1990), Sudworth (1908).

Peattie 1953). Both species were used locally for such purposes as shingles, fence posts, and firewood. They grow satisfactorily outside of their native range and have received moderate use as ornamentals (Burke 1975; Sargent 1875; Wilson 1938). Fruits of California torreya were collected for food by native Californians, and the characteristics of its oil compare favorably with those of pine-nut oil for cooking purposes (Burke 1975). Squirrels have been observed eating fruits and seeds of Florida torreya and antler-rubbing scars provide evidence of use by deer (Bronaugh 1996; Nicholson 1990; Schwartz and Hermann 1993a).

Flowering and fruiting. Torreyas are dioecious. The male flowers are small, budlike, and clustered on the under sides of twigs in axils of leaves produced the previous year (Abrams 1955; Jepson 1925; Sargent 1933; Sudworth 1908). The female flowers are less numerous and occur on the lower sides of the current year's twigs. After fertilization, they develop singly into sessile, thin-fleshed arils that mature during the second season as green to purplish drupes 25 to 44 mm long (figure 1). When mature, the leathery cover eventually releases a 25- to 30-mm yellow-brown seed (Munz and Keck 1959) (figure 2). The thick woody inner seedcoat is irregularly folded into the female gametophyte, and the embryo is minute (figure 3).

Both species flower in March and April, with some flowers of Florida torreya appearing as early as January and some of California torreya extending into May (Rehder 1940; Sargent 1933; Stalter 1990; Weidner 1996). Under favorable growing conditions, Florida torreya produces male and female flowers about age 20 (Stalter 1990); in greenhouse conditions, 5-year-old sprouts produced pollen (Schwartz 1996).

Figure 1—*Torreya taxifolia*, Florida torreya: the fruit is sessile and drupe-like.

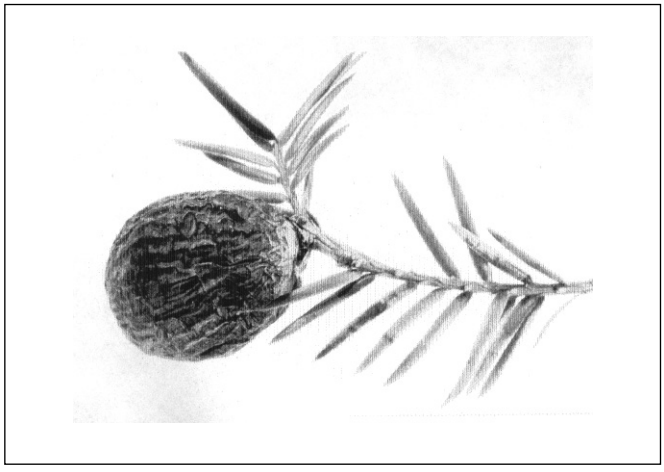


Figure 2—*Torreya*, torreya: large seeds of *T. californica*, California torreya (**left**) and *T. taxifolia*, Florida torreya (**right**).

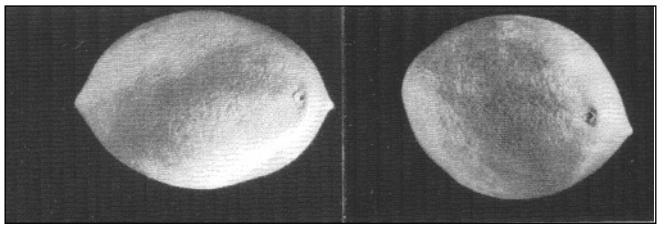
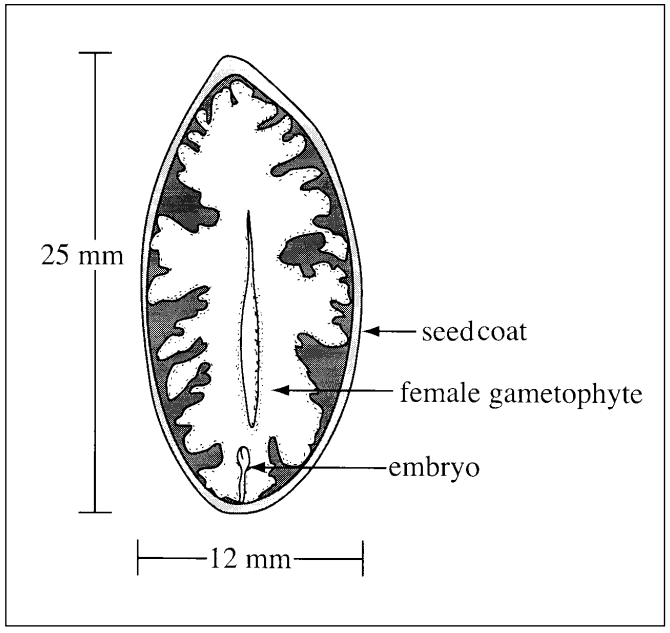


Figure 3—*Torreya californica*, California torreya: longitudinal section through a seed showing the folds of the inner seedcoat extending into the endosperm.



Information on the fruit production characteristics of both torreya species is sparse and inadequate. Fruits mature from August till November (Mirov and Kraebel 1939; Rehder 1940; Stalter 1990). At the Alfred B. Maclay Gardens in Tallahassee, Florida, fruit production from 8 trees was low and varied by tree and year. No fruits were produced in 4 years, and more than 100 fruits were available in 1985, 1986, 1987, and 1989 (Weidner 1996).

Collection, extraction and storage. Collection of Florida torreya fruits from the endemic population is not possible now because there are only scattered sexually mature male trees and no mature females (Bronaugh 1996; Schwartz and Hermann 1993a; Schwartz 1996). Trees in cultivation include less than 2 dozen reproductive females (Bronaugh 1996), so extraordinary diligence is required to collect any seeds that are produced. Fruits have been picked slightly green to gather them before the squirrels do and

then held in open storage until the outer cover turned dark; then the pulp was softened in water and removed by rubbing fruits against hardware cloth (Weidner 1996).

Fruit production of California torreya is common and widespread enough to forestall concerns about shortage; several hundred pounds may be collected in single commercial collections (Callahan 1996). The fruits are generally picked from the trees but are sometimes collected after they have been shed. Seed extraction is about the same as for Florida torreya, with the softened pulp removed by water pressure and some hand rubbing (Callahan 1996). Care is needed to avoid damage to the relatively tender seedcoat. Seed quality of California torreya is generally good and can be improved sometimes by separating light seeds through flotation.

Storage experience is short-term and fragmentary because torreya seeds are generally used as available. Based on incidental observations, the seeds may be recalcitrant, as high moisture content appears necessary to maintain their viability. California torreya has been stored in moist vermiculite or sphagnum moss at 2 to 7 °C for up to 3 years (Callahan 1996). Some seeds of both species will germinate in lengthy cool or warm stratification (Callahan 1996; Weidner 1996).

Seeds of California torreya averaged 324/kg (147/lb), with a range of 243 to 421/kg (110 to 191/lb) in 3 samples (Roy 1974). Florida torreya had 496 seeds/kg (225/lb) in 1 sample at a moisture content of 8.6% (Roy 1974).

Pregermination treatments and germination tests. Standard germination test procedures have not been developed yet for torreya seeds. Both species require lengthy after-ripening and stratification, but efforts made to date have not identified methods for timely germination testing of fresh or stored seeds.

As available, fresh seeds of Florida torreya have been tested at Alfred B. Maclay State Gardens according to the 9 variations of methodology specified in the recovery plan for the species (USFWS 1986). Warm stratification in a half and half mixture of Canadian peat and coarse sand for 6 months in a greenhouse at 13 to 18 °C has produced the best results. Gentle cracking of the distal end of the seedcoat before warm stratification produced somewhat higher germination than a preliminary 20-minute soak in 10% chlorine bleach or stratification alone (table 2) (Weidner 1996).

Germination averaged lowest for sowings made directly into outdoor beds. The germination results indicate that seedcrop quality or other factors differed from year to year, and results were also not very consistent for the same pretreatment and germination sequence.

Procedures have been prescribed for determining viability of torreya seeds quickly by a tetrazolium (TZ) test on excised embryos (Moore 1985). Seed preparation involves puncturing the seedcoat, soaking the seeds in water for 18 hours, and then cutting them open to expose nutritive tissue and the distal end of the embryo. The prepared seeds are soaked in a 1% TZ solution for 24 to 48 hours, depending on temperature; nutritive tissue and embryo are then further exposed and evaluated. Viable seeds have a completely stained embryo and nutritive tissue.

Nursery practices. Torreya germination is hypogeal. Both California and Florida torreyas can be reproduced from seeds but quantities grown are so small and infrequent that nursery practices are underdeveloped.

The protocols specified in the recovery plan (USFWS 1986) and the germination resulting therefrom (table 2) are evidently the most recent, systematic, and successful attempts to produce Florida torreya seedlings for outplanting. Seedlings are slow growing and very susceptible to damping-off, so repeated fungicide drenches are necessary.

Seeds of California torreya sown untreated in the fall will germinate late the next summer or in the second spring. Germination can be obtained by April of the first season by sowing in the fall and keeping the seedbed at 7 to 10 °C (Callahan 1996). Seeds generally have high viability—90 to

Table 2—*Torreya,* torreya: germination of *T. taxifolia* seeds

Pre-germination treatment*	Germination by seed year			
	1985	1990	1993	Average
6 months of warm stratification	69	13	80	54.0
Bleach + 6 months of warm stratification	77	0	85	54.0
Cracking + 6 months of warm stratification	100	25	86	70.3
3 mon of warm, then 3 months of cold stratification	85	38	58	60.3
Bleach + 3 months of warm, then 3 months of cold stratification	77	25	44	48.7
Cracking + 3 months of warm, then 3 months of cold stratification	62	38	35	45.0

Source: Weidner (1996).

98% germination. In a test of seeds stratified for 3 months, 92% germinated in 232 days after sowing (Mirov and Kraebel 1939). Two growing seasons are required to produce seedlings 15 to 25 cm tall (Callahan 1996; Wilson 1996).

Both species sprout from stumps or root crowns and can be propagated vegetatively. Metcalf (1959) described sprouting of California torreya as vigorous—"like redwood." Stalter (1990), Godfrey (1988), and others indicated that the current endemic Florida torreya population probably originated largely from vegetative propagation, but Schwartz and Hermann (1993a) concluded that most originated from seeds.

The urgency of conserving Florida torreya has stimulated development of its reproduction by cuttings (Bailo and others 1998; Nicholson 1988, 1993). Up to 91% of cuttings collected in November from trees throughout the species' native range rooted in a mixture of pumice, peat, and perlite mixture. The cuttings were potted and grown for 2 years and then shipped to botanic gardens and research institutions. A database on living Florida torreya material is maintained by The Center for Plant Conservation, headquartered at the Missouri Botanical Garden, St. Louis, Missouri.

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Euphorbiaceae—Spurge family

Triadica sebiferum (L.) Small

tallowtree

Franklin T. Bonner

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Synonym. *Sapium sebifera* (L.) Roxb.

Other common name. Chinese tallowtree.

Growth habit, occurrence, and use. Tallowtree—*Triadica sebiferum* (L.) Small—is a small deciduous tree that attains heights of about 10 m at maturity. A native of China, the species has been widely planted in the coastal plain from South Carolina and Florida to Texas, Oklahoma, and Arkansas. The bright red fall foliage makes the tree a popular ornamental, and the seeds have some value as wildlife food. In Asia, oils are extracted from the seeds and waxes from the seedcoats for use in a wide variety of products, including diesel fuel additives, soaps, candles, and cloth dressings (Bringi 1988; Samson and others 1985; Singh and others 1993; Vines 1960). Tallowtree readily escapes from cultivation and is common along roadsides of the Gulf Coast, where many consider it a pest species.

Flowering and fruiting. Both pistillate and staminate flowers are borne on the same yellowish green spike in the spring. The fruit, ripening in October to November, is a rounded, 3-lobed capsule, 8 to 13 mm in diameter (Vines 1960). Its greenish color changes to a brownish purple at maturity (Bonner 1974). There are 1 to 3 white waxy seeds per capsule (figures 1 and 2). In India, this species bears fruit as early as the third year after planting, and mature trees can yield 20 to 25 kg (Singh and others 1993).

Collection, cleaning, and storage of seeds. The dry capsules can be collected from the trees by hand after dehiscence (fruit-splitting) has started. Seeds can be removed from the capsules by gentle flailing in burlap bags or by being run through macerators at slow speeds. On a sample of capsules from a tree in central Mississippi, the following data were obtained (Bonner 1974):

Capsules per volume	30,300/hl (10,700/bu)
Seeds per weight	6,100/kg (2,780/lb)
Moisture content of seeds (% of fresh weight)	6
Sound seeds (% of total seeds)	90

Figure 1—*Triadica sebiferum*, tallowtree: seed.

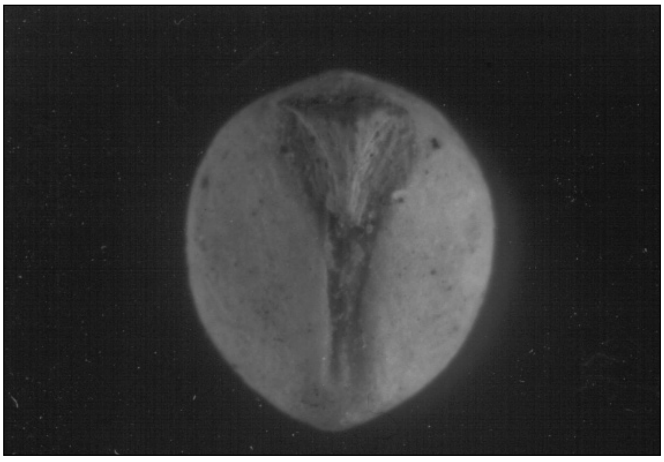
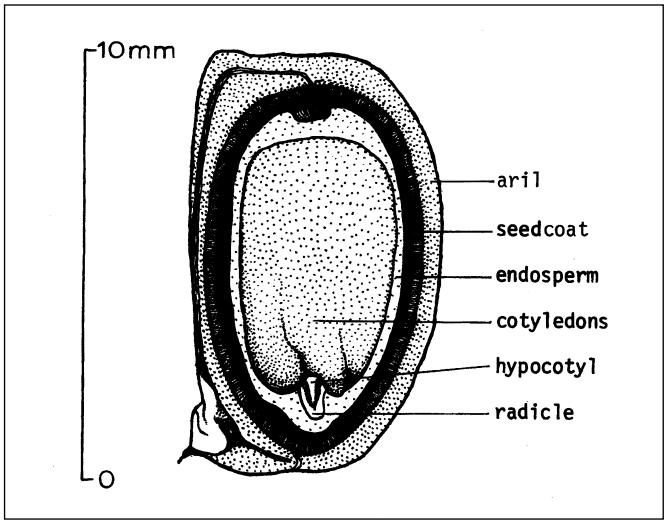


Figure 2—*Triadica sebiferum,* tallowtree: longitudinal section through a seed.



There are no known storage tests with seeds of tallow tree, but drying the sample noted above to 6% without killing the seeds indicates that they are orthodox in storage behavior. Short-term storage at low temperatures and seed moisture contents should be no problem. The seeds have a lipid content of about 20% (Zubair and others 1978), how-

ever, so sub-freezing temperatures should be used for any storage over 5 years.

Germination tests. Seeds of tallowtree are not dormant and do not typically require pretreatment. Germination results of 60 to 62% in germination beds have been reported from India (Singh and others 1993). Fresh seeds from the Mississippi collection had a laboratory germination of 38% after 30 days on moist Kimpak at day-night temperatures of 30 and 20 °C. The seeds received 8 hours of light during the day temperature. Moist stratification at 2 °C for 34 days increased the rate of germination but did not boost the percentage. Sixty days of stratification apparently induced a deep secondary dormancy (Bonner 1974). Tallowtree can also be propagated by cuttings from root suckers (Singh and others 1993).

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Pinaceae—Pine family

Tsuga Carr.

hemlock

Jill R. Barbour, Robert H. Ruth, and Robert P. Karrfalt

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Growth habit, occurrence, and use. Trees of the hemlock genus—*Tsuga* spp.—are tall, straight, late successional climax evergreens with conical crowns and slender, horizontal to pendulous branches. Fourteen species have been reported; 4 of these are native to the United States and the others to the Himalayas, China, Taiwan, and Japan. The name *tsuga* is a Japanese word meaning "tree-mother" (Dirr 1998). Native American names for the North Country (that is, Canada), *hoe-nadia*, and for the lands of upper New York, *oh-neh-tah,* both mean "land of the hemlock" (Dirr 1998).

Of the 4 native species in the United States (table 1), both eastern and western hemlocks are used commercially for lumber and pulpwood. The bark of eastern hemlock has been a source of tannin for the leather industry. In central and southern Oregon and some other areas, mountain hemlock has become an important part of the softwood sawtimber volume.

Much of eastern hemlock has been severely affected by the hemlock woolly adelgid—*Adelges tsuga*e Annand—in New England and the mid–Atlantic region (Dirr 1998). The hemlock woolly adelgid has also been noted on Carolina hemlock in the Tallulah Gorge in northeastern Georgia (Price 2002). Although the hemlock woolly adelgid occurs on mountain and western hemlocks from southern California to southeastern Alaska, these 2 species are resistant to the insect (McClure and others 2001).

Carolina hemlock overlaps the southern range of eastern hemlock, but it is a smaller tree with longer needles and cones. The wood serves the same uses as eastern hemlock, but the species is not abundant and of only minor commercial importance. Carolina hemlock is especially suitable for ornamental plantings.

Mountain hemlock is important mainly for watershed protection and the scenic beauty it adds to subalpine environments of Pacific Northwest mountain ranges. Its populations are disjunct due to the physical separation of its high-elevation sites. Due to the disjunct nature of its distribution, mountain hemlock was included in a world list of threatened species (Farjon and others 1993). It varies in size from a sprawling shrub at the timberline to a medium-sized forest tree.

Geographic races. Eastern, western, and mountain hemlocks have long north–south ranges and grow in a variety of habitats. Through natural selection, they apparently have developed numerous genetic types, each adapted to its local habitat.

Table 1—*Tsuga*, hemlock: nomenclature and occurrence

Scientific name	Common name(s)	Occurrence
***T. canadensis* (L.) Carr.**	**eastern hemlock,** Canada hemlock, hemlock	Nova Scotia to S Ontario, S to N Georgia & Alabama
***T. caroliniana* Engelm.**	**Carolina hemlock**	Mountains of Virginia to South Carolina to Georgia & Tennessee
***T. heterophylla* (Raf.) Sarg.**	**western hemlock,** Pacific hemlock, hemlock	Pacific Coast from Alaska to Washington, Oregon, & California & in mtns of N Idaho & NW Montana
***T. mertensiana* (Bong.) Carr.**	**mountain hemlock,** black hemlock	Pacific Coast regions from Cook Inlet, Alaska, to central California & to W Montana

Source: Ruth (1974)

A series of experiments with eastern hemlock (Baldwin 1930; Nienstaedt 1958; Olson and others 1959; Stearns and Olson 1958) showed that seedlings grown from southern seed sources tend to harden-off and go dormant later in the autumn and make more total growth (and the seeds requires less stratification) than those from northern sources. Southern seeds germinate best when temperatures approach 21 °C, whereas northern seeds do best near 13 °C. Seedlings from southern sources planted in Wisconsin grew late into the fall and were damaged more severely by frost than were their northern counterparts.

Similar results were obtained with western hemlock from 18 western provenances planted at various sites in Great Britain. Western hemlock seedlings from southern parts of this species' native range grew faster and set terminal buds later in the season than those from the North. However, when planted in northern Great Britain, they suffered severe damage from frost and cold winds. Frost damage was reduced if seedlings were planted under a high forest cover (Lines and Aldhous 1962, 1963; Lines and Mitchell 1969). Seed weight was found to decrease significantly from south to north, with collections from Alaska expected to have at least 110,000 more seeds/kg (50,000/lb) than western hemlock seeds from Oregon (Buszewicz and Holmes 1961). Kuser and Ching (1981) found significant differences among provenances in 100-seed weights, but there were only low correlations of seed weight with latitude, elevation, or distance from the Pacific Ocean. An increase in elevation on Vancouver Island, British Columbia, tended to increase germination rate and total germination (Edwards 1973).

Provenances of western hemlock with the fastest growing seedlings are from the southern part of the range; those with the slowest growing seedlings are from the northern part of the range as well as from the upper elevational extremes in the Rocky Mountains (Kuser and Ching 1981). In the case of western hemlock, the tree seed zones delineated by the Western Forest Tree Seed Council (WFTSC 1966b) may be used in Oregon and Washington. Those developed by the Organization for Economic Cooperation and Development (Piesch and Phelps 1970) may be used in British Columbia. A seed transfer zone map has been published for Oregon (Randall 1996).

Jeffrey hemlock—*Tsuga* × *jeffreyi* (Henry) Henry—has been reported as a cultivated hybrid of western and mountain hemlocks (Little 1979; Means 1990; Rehder 1949). Some French taxonomists proposed that mountain hemlock itself is an intergeneric hybrid of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock and they renamed it *Tsuga–Picea hookeriana* (Campo-Duplan and Gaussen 1948; Vabre-Durrieu 1954a&b). They considered a California form of mountain hemlock known as *Tsuga crassifolia* Flous to be a cross of mountain hemlock and Engelmann spruce (*Picea engelmannii* Parry ex Engelm). These hypotheses were rejected by American foresters, largely because of the absence of backcrosses and hybrid swarms in the field (Duffield 1950; Means 1990).

Many horticultural varieties of hemlock, including compact, weeping, spreading, and columnar forms, have been described (Dallimore and Jackson 1957; den Ouden and Boom 1965; Rehder 1940, 1949; Swartley 1945). They are widely planted as ornamentals throughout the temperate parts of the Northern Hemisphere.

Flowering and fruiting. Hemlocks are monoecious plants. Male and female strobili develop in clusters near the ends of lateral branches; each one consists of a central axis with spirally arranged microsporophylls. The male sporangia open transversely and the pollen is simple (Radford and others 1968). In mountain hemlock, pollen release is both protogynous and synchronous with female receptivity (Means 1990). The pollen is extremely sensitive to drying, which can prevent seed development in eastern hemlock (Godman and Lancaster 1990).

Ovulate strobili are erect, with nearly orbicular scales (each scale has 2 basal ovules), subtended by a membranous bract about the same length as the scale; they occur terminally on the lateral shoots of the previous year. In western hemlock, the total number of ovuliferous scales per cone is about 23 and about 70% of the scales are fertile (Colangeli and Owens 1989a). High temperatures in July the year before cone production favor flower initiation in mountain hemlock (Means 1990).

Hemlock is the only genus of the Pine family in which the mechanism of pollination involves nonmicropylar germination. Because of this difference, western hemlock seed cones are receptive for a much longer period than those of other conifers. Cones are receptive from shortly after bud burst until cone closure. The average number of days between bud burst and cone closure for western hemlock was 34 days in 1983 and 23 days in 1984 (Colangeli and Owens 1989a). Maximum pollination and seed efficiency (filled seed divided by the potential number of seeds per cone) is obtained when 50 to 75% of the cones have emerged beyond the cone scales (Bramlett and others 1977; Colangeli and Owens 1989a).

Hemlock pollen does not enter the cone micropyle but attaches to the waxy layer of the exposed portion of the bracts and ovuliferous scales. The bracts of western hemlock

can trap more than 100 pollen grains, the average pollen grain count per bract from controlled pollinations being 34, with a range from 2 to 116 (Colangeli and Owens 1989a). The ovuliferous scales elongate over the bracts, trapping the pollen between the bracts and scales. About 4 to 7 days after pollen germination, the pollen tubes grow into the micropyles; usually 1 to 6 pollen tubes and sometimes up to 10 pollen tubes have been found in each micropyle (Colangeli and Owens 1989a). In western hemlock, pollen is not essential for seed cone enlargement and unpollinated ovules can continue seedcoat development, but the seed will not have an embryo or gametophytic tissue (Colangeli and Owens 1990a).

Cones mature in 1 season and are small, pendant, globose to ovoid or oblong, with scales longer than the bracts (figure 1). Carolina hemlock has the largest seeds of the native hemlocks, followed by mountain hemlock and eastern hemlock, with western hemlock having the smallest seeds (table 2; figure 2). Eastern hemlock has the smallest cones; they measure 1.5 to 2.5 cm by 1 to 1.5 cm. Eastern hemlock trees grown from eastern and southern sources have larger cones than do those grown from northern and western sources (Godman and Lancaster 1990). Western hemlock cones measure 1 to 3.0 cm by 1to 2.5 cm; Carolina hemlock cones measure 2.5 to 4 cm by 1.5 to 2.5 cm. Mountain hemlock have the largest cones, which measure 3 to 6 cm by 1.5 to 3 cm (FNAEC 1993; Harlow and Harrar 1968; Hough 1947; Sargent 1933).

Cone production of hemlock usually begins when trees are 20 to 30 years of age, a little later if trees are shaded. All 4 species of hemlock bear some cones almost every year and large crops are frequent (table 3). Cones often remain on the hemlocks well into the second year, being especially conspicuous on the tops of mountain hemlock. Wisconsin had good eastern hemlock cone crops on 61% of the 32 years recorded (Godman and Lancaster 1990). Eastern hemlock trees as old as 450 years have been seen bearing cones.

Western hemlock bear cones every year with heavy crops every 3 to 4 years; in Alaska good crops occur every 5 to 8 years (Packee 1990). In Washington and Oregon, mountain hemlock trees 175 to 250 years old bear medium to heavy cone crops at 3-year intervals (Means 1990). Despite the frequency of cone crops, seed viability in hemlocks is generally low. Less than half the seeds in a cone are viable (Burns and Honkala 1990).

The period of dissemination of western hemlock seeds (table 4) can extend over a full year but the seeds are only viable during their first growing season (Packee 1990; Harris 1969). Most western hemlock seeds fall within 610 m from the tree, whereas eastern hemlock seeds fall within tree height due to their small wings (Godman and Lancaster 1990). Seeds remaining in cones are usually sterile in eastern hemlock.

Figure 1—*Tsuga*, hemlock: cones of *T. canadensis*, eastern hemlock (**upper left**); *T. mertensiana*, mountain hemlock (**lower left**); *T. carolina*, Carolina hemlock (**center**); and *T. heterophylla*, western hemlock (**right**).

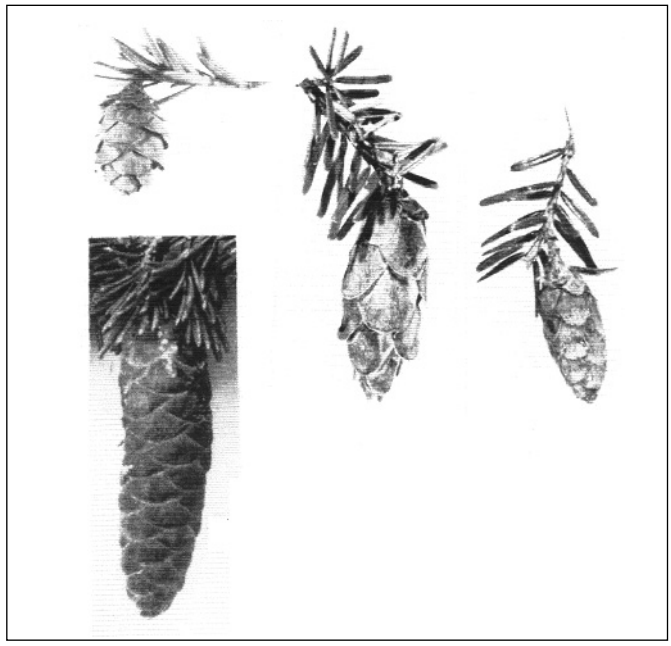


Table 2—*Tsuga*, hemlock: seed yield data

Species	Seeds (x1,000)/weight				Samples
	Range		Average		
	/kg	/lb	/kg	/lb	
T. canadensis	273–794	124–360	412	187	69
T. caroliniana	167–213	76–97	—	—	2+
T. heterophylla	417–1,120	189–508	573	260	106
T. mertensiana	132–459	60–208	251	114	6

Sources: Burns and Honkala (1990); Buszewicz and Holmes (1961), Hill (1969), Rafn (1915), Toumey and Korstian (1952), Toumey and Stevens (1928), Ruth (1974).

Table 3—*Tsuga*, hemlock: height, seed-bearing age, seedcrop frequency, and cone ripeness criteria

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yr)	Years between large seed-crops	Cone ripeness criteria	
					Pre-ripe color	Ripe color
T. canadensis	18–30	1736	20–30	2–3	Yellow-green	Purple-brown
				15	Green	Tan to brown
T. caroliniana	12–21	1881	—	—	Purple	Light brown
T. heterophylla	18–75	1851	20–30	5–8	Green with purple tips	Brown with red-brown tips
T. mertensiana	7.5–45	1854	20–30	1–5	Yellow-green to brown	Brown

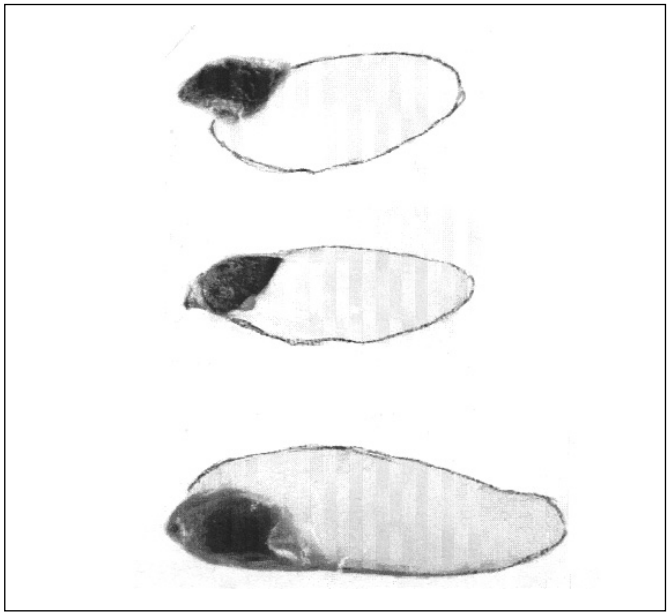
Sources: Burns and Honkala (1990), den Ouden and Boom (1965), Franklin (1968), Frothingham (1915), Harlow and Harrar (1968), Harris (1969), Hough (1947), Merrill and Hawley (1924), Olson and others (1959), Ruth (1974), Ruth and Berntsen (1955), Sudworth (1908).

Table 4—*Tsuga,* hemlock: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
T. canadensis	Southern range to northern range	Apr–early June	Sept–Oct	Sept–winter
T. caroliniana	North Carolina to South Carolina	Mar–Apr	Aug–Sept	—
T. heterophylla	Oregon to Washington	Apr–May	Sept–Oct	Oct–May
	S British Columbia	—	Sept 15	Oct–June
	SE Alaska	Late May-June	Sept–Oct	Oct
	W central Oregon	Mid to late Apr	—	Sept–May
	Idaho	May 27–June 5	Aug	Sept 17–winter
T. mertensiana	Oregon	June	Late Sept–Oct	—
	British Columbia, Alaska	June–mid-July	Late Sept-Nov	—
	Bitterroot Mtns, Idaho	Aug	—	—

Sources: Allen (1957), Burns and Honkala (1990); Ebell and Schmidt (1963), Frothingham (1915), Garman (1951), Gashwiler (1969), Godman (1953), Green (1939), Harris (1967), Harris (1969), Heusser (1954), Hough (1947), James (1959), Leiberg (1900), Radford and others (1964), Ruth (1974), Ruth and Berntsen (1955).

Figure 2—*Tsuga*, hemlock: seeds of *T. canadensis*, eastern hemlock (**top**); *T. heterophylla*, western hemlock (**center**); and *T. carolina*, Carolina hemlock (**bottom**).

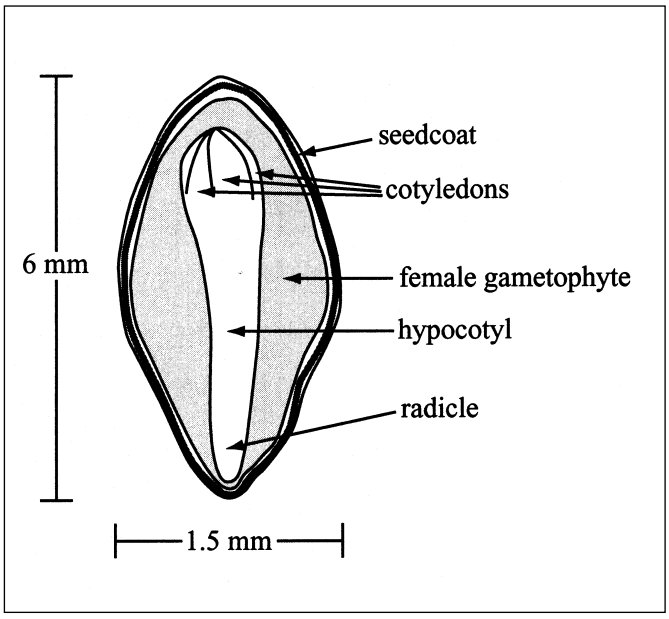


Western hemlock generally produces less than 40 seeds per cone; usually less than 20 of these are filled (Edwards 1976). At a clone bank in Victoria, British Columbia, the average number of seeds per cone was 34, and 22 seeds were filled when counted in 1983 and 1986 (Colangeli and Owens 1990b). The number of filled seeds counted on the exposed cut-face of a cone is a good predictor of total filled seeds per cone (Meagher 1996). The number of cones needed to estimate total filled seeds within ± 5 seeds ranged from 3 to 60 cones (Meagher 1996).

Prepollination ovule abortion produces small, flat seeds. Colangeli and Owens (1990b) found that it accounted for an average of 11 and 14% reduction in filled-seed yield in 1983 and 1986, respectively. Postpollination ovule abortion occurred in about 4% of the ovules, corresponding to less than 1 seed per cone (Colangeli and Owens 1990b). Insufficient pollination—which is usually the reason for low seed set—resulted in 25% empty seeds in 1983 and 66% empty seeds in 1986 (Colangeli and Owens 1990b).

Embryos have 3 to 6 cotyledons (figure 3) (Sargent 1933). Kuser and Ching (1981) found provenance variation

Figure 3—*Tsuga mertensiana*, mountain hemlock: longitudinal section through a seed.



in cotyledon number in western hemlock. Seedlots from the Rocky Mountains produced higher frequencies (15%) of 4-cotyledon seedlings than those from the Cascade Mountains or coastal zones (11%). The embryo extends the full length of the seed. Olson and others (1959) reported that embryos from eastern hemlock are about 3 mm long and 0.5 to 0.7 mm in diameter.

Collection of fruits. Hemlock cones are small and, therefore, more difficult to harvest than the larger cones of many conifers. They are most easily collected from tops of trees felled during harvest cuttings, but it is important that seeds from such collections are checked for maturity. Usually cone collection is delayed until shortly before seed dispersal to ensure full maturity of the seeds. Cones also can be harvested by the use of ladders, pole pruners, and various kinds of climbing equipment.

Based on a study of western hemlock in southern British Columbia, Allen (1958) recommended September 15th as a suitable date to begin cone collection even though cones are still green and hard. Seeds collected earlier (August 30th) had lower total germination. The germination rate of seeds collected September 15th was improved by storage and stratification. Seeds of western hemlock cones that are stored for 3 to 6 months before seed extraction had higher percentages of germinating seeds (91%) than did seeds from cones stored for 1 month before extraction (75%) (Leadem 1980). Also working with western hemlock, Harris (1969) found a few seeds viable when extracted as much as 70 days before seed dispersal. When cones were left on the tree, the percentage viability increased gradually until almost dispersal time.

Extraction and storage of seeds. Handling procedures for hemlock cones and seeds follow those of other conifers. Usually cones are stored—often for several weeks and sometimes months—in permeable sacks in open-sided cone drying sheds while awaiting processing. This covered storage serves as a preliminary curing process. Green cones tend to mold during storage, especially if stored without surface drying. Adequate air circulation is needed around each sack to minimize heating and mold buildup. Under proper conditions, western hemlock seeds may remain in the cones up to 6 months without detrimental effects upon seed quality. Leadem (1980) found that seeds from cones refrigerated at 2 °C had no better quality than seeds from cones stored outdoors.

An additional, or sometimes alternate, procedure is to place cones in a heated room for up to 36 hours before actually placing them in a drying kiln. This avoids exposing seeds that are nearly saturated with water to high kiln temperatures, a procedure that damages some conifer seeds. It also reduces kiln time and cost.

There are few problems in extracting seeds from hemlock cones. According to Baldwin (1930), mature hemlock cones need little artificial heat to open. Kiln-drying temperatures range from 31 to 43 °C, with drying time about 48 hours (Deffenbacher 1969; Isaacson 1969; Ruth 1974; Ward 1969). In the West, few hemlock cones are processed, and kiln schedules generally follow those for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and pine (*Pinus* spp.).

Eastern hemlock cones that are picked green, and thus are difficult to open, usually can be opened by exposure to repeated cycles of moistening followed by drying at 38 °C. Eastern hemlock cones collected just as they turn tan will open readily upon drying (Olson and others 1959). Mold-infested cones often open poorly, making seed extraction difficult. Seeds are extracted by tumbling or shaking the cones during or immediately after kiln-drying. On the tree, western hemlock cones open and close readily in response to changing moisture conditions and require many flexings of the cone scales before all seeds are dislodged; with kiln-drying and tumbling or shaking, a single opening of the cone scales appears sufficient for good seed extraction (Harris 1969).

Seeds are nearly surrounded by their wings (figure 2). Unlike the seeds of fir, Douglas-fir, and some pines, hemlock seeds have an entire wing that can be detached without serious damage to the seeds themselves (AOSA 2001).

Seeds are de-winged, and wing parts and foreign matter removed in a fanning mill or gravity separator. Minimum standards of 90% purity and 60% viability have been established for seedlots of western hemlock (WFTSC 1966a). The low viability often reported for eastern hemlock may be due to the difficulty of separating out low-quality seeds (Olson and others 1959). Care should be taken during processing to minimize the seed mortality that results from bruising or cracking the seedcoat.

For eastern hemlock, 0.35 hl (1 bu) of cones weigh about 15.5 kg (34 lb) or 1 liter (1 qt) of cones weights 0.44 kg (1 lb) (Eliason 1942) and yields 0.6 to 0.7 kg (1.4 to 1.5 lb) of seeds with a moisture content of 7.1% (Hill 1969; Toumey and Korstian 1952). Eastern hemlock seed yield per 100 kg (220 lb) of cones is 3.1 kg to 6.2 kg (6.8 to 13.6 lb) of seeds (Barton 1961; Ruth 1974). For western hemlock, there were 20,000 cones in 0.35 hl (1 bu) (Kummel and others 1944) and 0.45 kg (1 lb) of seeds was extracted from 0.35 hl (1 bu) of cones (Toumey and Korstian 1952).

Annual seeding and planting programs are dependent on successful seed storage (table 5). Western hemlock seeds keep best below freezing, and general practice is to store them at –18 °C. Barton (1954a) showed that viability was maintained better at this temperature than at –11 or –4 °C, with distinct differences showing up after only 2 years of storage. Viability can be maintained for at least 5 years, and this generally bridges the gap between large seedcrops.

Eastern hemlock seeds are stored both above and below freezing. They have been kept for 2 to 4 years in jars or plastic bags in a refrigerator maintained a few degrees above freezing, but retention of viability varied between seedlots (Olson and others 1959).

Mountain hemlock seeds are also stored at –18 °C. Mountain hemlock seedlots vary in their ability to withstand short-term stress, indicating that the genetic makeup of the seedlot may affect long-term seed storage. Accelerated aging (37.5 °C) treatments, varying from 0 to 21 days at 3-day intervals on mountain hemlock seeds, resulted in a complete loss of viability for stratified seeds at 12 days and for unstratified seeds at 18 days (El-Kassaby and Edwards 1998). The average viability for stratified seedlots decreased from 88% before aging to 3.6% after 9 days of aging. The average viability for unstratified seedlots decreased from 91% to 2% over the same time period (El-Kassaby and Edwards 1998).

Moisture content of hemlock seeds in storage should be maintained between 6 and 9%. In longevity tests of seedlots stored at 5 °C with 6 to 10% moisture contents, a seedlot of western hemlock had 13% germination after 15 to 16 years, and another of mountain hemlock had 2% after 11 to 20 years (Schubert 1954). A study with western hemlock (Lavender 1956) demonstrated that temperatures and humidity levels generally experienced between removal of seeds from storage and seeding operations or testing procedures do not appreciably reduce viability. There was good viability retention of seeds removed from storage and stored at 20 °C and 30% relative humidity for as much as 11 weeks.

Pregermination treatments. Dormancy is variable in hemlock, with some seedlots requiring pregermination treatment and others germinating satisfactorily without treatment (Baldwin 1934; Bientjes 1954; Olson and others 1959). Because cold stratification (1 to 4 °C) of mature seeds shortens incubation time and may substantially increase germination, cold stratification is recommended prior to testing (except for seeds known to be nondormant) (table 6).

Stratification clearly accelerates and improves total germination of eastern hemlock (Baldwin 1930, 1934; Stearns and Olson 1958). For eastern hemlock seeds that have not been stratified, germination is improved by exposing seeds to 8- to 12-hour photoperiods at a temperature of about 21 °C alternating with dark periods at about 13 °C (Olson and others 1959). A long stratification period (70 days) increased germination percentages for Coffman (1975), who germinated seeds at 18 °C in darkness or with a $^1/_2$ hour of red light daily (615 nm, 0.056 g-cal/cm^2/min). Viable stratified, irradiated seeds showed 58% germination; viable stratified, non-irradiated seeds showed only 37%. Coffman also found that gibberillic acid (GA), kinetin, or a mixture of the two, inhibited the effect of prechilling, even in the presence of red light. There was nearly a complete lack of germination of unstratified eastern hemlock seedlots kept under red light (Coffman 1975).

Table 5—*Tsuga,* hemlock: seed storage conditions

Species	Seed moisture (%)	Temp (°C)	Viable period (yrs)
T. canadensis	—	5	4
	6–8	1–3	—
	—	–3	—
T. heterophylla	7–9	–18	5–7
	6–8	0	—
	8	–18	5+
	8	–18	3+
	—	21	2–3

Sources: Allen (1957), Barton (1954b, 1961), Jones (1962), Ruth (1974).

Table 6—*Tsuga*, hemlock: stratification treatments

Species	Medium	Temp (°C)	Time (days)
T. canadensis	Moist sand or peat	1–5	30–120
T. caroliniana	Peat moss	3–5	30–90
T. heterophylla	Moist sand	1–5	21–90
	Plastic bag*	1–2	21–56
T. mertensiana	Moist sand	5	90

Sources: Allen (1958), Babb (1959), Deffenbacher (1969), Devitt and Long (1969), Eide (1969), Olson and others (1959), Ruth (1974), Swingle (1939), Walters and others (1960), Ward (1969), Weyerhaeuser (1969).
* Seeds were presoaked in tap water for 24 to 36 hours.

Germination of eastern hemlock seeds declines depending on the frequency and degree of drying following the imbibition phase and on the intensity of light. Eastern hemlock seeds incubated in open petri dishes at a low light level (645 lux) showed various germination values, from 50.2% with decomposed birch medium to 0% with filter paper. Seeds incubated in open petri dishes with decomposed birch medium that were exposed to a moderate light level (4,682 lux) exhibited delayed initial germination and significantly reduced total germination to half that at low light conditions (Coffman 1978). The intensity of light had no effect on seeds in covered petri dishes where a high moisture content was maintained.

Seeds of western hemlock stratified for 3 weeks at 1 °C germinated faster than untreated seeds; longer stratification periods caused additional but smaller increases in the rate of germination (Bientjes 1954; Ching 1958). Stratification of western hemlock seeds apparently has its main effect on speed of germination; it has only a minor effect on total germination percentage. Seedlots stratified for 1 week reached R_{50} (the number of days to reach 50% germination) 2.5 days sooner than did unstratified seedlots. Seedlots stratified for 4 weeks reached R_{50} 4.5 days sooner, and seedlots stratified for 16 weeks reached R_{50} 10.5 days sooner than did unstratified seedlots (Edwards 1973). Unstratified seedlots of western hemlock required nearly 2.5 weeks (18 days) to produce the same number of germinants as did seedlots stratified for 3 months in 10 days (Edwards 1973). Western hemlock seeds stratified for 1 week in plastic bags germinated about 1 day sooner than seeds stratified on filter paper (Edwards 1973). Presoaking the seeds for 48 hours was as effective in reducing the germination rate as was 1 week of stratification on filter paper (Edwards 1973). Immature western hemlock seeds tend to have lower total germination as a result of stratification (Allen 1958).

Experiments in Great Britain showed slightly increased rates of germination following stratification when western hemlock seeds were exposed to light but none when they were germinated in darkness (Buszewicz and Holmes 1961). Stratified western hemlock seeds tended to reduce the sensitivity to photoperiod (Edwards and Olsen 1973). Germination rate increased under a 4-hour photoperiod (300 to 350 foot candles or 3,228 lux); whereas 16 hours or more of photoperiod depressed germination rate below those in complete darkness at a constant 20 °C temperature (Edwards and Olsen 1973). Eight hours of light did not have a difference in germination from the no light treatment (Edwards and Olsen 1973).

Light significantly reduces germination rate for mountain hemlock seeds regardless of stratification. Unstratified and stratified seeds germinated in 8 hours of light (100 lux at filter paper surface) a week later than seeds grown in darkness (Edwards and El-Kassaby 1996). The R_{50} values for seeds incubated in light was almost double (6 days more) that of seeds incubated in darkness (Edwards and El-Kassaby 1996). Stratification increased the speed of germination slightly, but it did not alleviate the light effect nor did it effect total germination (Edwards and El-Kassaby 1996). Mountain hemlock seeds germinated 91% in the dark and 90% with light: mountain hemlock seeds can germinate as well or better without light (Edwards and El-Kassaby 1996).

Germination may begin while seeds are still in stratification if kept too long, with subsequent problems of drying out and mechanical damage during sowing. Careful regulation of seed moisture content and temperature can prevent germination from beginning in stratification. Seeds need to be kept at full imbibition but surplus water should be totally or mostly removed. Radicals will only elongate with surplus water present. Keeping temperatures closer to freezing and constant is also a good precaution. Temperature in the 1 to 2 °C range will retard germination more effectively than allowing temperatures to rise to near 5 °C. Personnel should limit entry into the stratification cooler to minimize temperature fluctuations.

Germination tests. The Association of Official Seed Analysts (AOSA 2001) have prescribed standard germination test conditions for eastern and western hemlocks (table 7). It is recommended that eastern hemlock seeds be prechilled for 28 days at 3 to 5 °C followed by 28 days in a germinator at 15 °C. The rules call for placing western hemlock seeds directly in germinators at 20 °C for 28 days. Stratification is not required as part of the standard germination test procedure for western hemlock seeds but a paired germination test with 21 days of stratification can be performed and it is common practice to stratify seeds prior to nursery sowing. Seeds of both species should be exposed to light no more than 8 hours daily during this period. A tetrazolium staining technique for estimating seed viability may be used on western hemlock, but results may tend to underestimate seed quality (Buszewicz and Holmes 1957).

The International Seed Testing Association (ISTA 1999) rules used for exporting seeds are similar to domestic rules except that the germination test period for western hemlock is extended to 35 days. Standard procedures have not been developed for Carolina and mountain hemlock, so test conditions follow those for the associated eastern or western hemlocks.

Mountain hemlock seed germination is very sensitive to the total accumulation of heat even though it has been known to germinate on snow but much more slowly (Franklin and Krueger 1968). Stratification as long as 120 days does not compensate for sub-optimal temperatures. For mountain hemlock seed testing germination, stratification for 90 days at 4.5 °C is recommended with germination temperature set at a constant 20 °C (480° daily heat sum) (table 6).

In a laboratory study, as the heat sums rose from 280 to 440% daily heat sums the germination rate increased but final germination was not affected by temperature (El-Kassaby and Edwards 2001). Heat sum is the addition of temperatures above 0 °C for 24 hours. The threshold heat sum for mountain hemlock seed germination lies close to 400% daily heat sum which does not occur at high elevations until August in British Columbia, Canada (El-Kassaby and Edwards 2001). Stratification treatments did not have a significant effect on rate or final germination (El-Kassaby and Edwards 2001).

Correlations between latitude and total germination (r= 0.482) and between mountain hemlock seed weight and latitude (r = – 0.482) were found to be significant (*p* less than

Table 7—*Tsuga*, hemlock: stratification period, germination test conditions, and results

Species	Cold stratification* (days)	Daily light period (hrs)	Germination test condions† Temp (°C) Day	Night	Days	Germination rate (%)	(days)	Germination (%)	Samples
T. canadensis	60–120	—	30	20	60	10–55	15–30	38	15
	0–30	—	22	22	—	6–62	28	10–66	9–12
	21–30	8	16	16	28	—	—	—	—
	20	8	15	15	28	—	—	60	3
	40	8	15	15	28	—	—	45	3
	90	8	15	15	28	—	—	61	9
T. caroliniana	0	8	30	20	28	—	—	40–80	9
	21–30	8	30	20	28	—	—	51–57	3
	0–120	16	22	22	34	—	—	82–91	5
T. heterophylla	0	8	20	20	28–35	49	21	53	146
	0–90	—	16	11	30	38	20–30	56	25
	0	8	15	15	35	—	—	86	44
	28	8	15	15	35	—	—	86	43
T. mertensiana	0–90	—	30	20	25–30	62–75	16–20	47	4
	—	Dark	20	20	28	—	—	91	19
	—	8	20	20	28	—	—	90	19
	90	—	30	20	60	61	16	62	1
	0	8	20	20	28	—	—	81	4
	28	8	20	20	28	—	—	97	3
	90	8	20	20	28	—	—	72	5

Sources: AOSA (2001), Buszewicz and Holmes (1961), Edwards and El-Kassaby 1996, Hill (1969), ISTA (1999), Ruth (1974), USDA FS (2002)

* Temperatures were –16 to –15 °C.

† Moisture-holding media were either blotters, Kimpak®, sand, or peat.

or equal to 0.05) (Edwards and El-Kassaby 1996). As seed source was moved further north in latitude, the seed weight decreases because the seeds are smaller. Germination parameters are under strong genetic control with broad sense heritabilities, h_2, ranging from 0.30 to 0.85 for stratified seeds and 0.45 to 0.84 for unstratified seeds (El-Kassaby and Edwards 1998).

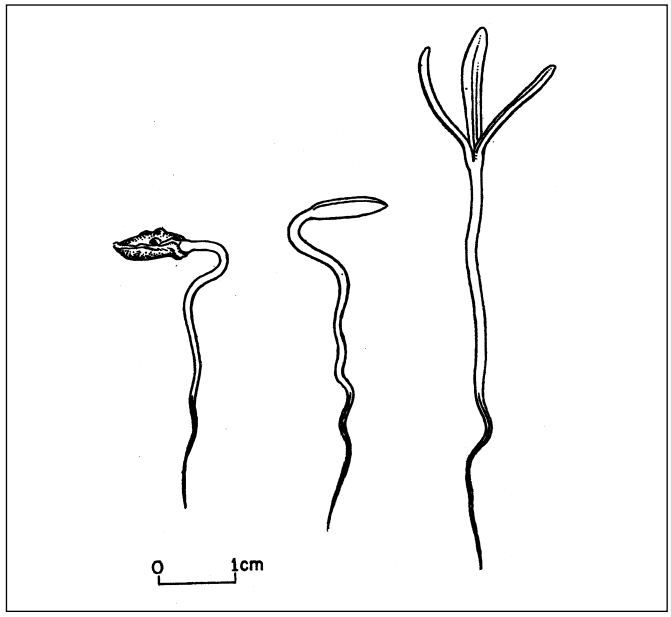
Final germination percentage of western hemlock seeds is affected by germination temperature. Greater total germination occurred at a constant temperature of 20 °C than under lower, higher, or alternating temperatures (Bientjes 1954; Buszewicz and Holmes 1961; Ching 1958). When alternating temperatures are used, keeping seeds in the dark improves germination (Buszewicz and Holmes 1961).

Western hemlock seeds from northern populations tended to germinate early, by about 4 days/degree of latitude, at 7 °C after 10 days of chilling (Campbell and Ritland 1982). Western hemlock seeds from high-elevation populations in the coast range germinated more rapidly than seeds from low or middle elevation population. For populations in the Cascades, seeds from both high- and low-elevation sources germinated more rapidly than seeds from middle elevations (Campbell and Ritland 1982). Lengthening stratification tended to decrease differences among provenances.

Observations of eastern hemlock (Olson and others 1959) illustrate ontogeny of seed germination, which is epigeal (figure 4). The first indicator of a viable seed is splitting of the seedcoat for half to two-thirds of its length, followed by the appearance of the pointed, bright-red root tip. The root grows at the rate of 2 to 3 mm/day, curving abruptly after emergence. After a few days, the hypocotyl also begins to grow, reaching 2 to 3 cm in length in 1 to 3 weeks. Normally, there is a pause in development after the cotyledons open, which may arbitrarily be considered the end of germination.

Nursery practice. Hemlock seedlings are difficult to grow in the nursery. They are easily damaged in the hot sun, and their small size the first year makes them particularly susceptible to frost heaving. Because of these difficulties, natural regeneration has in the past been favored over planting seedlings. Natural regeneration of western hemlock usually has been adequate, and a common procedure for mixed stands is to plant or seed associated species and expect hemlock to come in on its own, which it usually does. With increasing intensity of management, demand for western hemlock seedlings has increased, and production procedures were developed (Deffenbacher 1969; Devitt and Long 1969; Eide 1969; Isaacson 1969; Ward 1969; Weyerhaeuser 1969).

Figure 4—*Tsuga canadensis*, eastern hemlock: seedling development at 2, 4, and 7 days after germination.



At some nurseries (Eide 1969; Weyerhaeuser 1969), western hemlock seeds are soaked for 24 to 36 hours prior to stratification. The speed of germination was increased by soaking seeds in tap-water for 33 hours at room temperature (Bientjes 1954). Prolonged soaking for 96 to 120 hours, however, reduced the germination rate (Ching 1958).

Most nursery managers stratify western hemlock seeds and sow them in the spring. Seeds are moistened, excess water drained off, then the seeds are stratified at 1 to 2 °C from 21 to 42 days in a polyethylene bag. No stratification medium is used. Seed moisture content for optimum germination should be about 60% (Devitt 1969). Soil moisture content should be high but with drainage adequate to keep the ground water level below the rooting zone. Seedbeds may need screening to protect seeds from birds and rodents.

At one nursery (Eide 1969), seeds were sown on the surface and covered with burlap and sprinkled as needed to maintain moisture. After germination and penetration of the radicle into the soil, the burlap is removed and seedlings are mulched with peat moss. Additional peat moss is added during the growing season. Seedlings go into the winter with 13 to 19 mm ($^1/_2$ to $^3/_4$ in) of mulch to minimize frost heaving. About 50% shade is provided the first season.

For nursery production of eastern hemlock seedlings, spring-sowing of stratified seed is preferred over fall-sowing (Hill 1969; Olson and others 1959). Good eastern hemlock seeds planted under favorable conditions usually survive superficial contamination with mold, and use of fungicides

is not recommended unless serious contamination is present. Nursery seedlings are very subject to damping-off by *Rhizoctonia* spp. during the first few months after germination and this can be aggravated by over-fertilization. It can be prevented (and weed seeds killed) with fumigation. Damping-off after germination can be controlled with fungicide (Olson and others 1959). One nursery growing western hemlock treats seedbeds when necessary with captan or thiram and has not had a serious problem with damping-off diseases. They also have treated hemlock seedlings with animal repellant to protect them from damage after outplanting (Eide 1969).

In nursery experiments in Great Britain, partial soil sterilization with formalin drench or chloropicrin injection improved growth of western hemlock. Moderate to large height increases were obtained with either treatment. Both sterilants used together often gave even better growth response, although treatment effects were not additive (Benzian 1965).

Only a few reports are available on nutrient requirements of hemlock. Western hemlock in British Columbia requires a well-drained acid soil with pH about 4 to 5 and an organic matter content of 5 to 6% (Devitt 1969). In Washington, it grows well at pH 5.3 to 5.4 with at least 15% soil organic matter (Eide 1969). In Great Britain, western hemlock made maximum growth on acid soil at about pH 4.5 and responded favorably to fertilization with nitrogen, phosphorus, and potassium. It showed a definite tip burn when suffering a copper deficiency, but seedlings recovered when sprayed with Bordeaux mixture. Water deficits during a dry summer apparently prevent response to nitrogen fertilization (Benzian 1965), but on the other hand, late summer watering can delay hardening-off and may increase the risk of frost damage (Olson and others 1959).

Seedlings are small at the end of the first growing season in the nursery and usually are held over and lifted after the second or third season. Seedlings frequently are transplanted for 1 year and then outplanted as 2+1 or 3+1 planting stock (Devitt and Long 1969; Olson and others 1959; Ward 1969). To overcome the difficulties of germination and frost heaving in the bareroot bed, plug+1 or plug+2 seedlings are used more commonly now than directly sowing seeds in the nurserybed (Romeriz 1997). In this system, a miniplug seedling is started in the greenhouse and then transplanted to the bareroot nurserybed.

Desired densities range from 323 to 538 seedlings/m^2 (30 to 50/ft^2) and tree percentages run from 15 to 50 (Deffenbacher 1969; Devitt and Long 1969; Eide 1969; Isaacson 1969; Ward 1969; Weyerhaeuser 1969). Experience in Great Britain indicates that a large proportion of losses in the nursery occur before seedling emergence. A high variability in tree percentage requires large safety factors in nursery sowings, resulting in an occasional surplus of seedlings (Buszewicz and Holmes 1961). The use of western hemlock plug transplants (Klappart 1988) reduces the number of seeds used and produces a larger, higher quality seedling in less time (Smith 1997). The production of container seedlings for outplanting is also widely practiced for western hemlock (Smith 1997).

Most hemlocks are now grown in containers in greenhouses under intensive culture instead of in bareroot nurseries. Styrofoam® blocks are the most common containers used and the sizes vary from 60, 77, to 112 trees/block with 77 trees/block the most commonly used. There are two outplanting regimes that dictate the propagation procedure in the greenhouse. The spring-planting regime requires that seeds be sown around February 1st, with the seedlings outplanted in the spring of the next year. Seeds are sown around January 15th for the summer-planting regime, with the seedlings being outplanted in the summer of the same year (Girard 2002).

Seeds are stratified for 21 days before sowing to achieve rapid, uniform germination and are germinated at 20 to 25 °C with light. It is the usual practice to sow with equipment more than 1 seed per cavity when germination falls below 90%. Once the seeds are fully germinated the photoperiod is increased to 20 hours/day and maintained until late April to keep the terminal bud from setting prematurely. The container medium is usually peat moss that may be amended with perlite or fir sawdust. Containers are lightly filled with medium to allow hemlock's large root system to grow. Controlled-release fertilizer is added to the medium at 4 kg/m^3 of medium in addition to lime to raise the pH and trace elements. The seeds are lightly covered with a sandy grit. A complete soluble fertilizer is added to the irrigation water every time the seedlings are watered. Frequency of irrigation is determined by weighing the containers after watering and then re-irrigating once the container weight drops below the target level (Girard 2002).

The seedlings are induced to set a terminal bud in the greenhouse by photoperiod reduction achieved through retractable darkout systems. Western hemlock seeds from southern sources require about a 4-week darkout period of 10 hours/day of light and 14 hours/day darkness. Seeds from northern sources only require about 2 weeks of darkness in the July following sowing to set buds. The short-day induction period is not begun until the trees have reached a minimum height of 15 cm (77 cavities/block). Seedlings will

continue height growth during the short-day treatment so it is important to initiate bud induction early enough to maintain a good shoot to root ratio. Following the darkout period, seedlings are subjected to moderate moisture stress to maintain budset. Nurseries favor greenhouse systems that have roofs that open to subject the planting stock to full light conditions following budset. In nurseries lacking those systems, containers are usually moved outside growing compounds (Girard 2002).

For 77 cavities/block stocktypes, the target seedling height for outplanting is 30 cm (12 in), with no more than a maximum of 40 cm (16 in) height. The minimum caliper for outplanting is 3 mm and the target is 3.5 mm. It takes about 25 weeks from sowing to grow a target seedling. For spring-planted crops, ambient greenhouse temperatures are reduced to about 2 °C in the late fall to further develop dormancy. A frost hardiness test is performed to determine dormancy before the seedlings are lifted for cold storage. A sample of seedlings are frozen to –15 °C and injury is determined through variable chlorophyll inflorescence (Girard 2002).

For extraction of seedlings from the growing containers, most nurseries use automatic pin extractor machines. The containers are laid on their sides and metal pins push the plugs out of the containers and the seedlings are then graded for quality. For summer outplanting (late August and early September), seedlings are not stored before planting. The seedlings are lifted while still growing, shipped, and planted within 24 hours (Girard 2002).

Spring-outplanted seedlings are lifted from containers in December and stored for up to 3 months in cold storage at –2 to –5 °C. Seedlings are placed in an upright position within a waxed cardboard box. Boxes filled with seedlings to be stored frozen have a brown paper liner with an inner plastic membrane to retain moisture. Frozen seedlings are allowed to thaw 3 to 5 days in a thawing shed before they are shipped to the field for planting (Girard 2002).

Eastern hemlock is sometimes propagated vegetatively. Dormant cuttings taken in January to mid-February should be placed in beds with bottom heat, but results can be variable (Dirr and Heuser 1987).

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Fabaceae—Pea family

Ulex europaeus L.

common gorse

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Growth habit, occurrence, and use. Gorse is a leafless, spined shrub introduced from western Europe. In its homeland, it grows 1 to 2 m tall and is primarily a non-aggressive invader of disturbed areas that is recognized as useful for wildlife protection, soil stabilization, and revegetation. It has also been cultivated as an ornamental and as forage for livestock, which feed on the soft, new growing shoots. Its major use in the past, however, was for hedgerows to contain livestock before barbed wire (Jobson and Thomas 1964). As a useful plant, European settlers carried gorse to many parts of the world where it quickly escaped from cultivation and formed aggressive feral populations. These feral plants grow 3 to 5 m tall in dense, spiny, impenetrable stands that exclude desirable vegetation in pasture lands (Hill 1983; Sandrey 1985) and, in open forests, interfere with reforestation and forest management (Balneaves and Zabkiewicz 1981; Zabkiewicz 1976). Gorse is presently recognized as one of the worst weeds in New Zealand, Chile, and Tasmania and is recognized as a weed in at least 15 other countries or island groups around the world (Holm and others 1979).

In North America, gorse is still used to a limited extent as an ornamental for its dense yellow flowers. In the eastern United States, scattered feral populations have been recorded, but apparently these are not of an aggressive nature. By contrast, along the Pacific Coast, gorse is found scattered along the coastline from San Francisco, California, north to Vancouver, British Columbia (Markin and others 1994). Through most of this area, it is found in small, scattered populations that are usually targeted for intensive control programs to keep them from expanding. The major outbreak along the southwestern coast of Oregon covers at least 15,000 ha and is a major problem in forest management. This gorse population interferes with reforestation and, because of the plant's highly flammable nature, creates an extreme fire hazard (Herman and Newton 1968). Gorse also infests 14,000 ha at higher elevations on the islands of Hawaii and Maui in Hawaii (Markin and others 1988).

As a useful agricultural and ornamental plant in its native range, methods for propagating gorse have been developed in Europe (Rudolf 1974). As a major weed through the rest of the world, no effort has been made to propagate it for sale or outplanting. However, very extensive work has been done in studying the regeneration, reproduction, and propagation of this plant for research purposes and to develop control methods, particularly in New Zealand. A more recent need has been to propagate gorse to be used as food for insects being tested as potential biocontrol agents (Markin and Yoshioka 1989).

Flowering and fruiting. The small, bright yellow, pea-like flowers (Whitson and others 1991) are very similar in size and appearance to those of the closely related Scotch broom—*Cytisus scoparius* (L.) Link—with which it shares much of its range on the Pacific Coast. In Europe, gorse blooms in late spring, usually for 1 month; depending upon the latitude, this can occur from late February to early June. On the Oregon coast, gorse blooms from February to early May; in Hawaii, it blooms from December to May, peaking in February and April. Flowers may be solitary or in clusters, but because they are often synchronized in blooming, an entire plant will sometimes be covered with thousands of blooms. The flowers are insect-pollinated and require a large insect that, while probing for nectar, can trip and release the stamens held in the keel on the lower surface of the flower. The major pollinator in North America and Hawaii is the common honey bee (*Apis mellifera* L.). When massive blooms occur in areas where feral bees are scarce, poor pod set may be seen in limited areas (a desirable feature for land managers). Beekeepers, however, recognize the bloom as an excellent source of early spring pollen that can be used to build up their hives, and they usually move hives in to take advantage of the bloom, resulting in adequate pollination (Sandrey 1985). One method of control that has been used in Hawaii is restricting commercial bees in an effort to reduce seed production.

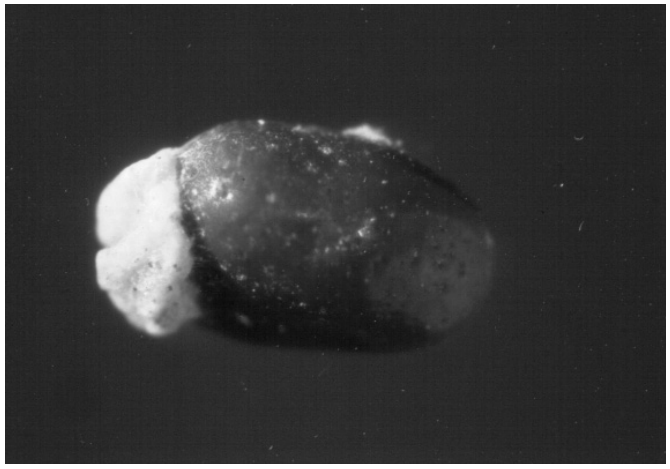
The mature fruit is a typical, small (1 to 1.5 cm), black legume (pod) that contains 1 to 12 seeds, although the average is 4 to 5. After pollination, a legume requires 2 months to mature, so peak legume set occurs 2 months after peak flowering. In Oregon, this is mid-May through July; in Hawaii, peak legume set is in May and is finished by the first of July. On maturing and drying, the legumes open violently (dehisce), naturally dispersing the seeds 1 to 3 m out from the parent plant. In Oregon and Hawaii, natural germination usually occurs during the wetter winter and spring months.

Fruit collection; seed extraction and storage. As an aggressive, noxious weed, there is no demand for the commercial collection of seeds. Researchers obtain the seeds they need by collecting the mature black legumes individually or by cutting a branch containing them. When allowed to dry out in a cloth sack at room temperature, the legumes naturally dehisce, releasing the seeds. The mature brown seeds are generally spherical, 1.25 to 2 mm in diameter (figure 1). Each seed initially contains an elaiosome, a yellow, fleshy appendage, rich in oil and protein (Pemberton and Irving 1990) that attract ants; this is another method of seed dispersal (Weiss 1909). The gorse seedcoat is notorious for its hardness (it is water impermeable), which gives the seeds a very long field life and has created major problems in managing this weed (Butler 1976; Chater 1931; Moss 1959). Seed numbers range from 145,000 to 159,000/kg and average about 150,000/kg (66,000 to 72,000/lb and average about 68,000/lb) (Rudolf 1974). The seeds are orthodox in storage behavior and can be kept indefinitely in ordinary cool, dry storage.

Pregermination treatments. Germination of mature, well-dried seeds varies greatly according to the literature but can be as low as 10 to 30% in 6 months. In the field, the seeds have a long life; it has been estimated that they can remain viable for up to 26 years or more (Moss 1959).

Because of the seedcoat's hardness, a number of different pregermination treatments have been tried. In the field, the most common method to trigger germination is fire. When a gorse area burns, the seeds in the top centimeter or two of duff are destroyed, but the deeper seeds survive and most of these are often triggered into germinating (Rolston and Talbot 1980; Zabkiewicz and Gaskin 1978). In the laboratory, this can be duplicated by heating the seeds from 60 to 80 °C for 30 minutes in an oven (Butler 1976; Moss 1959). Placing gorse seeds in boiling water for 30 seconds and then cooling them in cold water can increase germination to over 90% (Millener 1961).

Figure 1—*Ulex europaeus*, common gorse: seed.



Other methods of germination include soaking in concentrated sulfuric acid for $^1/_2$ to $1^1/_2$ hours, and mechanical scarification (Buttler 1976), most simply done with emery paper (Moss 1959).

Germination tests. Because of the noxious nature of gorse in North America, standardized germination tests for quality control have not been developed. In Europe, where gorse is a beneficial native plant, germination tests at one time were apparently developed in which seeds were tested in germinators or sand flats at 20 °C for 30 days using 400 pretreatment seeds/test (Rudolf 1974). Researchers have reported no problem in obtaining germination by planting scarified seeds 1 cm deep in different media. First signs of germination are usually seen within 10 days of planting. In 15 to 25 days, seedlings are small rosettes with true leaves, approximately 1.5 cm in diameter. Small leaves continue to form until the plant is approximately 5 cm tall, at which time the first spines are produced. During the remainder of its life, the plant produces no more leaves, only spines. The juvenile stage of the plant, from seed germination until spines begin to form, requires 4 to 6 months in the field. In Europe, large-scale germination in pots and direct seeding into the field have been practiced in the past (Rudolf 1974).

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Ulmaceae—Elm family

Ulmus L.

elm

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Growth habit, occurrence, and use. About 20 species of elm—the genus *Ulmus*—are native to the Northern Hemisphere. There are no native elms in western North America but some are found in northeastern Mexico (Johnson 1973). American elms are much loved as street trees for their arching branches and most elms species are valued for their hard, tough wood and many have been planted for environmental purposes. The natural ranges of 13 of the more important species are listed in table 1.

Since the 1930s, however, most elms in North America have been killed by the Dutch elm fungus, *Ophiostoma ulmi* (Buisman) Nannf., or by phloem necrosis, which is caused by a microplasma-like organism (Sinclair and others 1987). The Dutch elm disease was discovered in 1930 in Ohio. Dutch elm disease is transmitted when the European elm beetle, *Scolytus multistriatus* (Marsham), and the native elm bark beetle, *Hylurgopinus rufipes* Eichoff, feed on the tree (Burns and Honkala 1990). Phloem necrosis is spread by the

Table 1—*Ulmus,* elm: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***U. alata* Michx.**	**winged elm,** cork elm, wahoo	Virginia to Missouri, S to Oklahoma & E Texas, E to central Florida
***U. americana* L.**	**American elm,** water elm, soft elm, white elm	Quebec to E Saskatchewan, S to North Dakota, Oklahoma, & Texas, E to central Florida
***U. crassifolia* Nutt.**	**cedar elm,** basket elm, red elm, southern rock elm	SW Tennessee, Arkansas, & S Oklahoma to S Texas, Louisiana & W Mississippi
***U. glabra* Huds.** *U. scabra* Mill. *U. montana* With. *U. cammpestris* L. in part	**Scots elm,** Scotch elm, Wych elm	N & central Europe & Asia Minor
***U. japonica* (Sarg. ex Rehd.) Sarg.** *U. campestris* var. *japonica* Rehd. *U. davidiana* var. *japonica* (Rehd.) Nakai	**Japanese elm**	Japan & NE Asia
***U. laevis* Pall.** *U. pedunculata* Pall. *U. effusa* Willd.; *U. racemosa* Borkh.	**Russian elm,** spreading elm, European white elm'	Central Europe to W Asia
***U. minor* Mill.** *U. carpinifolia* Gled.	**Smoothleaf elm,** field elm,	Central & S Europe, England, Algeria, & Near East
***U. parvifolia* Jacq.** *U. chinensis* Pers.	**Chinese elm,** leatherleaf elm, lacebark elm	N & central China, Korea, Japan, & Formosa
***U. procera* Salisb.**	**English elm**	S & central England, NW Spain
***U. pumila* L.**	**Siberian elm,** Chinese elm, dwarf Asiatic elm	Turkestan, E Siberia, & N China
***U. rubra* Mühl.** *U. fulva* Michx.	**slippery elm,** grey elm, red elm, soft elm (lumber)	SW & Quebec to E North Dakota, S to W Oklahoma & SE & E Florida
***U. serotina* Sarg.**	**September elm,** red elm	Kentucky and S Illinois, S to N Alabama & NW Georgia; also in Arkansas & E Oklahoma
***U. thomasii* Sarg.** *U. racemosa* Thomas	**rock elm,** cork elm	Vermont to S Ontario, central Minnesota & SE South Dakota, S to E Kansas, E to Tennessee & New York

Sources: Brinkman (1974), Maisenhelder (1966), Rudolf (1937).

whitebanded elm leafhopper, *Scaphoideus luteolus* (Van Duzee) and root grafts (Burns and Honkala 1990). Only Chinese, Japanese, and Siberian elms (Krüssman 1960) are resistant to these diseases. Although American elms now are only a small percentage of the large-diameter trees in mixed forest stands, beautiful old specimens of American elm still exist in some isolated city parks and along streets, for example, in Central and Riverside Parks in Manhattan (Barnard 2002).

Flowering and fruiting. Elm flowers are perfect. Selfing rarely occurs in elms due to their high degree of self-incompatibility, with the exception of Siberian elm, which is self-compatible (Townsend 1975). American elm has twice as many chromosomes (2n = 56) as the other elm species common to North America, making it hard to cross-pollinate different species to impart disease resistance to American elm (Burns and Honkala 1990).

Most of the elms commonly grown in North America have protogynous flowers, where the stigma becomes receptive to pollen before the male anthers dehisce (Burns and Honkala 1990). Three species—rock, Siberian and Russian elms—have protandrous flowers, where the male anthers dehisce before the stigma is receptive. The elms are one of the few tree genera where the normal flowering period varies more than 2 to 3 weeks among species that are sexually compatible (Santamour 1989). Five floral stages have been identified: (1) stigma visible; (2) stigma lobes reflexed above anthers; (3) anthers dehiscing; (4) anther dehiscence complete and stigma wilting; (5) stigma shriveled, ovule green, and enlarged (Lee and Lester 1974). Pollination at stage 2 yielded the most viable seed (81%) followed by stage 1, stage 3, stage 4, and finally stage 5 (Lee and Lester 1974).

The perfect, rather inconspicuous inflorescences usually are borne in the spring before the leaves appear except for cedar, lacebark, and red elms, which flower in the fall (table 2). The inflorescences are fascicles, racemes, or racemose cymes measuring <2.5 up to 5 cm long (Fernald 1970). American, Scots, and rock elms have pendulous inflorescences (FNAEC 1997). Individual flowers are borne on pedicels measuring 0.4 to 1 cm long. The flowers have a calyx with 3 to 9 lobes, 3 to 9 stamens, and white stigmas with 2 styles (Fernald 1970; Radford and others 1968). Most of the elm species have reddish anthers,which gives the trees their characteristic flower color (FNAEC 1997; Johnson 1973).

The fruit is a 1-cell samara that ripens a few weeks after pollination and consists of a compressed nutlet surrounded by a membranous wing (figures 1 and 2). Winged, cedar, slippery, red, and rock elm seeds have pubescent samaras (Hora 1981). The seed is centrally located within the wing for slippery, Siberian, lacebark, and Scots elms (Hora 1981). The apex of the wing can be shallowly or deeply notched (FNAEC 1997). American elm seeds have 2 inward curving beaks at the wing's apex (Dirr 1998). Elm seeds have no endosperm and are dispersed by wind, water, or animals (Burns and Honkala 1990). Most species produce good seedcrops at 2- or 3-year intervals (table 3).

Collection of fruits. Elm seeds can be collected by sweeping them up from the ground soon after they fall or by beating or stripping the seeds from the branches. The large seeds of rock elm are greatly relished by rodents (Dore 1965), however, and usually must be picked from the trees. American elm samaras fall within 91 m of the parent tree (Burns and Honkala 1990). Rock elm samaras are carried no more than 40 to 45 m from the parent tree, but their buoyant

Table 2—*Ulmus*, elm: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal	Seed size (mm)
U. alata	—	Feb–Apr	Apr	Apr	6–8
U. americana	From S to Canada	Feb–May	Late Feb–June	Mid-Mar–mid-June	13
U. crassifolia	SE US	Aug–Sept	Sept–Oct	Oct	6–13
U. glabra	Europe & Asia Minor	Mar–Apr	May–June	May–June	15–25
U. japonica	Japan	Apr–May	June	—	—
U. laevis	Massachusetts	Apr–May	May–June	May–June	10–15
U. parvifolia	NE US	Aug–Sept	Sept–Oct	Sept–Oct	10
U. pumila	E central US	Mar–Apr	Apr–May	Apr–May	10–14
U. rubra	F S to Canada	Feb–May	Apr–June	Apr–June	12–18
U. serotina	SE US	Sept	Nov	Nov	10–13
U. thomasii	NE US	Mar–May	May–June	May–June	13–25

Sources: Asakawa (1969), Brinkman (1974), Burns and Honkala (1990), Dirr (1998), FNAEC (1997), Hora (1981), Little and Delisle (1962), Loiseau (1945), Pammel and King (1930), Petrides (1958), Rehder (1940), Spector (1956), Stoeckeler and Jones (1957), Sus (1925) ,Vines (1960), Wappes (1932), Wyman (1947).

Figure 1—*Ulmus*, elm: samaras of *U. alata*, winged elm (**top left**); *U. americana*, American elm (**top right**); *U. parvifolia*, Chinese elm (**middle left**); *U. pumila*, Siberian elm (**middle center**); *U. rubra*, slippery elm (**middle right**); *U. crassifolia*, cedar elm (**bottom left**); and *U. thomasii*, rock elm (**bottom right**).

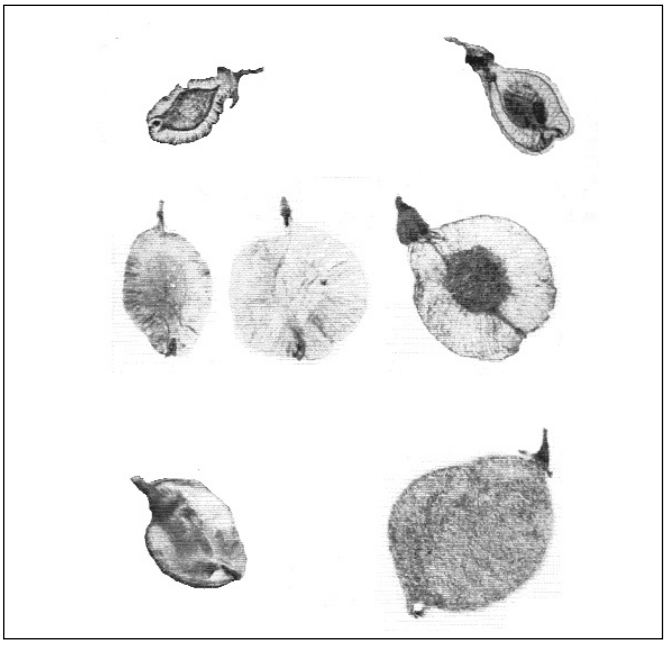


Figure 2—*Ulmus alata*, winged elm: longitudinal section through a seed.

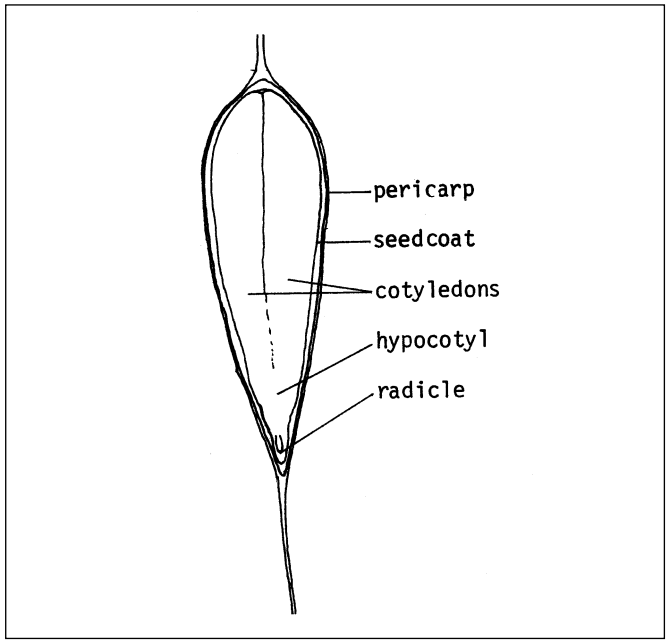


Table 3—*Ulmus,* elm: height, seed-bearing age, seed crop frequency, and fruit ripeness criteria

Species	Height at maturity (ft)	Year first cultivated	Minimum seed-bearing age (yr)	Years between large seedcrops	Ripe fruit color when ripe
U. alata	50	1820	—	—	Reddish green
U. americana	120	1752	15	—	Greenish brown
U. crassifolia	100	—	—	—	Green
U. glabra	130	Long cultivated	30–40	2–3	Yellow-brown
U. japonica	100	1895	—	2	—
U. laevis	100	Long cultivated	30–40	2–3	Yellow-brown
U. parvifolia	80	1794	—	—	Brown
U. pumila	80	1860	8	45	Yellow
U. rubra	70	1830	15	2–4	Green
U. serotina	60	1903	—	2–3	Light green to brownish
U. thomasii	100	1875	20	3–4	Yellow or brownish

Sources: Brinkman (1974), Burns and Honkala (1990), Dore (1965), FNAEC (1997), George (1937), Little and Delisle (1962), McDermott (1953), Van Dersal (1938), Vines (1960), Wappes (1932).

samaras can be carried by water and are frequently found along stream and lake banks (Burns and Honkala 1990). In rock elm, 90 to 100% of the mature seeds are viable and the seeds ripen about 2 to 3 weeks after American elm seeds (Burns and Honkala 1990).

Storjohann and Whitcomb (1977) collected lacebark elm seeds at Oklahoma State University and found that 75 to 80% of the seeds were empty. They also found that lacebark elm seeds are the most viable if collected before a hard freeze. Freshly collected fruits should be air-dried for a few days before being sown or stored. The number of seeds per weight varies widely, even within species (table 5).

Extraction and storage of seeds. Although the fruits can be de-winged by putting them into bags and beating with flails, this has been found to damage the seeds of American and Siberian elms (Cram and others 1966; George

1937). Elm seeds can be cleaned with an air-screen cleaner in a reverse procedure—blowing out the seeds, and catching the heavier leaves and twigs (Myatt 1996) with the air vents wide open on both sides of the cleaner. A large round-holed 9.9-mm screen (#25) is placed on top of the cleaner to separate the seeds from the leaves and a small round-holed 2.4-mm screen (#6) is placed on the bottom to separate the twigs from the seeds (Myatt and other 1998). Only 3 to 7% of the seeds blown out of the air chute in the back of the air-cleaner were good seeds (Myatt and others 1998).

Fruits usually are sown or stored with the wings attached. Elm seeds are orthodox in storage behavior and should be stored at low temperatures and moisture contents in sealed containers (table 4). Dessication of smoothleaf elm seeds to 3.3% moisture content did not reduce germination (Tompsett 1986). When the temperature of storage was increased at constant moisture contents, seed longevity was reduced within the range of –13 to 52 °C. Smoothleaf elm seeds stored at 22% moisture content (fresh-weight basis) died after 7 days at –75 C°, but seeds stored at 19% moisture content lost no germination ability. Lowering the storage temperature from –13 to –75 °C did not increase seed longevity. Tompsett (1986) found that a 5% moisture content and a temperature of –20 °C or lower maintains the long-term seed viability for smoothleaf elm seeds. Tylkowski (1989) reported that Russian elm seeds dried to 10% moisture could be stored at –1 to –3 °C for 5 years without losing any viability; however, after 6 years of storage, a 20% decrease in germination was observed. Siberian elm seeds with 3 to 8% moisture content have been stored at 2 to 4 °C in sealed containers for 8 years (Dirr and Heuser 1987). Air-dried Scots elm seeds stored at 1 to 10 °C were only viable for 6 months (Dirr and Heuser 1987).

Dried American elm seeds stored at 0, 10, and 20 °C declined from 65 to 70% germination before storage to less than 10% after 10.5 months of storage (Steinbauer and Steinbauer 1932). Another lot of dried American elms seeds stored at 20 °C exhibited a steady, continuous decline in germination when stored for 14 to 51 weeks compared to fresh seed germination values (Steinbauer and Steinbauer 1932). Barton (1939, 1953) found that a 75% germination value for American elm seeds was retained after 15 years of seed storage at –4 °C with a 3% seed moisture content .

Pregermination treatments. Under natural conditions, elm seeds that ripen in the spring usually germinate in the same growing season; seeds that ripen in the fall germinate in the following spring. Although seeds of most elm species require no presowing treatment, practically all the seeds in some seedlots of American elm remain dormant until the second season (Rudolf 1937). Dormant American elm seedlots should receive cold stratification for 2 to 3

Table 4—*Ulmus,* elm: seed storage conditions

Species	Seed moisture (%)	Storage temp (°C)	Viable period (yr)
U. alata	Air-dried	4	1
U. americana	3–4	–4	15
	Air-dried	4	2
U. crassifolia	Air-dried	4	1
U. glabra	Air-dried	1–10	0.5
U. laevis	Air-dried	22	0.5
U. parvifolia	10–15	0	0.5
U. pumila	3–5	2–4	8
U. thomasii	Air-dried	Cold	—

Sources: Barton (1939, 1953), Brinkman (1974), Heit (1967a&b), Kirby and Santelmann (1964), Rohmeder (1942), Sus (1925).

Table 5—*Ulmus,* elm: seed yield data

Species	Place collected	Fruit/vol		Cleaned seeds (x1,000)/weight				Samples
				Average		Range		
		kg/hl	lb/bu	/kg	/lb	/kg	/lb	
U. alata	Mississippi	—	—	245	112	222–269	101–119	4
U. americana	—	5.8	4.5	156	71	106–240	48–109	14
U. crassifolia	Mississippi	—	—	147	67	130–135	59–61	5
U. glabra	Europe	4–6.5	3–5	88	40	66–99	30–45	12+
U. japonica	Japan	—	—	12.8	6	—	—	2+
U. laevis	Russia	—	—	140	63	117–205	53–93	20+
U. parvifolia	US, Japan	—	—	265	121	250–372	114–169	6+
U. pumila	—	—	—	158	72	88–261	40–119	35+
U. rubra	—	—	—	90	41	77–119	35–54	10
U. serotina	—	—	—	328	149	—	—	—
U. thomasii	—	7.7–10.3	6–8	15	7	11–15	5–7	5

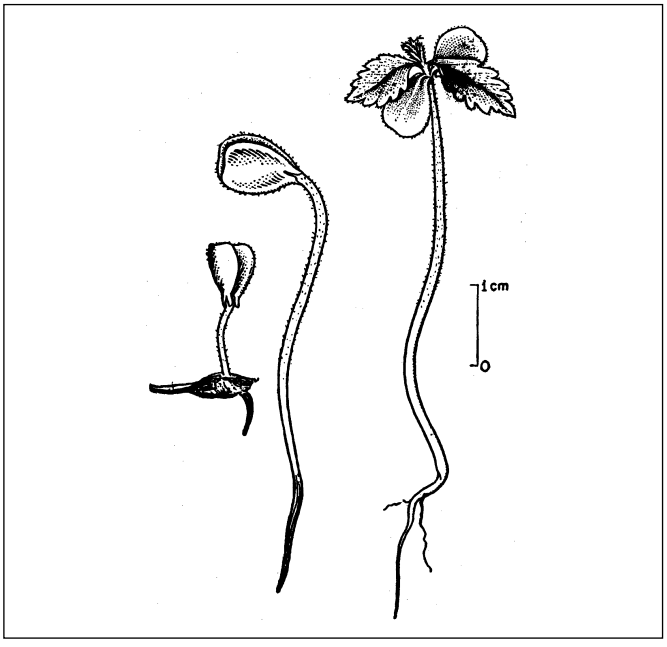
Sources: Asakawa (1969), Brinkman (1974), Engstrom and Stoeckeler (1941), Goor (1955), Gorshenin (1941), Heit (1969), Rafn and Son (1928), Stoeckeler and Jones (1957), Sus (1925), Swingle (1939), Taylor (1941), Van Dersal (1938), Wappes (1932).

months (Dirr and Heuser 1987). Seeds of slippery elm, especially from northern sources, also may show dormancy; 70% of fresh seeds germinated and 57% germinated after 2 months of cold, moist stratification (Dirr and Heuser 1987). Stratification at 5 °C for 60 to 90 days before sowing improves germination of cedar, smoothleaf, and September elms (Brinkman 1974; Dirr and Heuser 1987; Maisenhelder 1968).

Winged, Scots, Japanese, English, Russian, Siberian, and rock elms have no pregermination requirements (Dirr and Heuser 1987). Fresh seedlots of Scots elm germinated at 98%, but after 2 months of cold, moist stratification, only 88% germinated (Dirr and Heuser 1987). English elm rarely produces seeds, but fresh seeds will germinate at 100% with or without 2 months of stratification (Dirr and Heuser 1987). Fresh Siberian elm seeds germinated 96% and cold stratification did not improve germination (Dirr and Heuser 1987). Fresh lacebark elm seeds will germinate without pretreatment, but once dried they require 1 to 2 months of cold, moist stratification (Dirr and Heuser 1987).

Germination tests. Official testing rules for American elm call for alternating temperatures of 30 °C (day) for 8 hours and 20 °C (night) for 16 hours for 14 days on wet blotters and 10 days at a constant 20 °C for Chinese and Siberian elms (AOSA 2001). American elm seeds can also germinate well at alternating temperatures of 21 °C (day) and 10 °C (night) (Burns and Honkala 1990). The International Seed Testing Association (1999) suggests testing for 14 days on wet blotters for all 3 species. ISTA also suggests removal of the pericarp if germination is slow. Germination tests of most species may also be made on sand or peat in germinators at alternating temperatures of 30 °C (day) and 20 °C (night). Rock elm seeds germinated 70 to 80% in a peat moss medium (Burns and Honkala 1990). Light requirements may vary among species (table 6). American elm can germinate in darkness but germination is increased with the addition of light (Burns and Honkala 1990).

Figure 3—*Ulmus americana*, American elm: seedling development at 1, 3, and 21 days after germination.



Germination is epigeal (figure 3); it usually peaks within 10 days. Seedlots of stratified seeds complete germination in 10 to 30 days. With American elm seeds, germination can extend up to 60 days; seeds can lay on flooded ground for a month without adversely affecting germination (Burns and Honkala 1990). Radicles of rock elm emerge in 2 to 3 days in a petri dish and are 2.5 to 3.8 cm (1 to 1.5 in) long by the 5th day; cotyledons opened about the 5th or 6th day (Burns and Honkala 1990). Winged elms cotyledons are oval with shallowly notched apexes and heart-shaped bases and may persist 1 to 2 months on the seedling with primary leaves appearing 1 week after germination in natural forest conditions (Burns and Honkala 1990).

Nursery practice. Seeds of elm species ripening in the spring are usually sown immediately after collection, whereas seeds of fall-ripening species or of species requiring stratification are usually planted the following spring (table 7). Beds should be kept moist until germination is complete; shading is not usually necessary. From 5 to 12% of the viable cedar elm seeds sown can be expected to produce plantable stock (Burns and Honkala 1990). One-year-old seedlings usually are large enough for field planting. Rock elm seedlings have a persistent dormant bud, so seedlings rarely develop more than a single pair of true leaves in the first growing season (Burns and Honkala 1990). In northern Wisconsin, rock elm 1.5+0 nursery stock averaged 27 cm (10.6 in) in height 5 years after planting and 52 cm (20.5 in) in height 10 years after planting; first-year survival was 85% and 10th-year survival was 32% (Burns and Honkala 1990). To improve survival in semiarid regions, trees often are transferred into containers after 1 year in the seedbeds (Goor 1955). Slippery elm is commonly used as rootstock when grafting hybrid elms (Burns and Honkala 1990).

Table 6—*Ulmus,* elm: germination test conditions and results

Species	Germination test conditions* Medium	Temp (°C) Day	Night	Days	Germinative energy Amount (%)	Germinative capacity Period (days)	Avg (%)	Samples	Purity (%)
U. alata	Soil	32	21	15	76	7	91	6	—
U. americana	Paper pads	30	20	14	—	—	—	—	—
	Kimpak	30	20	28	—	—	67	1	—-
	—	—	—	13–60	55	7	64	15	92
U. crassifolia	Soil	32	21	80	56	78	56	2	—
U. glabra	Germinator or sand	21–30	20–25	30–60	—	—	44	72+	—
U. laevis	Germinator or sand	21	21	30	—	—	65	22+	85
U. parvifolia	Paper pads	20–29	20	10–60	—	—	55	2+	64
U. pumila	Paper pads	—	—	10	—	—	—	—	—
	Kimpak	30	20	28	—	—	81	1	—
	Germinator or sand	20–30	20	30	55	10	76	48	90
U. rubra	Sand	30	20	60	21	10	23	5	94
U. serotina	Soil	32	21	30	68	20	72	1	—
U. thomasii	Sand or petri dish	30	20	30	77	8	81	11	95

Sources: Arisumi and Harrison (1961), AOSA (2001), Engstrom and Stoeckeler (1941), Gorshenin (1941), Heit (1967a&, 1968), ISTA (1999), Johnson (1946), Kirby and Santelman (1964), Maisenhelder (1968), McDermott (1953), NBV (1946), Rafn and Son (1928), Rohmeder (1942), Spector (1956), Stoeckeler and Jones (1957), Sus (1925), Swingle (1939), USDA FS (2002), Wappes (1932).

* Light for 8 hours or more per day is recommended for American elm (AOSA 2001; ISTA 1999; McDermott 1953). Light is neither required nor inhibitory for germination of winged elm (Loiseau 1945), and Chinese and Siberian elms (AOSA 2001; ISTA 1999).

Table 7—*Ulmus,* elm: nursery practice

Species	Sowing season*	Seedlings/area /m²	/ft²	Sowing depth mm	in	Tree percent	Out-planting age (yrs)
U. alata	Summer	—	—	0–6.4	0–1/4	—	1
U. americana	Spring	5	2	6.4	1/4	12	1
U. crassifolia	Spring	—	—	0–6.4	0–1/4	—	1
U. glabra	Summer	—	—	0–6.4	0–1/4	—	—
U. laevis	Summer	—	—	0-6.4	0–1/4	6	1–2
U. parvifolia	Spring	25–30	2–3	4.8–6.4	3/16–1/4	12–20	1–2
U. pumila	Summer	—	—	6.4	1/4	3–7	1–2
U. rubra	Spring	25	2	6.4	1/4	—	1
U. serotina	Spring	—	—	0–6.4	0–1/4	—	1
U. thomasii	Spring	15–38	1–4	6.4	1/4	—	2

Sources: Baker (1969), Deasy (1954), Engstrom and Stoeckeler (1941), George (1937), Kirby and Santelman (1964), Rohmeder (1942), Stoeckeler and Jones (1957), Sus (1925), Swingle (1939), Toumey and Korstian (1942).

* Spring-sowing was preceded by stratification in sand or in a plastic bag at 4 to 5 °C for 60 days.

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Lauraceae—Laurel family

Umbellularia californica (Hook. & Arn.) Nutt.

California-laurel

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Growth habit, occurrence, and uses. The genus *Umbellularia* contains a single species—*Umbellularia californica* (Hook. & Arn.) Nutt.—that has many common names (Coombes 1992; Stein 1990), the best known being California-laurel, California-olive, Oregon-myrtle, myrtlewood, bay, laurel, and pepperwood. California-laurel is a broad-leaved evergreen that matures either as a shrub or tall forest tree. Over much of its range, it attains heights of 12 to 24 m and diameters of 46 to 76 cm, but near the ocean, in the chaparral, and on other severe or rocky sites it is confined to prostrate or shrub sizes (Harlow and others 1979; Jepson 1910). In the protected bottomlands of southern Oregon and northern California, mature trees are 91 to 305 cm in diameter and 30 or more m tall (Harlow and others 1979). A maximum circumference of 1,387 cm at 137 cm above ground (AFA 2000) and a maximum height of 53.3 m have been reported (Sargent 1961).

Several racial variations are recognized. *Umbellularia californic*a forma *pendula* Rehd. is an uncommon, broad-spreading tree distinctive for its pendulous branchlets that contrast strongly with typically ascending branch growth (Jepson 1910; Rehder 1940). *U. californica* var. *fresnensis* Eastwood has fine white down on the lower surfaces of leaves and branches of the panicle (Eastwood 1945). Several forms that Jepson (1910) describes—gregarious, rockpile, dwarf, and prostrate—may indicate other varietal differences.

The range of California-laurel spans more than 11 degrees of latitude, from near the 44th parallel in the Umpqua River Valley of Douglas County, Oregon, south beyond the 33rd parallel in San Diego County, California, nearly to the Mexican border. California-laurel is widely distributed in the coast ranges and less abundantly in inland valleys and the Siskiyou and Sierra Mountains (Sudworth 1908). It may be found from sea level to 1,220 m in much of its range, and from 610 to 1,520 m in southern California (Jepson 1910). Pure, dense stands of California-laurel develop in some areas, but more often it is intermixed with other tree and shrub species. It grows in many kinds of soils under both cool-humid and hot-dry atmospheric conditions (Stein 1990). In xeric climates, it is most prominent where soil moisture is favorable—on alluvial deposits or protected slopes, along watercourses, near springs and seeps—but in its shrub form, it also is found on dry slopes and is a common component of chaparral (Sampson and Jespersen 1963).

All parts of the tree have served human needs. Wood of this species compares favorably in machining quality with the best eastern hardwoods (Davis 1947) and is used for woodenware, interior trim, furniture, paneling, veneer, and gunstocks. Burls and other growths with distorted grain are especially prized for making the gift and novelty items that are marketed extensively as "myrtlewood." Dried leaves are used for seasoning meats and soups (McMinn 1970). In an earlier day, Hudson Bay Company trappers brewed a comforting tea from the leaves to overcome chill (Ross 1966). David Douglas learned that hunters made a drink from the bark and declared it "by no means an unpalatable beverage" (Harvey 1947). Native Americans ate substantial quantities of the fruit and seeds, made a drink from the bark of the roots, and used the leaves for several internal and external medicinal purposes, including vermin control (Chesnut 1902).

Extracts of the leaves, seeds, and wood have strong chemical properties and should be used with caution. Vapor from the aromatic leaves can cause sneezing, headache, sinus irritation, other severe discomforts, and even unconsciousness (Drake and Stuhr 1935; Peattie 1953). The leaves contain considerable menthol (Stein 1974) and the ketone umbellulone, which when extracted from the leaf oil, interferes strongly enough with respiration, heartbeat, and blood circulation to cause death in laboratory animals (Drake and Stuhr 1935). Umbellulone also has fungicidal and germicidal properties (Drake and Stuhr 1935). Oils from the wood,

leaves, and seeds have been sold for pharmaceutical purposes such as treating catarrh, nervous disorders, rheumatism, meningitis, intestinal colic, and dyspepsia (Peattie 1953; Sargent 1895; Stuhr 1933).

California-laurel is used to a moderate extent as an ornamental evergreen. It has thick, glossy, medium-to-dark green persistent leaves that turn orange or yellow before they drop individually and contrasting pale yellow flowers. The very dense aromatic foliage often shapes naturally into a pleasing, symmetrical, rounded crown. Since it was first cultivated in 1829 (Rehder 1940), it has demonstrated the ability to grow well far outside its natural range (Stein 1958). It can be grown as a decorative potted plant for lobbies and patios and will tolerate moderate pruning (Kasapligil and Talton 1973).

California-laurel also has wildlife values—young sprouts are choice browse in spring and summer. Year-long use is rated by Sampson and Jespersen (1963) as good to fair for deer (*Odocoileus* spp.) and fair to poor for cattle, sheep, and goats. Longhurst and others (1952) list it as a principal browse species for deer in the north coastal ranges of California. Silver gray-squirrels (*Sciurus griseus*), dusky-footed wood rats (*Neotoma fuscipes*), and Steller's jays (*Cyanocitta stelleri*) feed on the seeds extensively (Bailey 1936; Van Dersal 1938). Hogs eat both seeds and roots (Jepson 1910; Van Dersal 1938).

Flowering and fruiting. California-laurel flowers regularly and often profusely. The small, pale yellow, perfect flowers grow on short-stemmed umbels that originate from leaf axils or near the terminal bud (figure 1). Flower buds develop early; those for the following year become prominent as current-year fruits are maturing. Within its long north–south range, California-laurel has been reported to flower in all months from November to May, beginning before new leaves appear (Jepson 1910; Kasapligil and Talton 1973; Rehder 1940; Unsicker 1974). The flowering period may stretch into late spring and summer with the occasional appearance of flowers originating in axils of the current year's developing leaves (Sargent 1895). California-laurel flowers at an early age; flowers have been observed on short whiplike shrubs and on 1-year-old sucker growth that originated on a long broken stub. Small insects appear to be the chief pollinaters (Kasapligil 1951).

Seedcrops are abundant in most years (Stein 1974). Although umbels bear 4 to 9 flowers each, generally only 1 to 3 fruits set (Jepson 1910). The age when a tree first bears fruit, the age for maximum production, and the average quantity produced have not been reported. Seeds are produced in abundance after trees are 30 to 40 years old (Harlow and others 1979). Damage to developing seedcrops by insects, birds, or diseases has not been reported.

Collection, extraction, and storage. The fruits—acrid drupes each containing a single, large, thin-shelled seed—ripen in the first autumn after flowering (Rehder 1940; Sargent 1895; Sudworth 1908). As the drupes mature, their thin, fleshy hulls change from medium green to speckled yellow green (Britton 1908; Sudworth 1908) (figure 1), pale yellow (Eliot 1938), or various other hues, ranging from yellow-green tinged with dull red or purple (Peattie 1953; Sargent 1895) through purplish brown (Jepson 1910; Kasapligil 1951) to purple (Kellogg 1882; Sargent 1892; Torrey 1856). Ripe drupes may be yellow-green on one tree and dark purple on an adjacent tree (Stein 1974).

Drupes fall stemless to the ground in late autumn or winter and are dispersed by gravity, wind, animals, and water (McBride 1969). Seeds are collected simply by gathering fallen drupes—if squirrels and other animals don't get there first. Shaking ripe drupes from the tree should provide a good means for making quick, efficient collections.

When soft, the fleshy hulls are readily removed from the seeds by hand. The hulls can also be removed easily by machines used for de-pulping drupes if quantity processing is required. Mirov and Kraebel (1937) obtained about 300 cleaned seeds (figure 2) from 0.45 kg (1 lb) of drupes. For 8 samples processed at Davis, California (Lippitt 1995), the seed count averaged 547/kg (248/lb) and ranged from 403 to 675/kg (183 to 306/lb).

Figure 1—*Umbellularia californica*, California-laurel: yellow-green mature drupe suspended from its conical capula.

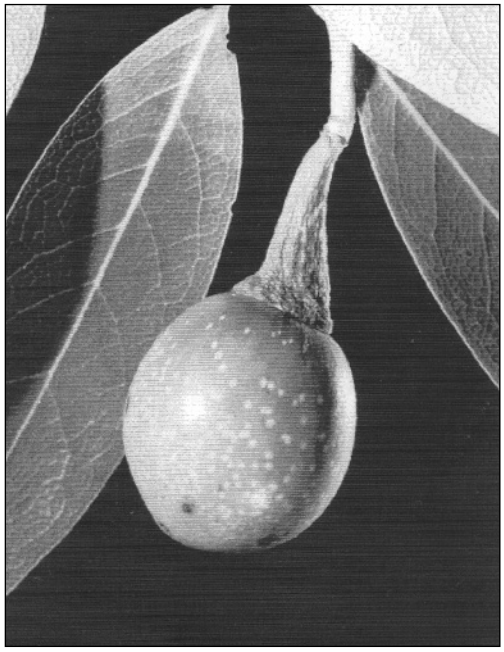


Figure 2—*Umbellularia californica*, California-laurel: exterior views of cleaned seeds.

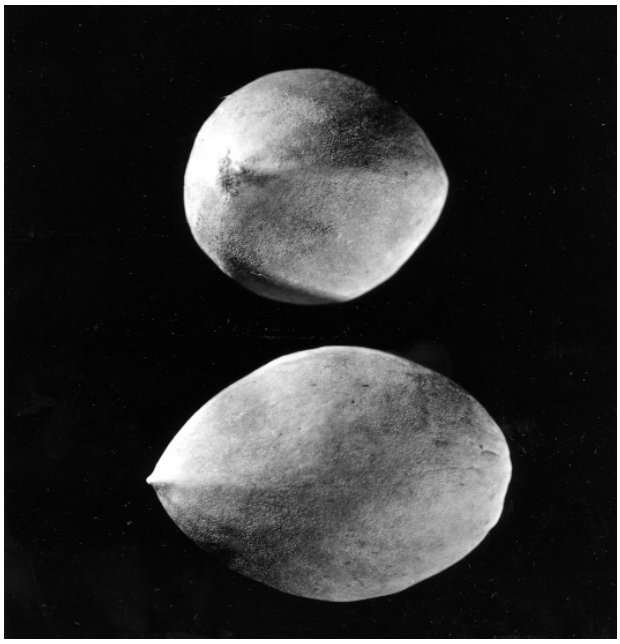
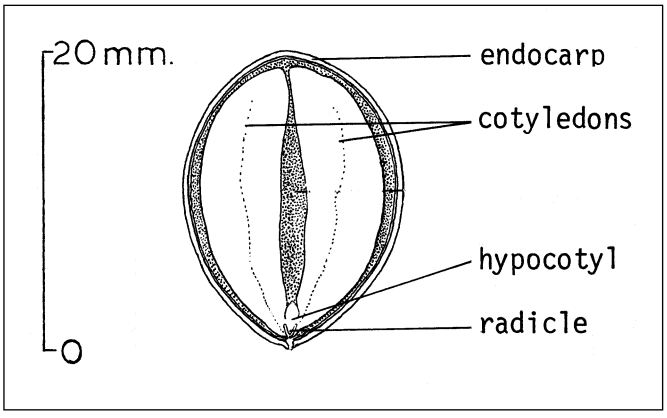


Figure 3—*Umbellularia californica*, California-laurel: tudinal section through a seed.

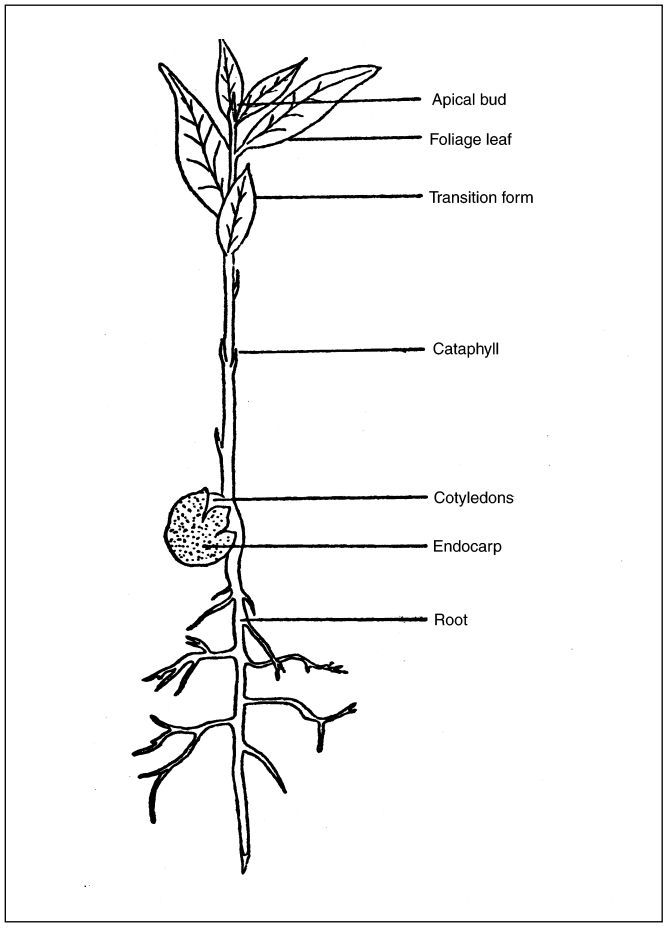


Seeds of California-laurel have lost viability in storage even at low temperatures, so yearly collection of fresh seeds is advised (Stein 1974). Viability has been maintained for 6 months when seeds were stored at 3 °C in wet, fungicide-treated vermiculite (McBride 1969). Storage trials have been very limited and tests of cool, moist storage at different moisture contents are needed. Highest germination (81%) was obtained from a seedlot with 32% moisture content (Lippitt 1995). Under favorable natural conditions, seeds on the ground retain their viability over winter, but under adverse conditions, viability may prove transient.

Seed treatment and germination. Fresh untreated seeds will germinate under room or outdoor conditions in peat moss, sawdust, vermiculite, or light-textured soil but may require 3 months or longer (Kasapligil 1951; Mirov and Kraebel 1937; Stein 1974). Germination can be speeded by scarifying, cracking, or removing the endocarp or by stratifying the seeds, but it still may require about 2 months (Kasapligil 1951; McBride 1969; Stein 1974). In light soil, 20 to 25% of untreated seeds germinated; with stratification, germination nearly doubled (Stein 1974). In 16 lots of seeds collected in 1969 from Oregon and California sources, germination by the end of March ranged from 0 to 82% after January planting deep in pots of peat or vermiculite. Parts of seedlots held in a refrigerator at 4.4 °C from November to January germinated somewhat better than those immediately planted outdoors in a peat–vermiculite mixture. The better seedlots germinated equally well in several contrasting test conditions (Stein 1974).

In comparison tests made in petri dishes, California-laurel germination was highest in 30 days under a temperature regime of 16 °C day, 7 °C night, and when evaporative stress was minimal (McBride 1969). Germination did not appear affected by light level but was highest in soil with moisture tension at 4 to 10 atmospheres.

Figure 4—*Umbellularia californica*, California-laurel: 4-month-old seedling (from Stein 1974, courtesy of Baki Kasapligil 1951).



Seedling development and nursery practice. Under forest conditions, germination has been reported to take place in autumn soon after seedfall (Harlow and others 1979; Sargent 1895; Sudworth 1908) or in late winter and spring (Stein 1958, 1974). Covered seeds germinate best, but the large seeds do not bury readily without ground disturbance or silt deposition by high water. Seedling establishment is uncommon in the drier parts of California except in protected areas and where the ground is disturbed (Jepson 1910).

Germination is hypogeal, and the fleshy cotyledons remain within the endocarp and attached to the seedling until midsummer, when the plant may be 15 to 20 cm tall (Kasapligil 1951; Sargent 1895). Generally, there are 2 large cotyledons, sometimes 3, and no endosperm (figure 3) (Kasapligil 1951).

Young California-laurel seedlings appear flexible in their growth requirements. In the first 120 days, seedlings potted in vermiculite grew well at several levels of temperature, evaporative stress, soil moisture, and soil nutrients (McBride 1969). Seedlings grown at 18% or more of full sunlight produced the most dry weight. Seedlings produce leaves of several transitional forms as they develop (figure 4) and do not branch until they are 2 or 3 years old unless so induced by removal of the terminal bud (Kasapligil 1951). They soon develop a moderately stout taproot and are difficult to transplant if more than 1 year old unless grown in containers. Recovery after transplanting is often slow, and height growth may be limited for several seasons.

California-laurel may also be reproduced by cuttings (Stein 1974). Under field conditions, it sprouts prolifically from the root collar, stump, and fallen or standing trunk.

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Ericaceae—Heath family

Vaccinium L.

blueberry, cranberry

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Occurrence, growth habit, and uses. There are about 150 to 450 species (the number varies by authority) of deciduous or evergreen shrubs (rarely trees or vines) in *Vaccinium* (Huxley 1992b; LHBH 1976; Vander Kloet 1988). The majority of species are native to North and South America and eastern Asia (LHBH 1976; Vander Kloet 1988). Some of the more commonly cultivated North American species are listed in table 1. Like other members of the Ericaceae, *Vaccinium* species require an acidic (pH 4.0 to 5.2) soil that is moist, well drained, and high in organic matter (3 to 15%). Symptoms of mineral nutrient deficiency arise if soil pH exceeds optimum levels (LHBH 1976). Sparkleberry is one exception that grows well in more alkaline soils (Everett 1981). Many species of *Vaccinium* establish readily on soils that have been disturbed or exposed (Vander Kloet 1988).

Many species of *Vaccinium* are rhizomatous, thus forming multi-stemmed, rounded to upright shrubs or small trees ranging in height from 0.3 to 5.0 m (table 1). Cranberry forms a dense evergreen ground cover about 1 m in height (Huxley 1992b; Vander Kloet 1988).

Several species of *Vaccinium* are valued for their edible fruits. Historically, Native Americans consumed blueberries fresh or dried them for winter consumption (Vander Kloet 1988). In addition, they steeped the leaves, flowers, and rhizomes in hot water and used the tea to treat colic in infants, to induce labor, and as a diuretic (Vander Kloet 1988). Currently, most commercial blueberry production occurs in North America, where highbush blueberry accounts for more than two-thirds of the harvest (Huxley 1992a). Another species, rabbiteye blueberry, is more productive, heat resistant, drought resistant, and less sensitive to soil pH than highbush blueberry, but it is less cold hardy (Huxley 1992a; LHBH 1976). In more northern latitudes, the low-growing lowbush and Canadian blueberry bushes occur in natural stands. Their fruits are harvested for processing or the fresh fruit market (LHBH 1976).

Although cranberry has been introduced successfully into cultivation in British Columbia, Washington, and Oregon, Wisconsin and Massachusetts remain the largest producers; the crops for 2000 were estimated at 2.95 and 1.64 million barrels, respectively (NASS 2001).

Evergreen huckleberry grows along the Pacific Coast and is valued for its attractive foliage, which is often used in flower arrangements (Everett 1981). Species of *Vaccinium* also are prized as landscape plants. Lowbush forms are used to form attractive ground covers or shrubs. Two cultivars of creeping blueberry (*V. crassifolium* Andrews)—'Wells Delight' and 'Bloodstone'—form dense ground covers usually < 20 cm in height, varying only in texture and seasonal color change (Kirkman and Ballington 1985). Shrub-forming species add interest to the landscape with their attractive spring flowers and brilliantly colored fall foliage (Dirr 1990). Bird lovers also include *Vaccinium* spp. in their landscapes as the shrubs attract many birds when fruits ripen. In the wild, species of *Vaccinium* also serve as a source of food for many mammals (Vander Kloet 1988).

Geographic races and hybrids. Breeding programs have focused on improvement of species of *Vaccinium* since the early 20th century (Huxley 1992a). As a result, numerous hybrids and cultivars exist, each suited to specific growing conditions.

Flowering and fruiting. Perfect flowers are borne solitary or in racemes or clusters and are subterminal or axillary in origin (Vander Kloet 1988). White flowers, occasionally with a hint of pink, occur in spring or early summer, usually before full leaf development (table 2) (Dirr 1990). Rabbiteye and lowbush blueberries are generally self-sterile and must be interplanted to ensure fruit-set. Highbush blueberries are self-fertile, although yields can be improved by interplanting with different cultivars (Huxley 1992a). When mature, fruits of blueberries are many-seeded berries (figure 1), blue to black in color, often glaucous, ranging in size from 6.4 to 20 mm in diameter with a per-

Table 1—*Vaccinium,* blueberry and cranberry: nomenclature, plant height, and natural occurrence

Scientific name & synonym(s)	Common name(s)	Plant height (cm)	Occurrence
***V. angustifolium* Ait.** *V. lamarckii* Camp *V. nigrum* (Wood) Britt. *V. angustifolium* var. *hypolasium* Fern. var. *laevifolium* House var. *nigrum* (Wood) Dole var. *brittonii* Porter ex Bickn.	**lowbush blueberry,** late sweet blueberry, low sweet blueberry	18 ± 9	Labrador & Newfoundland; W to Manitoba & Minnesota; S to Illinois, Delaware, & Pennsylvania; mtns of Virginia & West Virginia
***V. arboreum* Marsh.** *V. arboreum* var. *glaucescens* (Greene) Sarg. *Batodendron andrachniforme* Small *Batodendron arboreum* (Marsh.) Nutt.	**sparkleberry,** farkleberry	311 ± 102	Virginia to central Florida, W to E Texas, central Oklahoma & SE Mississippi
***V. corymbosum* L.** *V. constablaei* Gray *V. corymbosum* var. *albiflorum* (Hook.) Fern. *V. corymbosum* var. *glabrum* Gray *Cyanococcus corymbosus* (L.) Rydb. *Cyanococcus cuthbertii* Small	**highbush blueberry,** American blueberry, swamp blueberry	230 ± 60	Atlantic Coast; W to E Texas & Illinois; absent from Mississippi, central Ohio, W Kentucky, W Tennessee, West Virginia, & central Pennsylvania
***V. macrocarpon* Ait.** *Oxycoccus macrocarpus* (Ait.) Pursh	**cranberry,** large cranberry, American cranberry	6 ± 3	Newfoundland, W to Minnesota, S to N Illinois, N Ohio, & central Indiana; Appalachian Mtns to Tennessee & North Carolina
***V. myrtilloides* Michx.** *V. angustifolium* var *myrtilloides* (Michx.) House *V. canadense* Kalm ex A. Rich. *Cyanococcus canadensis* (Kalm ex A. Rich) Rydb.	**Canadian blueberry,** velvet-leaf blueberry, velvetleaf huckleberry, sour-top blueberry	35 ± 14	Central Labrador to Vancouver Island, Northwest Territories SE to Appalachian Mtns
***V. ovatum* Pursh.**	**California huckleberry,** evergreen huckleberry, shot huckleberry	82 ± 42	Pacific Coast, British Columbia to California
***V. oxycoccos* L.** *V. palustre* Salisb. *Oxycoccus palustris* Pers. *Oxycoccus quadripetalus* Gilib.	**small cranberry**	2 ± 1	North American boreal zone to the Cascade Mtns in Oregon & to Virginia in the Appalachian Mtns
***V. virgatum* Ait.** *V. virgatum* var. *ozarkense* Ashe *V. virgatum* var. *speciosum* Palmer *V. parviflorum* Gray; *V. amoenum* Ait. *V. ashei* Rehd.; *V. corymbosum* var. *amoenum* (Ait.) Gray *Cyanococcus virgatus* (Ait.) Small *Cyanococcus amoenus* (Ait.) Small	**rabbiteye blueberry,** smallflower blueberry	300 ± 100	SE United States
***V. vitis-idaea* L.**	**lingonberry,** cowberry, foxberry, mountain cranberry	7 ± 3	New England & scattered throughout Canada; native to Scandinavia

Sources: GRIN (1998), Huxley (1992b), Vander Kloet (1988).

sistent calyx (table 3) (LHBH 1976). Cranberry fruits are many-seeded berries that are red at maturity and range from 1 to 2 cm in diameter (Huxley 1992b).

Collection of fruits, seed extraction, and cleaning. Small quantities of ripe fruits may be collected by hand-picking. Larger quantities, however, are usually harvested mechanically (Huxley 1992a). To extract seeds, fruits should be placed in a food blender, covered with water, and thoroughly macerated using several short (5-second) power bursts. More water is added to allow the pulp to float while the sound seeds (figures 2 and 3) settle to the bottom. Repeating this process several times may be necessary to achieve proper separation of seeds and pulp (Galletta and Ballington 1996). Seed weights are listed in table 3.

Table 2—*Vaccinium,* blueberry and cranberry: phenology of flowering and fruiting for cultivated species

Species	Flowering	Fruit ripening	Mature fruit color
V. angustifolium	May–June	July–Aug	Blue to black; glaucous
V. arboreum	May–June	Oct–Dec	Shiny black to glaucous blue
V. corymbosum	June	June–Aug	Dull black to blue & glaucous
V. macrocarpon	May–June	Sept–Oct	Red
V. myrtilloides	—	—	Blue & glaucous
V. ovatum	Mar–July	Aug–Sept	Blue & glaucous to dull black
V. virgatum	Mar–May	June–Aug	Black or glaucous blue
V. vitis-idaea	May–June	Aug	Red

Source: Ballington (1998), Crossley (1974), Dirr (1990), Vander Kloet (1988)

Figure 1—*Vaccinium*, blueberry: fruits (berries) of *V. angustifolium*, lowbush blueberry (**top**); *V. corymbosum*, highbush blueberry (**bottom**).

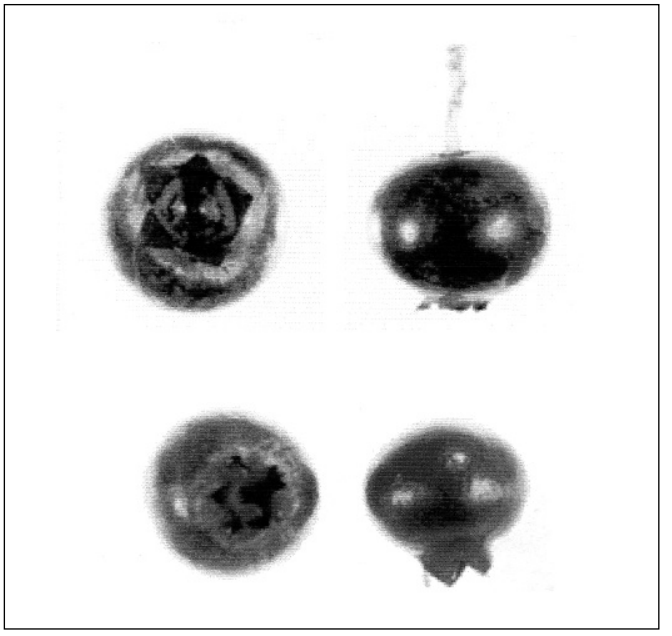


Table 3—*Vaccinium,* blueberry and cranberry: fruit and seed sizes of cultivated species

Species	Berry diameter (mm)	Cleaned seeds/weight /kg	/lb
V. angustifolium	8 ± 1	3.90×10^6	1.45×10^6
V. arboreum	8 ± 1	1.01×10^6	4.59×10^5
V. corymbosum	8 ± 1	2.20×10^6	1.00×10^6
V. macrocarpon	12 ± 2	1.09×10^6	4.95×10^5
V. myrtilloides	7 ± 1	3.81×10^6	1.73×10^6
V. ovatum	7 ± 1	2.99×10^6	1.36×10^6
V. oxycoccos	9 ± 2	1.46×10^6	6.62×10^5
V. virgatum	12 ± 4	—	—
V. vitis-idaea	9 ± 1	3.54×10^4	1.61×10^4

Sources: Huxley (1992b), Vander Kloet (1988).

Seed storage. There have been no long-term studies of blueberry seed storage, but there is enough information to suggest that the seeds are orthodox in their storage behavior. Sparkleberry seeds, for example, still germinated after being buried in the soil for 4 years in Louisiana (Haywood 1994). Aalders and Hall (1975) investigated the effects of storage temperature and dry seed storage versus whole-berry storage of lowbush blueberry. Seeds extracted from fresh berries and sown immediately germinated with 80% success. However, seeds stored dry at room temperature exhibited poor germination. Seeds stored dry at –23, –2, or 1 °C germinated in higher percentages than those stored in berries (uncleaned) at the same temperatures. Germination was not significantly different among the temperatures for dry stored seeds, nor between dry and whole-berry storage at –23 °C. However, if storage temperature was maintained at –2 or 1 °C, dry storage proved preferable to whole-berry storage.

Pregermination treatments. It has been well established that seeds of various species of *Vaccinium* are photoblastic and require several hours of light daily for germination (Devlin and Karczmarczyk 1975, 1977; Giba and others 1993, 1995; Smagula and others 1980). Although much debated, it appears that seeds of some *Vaccinium* species do not require any pretreatment for satisfactory germination. Devlin and Karczmarczyk (1975) and Devlin and others (1976) demonstrated that cranberry seeds would germinate after 30 days of storage at room temperature if light requirements were fulfilled during germination. Aalders and Hall (1979) reported that seeds of lowbush blueberry will germinate readily if they are extracted from fresh fruit and sown immediately. The literature regarding pretreatments for highbush blueberry is not conclusive. However, cold requirements among the various species appear to be species-specific. Although seeds of many species will germinate if sown immediately after they are extracted from fresh fruit, a dry cold treatment of 3 to 5 °C for about 90 days may increase germination or become necessary if

seeds are allowed to dry (Ballington 1998). Gibberellic acid (GA_3 or GA_{4+7}) treatment has been shown to promote germination. Although GA does not increase total germination, it reduces the hours of light necessary or in some instances overcomes the light requirement, thus stimulating early and uniform germination (Ballington 1998; Ballington and others 1976; Devlin and Karczmarczyk 1975; Giba and others 1993; Smagula and others 1980).

Germination tests. In studies to investigate the light requirement for seed germination of lowbush blueberry, Smagula and others (1980) found that seeds germinated in light exhibited an increase in both germination rate and cumulative germination in comparison to seeds germinated in darkness. Gibberellic acid treatment enhanced germination in the light as well as dark germination, with 1,000 ppm (0.1%) sufficient to overcome dark inhibition. Seed germination of highbush blueberry can be enhanced by GA_3 (Dweikat and Lyrene 1988). In 4 weeks, 4% germination of nontreated seeds was reported, whereas 50% germination of seeds treated with 900 ppm GA_3 (0.09%) was reported. Higher concentrations did not significantly affect germination. Ballington and others (1976) found that GA treatments did not influence the final germination percentage of seeds of 'Tifblue' rabbiteye blueberry. However, treatment of seeds with 100 (0.01%), 200 (0.02%), or 500 ppm (0.05%) GA_{4+7} resulted in seedlings that reached transplanting size 2 to 4 weeks earlier than did control or GA_3 treatments. The effects of GA treatment on seed germination of cranberry is similar. Devlin and Karczmarczyk (1977) found that cranberry seeds failed to germinate without light. However, seeds treated with 500 ppm GA showed 69% germination after 20 days in the dark following treatment. They also reported that, under low light conditions, GA stimulated early germination.

Aalders and others (1980) demonstrated that seed size may be an indication of seed viability in clones of lowbush blueberry. Seeds that passed through a screen with openings of 600 μm germinated poorly (1 to 14%), whereas seeds retained on that screen germinated in higher percentages (5 to 74%). In general, they reported that larger seeds germinated in higher percentages, although optimal size was clone specific.

Nursery practice and seedling care. Due to seedling variability, sexual propagation is normally restricted to breeding programs. Seeds $\geq$ 600 μm in diameter should be allowed to imbibe a solution of 200 to 1000 ppm (0.02 to 0.1%) GA before being sown on the surface of a suitable medium and placed under mist to prevent desiccation. Germination during periods of high temperature should be avoided if no GA treatment is applied, as Dweikat and Lyrene (1989) have suggested that high temperatures may inhibit germination. Seedlings should be transplanted to a site with ample moisture where an appropriate pH can be maintained. For field production, soil should contain high amounts of organic matter, and plants should be mulched with 10 to 15 cm of organic matter (Huxley 1992a).

Asexual propagation—by division and also by rooting softwood or hardwood stem cuttings—is widely practiced commercially for clonal propagation (Huxley 1992a). Lowbush blueberry can be propagated easily from rhizome cuttings 10 cm (4 in) in length taken in early spring or autumn (Dirr and Heuser 1987). However, the new shoots form flower buds almost exclusively, and the resulting plants develop slowly due to excessive flowering (Ballington 1998). Successful propagation of highbush and rabbiteye blueberry by means of softwood or hardwood cuttings has also been reported (Mainland 1993). A much easier species to root, cranberry can be propagated by stem cuttings taken any time during the year and treated with 1,000 ppm (0.1%) indolebutyric acid (IBA) (Dirr and Heuser 1987). Micropropagation procedures for various species of *Vaccinium* have also been reported (Brissette and others 1990; Dweikat and Lyrene 1988; Lyrene 1980; Wolfe and others 1983). These procedures involve rapid *in vitro* shoot multiplication followed by *ex vitro* rooting of microcuttings, utilizing standard stem cutting methods.

Figure 2—*Vaccinium*, blueberry: seeds of *V. angustifolium*, lowbush blueberry (**A**); *V. arboreum*, sparkleberry (**B**); *V. virgatum*, rabbiteye blueberry (**C**); *V. corymbosum*, highbush blueberry (**D**); *V. macrocarpon*, cranberry (**E**); *V. myrtilloides*, Canadian blueberry (**F**); and *V. ovatum*, California huckleberry (**G**).

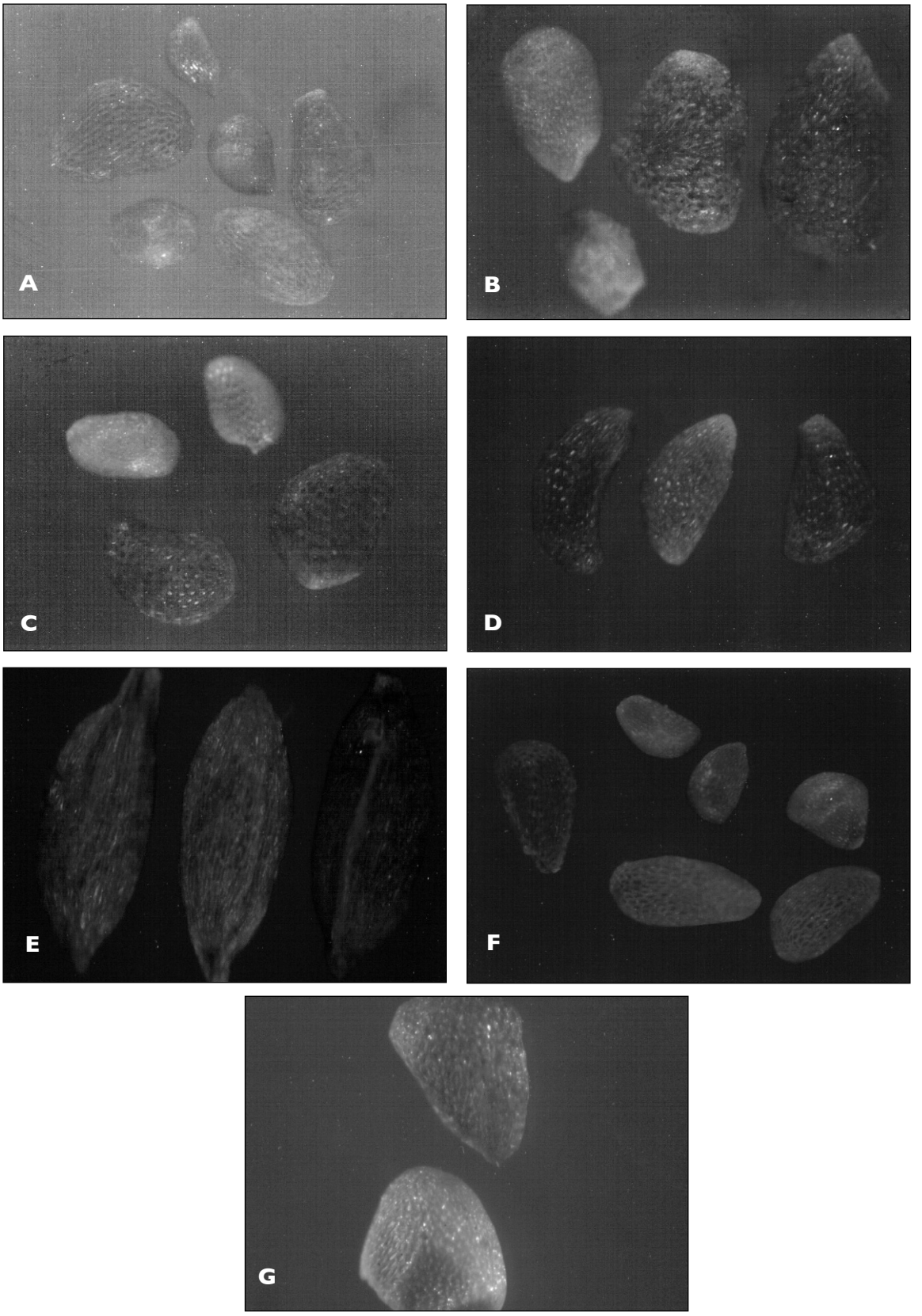
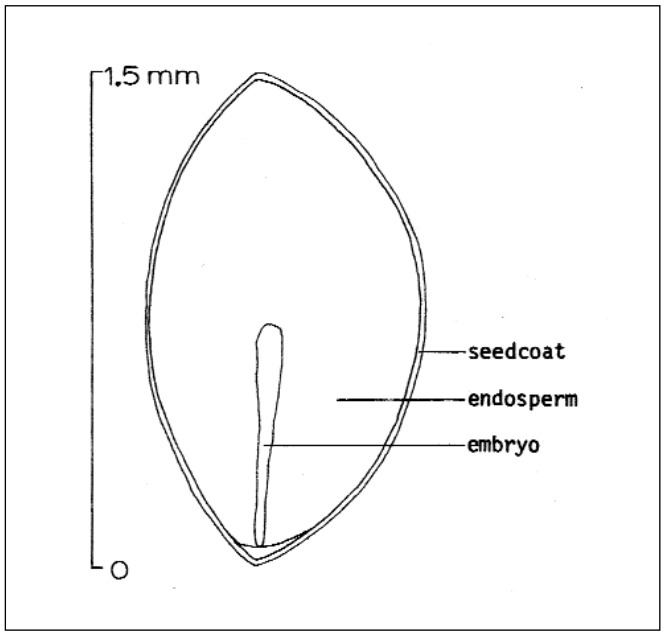


Figure 3—*Vaccinium corymbosum*, highbush blueberry: longitudial section of a seed.



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Euphorbiaceae—Spurge family

Vernicia fordii (Hemsl.) Airy-Shaw

tung-oil tree

Franklin T. Bonner

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Synonyms. *Aleurites fordii* Hemsl.

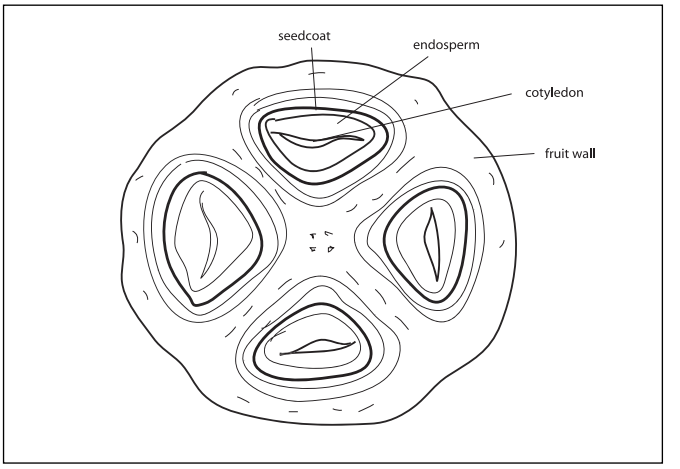
Occurrence and uses. Tung-oil tree—*Vernicia fordii* (Hemsl.) Airy-Shaw—is a native of central Asia. The species was introduced into the southern United States in 1905 as a source of tung oil (a component of paint, varnish, linoleum, oilcloth, and ink) that is extracted from the seeds. The use of this ingredient has declined in recent years in this country, but there are numerous research and breeding programs still underway in Asia. Extensive plantations were established along the Gulf Coast from Texas to Florida, and the tree has become naturalized (invasive) in some areas (Brown 1945; Brown and Kirkman 1990; Vines 1960). It has also been planted in Hawaii (Little 1979). Tung-oil tree is small, with a rounded top, and seldom reaches more than 10 m in height in the United States (Vines 1960).

Flowering and fruiting. Flowering is monoecious, but sometimes all staminate, or rarely all pistillate (Potter and Crane 1951). The white pistillate flowers with red, purple, or rarely yellow throats appear just before the leaves start to unfold in the spring. Borne in conspicuous, terminal cymes approximately 3.7 to 5 cm in diameter, the flowers create a showy display in large plantations. The fruits are 4-celled indehiscent drupes (figure 1), 3 to 7.5 cm in diameter, that ripen in September to early November (Bailey 1949; Potter and Crane 1951; Vines 1960). The seeds, 2 to 3 cm long and 1.3 to 2.5 cm wide, are enclosed in hard, bony endocarps (figures 2 and 3). They are sometimes referred to as stones or nuts. There may be 1 to 15 seeds per fruit, but the average is 4 to 5 (Potter and Crane 1951). The seeds are poisonous. Fruit production begins at about age 3, with commercial production by age 6 or 7 (Potter and Crane 1951). Good trees will yield 45 to 110 kg of seeds annually (Vines 1960).

Collection, cleaning, and storage. Fruits are shed intact in October or November (McCann 1942) and seeds may be collected from the ground. The fruit hulls should be removed as there is some evidence that hull fragments delay germination (Potter and Crane 1951). Cleaning is not a major problem. There are no definitive storage data for tung-oil tree seeds, but they are considered short-lived and are normally planted the spring following harvest. Their high oil content suggests that storage for long periods may be difficult.

Figure 1—*Vernicia fordii*, tung-oil tree: immature fruit (photo courtesy of Mississippi State University's Office of Agricultural Communications).

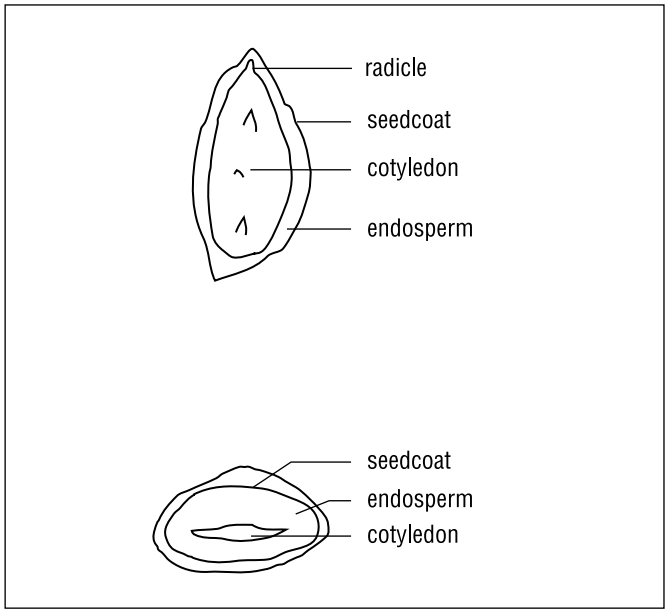
Figure 2—*Vernicia fordii*, tung-oil tree: cross-section of a fruit (adapted from McCann 1942).



Germination. No pretreatments are usually needed for germination. Seeds may be planted dry, or soaked in water for 2 to 5 days before sowing. The latter treatment is said to speed emergence (Potter and Crane 1951). Seeds typically germinate in 4 to 5 weeks (Vines 1960). Some growers have stratified seeds overwinter in moist sand at 7 °C (Potter and Crane 1951), but there does not appear to be much need for this treatment. There are no standard germination test prescriptions for this species.

Nursery practices. Seedling production of tung-oil tree is usually in row plantings instead of beds. Seeds should be planted 5 cm (2 in) deep, 15 to 20 cm (6 to 8 in) apart, in rows 1.5 m (5 ft) apart (Potter and Crane 1951). A good transplant size is 30 to 60 cm (1 to 2 ft). The tree can also be propagated vegetatively with hardwood cuttings (Vines 1960).

Figure 3—*Vernicia fordii*, tung-oil tree: longitudinal (**top**) and median (**bottom**) cross-sections of seeds.



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Caprifoliaceae—Honeysuckle family

Viburnum L.

viburnum

Franklin T. Bonner, John D. Gill, and Franz L. Pogge

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Growth habit, occurrence, and use. Among the 135 or so viburnum species, 12 that are either native to North America or have been introduced are discussed here (table 1). All 12 species are deciduous shrubs or small trees. Their characteristics place the viburnums among the most important genera for wildlife food and habitat and environmental forestry purposes. The attractive foliage, showy flowers, and fruits of viburnums have ensured their widespread use as ornamental plants as well. The fruits of most species are eaten by white-tailed deer (*Odocoileus virginianus*), rabbits (*Sylvilagus floridanus*), chipmunks (*Tamias striatus*), squirrels (*Sciurus* spp.), mice (*Reithrodontomys* spp.), skunks (*Mephitis mephitis*), ruffed grouse (*Bonasa umbellus*), ring-necked pheasants (*Phasianus colchicus*), turkeys (*Meleagris gallopavo*), and many species of songbirds. The twigs, bark, and leaves are eaten by deer, moose (*Alces americana*), rabbits, and beaver (*Castor canadensis*) (Martin and others 1951). The fruits of hobblebush, nannyberry, blackhaw, and

Table 1—*Viburnum,* viburnum: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***V. acerifolium* L.**	**mapleleaf viburnum,** dock-mackie, mapleleaf arrowwood, & Texas possum-haw	Minnesota to Quebec, S to Florida
***V. dentatum* L.** *V. pubescens* (Ait.) Pursh	**southern arrowwood,** roughish arrowwood, arrowwood viburnum	Massachusetts, S to Florida & E Texas
***V. lantana* L.**	**wayfaringtree,** wristwood, wayfaringtree virbunum	Native of Europe & W Asia; introduced from Connecticut to Ontario
***V. lantanoides* Michx.** *V. alnifolium* Marsh. *V. grandifolium* Ait.	**hobblebush**, hobblebush viburnum, moosewood, tangle legs, witch-hobble	Prince Edward Island to Michigan, S to Tennessee & Georgia
***V. lentago* L.**	**nannyberry,** blackhaw, sheepberry, sweet viburnum	Quebec to Saskatchewan, S to Missouri, Virginia, & New Jersey
***V. nudum* var. *nudum* L.** *V. cassinoides* L.	**possumhaw,** swamphaw	Coastal Plain, from Connecticut to Florida & Texas; N to Arkansas & Kentucky
***V. nudum* var. *cassinoides* (L.) Torr. & Gray**	**witherod viburnum,** wild-raisin, witherod	Newfoundland to Manitoba, S to Indiana, Maryland, & mtns of Alabama
***V. opulus* L** *V. opulus* var. *amerieanum* Ait. *V. trilobum* Marsh.	**European cranberrybush,** cranberrybush, Guelder rose, highbush-cranberry	Native of Europe; escaped from cultivation in N US & Canada
***V. prunifolium* L.**	**blackhaw,** stagbush, sweethaw	Connecticut to Michigan, S to Arkansas & South Carolina
***V. rafinesquianum* J. A. Schultes** *V. affine* Bush ex Schneid. *V. affine* var. *hypomalacum* Blake	**downy arrowwood,** Rafinesque viburnum	Manitoba to Quebec, S to Arkansas & Kentucky
***V. recognitum* Fern.**	**smooth arrowwood,** arrowwood	New Brunswick to Ontario, S to Ohio & South Carolina
***V. rufidulum* Raf.**	**rusty blackhaw,** southern blackhaw, bluehaw, blackhaw, southern nannyberry	Virginia to Kansas, S to E Texas & N Florida

Sources: Dirr and Heuser (1987), Little (1979), Vines (1960).

European cranberrybush are eaten by humans also (Gill and Pogge 1974). Medicinal uses have been found for fruits of European cranberrybush, blackhaw, hobblebush, and rusty blackhaw (Gould 1966; Krochmal and others 1969; Vines 1960). Most species prefer moist, well-drained soils, but drier soils are suitable for some, notably blackhaw, mapleleaf viburnum, and witherod viburnum. Soil texture and pH requirements are less critical than in most other genera; hobblebush, mapleleaf viburnum, and nannyberry are particularly tolerant of acidic soil (Rollins 1970; Spinner and Ostrum 1945). Most species are also shade tolerant, particularly hobblebush, mapleleaf viburnum, and the 3 arrowwoods (Gould 1966; Hottes 1939). The species that more typically thrive in the open or in partial shade include blackhaw, European cranberrybush, nannyberry, and witherod viburnum.

Flowering and fruiting. The small white, or sometimes pinkish, flowers are arranged in flattened, rounded, or convex cymes (figure 1). Flowers are typically perfect, but the marginal blossoms in hobblebush and European cranberrybush are sterile. In some cultivated varieties of European cranberrybush, all flowers may be sterile (Rollins 1970). Flowering and fruit ripening dates are mostly in May–June and September–October, respectively, but vary among species and localities (table 2). Pollination is primarily by insects (Miliczky and Osgood 1979). The fruit is a 1-seeded drupe 6 to 15 mm in length, with soft pulp and a thin stone (figures 2, 3, and 4). As viburnum drupes mature, their

Figure 1—*Viburnum lentago*, nannyberry: cluster of fruits (a compound cyme) typical of the genus.

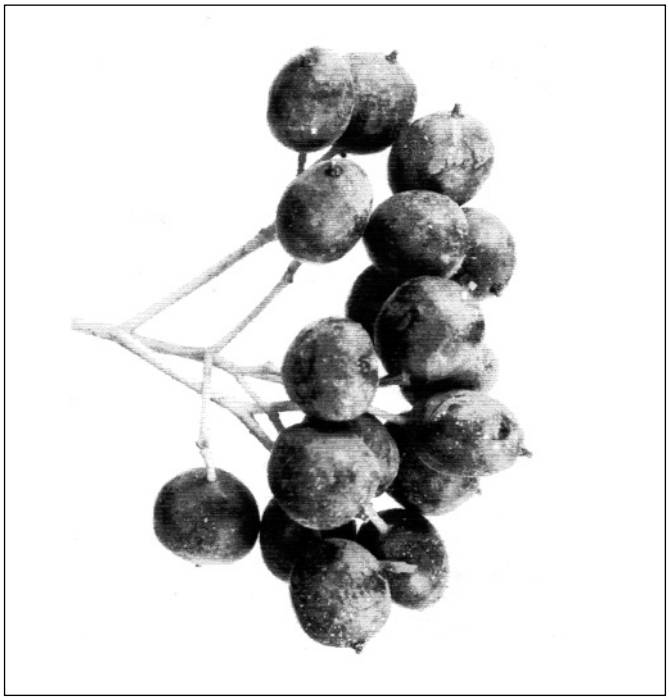


Table 2—*Viburnum,* viburnum: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
V. acerifolium	Midrange	May–Aug	July–Oct	Fall
	West Virginia	—	Late Oct	Nov–Dec
	South	Apr–May	Late July	Fall–Spring
V. dentatum	Midrange	May–June	Sept–Oct	to Dec
	Extremes	June–Aug	July–Nov	to Feb
V. lantana	Midrange	May–June	Aug–Sept	Sept–Feb
V. lantanoides	Midrange	May–June	Aug–Sept	Fall
	West Virginia	—	Late Sept	Oct–Nov
	New York	May	Aug–Sept	Aug–Oct
V. lentago	Midrange	May–June	Sept–Oct	Oct–May
	Extremes	Apr–June	Mid July	Fall–Spring
V. nudum var. *nudum*	South	Apr–June	Sept–Oct	—
V. nudum var. *cassinoides*	Midrange	June–July	Sept–Oct	Oct–Nov
	Extremes	May–July	July–Oct	—
V. opulus	Midrange	May–June	Aug–Sept	Mar–May
	Extremes	May–July	Sept–Oct	Oct–May
V. prunifolium	Midrange	Apr–May	Sept–Oct	to Mar
	Extremes	Apr–June	July–Aug	Oct–Apr
V. rafinesquianum	Midrange	June–July	Sept–Oct	Oct
	Extremes	May–June	July–Sept	—
V. recognitum	North	May–June	Aug–Sept	to Dec
	South	Apr–May	July–Aug	to Feb
V. rufidulum	South	Mar–Apr	Sept–Oct	Dec
	North	May–June	—	—

Sources: Brown and Kirkman (1990), Donoghue (1980), Gill and Pogge (1974).

Figure 2—*Viburnum*, viburnum: single fruits (drupes) of *V. nudum* var. *cassinoides*, witherod viburnum (**top left**); *V. lentago*, nannyberry (**top right**), *V. rafinesquianum*, downy arrowwood (**bottom left**); and *V. opulus*, cranberrybush (**bottom right**).

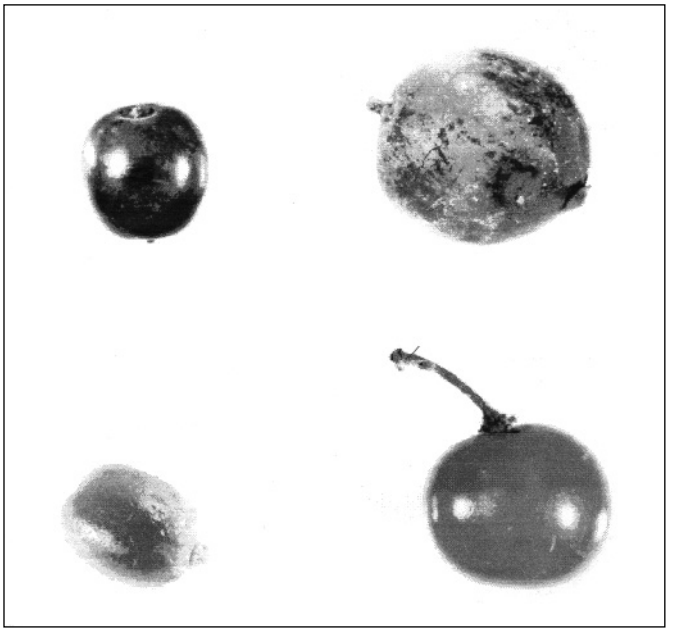
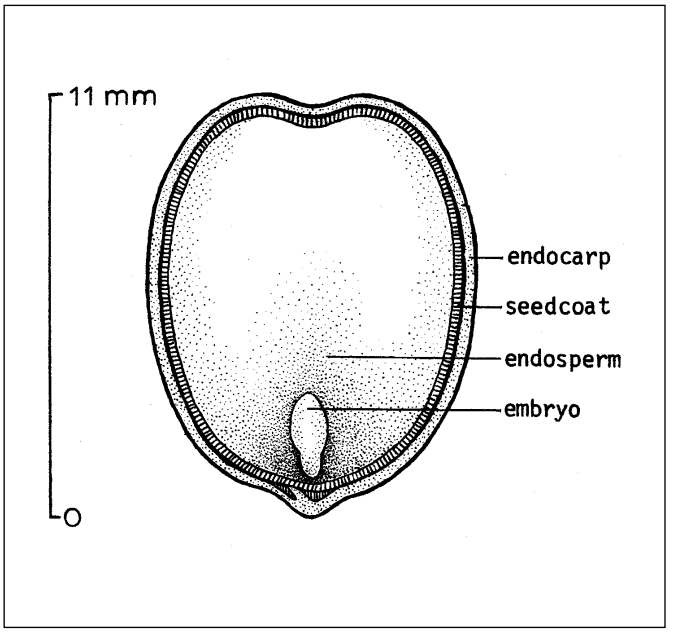


Figure 3—*Viburnum*, viburnum: cleaned seeds (stones) of (**top left to right**) *V. acerifolium*, mapleleaf viburnum; *V. lantanoides*, hobblebush; *V. nudum* var. *cassinoides*, witherod viburnum; *V. dentatum*, southern arrowwood; *V. lantana*, wayfaringtree; and (**bottom left to right**) *V. lentago*, nannyberry; *V. rafinesquianum*, downy arrowwood; *V. recognitum*, smooth arrowwood; *V. opulus*, European cranberrybush.

skins change in color from green to red to dark blue or black when fully ripe (Fernald 1950; Vines 1960). This color change is a reliable index of fruit maturity for most members of the genus in North America. The drupes of European cranberrybush, however, remain orange to scarlet when fully ripe (Fernald 1950). Age of viburnums at first fruiting varies among species, from 2 to 3 years up to 8 to 10 years (table 3). Production is usually meager in early

Figure 4—*Viburnum lentago*, nannyberry: longitudinal sections through a stone.



fruiting years, but most species produce fruit nearly every year. Species such as mapleleaf viburnum and hobblebush that grow in deep shade seldom produce large crops (Gould 1966). Much of the wildlife-habitat and ornamental value in viburnums is due to persistence of their fruits through winter (table 2). Dispersal is accomplished by animals or gravity.

Collection, extraction, and storage. The drupes may be hand-picked when their color indicates full physiological maturity (dark blue or black). After collection, care must be taken to prevent overheating as with all fleshy drupes. If whole drupes are to be sown, they should be spread out to dry before storage. If seeds are to be extracted, drying should be minimized to prevent toughening of the drupe coats. Extraction is recommended because there are good indications that cleaned seeds show higher levels of germination (Smith 1952). Extraction can be easily accomplished by maceration with water. Because good seeds should sink in water, the pulp can be floated off. An alternative method is to wash the pulp through screens with hoses. The seeds should then be dried for storage. Viburnum seeds are orthodox in storage behavior. Viability of air-dried seeds was maintained for 10 years by storage in a sealed container at 1 to 4 °C (Heit 1967). Whole fruits can be stored similarly (Chadwick 1935; Giersbach 1937). Average seed weight data are listed in table 4. Soundness in seed lots of several species has ranged from 90 to 96% (Gill and Pogge 1974).

Germination. Seeds of most viburnum species are difficult to germinate. The only official testing recommendation for any viburnum is to use tetrazolium staining (ISTA

Table 3—*Viburnum,* viburnum: growth habit, height, seed-bearing age, and seedcrop frequency

Species	Growth habit	Height at maturity (m)	Year first cultivated	Seed-bearing age (yrs)	Years between large seedcrops
V. acerifolium	Erect shrub	2	1736	2–3	1
V. dentatum	Erect shrub	5	1736	3–4	—
V. lantana	Shrub or tree	5	—	—	—
V. lantanoides	Erect or trailing shrub	3	1820	—	3 or 4
V. lentago	Shrub of tree	10	1761	8	1
V. nudum var. *nudum*	Shrub or tree	1.8	—	—	—
V. nudum var. *cassinoides*	Erect shrub	3	1761	—	1
V. opulus	Erect shrub	4	—	3–5	—
V. prunifolium	Shrub or tree	5	1727	8–10	1
V. rafinesquianum	Shrub	2	1830	—	—
V. recognitum	Erect shrub	3	—	5–6	—
V. rufidulum	Shrub or tree	3.5	—	5	—

Source: Gill and Pogge (1974).

Table 4—*Viburnum,* viburnum: fruit and seed weight and yield data

Species	Dried fruits/wt		Cleaned seeds/weight				
			Range		Average		
	/kg	/lb	/kg	/lb	/kg	/lb	Samples
V. acerifolium	10,600	4,800	24,050–36,600	10,900–16,600	28,000	13,100	5
V. dentatum	—	—	32,200–71,900	14,600–32,600	45,000	20,400	6
V. lantana	—	—	9,250–29,100	4,200–13,200	19,200	8,700	2
V. lantanoides	16,700	7,580	—	—	25,350	11,500	11
V. lentago	4,850	2,200	4,850–27,350	2,200–12,400	13,000	5,900	21
V. nudum var. *cassinoides*	6,600	3,000	55,100–63,950	25,000–29,000	60,850	27,6003	
V. opulus	12,100	5,500	20,700–39,250	9,400–17,800	30,000	13,600	12
V. prunifolium	—	—	8,800–13,230	4,000–6,000	10,600	4,800	5
V. rufidulum	5,200	2,360	—	—	—	—	—

Source: Gill and Pogge (1974).

1993). Most species have an apparent embryo dormancy and some have impermeable seedcoats as well (Gill and Pogge 1974). Dormancy in seeds of southern species is more readily overcome than in seeds of northern species. Seeds of the more northern forms need warm stratification for development of the radicle, followed by cold stratification to break dormancy in the epicotyl (shoot). European cranberrybush germinated 97% after 14 weeks of alternating temperatures between 20 and 2 °C (Fedec and Knowles 1973). For this reason, seeds of northern species seldom germinate naturally until the second spring after they ripen. In contrast, seeds of some southern viburnums usually complete natural germination in the first spring after seedfall. They ordinarily do not exhibit epicotyl dormancy and do not require cold stratification. Among the 12 species discussed here, only possumhaw and southern arrowwood from the southern part of its range may not need cold stratification (table 5 and figure 5) (Barton 1951; Giersbach 1937). Scarification of seeds has not improved germination (Barton 1958). Germination tests of stratified seeds have been made in sand or soil, but modern procedures would use moist paper blotters. The commonly suggested temperatures are alternating from 20 °C (night) to 30 °C (day) (table 5), but European cranberrybush is reported to germinate well at a constant 20 °C (Fedec and Knowles 1973).

Nursery practice. The warm-cold stratification sequence (table 5) can be accomplished in nurserybeds. Seeds or intact drupes can be sown in the spring, to allow a full summer for root development (figure 6). The ensuing winter temperatures will provide the cold stratification needed to break epicotyl dormancy. The principal advantage of this method, compared to stratification in flats or trays, is

Table 5—*Viburnum,* viburnum: stratification treatments and germination test results

	Stratification treatments (days)			Germination percentage	
	Warm period* (first stage)	Cold period† (second stage)	Germination test duration‡	Avg (%)	Samples
V. acerifolium	180–510	60–120	60+	32	5
V. dentatum§	0	0	60	—	—
V. lantanoides	150	75	100	43	3
V. lentago	150–270	60–120	120	51	3
V. nudum var. *cassinoides*	60	90	120	67	2
V. opulus	60–90	30–60	60	60	3+
V. prunifolium	150–270	30–60	60+	75	2
V. rafinesquianum	360–510	60–120	—	—	—
V. recognitum	360–510	75	60+	69	2
V. rufidulum	180–360	0	—	—	—

Sources: Gill and Pogge (1974), Vines (1960).
* Seeds in a moist medium were exposed to diurnally alternating temperatures of 30/20 °C or 30/10 °C, but a constant 20 °C was equally effective for most species (Barton 1958).
† Seeds and medium were exposed to constant temperature of 5 or 10 °C. Temperatures of 1 to 6 °C are preferred now for cold stratification.
‡ At temperatures alternating diurnally from 30 (day) to 20 °C (night).
§ Seeds were collected in Texas; temperature was not critical for germination (Giersbach 1937).

Figure 5—*Viburnum dentatum*, southern arrowwood: seedling development at 1, 2, 11, and 29 days after germination; roots and shoots develop concurrently.

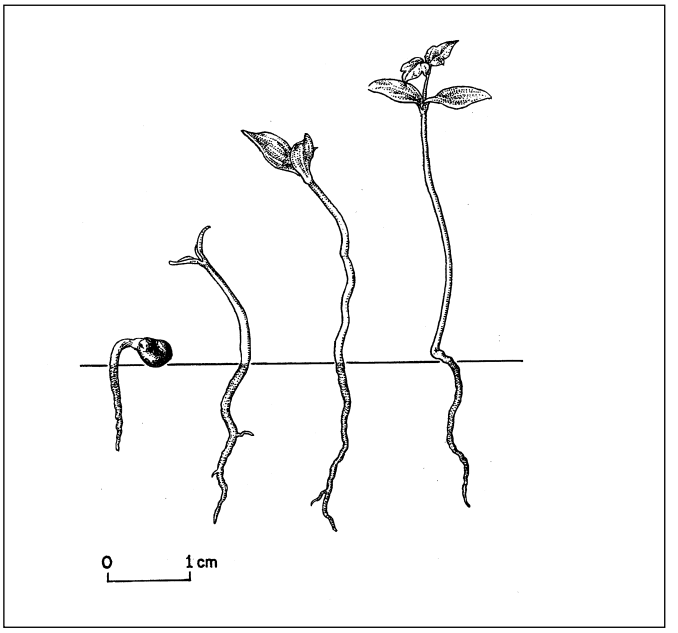
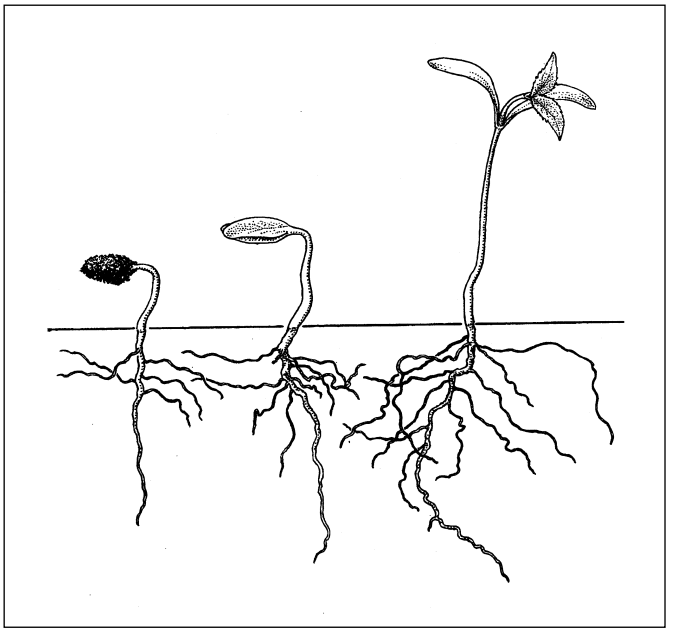


Figure 6—*Viburnum lentago*, nannyberry: seedling development from stratified seed—root development during warm stratification (about 150 days) (**left**); very little development during ensuing cold stratification (about 120 days) for breaking epicotyl dormancy (**middle**); subsequent development at germinating temperatures (**right**).



that seeds need not be handled after their roots emerge during the warm stratification period (Rollins 1970). Seeds of species with more shallow dormancy can be sown in the fall shortly after collection and extraction. For the several species that may be handled in this manner, the latest sowing dates for optimum seedling percentages in the ensuing year are listed in table 6. Sowing done somewhat earlier than these dates gave nearly as good results, but sowing at later dates reduced germination percentages.

The seeds may be broadcast on prepared seedbeds and mulched with sawdust (Rollins 1970). Alternatively, seeds can be sown in drills 20 to 30 cm (8 to 12 in) apart, covered with 12 mm ($^1/_2$ in) of soil, and mulched with straw (Gill and Pogge 1974). Straw mulch must be removed once germination begins, otherwise there is risk of loss due to damp-

Table 6—*Viburnum,* viburnum: latest allowable dates for sowing in nurserybeds and seedling percentages obtained in the following year

Species	Location	Latest allowable sowing date*	Seedling %†
V. acerifolium	New York	May 1	55
V. lantana	Ohio	Oct 21	90
V. lentago	Ohio	Oct 7	75
V. opulus	New York	July 1	87
V. prunifolium	New York	May 1	26
V. recognitum	New York	May 1	32

Sources: Giersbach (1937), Smith (1952).
* Sowing dates later than those listed resulted in reduced seedling percentages.
† Number of seedlings in a nurserybed at time of lifting expressed as a percentage of the number of viable seeds sown.

ing-off fungi. The recommended seedbed density for several viburnums is 215/m² (20/ft²) (Edminster 1947). Seedlings of some species may require shade for best development, although this depends on location and species. The most likely candidates for shading are the arrowwoods, hobblebush (Gould 1966), and mapleleaf viburnum. Seedlings should be ready for outplanting as 1+0 or 2+0 stock. A variety of techniques exist for rooting viburnum species by softwood cuttings, hardwood cuttings, or layering (Dirr and Heuser 1987).

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Verbenaceae—Verbena family

Vitex agnus-castus L.

lilac chastetree

John C. Zasada and C. S. Schopmeyer

Dr. Zasada retired from the USDA Forest Service's North Central Research Station; Dr. Schopmeyer (deceased) retired from the USDA Forest Service's National Office, Washington, DC

Other common names. chaste-tree, monks'-pepper tree, hemptree (Bailey 1949).

Growth habit, occurrence, and use. The genus *Vitex* occurs in both hemispheres in the tropical and subtropical zones. About 380 taxa have been described (Bredenkamp and Botha 1993). Lilac chastetree, a deciduous, strongly aromatic shrub or small tree, is one of the few species in the genus that is native to the temperate zones, but it is not native to North America (Bailey 1949). It has, however, naturalized in much of the southeastern United States.

In Washington on the west side of the Cascades, it attains a height of 1.8 m, increasing in more southerly latitudes to a height of 7.7 m in the low desert of southern California (Williamson 1967). Multiple stems support a broad spreading form, but shade trees with a single stem can be developed by pruning (Williamson 1967).

In the eastern United States, the species is hardy as far north as New York (USDA Hardiness Zone 6), but marginally so; it performs better further south, in USDA Hardiness Zones 8–9 (LHBH 1076; Dirr 1990; Moldenke 1968). This species is less hardy than negundo chastetree (*Vitex negundo* L.), which is also planted as an ornamental (Dirr 1990) and has been cultivated as an ornamental in southern Europe, the Middle East, India, and Brazil (Moldenke 1968). Lilac chastetree was introduced as an ornamental into the United States in 1570 (Rehder 1940). The species has value in shelterbelt plantings (Engstrom and Stoeckeler 1941).

Since the days of Dioscorides in the first century AD, seeds of this species have been noted for their ability to subdue sexual urges in men, hence the name "chastetree" (Moldenke 1968; Polunin and Huxley 1966). This property was recognized as being useful to celibates and this in turn led to the name "monks'-peppertree." However, these properties are questioned today. There is evidence that phytomedicines from the chastetree are useful in the treatment of menstrual disorders in women (Bohnert and Hahn 1990). Because of the aromatic pungency of fresh seeds, however, some people have considered the seeds as having aphrodisiac properties.

Other species (for example, negundo chastetree) are used in tropical and subtropical regions for biomass and fuelwood production because of their rapid growth, ability to coppice, and tolerance of a wide range of site conditions (Verma and Misra 1989).

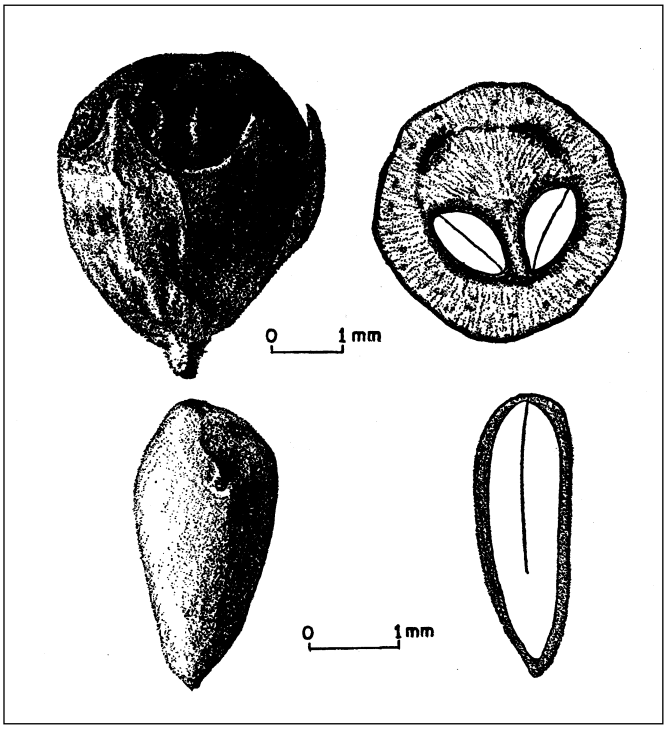
Varieties. Typical plants of the species have lavender flowers, but several other varieties have been cultivated in the United States (Rehder 1940; Dirr 1990). White chastetree, var. *alba* West., has white flowers. Hardy lilac chastetree, var. *latifolia* (Mill.) Loud., is characterized by broader leaflets and greater cold-hardiness. In addition, a form with pink flowers, f. *rosea* Rehder, has been propagated (Dirr 1990; Rehder 1940).

Flowering and fruiting. The fragrant flowers occur in dense spikes about 2.8 cm long; they bloom during the late summer and autumn in the United States (Bailey 1949). In Europe, flowering occurs from June to September (Moldenke 1968; Polunin and Huxley 1966). According to Dirr (1990), the plants will continue to flower as long as new growth is occurring; removing old flowers (deadheading) can prolong flowering.

The pungent fruits are small drupes about 3 to 4 mm in diameter that ripen in late summer and fall (Schopmeyer 1974). Good seedcrops occur almost every year (Engstrom and Stoeckeler 1941). Each drupe contains a rounded 4-celled stone about 3 mm long that is brownish to purple-brown and frequently partially covered with a lighter colored membranous cap. Each stone may contain from 1 to 4 seeds (figure 1) (Schopmeyer 1974).

Collection of fruits; extraction and storage of seeds. The fruits may be gathered in late summer or early fall by picking them from the shrubs by hand or by flailing or stripping them onto canvas or plastic sheets. Seeds can be removed by running the fruits dry through a macerator and fanning to remove impurities (Engstrom and Stoeckeler 1941). Seed weight per fruit weight is about 34 kg of

Figure 1—*Vitex agnus-castus*, lilac chastetree: fruit (**top left**) and transverse section through 2 seeds within a fruit (**top right**); cleaned seed (**bottom left**) and longitudinal section through a seed, with embryo taking up entire seed cavity (**bottom right**)



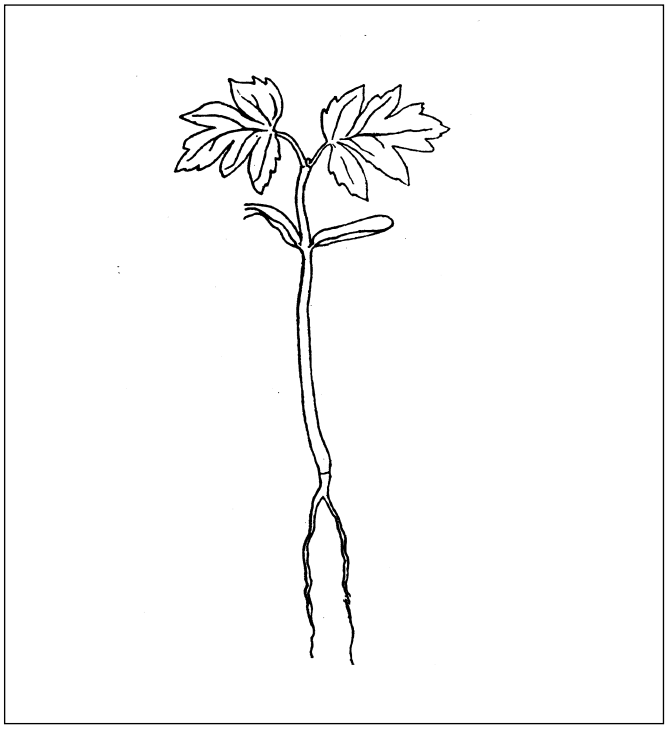
cleaned seed/45 kg of ripe fruit (75 lb/100 lb). Number of cleaned seeds varied from 74,800 to 130,000/kg (34,000 to 59,000/lb) in 4 samples (Schopmeyer 1974). Purity in 2 samples was 80%, and average soundness in 4 samples was 55%. In one test, seeds stored in moist sand and peat at 5 °C or 1 year showed no loss of viability (Schopmeyer 1974).

Germination. Seeds germinate readily without pretreatment (Dirr and Heuser 1987). However, stored seeds may exhibit dormancy that can be overcome by stratification in moist sand and peat for 90 days at about 5 °C. Germination tests should be made in sand flats for 40 days at 21 °C (night) to 30 °C (day) (Schopmeyer 1974). Germinative energy of stratified seeds was 18 to 60% in 10 to 22 days (3 tests). Germinative capacity of untreated seeds was 0.4% in 71 days (1 test); with stratified seeds, 20 to 72% (3 tests) (Schopmeyer 1974).

In another test, fresh seeds collected in January in southern California were sown without treatment in February in a greenhouse in Iowa. Germination was completed (percentage not stated) by April 20 when seedlings were 2 inches tall (King 1932). Germination is epigeal (King 1932) (figure 2).

Nursery practice. Stratified seeds of lilac chastetree should be sown in the spring and covered with 6 mm ($^1/_4$ in) of soil. On the average, about 16% of the viable seeds sown produce usable 2+0 seedlings (Engstrom and Stoeckeler 1941). Lilac chastetree can be readily propagated by greenwood cuttings collected before flowering, by hardwood cuttings in the fall, and layering (LHBH 1976; Dirr and Heuser 1987).

Figure 2—*Vitex agnus-castus*, lilac chastetree: seedling showing cotyledons and first leaves (from drawing by King 1932, used in 1948 edition).



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Vitaceae—Grape family

Vitis labrusca L.

fox grape

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Other common names. northern fox grape, plum grape, northern muscadine, swamp grape, wild vine.

Growth habit, occurrence, and use. Fox grape—*Vitis labrusca* L.—a deciduous, woody vine, grows naturally from New England to Illinois and south to Georgia and infrequently, Arkansas (Vines 1960). It may climb on trees to a height of 12 m. Fox grape hybridizes readily with other *Vitis* species, and it has been the most important grape in the development of North American viticulture (Vines 1960), notably the 'Concord' varieties (Cawthon and Morris 1982). The fruits are important as food for many birds and mammals.

Flowering and fruiting. The dioecious flowers are both borne in short panicles, 5 to 10 cm long, in May or June. The fruit clusters usually have fewer than 20 globose berries, 8 to 25 mm in diameter. The berries mature in August to October and drop singly. Mature berries are brownish purple to dull black and contain 2 to 6 brownish, angled seeds that are 5 to 8 mm long (Vines 1960) (figures 1 and 2). Seed maturity is indicated by a dark brown seedcoat (Cawthon and Morris 1982).

Collection, extraction, and storage of seeds. Ripe berries can be stripped from the vines by hand or shaken onto canvas sheets. The seeds can be extracted by placing the berries in screen bags with 1.4-mm openings (approximately 14-mesh) and directing a solid stream of water at about 181 kg (400 lb) of pressure onto them. This removes the skins and pulp, most of which will be washed through the screen. The remaining fragments can be washed off in a pail of water. Seeds can also be extracted by running berries through a macerator or hammermill with water and washing the pulp away (Bonner and Crossley 1974). Six samples of fox grape seeds ranged from 32,900 to 34,000/kg (14,920 to

Figure 1—*Vitis labrusca*, fox grape: seed.

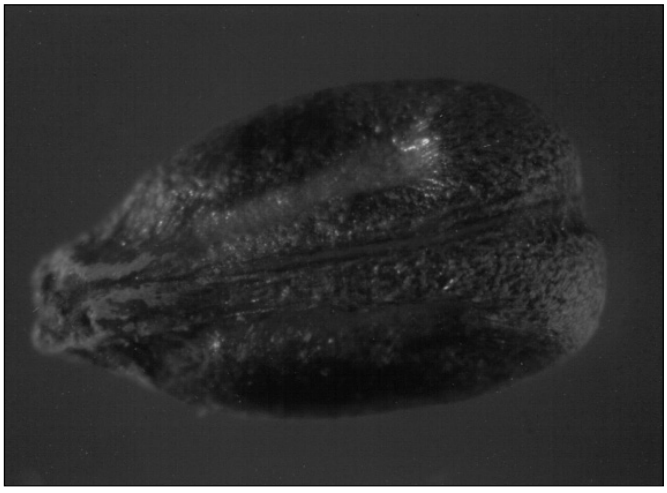
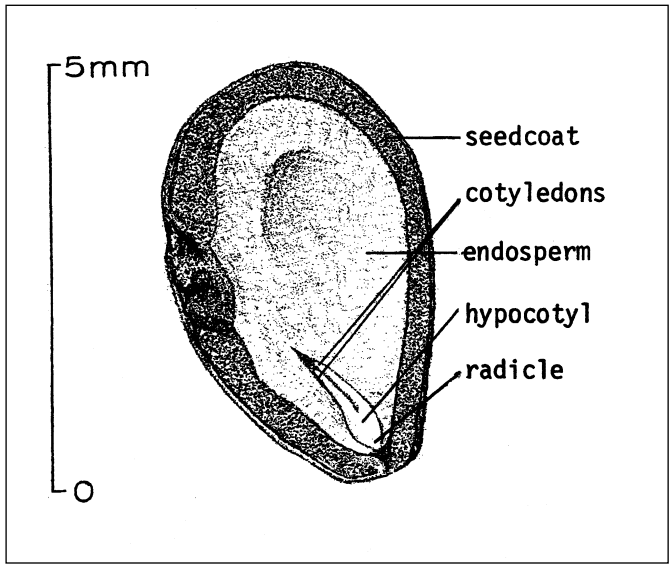


Figure 2—*Vitis labrusca*, fox grape: longitudinal section through a seed.



15,430/lb) at a moisture content of 10%; the average was 34,600 seeds (15,070/lb). No storage data are available for fox grape, but other *Vitis* species have been stored successfully at low moisture contents at 5 °C in sealed containers (Bonner and Crossley 1974; Vories 1981). These results suggest that fox grape seeds are orthodox in storage behavior and can be stored successfully for at least several years.

Pregermination treatments. Fox grape seeds exhibit dormancy that can be overcome by moist stratification at 2 to 5 °C for several months. There are no specific data for fox grape, but a similar wild species—riverbank grape, *V. vulpina* L.—requires 90 days of stratification for germination testing (AOSA 1993) and up to 4 months has been recommended for spring planting in nurseries (Vories 1981). Soaking stratified seeds in solutions of nutrients or growth substances for 12 hours before sowing has also been reported as helpful in Europe (Simonov 1963).

Nursery practice. Seedlings rarely run true to type; hence, propagation by cuttings is common (Vines 1960).

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Arecaceae—Palm family

Washingtonia filifera (L. Linden) H. Wendl.

California washingtonia

Stanley L. Krugman

Dr. Krugman retired from the World Bank and from the USDA Forest Service's National Office, Washington, DC

Synonyms. *Washingtonia filamentosa* (Frenzi) Kuntze, *Neowashingtonia filimentosa (*Frenzi) Sudworth.

Other common names. California Washington-palm, desert-palm, California fan-palm, California-palm.

Growth habit, occurrence, and use. The California washingtonia—the only palm native to California—is the largest of the native palms in the United States (Bomhard 1950). Its sturdy, massive, cylindrical trunk grows to a height of 18 to 23 m and tapers very gradually from a diameter of 51 to 91 cm at the base to slightly less at the top. It has a broad open crown with as many as 50 fan-shaped, much-folded leaves with petioles as long as 1.5 m. Dead leaves may remain on the trunk for many years, forming a dense, thatch-like shroud or skirt about the trunk down to within a few feet of the ground (Sudworth 1908). This species is native to rocky streambeds and edges of other sources of water bordering the Colorado Desert in southeastern California and in Yuma County, Arizona, and northern Baja California, Mexico (Bomhard 1950). It is now widely planted in southern California, Arizona, Texas, and along the Gulf Coast for ornamental and environmental forestry purposes along roads or in small stands.

Geographic races. Studies employing electrophoretic techniques suggest that the current populations in southern California are either relicts or recent recolonizations from seed dispersal from a refugium population in Baja California, Mexico (McClenaghan and Beauchamp 1986).

Flowering and fruiting. In August, small but showy clusters of white, vase-shaped flowers are borne, enclosed initially by a spathe (Jepsen 1910). The mature flower stalk may average 3.7 m in length and extend almost horizontally in the crown (Bomhard 1950). The flowers are perfect and occur annually in great abundance once the tree reaches reproductive maturity. The calyx is tubular and the corolla is funnel-shaped, with the stamens inserted in its tube (Jepsen 1910).

The fruit and seeds mature during December and January. The ripe fruit is a spherical or elongated black berry about 10 to 13 mm long, with thin flesh surrounding a single hemispherical seed (DeMason 1988; Jepsen 1910; Sudworth 1908). The seeds are pale chestnut in color and measure about 6 to 8 mm long by 3 mm thick (figure 1); there are about 2,300 to 2,700 seeds/kg (1,040 to 1,225/lb) (Sudworth 1908). They are flattened somewhat on the ventral side (figure 2). The lance-shaped embryo is located on the round side of the seed near the raphe (DeMason 1988). There is a large cotyledon, an epicotyl, a small root apex, a horny endosperm, and a thin seedcoat (DeMason 1988; Jepsen 1910). The seeds are mature at the time of fruit drop.

Extraction and storage of seeds. The fleshy covering on the seeds should by removed in a macerator. The cleaned seeds then may be stored or sown immediately. Seeds should not be permitted to dry out (DeLeon 1958). Seeds of this species have been stored successfully in sealed containers at 5 °C for up to 6 years (Quick 1968), but long-term storage is not recommended.

Figure 1—*Washingtonia filifera*, California washingtonia: seed.

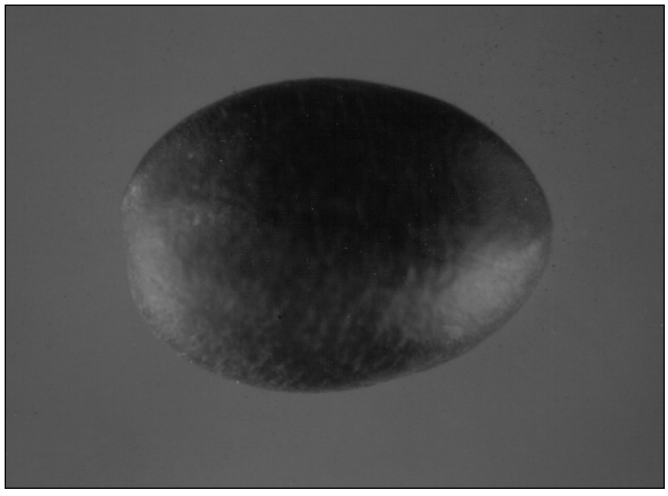
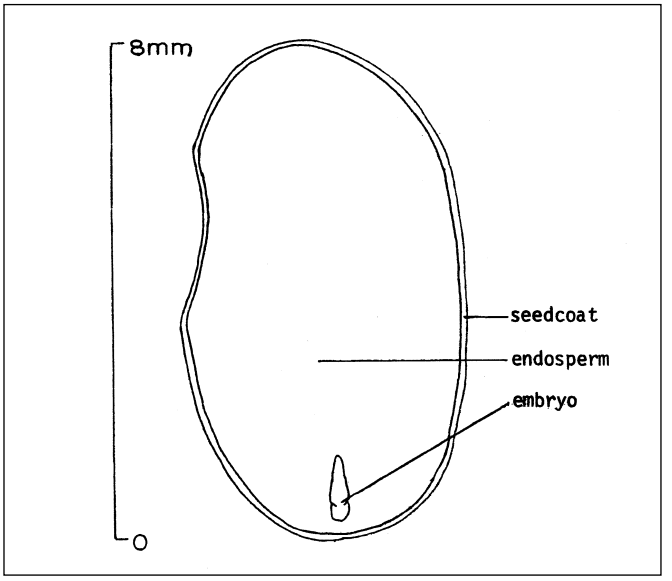


Figure 2—*Washingtonia filifera*, California washingtonia: longitudinal section through the embryo of a seed.



Germination and nursery practice. Fresh seeds with no treatment before sowing have germinated between 80 and 100% in 4 to 15 weeks (Emery 1969; McCurrach 1960). Seeds stored as long as 5 years also germinated well (87%) without a pretreatment. However, the time to reach maximum germination was reduced when stored seeds were stratified at 5 °C for 12 weeks before sowing (Quick 1968). Fresh or stratified seeds can be sown directly in a well-drained seedbed outdoors or in flats or other containers. Many growers prefer to sow the seed in a mixture of peat moss and sand or in just sand. Depth of cover has been 6 to 13 mm ($^1/_4$ to $^1/_2$ in), or a depth equivalent to the thickness of the seed (McCurrach 1960). Bottom heat for the containers has been recommended to speed germination and is also recommended during periods when cold nights can occur (Loomis 1950; Muirhead 1961). It should be noted that there is an allelopathic potential of the dry fruit of this species. Substances that inhibit germination were found in the pericarp (Khan 1982).

Germination is hypogeal (Tomlinson 1960). When a seed germinates, the shoot grows but the seed remains underground. With the appearance of an elongated second leaf, seedlings should be transplanted to individual containers containing soil mix enriched with leaf mold (Muirhead 1961). The transplants should be grown in partial shade to prevent excessive drying of the seedlings. During the subsequent growing period, the seedlings should be acclimated to heat by gradually removing the shade.

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Agavaceae—Century-plant family

Yucca L.

yucca

Robert R. Alexander, Floyd W. Pond, and Jane E. Rodgers

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Growth habit and occurrence. There are about 30 species of yucca native to North America and the West Indies. Although most of these long-lived, evergreen plants grow in the arid southwestern United States and on Mexican tablelands, yuccas are found up to 2,400 m in elevation in the mountains of Colorado (Arnott 1962; Webber 1953). Four western species are considered here (table 1). Great Plains yucca is a small acaulescent shrub 1 to 2 m tall, with narrow, swordshaped, spine-tipped, upright leaves 6 to 12 mm wide. Soaptree yucca is a medium to large caulescent shrub up to 9 m tall, with similar but wider (5 cm) and longer leaves (Arnott 1962; McKelvey 1947; Webber 1953). Tree-like in form, Joshua tree can exceed trunk lengths of over 3 m, with pseudodichotomous branching and long dark green leaves (Cornett 1991). Extensive stands of this sturdy tree can be found scattered throughout the Mojave Desert. The most common yucca in desert areas is Mohave yucca, a shrub or tree-like yucca reaching 1 to 5 m in height with rosettes at its tips (Jaeger 1940) .

Natural reproduction by seed is limited because of low rainfall (McKelvey 1947; Webber 1953). Most new plants sprout from underground rhizomes. Early growth of seedlings is very slow, and they often retain their succulent juvenile leaves for a year (Webber 1953). Soaptree yucca seedlings observed over a period of time on the Jornada Experimental Range in New Mexico averaged only about 20 cm high when 16 years old (Campbell and Keller 1932). At Joshua Tree National Park, it has been observed that Joshua tree and Mohave yucca grow 10 to 15 cm in their first year and roughly 2.5 cm annually thereafter (CALR 1995).

Uses. Yuccas are an important resource for Native Americans in the Southwest and Mexico. The buds, flowers, and legumes can be eaten raw, roasted, or boiled. The flower stalks of soaptree yucca can also be roasted like mescal. Rope, mats, sandals, baskets, and burlap cloth have been made from the fibers of the leaves. The roots of soaptree yucca, known as *amole*, have saponifying properties and have been used as a soap and as a laxative (Kearney 1969; Webber 1953). Bean and Saubel (1972) report that as a soap plant, Mohave yucca (the roots are called *hunuvat* by the Cahuilla) is one of the most famous in the Southwest. The inflorescent shoots of capsular yuccas are highly palatable to livestock and wildlife, and soaptree yucca has been used as an emergency ration for livestock during periods of drought. The chopped stems, when mixed with feed concentrates such as cottonseed meal, are palatable and nourishing (Kearney 1969; Webber 1953). Around the turn of the century, Joshua tree saw brief but unsuccessful commercial use as paper pulp and surgical splints (McKelvey 1938). These species have been cultivated occasionally as ornamentals; other species not covered here are commonly used horticulturally.

Table 1—*Yucca,* yucca: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***Y. brevifolia* Engelm.**	**Joshua tree,** tree yucca	Mojave Desert to SW Utah & W Arizona
***Y. elata* (Engelm.) Engelm.** *Y. radiosa* (Engelm.) Trel.	**soaptree yucca,** palmilla, soapweed, Spanish-bayonet	SW Texas, NW to central New Mexico & W central Arizona; Iron & Washington Cos., Utah
***Y. glauca* Nutt.** *Y. angustifolia* Pursh	**Great Plains yucca,** beargrass, soapweed, Spanish-bayonet	Texas N through Rocky Mtns & Great Plains to Montana & North Dakota
***Y. schidigera* Roezl ex Ortgies**	**Mojave yucca,** Spanish-dagger	S Mojave Desert, NW Sonoran Desert to Nevada, Arizona, & N Baja California

Source: Little (1979).

Flowering and fruiting. The greenish to creamy white flowers are perfect. They appear on terminal panicles from mid-May to mid-July (table 2). Under favorable environmental conditions, plants begin bearing flowers when about 5 to 6 years old. Soaptree yucca bears about 75 to 200 flowers per stalk, but only about 30% of these produce fruits (Campbell and Keller 1932). The fruit is a dehiscent capsule containing 120 to 150 flat, ovoid, black seeds (Campbell and Keller 1932; Ellis 1913). Capsules ripen from mid-July to late September (table 2). Seeds (figures 1 and 2) are wind disseminated in September and October.

Yucca pollination seldom occurs without the aid of females of 2 moth species—the yucca moth, *Pronuba yuccasella* (Riley), and *Prodoxus quinquepunctellus* (Chambers). These moths gather the pollen, place it in the stigmatic tube, and lay their eggs. The larvae feed exclusively on the maturing seeds but usually consume only a small (20%) portion (Bailey 1962; Ellis 1913; McKelvey 1947; Webber 1953).

Collection of fruits. Because the capsules are dehiscent, fruits should be collected just before or at the time the capsules open. They may be picked by hand or stripped from the plants onto canvas (Alexander and Pond 1974).

Extraction and storage of seeds. Seeds are easily extracted from dry capsules by hand if the sample is small (Alexander and Pond 1974). With larger samples, dry capsules should be run through a tumbler, revolving box, or drum with screen sides that permit the seeds to fall out. Chaff and other debris can then be winnowed or screened out. Cleaned seeds average 50,000/kg (22,680/lb) for soaptree and Great Plains yuccas (Arnott 1962) and 9,250/kg (4,200/lb) for Joshua tree and Mohave yucca. Seeds have been satisfactorily stored dry at room temperatures, so although no storage tests have been done, the seeds are obviously orthodox in storage behavior.

Pregermination treatments. Pretreatment is apparently not needed for successful germination (Arnott 1962), but there is evidence that yuccas exhibit some degree of hardseededness (Webber 1953). The germination period can be reduced by soaking seeds in water for 24 hours at room temperatures or by mechanically scarifying or removing the hard seedcoat at the hilum end.

Germination tests. Germination tests for soaptree and Great Plains yuccas have been run at temperatures between 28 and 32 °C, with soaked seeds placed between the folds of moist cotton. The germinative energy of both species after 4 days varied from 45 to 98% (72 samples), with the majority of the samples tested ranging from 80 to 90% (Webber 1953). Tests have also been run in flats in a greenhouse with untreated seeds. Germination after 20 days was 96% for soaptree yucca and 80% for Great Plains yucca (Arnott 1962). After 5 months, however, only 20% of the Great Plains yucca seeds sown had produced living seedlings, whereas all the soaptree yucca germinants were still alive.

Germination tests of Joshua tree seeds found maximum germination at 20 to 25 °C and inhibition at 10 to 15 °C

Figure 1—*Yucca*, yucca: seeds of *Y. elata*, soaptree (**top**); *Y. brevifolia*, Joshua tree (**center**); *Y. schidigera*, Mojave yucca (**bottom**).

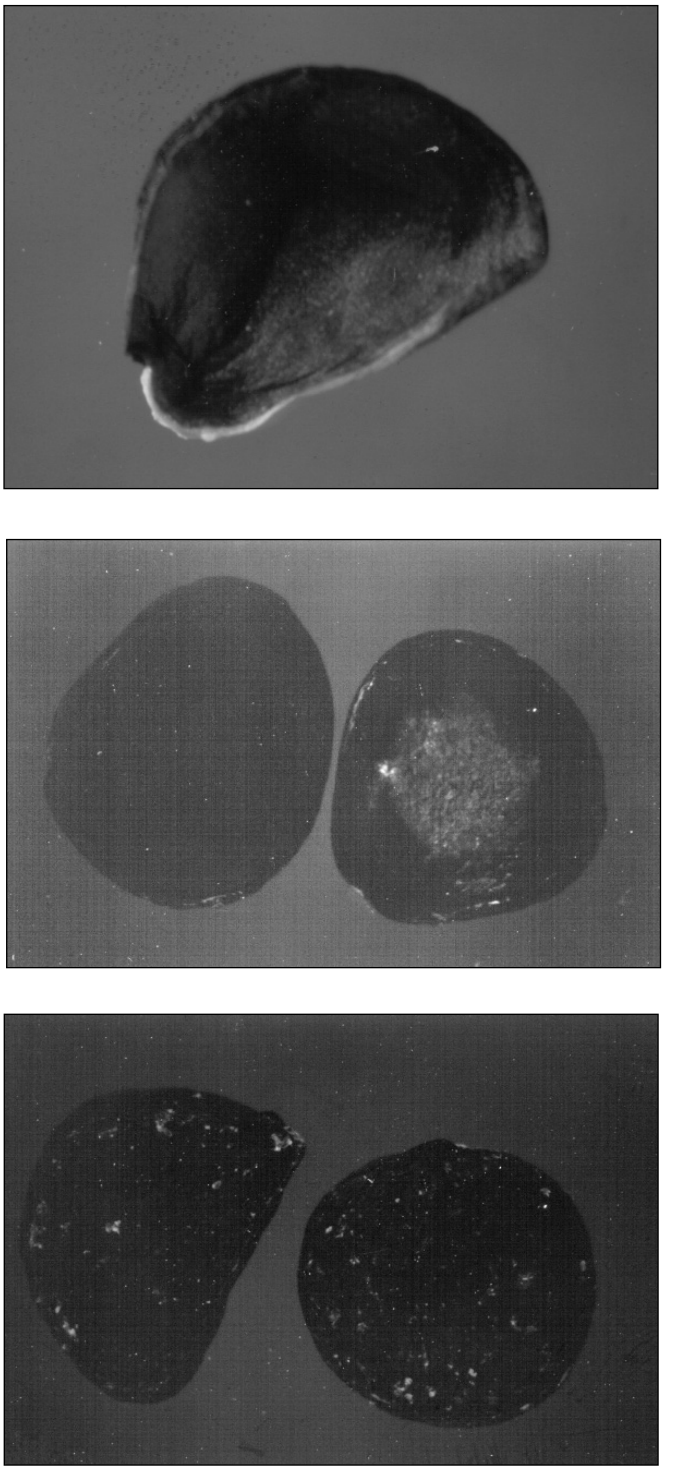
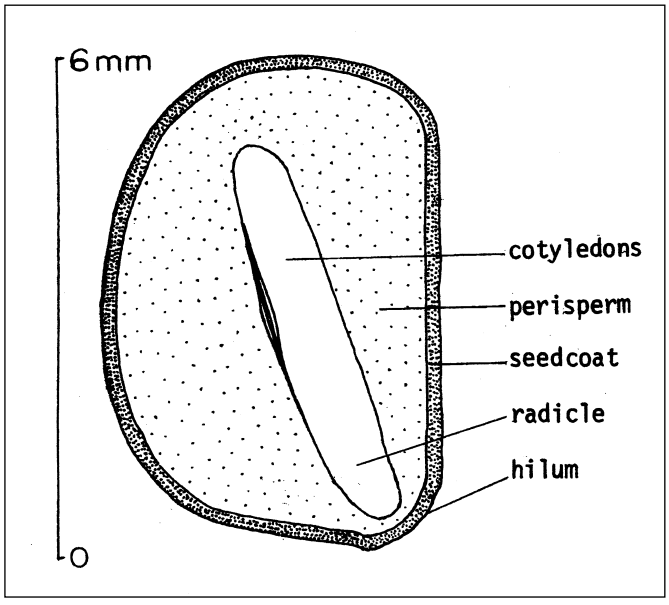


Table 2—*Yucca,* yucca: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
Y. brevifolia	—	Mar 1–Apr 1	July 1–Aug 1	—
Y. elata	S Arizona, New Mexico, & Texas	May 15–July 15	Aug 1–late Sept	Sept–Oct
Y. glauca	E Colorado	May 15–June 30	July–Aug	Sept
Y. schidigera	—	Late Mar–early May	Aug–Sept	—

Sources: Kay and others (1977), Kearney and Peebles (1969), McKelvey (1937), Webber (1953).

Figure 2—*Yucca elata*, soaptree yucca: longitudinal section through the embryo of a seed.



(McCleary and Wagner 1973). Seeds do not require scarification for germination (CALR 1995; Went 1948). Kay and others (1977) found that germination remained around 90% for sealed seeds in 3 environments (room temperature, 4 °C, and –15 °C) even after 35 months in storage. Germination treatments are similar for Mohave yucca (CALR 1995).

Nursery practice and seedling care. Most plants in botanical gardens or landscape plantings have been either 2- to 3-year-old wildings transplanted from the field or vegetative propagules. Joshua Tree National Park has successfully transplanted older Mohave yucca and Joshua tree specimens (CALR 1995). A few individuals and private nurseries have raised yucca plants from seeds. Good germination was obtained by soaking seeds in water at room temperature for at least 24 hours before sowing in the spring. Germination usually begins in 1 to 2 weeks but may continue for 2 to 3 years. Seedlings should be mulched the first winter if there is danger of frost. Seedlings should be ready for outplanting the second year (Hester 1933; Webber 1953). Yucca seedlings are foraged upon by mule deer (*Odocoileus hemionus*), rabbits (*Sylvilagus* spp.), woodrats (*Neotoma* spp.), and ground squirrels (*Citellus* spp.) (Cornett 1991).

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Zamiaceae—Sago-palm family

Zamia pumila L.

coontie

W. Gary Johnson

Mr. Johnson retired from the USDA Forest Service's National Seed Laboratory

Synonyms. *Zamia angustifolia* Jacq., *Z. debilis* Ait., *Z. floridana* A. DC., *Z. integrifolia* Ait., *Z. latifoliolata* Preneloup, *Z. media* Jacq., *Z. portoricensis* Urban, *Z. silvicola* Small, and *Z. umbrosa* Small.

Other common names. Florida arrowroot, sago [palm] cycad, comptie, Seminole-bread.

Growth habit, occurrence, and use. Coontie is a cycad (a low, palm-like plant) with the trunk underground or extending a short distance above ground. It is native to Georgia, Florida, and the West Indies and is found in pine–oak woodlands and scrub, and on hammocks and shell mounds. About 30 *Zamia* species are native to the American tropics and subtropics. *Zamia* classification in Florida has long been the subject of controversy. Traditionally, several species have been recognized, but many botanists now believe that all *Zamia* taxa in Florida belong to a single species (FNAEC 1993).

The taproot gradually contracts, pulling the plant downward, leaving only the upper part of the stem above soil level. Coontie fixes nitrogen in upward-growing branching roots that terminate in nodules with cyanobacteria (Dehgan 1995). Coontie lacks lateral buds and thus has no true lateral branches. However, branching sometimes does occur, by division of the terminal bud (Dehgan 1995). The leaves are pinnately compound with dichotomously branched parallel veins. The seeds remain attached to the seedlings for 2 or more years after germination. The cotyledons never emerge from the seed (Dehgan 1995).

Coontie was once common to locally abundant but is now considered endangered in Florida. The starchy stems of coontie, after water-leaching to remove a poisonous glycoside, were eaten by the native people and early settlers (FNAEC 1993; Witte 1977). It is considered a good candidate for local landscaping (Witte 1977).

Flowering and fruiting. Coontie is a cycad, a cone-bearing gymnosperm, with male and female cones appearing on different plants. The male cones are cylindrical, 5 to 16 cm long, and often clustered 2 to 5 per plant. The female cones are elongate-ovoid, up to 5 to 19 cm long (LHBH 1976; FNAEC 1993). The period of receptivity and maturation of seed is December to March (FNAEC 1993). Insects (usually beetles or weevils) pollinate coontie. Good seed set is helped by hand-pollination (Dehgan 1995).

Collection of cones, extraction, and storage. Two seeds are produced per cone scale. The seeds are drupe-like, bright orange, 1.5 to 2 cm long (FNAEC 1993). The seeds may be collected from dehiscing cones in the winter (January in Gainesville, Florida). The pulpy flesh should be partially dried by spreading out the seeds to air-dry for about a month. Then, the pulp should be removed and the seeds should be washed, scrubbed, and air-dried (Witte 1977). Another method involves soaking the seeds 24 hours in water, then putting the seeds with moist sand in a wide-mouth jar and using a variable-speed drill with an attached long-stemmed wire brush to remove the fleshy seed coat (sarcotesta) without damaging the stony layer (sclerotesta) (Dehgan and Johnson 1983). Seeds stored for 1 year at 5 °C germinated as well as or better than fresh seeds (Witte 1977).

Pregermination treatments and germination tests. The fleshy seedcoats contain a growth inhibitor; the stony layer is up to 2 mm thick and is impermeable to water; and the embryo is partially dormant (Dehgan and Johnson 1983). Germination often takes 6 to 12 months. Removal of the fleshy seedcoat and scarification of the stony layer by cutting or cracking resulted in germination of 80 to 100% in 1 week (Smith 1978). Soaking seeds in sulfuric acid for 1 hour followed by 48 hours in gibberellic acid yielded a 92% germination in 6 weeks with intermittent mist (Dehgan 1996). Seeds average 340/kg (154/lb).

Nursery practice and seedling care. Cycads need well-drained soil with a pH of 6.5. The best growth occurs with a combination of slow-release fertilizer and monthly application of 300 ppm 20:20:20 N-P-K liquid fertilizer.

Seedlings should be provided with micronutrients applied once or twice per year or fertilizers that contain micronutrients should be used (Dehgan 1996). For prevention of root rot, the soil should not be allowed to remain wet longer than 1 to 2 days. The only major insect problems are with magnolia scale (*Neolecanium cornuparvum* (Thro)) and mealybugs (*Pseudococcus* spp.) (Dehgan 1996). Root-pruning helps to develop branched roots. The roots should be clipped where they join the stem, the cut surface dipped in indole butyric acid (IBA), and the plants misted for 2 weeks (Dehgan 1996).

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Rutaceae—Rue family

Zanthoxylum L.

prickly-ash

Franklin T. Bonner

Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi

Growth habit and use. Most of the prickly-ashes—*Zanthoxylum* spp.—are large shrubs or small trees. The 3 species considered here are listed in table 1. In some areas they provide food and cover for wildlife. Their deciduous foliage is very aromatic, and the bark and fruit were once used for medicinal purposes, both as home remedies and in the drug industry (Vines 1960). The wood of *espino rubial* is used for boxes, pallets, local construction, and some furniture (Francis 1991).

Flowering and fruiting. The greenish white dioecious flowers are borne in inconspicuous axillary cymes on common prickly-ash and in large terminal cymes 5 to 15 cm in length on Hercules-club and espino rubial (figure 1) (Sargent 1965; Francis 1991). Phenological data are summarized in table 2. Prickly-ash fruits are globose, single-seeded capsules 5 to 6 mm in diameter. During ripening, they turn from green to reddish brown. At maturity, the round, black, shiny seeds hang from the capsules (figures 1–3).

Collection, extraction, and storage. Seeds may be stripped from clusters of mature capsules by hand as the capsules open, or entire clusters of unopened capsules may be picked when they turn reddish brown. Unopened capsules will discharge their seeds with gentle flailing after several days of air-drying. Seeds can be separated from capsule fragments by screening or winnowing (table 3). There are no storage test data known for this genus, but the seeds are probably orthodox in storage behavior. They can be dried to 10% moisture content without loss of viability, and seeds of common prickly-ash showed practically no loss in germinability after 25 months of storage in sealed containers at 5 °C (Bonner 1974).

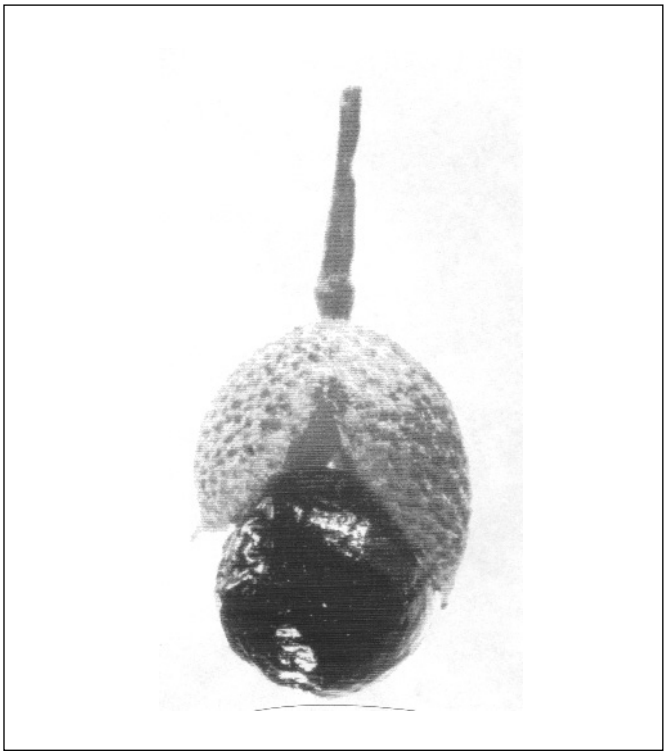
Figure 1—*Zanthoxylum clava-herculis*, Hercules-club: cluster of mature fruits.

Table 1—*Zanthoxylum,* prickly-ash: nomenclature, occurrence, and size

Scientific name	Common name(s)	Occurrence	Height at maturity (m)
***Z. americanum* Mill.**	**common prickly-ash,** toothache-tree, northern prickly-ash	Quebec to North Dakota, S to Oklahoma & Georgia	8
***Z. clava-herculis* L.**	**Hercules-club,** toothache-tree, southern prickly-ash, tingle-tongue, pepperbark	Oklahoma & Virginia, S to Florida & Texas	9–15
***Z. martinicense* (Lam.) DC.**	***espino rubial,*** *pino macho, ayúa,* yellow hercules, *bosú*	Greater & Lesser Antilles, Trinidad & Tobago, E Venezuela	20–25

Sources: Bailey (1949), Francis (1991), Little (1979), Sargent (1965).

Figure 2—*Zanthoxylum clava-herculis*, Hercules-club: single carpel and seed.



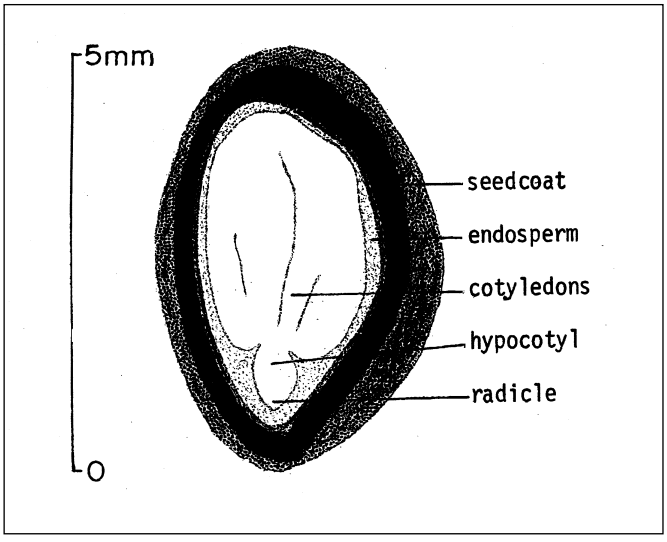
Germination. Seeds of common prickly-ash and Hercules-club exhibit strong dormancy, apparently imposed by the seedcoat. Scarification with concentrated sulfuric acid for 2 hours at about 21 °C has given fair results for Hercules-club, and stratification in moist sand for 120 days at 5 °C has helped germination of common prickly-ash (Bonner 1974). Germination of treated seeds of both species has been tested at diurnally alternating temperatures of 20 to 30 °C. (table 4). Seeds of espino rubial may have a similar dormancy, but there are no conclusive data. Untreated seeds sown in Puerto Rico produced only 5% germination (Francis 1991).

Table 2—*Zanthoxylum,* prickly-ash: phenology of flowering and fruiting

Species	*Flowering*	*Fruit ripening*
Z. americanum	Apr–May	June–Aug
Z. clava-herculis	Apr–June	July–Sept
Z. martinicense	Apr–May*	Aug–Sept

Sources: Vines (1960), Bonner (1974), Francis (1991).
* Primarily, but throughout the year in some areas.

Figure 3—*Zanthoxylum americanum*, common prickly-ash: longitudinal section of a seed (**left**) and seeds (**right**).



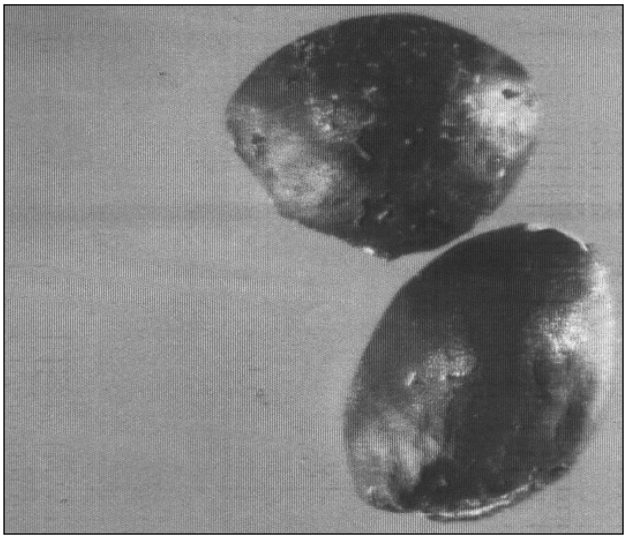


Table 3—*Zanthoxylum,* prickly-ash: seed data

Species	Place collected	Seed moisture (%)	Cleaned seeds/weight				
			Range		Average		
			/kg	/lb	/kg	/lb	Samples
Z. americanum	Minnesota	—	48,100–72,590	21,800–32,900	56,490	25,600	3
Z. clava-herculis	Mississippi	10	33,100–37,050	15,000–16,800	35,000	15,900	2
Z. martinicense	Puerto Rico	—	—	—	75,000	34,020	—

Sources: Bonner (1974), Francis (1991).

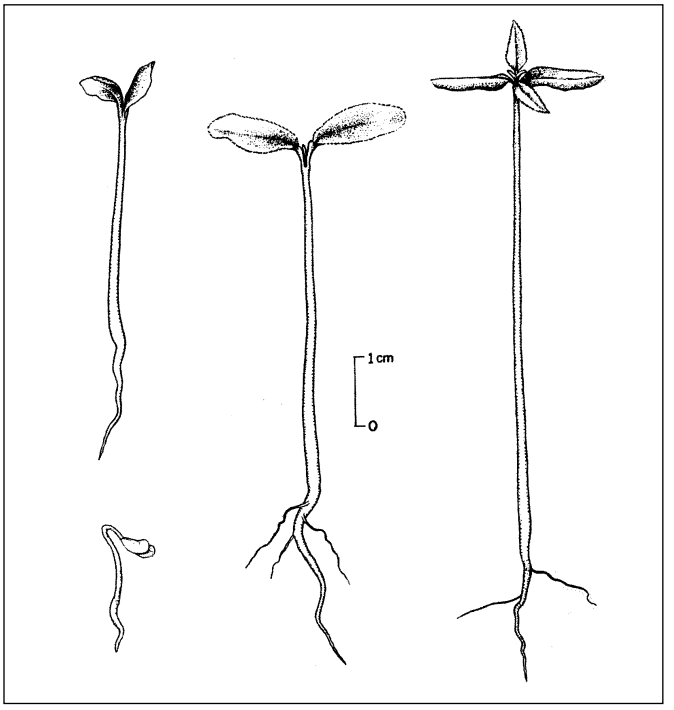
Table 4—*Zanthoxylum,* prickly-ash: germination test conditions and results

Species	Pregermination treatment	Germination test conditions: Daily light (hr)	Medium	Temp (°C): Day	Temp (°C): Night	Days	Germination rate: Amt (%)	Germination rate: Days	Germination %: Avg (%)	Germination %: Samples
Z. americanum	Stratified*	24	Sand	30	20	60	20	20	24	1
Z. clava-herculis	H_2SO_4	8	Blotterpaper	30	20	45	29	19	31	3

Source: Bonner (1974).

* In moist sand at 5 °C for 120 days.

Figure 4—*Zanthoxylum americanum*, common prickly-ash: seedling development at 1 (**left bottom**), 3 (**left top**), 13, and 18 days after



Nursery practice. Until more effective pregermination treatments are developed, fall sowing of untreated seed immediately after collection is recommended. Germination is epigeous (figure 4). Vegetative propagation from root cuttings and suckers is also possible (Dirr and Heuser 1987).

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Rhamnaceae—Buckthorn family

Ziziphus P. Mill.

jujube

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Growth habit and occurrence. There are about 100 species of this genus, which is composed of trees, shrubs, and lianas found chiefly in the tropical and subtropical regions of the world (Johnston 1963). There are 7 species native to the United States and Mexico, but none of them are of economic importance (Lyrene 1979). However, 2 exotic species, which are small deciduous trees, have been planted in this country for fruit production, wildlife food, and watershed protection (table 1). Common jujube—*Ziziphus jujuba* Mill.—the most commonly planted species, may grow to heights of 15 m at maturity (Vines 1960). This species has been cultivated for about 4,000 years in China and grown in this country for over 150 years (Bonner and Rudolf 1974; Lyrene 1979; Mowry and others 1953). Both common jujube and Christ-thorn—*Z. spina-christi* Willd.—are highly valued for fruit production and numerous agroforestry uses in Africa and Asia (Von Carlowitz 1986), where there are many selected cultivars.

Flowering and fruiting. The perfect, yellow flowers of common jujube appear in March to May in the United States, and the reddish-brown fruits mature from July to November. The fruits are globose to slender, fleshy drupes, which turn from green to dark reddish brown at maturity. If left on the tree, the fruits will turn black (Bailey 1939; Vines 1960). Common jujube drupes are oblong and 2.5 to 5 cm in length. They contain a 2-celled and 2-seeded pointed stone that is deeply furrowed, reddish brown to deep gray, oblong, and 2 to 2.5 cm long (figure 1) (Bonner and Rudolf 1974; Mowry and others 1953). Trees bear fruit as early as 1 to 4 years after planting (Lyrene 1979). Good crops are borne annually, and although they are popular for human consumption in Asia and Europe, the fruits from trees grown in the United States have apparently not been as edible. The crisp flesh of common jujube is whitish in color and has a sweet to subacid taste (Mowry and others 1953; Goor 1955; Vines 1960).

Collection, extraction, and storage. Jujube drupes may be picked by hand or flailed onto canvas sheets in the fall. Stones can be depulped by running them through a macerator with water and floating off the pulp. The cleaned stones are used as seeds. Seed yields are as follows (Goor 1955; Bonner and Rudolf 1974):

	Common jujube	Christ-thorn
Cleaned seeds/weight of drupes—kg/45 kg (lb/100 lb)	12–16 (25–35)	—
Cleaned seeds/weight—kg (lb)	1,650 (750)	1,500 (680)

No conclusive storage data are available for this genus, but dry storage at room temperature has been successful for Christ-thorn (Goor 1955). Because these seeds appear to be orthodox, storage at low moisture contents at 5 °C is suggested.

Pregermination treatments. Jujube seeds are moderately dormant and require treatment for prompt germination. Stratification recommendations for common jujube are 60 to 90 days in moist sand at 5 °C (Bonner and Rudolf 1974) or 3 months warm incubation, followed by 3 months cold stratification (Dirr and Heuser 1987). Some growers recommend scarification in sulfuric acid for 2 to 6 hours, followed by stratification at 5 °C for 60 to 90 days (Lyrene 1979). Very

Table 1—*Ziziphus*, jujube: nomenclature and occurrence

Scientific name	Common name(s)	Occurrence
***Z. jujuba* Mill.**	**common jujube,** jujube, Chinese date	Native to Asia, Africa, & SE Europe; planted in S US from Florida to California; naturalized along Gulf Coast from Alabama to Louisana
***Z. spina-christi* Willd.**	**Christ-thorn**	Native to arid & semi-aridregions of Africa & W Asia; planted in SW US

Sources: Bonner and Rudolf (1974), Vines (1960).

prompt germination was obtained for seeds of Christ-thorn in Israel by soaking them for 2 days in water at 21 to 38 °C. Shorter or longer periods were not as successful (Gindel 1947).

Germination tests. Germination tests with seeds treated as described above are summarized in table 2.

Nursery practice. Untreated stones of common jujube can be sown in drills in the fall; stones stratified for 90 days may be sown in the spring. They should be covered with 2.5 cm (1 in) of soil (Bonner and Rudolf 1974). In Israel, 2 days of water-soaking prior to sowing has been recommended for Christ-thorn (Gindel 1947). Intact drupes may also be sown in the nursery (Goor 1955). Germination is epigeal. Vegetative propagation is possible by root cuttings (Dirr and Heuser 1987).

Figure 1—*Ziziphus jujuba*, common jujube: longitudinal section through 2 seeds in a stone (**left**), exterior view of a seed after removal from a stone (**center**), exterior view of a seed (**right**).

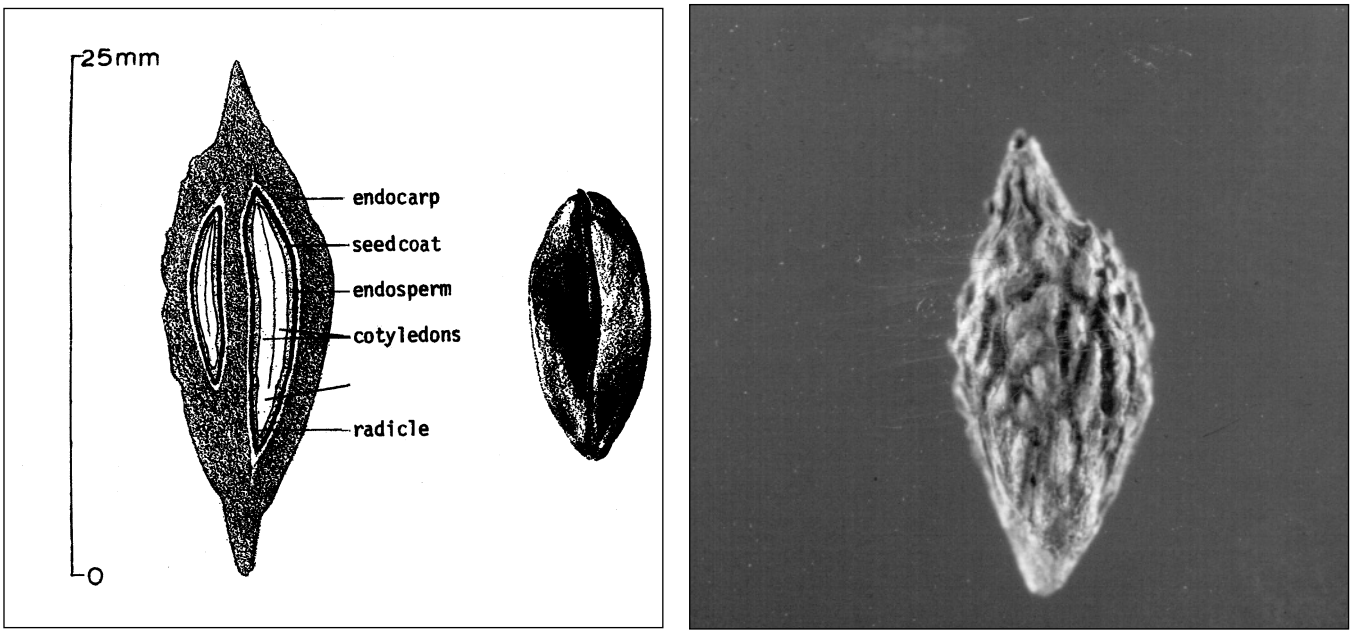

Table 2—*Ziziphus,* jujube: germination test conditions and results

	Germination test conditions				Germination rate		Germination %	
		Temp (°C)			Amt		Avg	
Species	Medium	Day	Night	Days	(%)	Days	(%)	Samples
Z. jujuba	Sand	30	21	50	—	—	31	2
Z. spina-christi	—	38	38	4	65	2	85	4

Source: Bonner and Rudolf (1974).

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Chenopodiaceae—Goosefoot family

Zuckia brandegei (Gray) Welsh & Stutz ex Welsh

siltbush

Nancy L. Shaw, Rosemary L. Pendleton, and Emerenciana G. Hurd

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Other scientific names. *Zuckia arizonica* Standley, *Atriplex brandegei* (Gray) Collotzi, *Grayia brandegei* (Gray).

Other common names. spineless hopsage, applebush, saltbush.

Growth habit, occurrence, and use. Siltbush is an autumn-deciduous shrub or sub-shrub ranging from 0.1 to 0.8 m in height (Goodrich and Neese 1986). Stems of the current year are thornless and erect or ascending, branching from a persistent, woody base. Leaves are gray-scurfy and entire to lobed. Overwintering leaf buds are prominent, axillary, and globose (Welsh and others 1987).

A narrowly distributed edaphic endemic, siltbush is largely restricted to the Colorado River drainage of central and eastern Utah and northeast Arizona, southwest Wyoming, western Colorado, and northwest New Mexico (Smith 1974; Stutz and others 1987; Welsh and others 1987). It grows in isolated monotypic populations on weathered, often saline or seleniferous, fine-textured to sandy substrates in desert shrub to lower juniper communities at elevations from 1,280 to 2,240 m (Goodrich and Neese 1986). Although a poor competitor, siltbush is a stress-tolerant species capable of surviving on sites unfavorable for establishment of other species and enduring long periods of adverse environmental conditions. It is a potential revegetation species for mined lands and other disturbed sites within its native range (Pendleton and others 1996).

Geographic races and hybrids. Type specimens of *Zuckia brandegei* were originally described as *Grayia brandegei* Gray (Gray 1876). Stutz and others (1987) later identified 2 chromosome races. Diploid populations (2X = 18) are small plants with narrow, linear leaves that are mostly restricted to south-central Utah and northeastern Arizona. Tetraploids (4X = 36) are larger plants with large ovate to lanceolate leaves that occur primarily as isolated populations in northeastern Utah, south-central Wyoming, eastern Colorado, and northwestern New Mexico. Based on distribution patterns and interpopulation differences, Stutz and others (1987) suggested that the larger plants may be autotetraploids of polyphyletic origin and designated them *G. brandegei* A. Gray var. *plummeri* Stutz and Sanderson var. nov. in honor of A. P. Plummer, pioneer shrub scientist.

Welsh (1984) and Welsh and others (1987) transferred *G. brandegei* to the genus *Zuckia*, renaming it *Z. b.* (Gray) Welsh & Stutz ex Welsh var. *brandegei* and reduced *Z. arizonica* Standley, the only species previously in the genus, to *Z. b.* Welsh & Stutz ex Welsh var. *arizonica* (Standley) Welsh. *Z. b.* var. *arizonica* is diploid (Sanderson 2000) and is found in scattered populations from northern Arizona to northeastern Utah (Goodrich and Neese 1986). Dorn (1988) later transferred *G. b.* var. *plummeri* to *Z. b*. var. *plummeri* (Stutz & Sanderson) Dorn. Transfers from *Grayia* to *Zuckia* were made on the basis of fruit morphology, branching pattern, and pubescence type. Goodrich and Neese (1986) concurred with these distinctions but with the reservation that *Grayia* "could logically be expanded to include *Zuckia*."

Naturally occurring hybrids of siltbush with shadscale (*Atriplex confertifolia* (Torr. And Frem.) Wats.) and Castle Valley clover (*A. gardneri* (Moq.) D. Dietr. var. *cuneata* (A. Nels.) Welsh) were reported by Drobnick and Plummer (1966). Blauer and others (1976) obtained viable seeds, but no seedlings, by artificially pollinating pistillate flowers of fourwing saltbush with tetraploid siltbush pollen.

Flowering and fruiting. All siltbush varieties are monoecious and heterodichogamous (Pendleton and others 1988). Plants are protogynous (producing pistillate, then staminate flowers) or protandrous (producing staminate, then pistillate flowers) in about equal numbers. Within each plant, temporal separation of pistillate and staminate phases is nearly complete, generally precluding self-fertilization.

Staminate flowers each consist of 4 or 5 stamens and a 4- or 5-lobed perianth. They develop in clusters of 2 to 5 in bract axils (Goodrich and Neese 1986; Welsh and others 1987). Pistillate flowers are 1 to several in bract axils with each enveloped by 2 united bracts. The bracts are either dorsiventrally flattened and unequally 6-keeled with the seed horizontal (*Z. b*. var. *arizonica*) (figures 1 and 2) or obcompressed and thin-margined with the seed vertical (*Z. b.* var. *bradegei* and *Z. b.* var. *plummeri*) (Goodrich and Neese 1986; Welsh and others 1987) (figures 1 and 2). Plants of all varieties flower in late spring or summer and fruits ripen in mid to late summer or fall (Blauer and others 1976; Pendleton and others 1988) (table 1).

Protogynous plants generally produce more seeds, but protandrous plants may be equally productive in wet years or in years with low seed predation (Pendleton and others 2000). Fruits are dispersed slowly, with some usually remaining dormant on the plant through winter (Blauer and others 1976). Seeds are light yellowish brown at maturity (Hurd and Pendleton 1999) (figure 3). The outer layer of the seedcoat is elastic when imbibed. The embryo is well developed, with pale yellow cotyledons and an elongate, inferior radicle encircling the perisperm (figure 3). Seedling development is epigeal (figure 4).

Collection of fruits and seed extraction and cleaning. Fruits are collected by hand- stripping or beating and air-dried. Coarse debris may be removed with an air-screen machine or a seed blower, or by screening. Careful rubbing to remove bracts prevents radicle damage. The final product may consist of debracted utricles (Meyer and Pendleton 1990; Pendleton and Meyer 1990) or seeds (figure 3). Weight of bracted utricles and seeds and seed fill data are provided in table 2.

Figure 1—*Zuckia brandegei*, siltbush: bracted utricles.

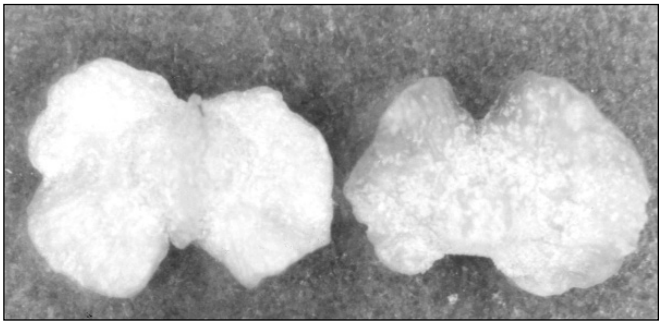
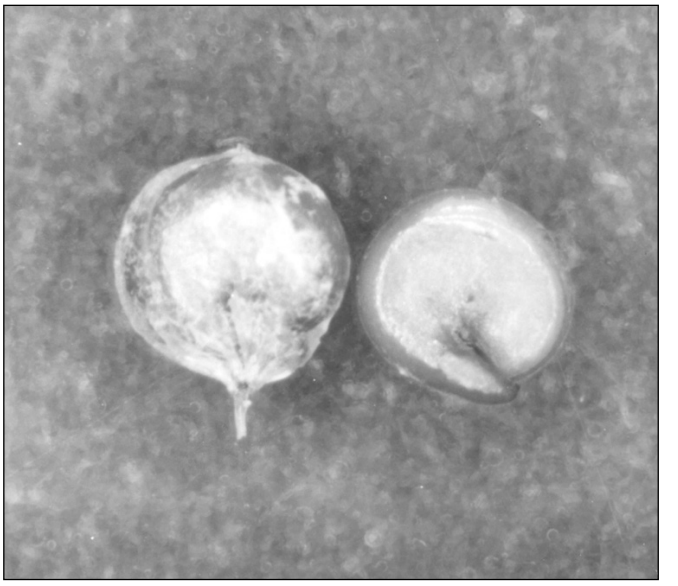


Figure 2—*Zuckia brandegei*, siltbush: utricle (**left**) and seed (**right**)



Storage. Germination of seeds incubated at 1 to 3 °C in constant darkness was 87% after 2 years of storage in cloth bags in a warehouse (Stevens and Jorgensen 1994; Stevens and others 1981). Germination from year 2 to year 4 was 88%, dropping to 57% by year 5, 13% by year 7, and 0% after 15 years. Viability of bracted utricles stored in paper bags at room temperature and debracted utricles from the same collection stored in a freezer at – 80 °C was 97% after 7 years as determined by tetrazolium chloride testing (Hurd and Pendleton 1994).

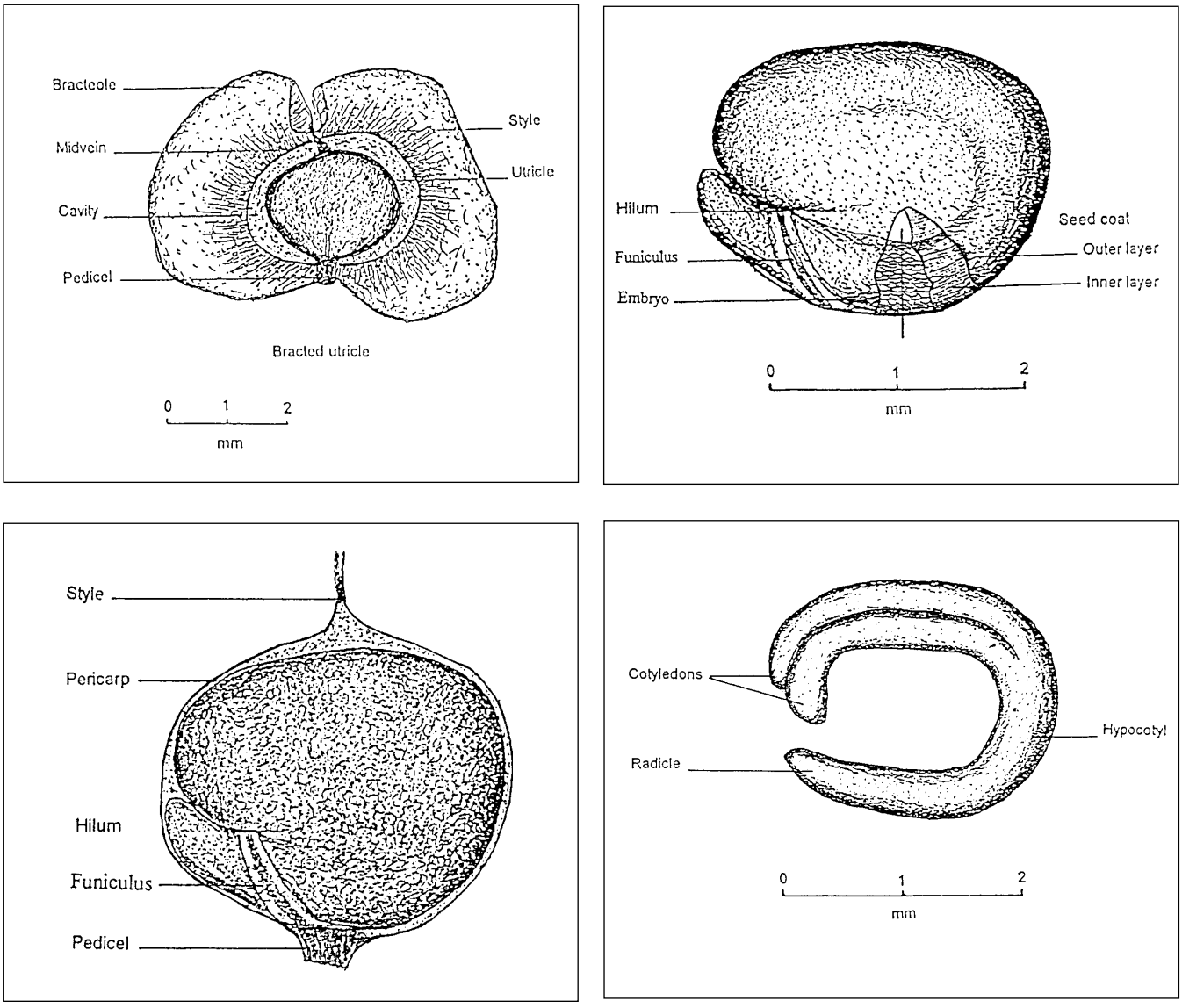
Pregermination treatments. Germination experiments have been conducted with seeds of *Z. b.* var. *brandegei* and *Z. b.* var. *plummeri*. Seeds of warm-winter populations may germinate opportunistically over a wide range of

Table 1—*Zuckia brandegei*, siltbush: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
Z. brandegei	Central Utah	Mid-June–mid-Aug	Late Sept–early Oct	Jan or later
	Uinta Basin, Utah	May–June	Sept	—
	Sanpete Co., Utah	Mid-May–July	July–late Sept	—
	—	—	Sept 10–Dec 15	—

Sources: Blauer and others (1976), Goodrich and Neese (1986), Pendleton and others (1988), Plummer and others (1968).

Figure 3—*Zuckia brandegei*, siltbush: bracted utricle (**top left**), seed (**top right**), utricle (**bottom left**), and embryo (**bottom right**).



constant temperatures (15 to 30 °C) when water is available (Meyer and Pendleton 1990). Seeds of cold-winter populations are dormant at fall and winter temperatures, germinating in early spring following exposure to overwinter chilling. Germination generally increased with duration of wet prechilling at 1 °C for up to 8 weeks, dry after-ripening for up to 14 months, or removal of bracts (Meyer and Pendleton 1990; Pendleton and Meyer 1990).

Techniques and criteria recommended for characterizing normal seedlings, excising embryos, and testing viability are as described for spiny hopsage (Shaw 1992):

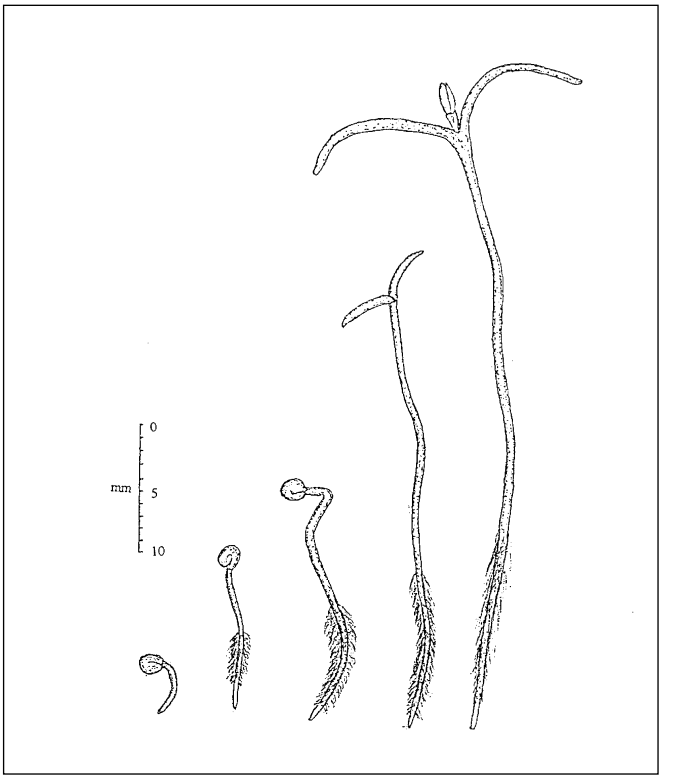
- Normal seedling—Epigeal, with thin, 10- to 15-mm-long hypocotyls; small, narrow cotyledons; short epicotyl; and well-developed root hairs (figure 4).
- Excised embryo—Seeds soaked in water at 28 °C for 12 hours and then drained can have their embryos excised with sharp needles; these embryos germinate rapidly at 15/5 or 15 °C and should be evaluated for presence of normal seedlings.
- Viability—Seeds soaked in water at 28 °C for 12 hours, and then drained can be pierced through the perisperm with a sharp probe or needle, then they are

Table 2—*Zuckia brandegei*, siltbush: fruit and seed characteristics

Species	Bracted utricles (x1,000)/weight				Seeds (x1,000)/weight				Filled seed %	
	Range		Average		Range		Average			
	/kg	/lb	/kg	/lb	/kg	/lb	/kg	/lb	Range	Average
Z. brandegei	263–312	119–142	284	129	555–769	252–349	—	—	5–27	16
Z. brandegei var. *arizonica*	372–1,061	169–481	732	332	420–794	191–360	418–561	190 – 254	7–21	15

Sources: Pendleton and others (1988), Plummer and others (1968), Smith (1974).

Figure 4—*Zuckia brandegei*, siltbush: seedling development.



soaked in a 1% 2,3,5-triphenyl tetrazolium chloride solution for 4 to 8 hours at 28 °C; the seedcoat is translucent after soaking, making excision unnecessary for evaluation of staining.

Nursery culture and direct seeding. Because few data are available, recommendations for spiny hopsage (see Grayia, page 567) may be used as guidelines for establishing siltbush from seed. Based on studies conducted in south-central Utah, Monsen (1996) found that siltbush seedlings develop more rapidly than those of spiny hopsage. Root systems of bareroot stock are much more extensive after 1 growing season. Palatability is low to moderate (Monsen 1996; Stutz 1995). Plants may attract rodents, other small animals, and occasionally deer.

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Part III

Appendices

Metric to English

To convert from	To	Multiply by
millimeters	sixteenths of an inch	0.6301
millimeters	eighths of an inch	0.3150
millimeters	fifths of an inch	0.1968
millimeters	fourths of an inch	0.1574
millimeters	thirds of an inch	0.1181
millimeters	halves of an inch	0.07874
millimeters	inches	0.03937
centimeters	inches	0.3937
meters	feet	3.281
number per hectoliter	number per bushel	0.3524
kilograms per hectoliter	pounds per bushel	0.777
grams per hectoliter	ounces per bushel	0.0124
number per kilogram	number per pound	0.4536
number per gram	number per pound	453.6
number per gram	number per ounce	28.35
number per square meter	number per square foot	0.0929
number per linear meter	number per linear foot	0.3048
degrees Centigrade (°C)	degrees Fahrenheit (EF)	(1.8 H °C) + 32
hectares	acres	2.471

English to metric

To convert from	To	Multiply by
sixteenths of an inch	millimeters	1.587
eighths of an inch	millimeters	3.175
fifths of an inch	millimeters	5.080
fourths of an inch	millimeters	6.350
thirds of an inch	millimeters	8.467
halves of an inch	millimeters	12.70
inches	centimeters	2.540
feet	meters	0.3048
number per bushel	number per hectoliter	2.838
pounds per bushel	kilograms per hectoliter	1.287
ounces per bushel	grams per hectoliter	80.44
number per pound	number per kilogram	2.205
number per pound	number per gram	0.002205
number per ounce	number per gram	0.03527
number per square foot	number per square meter	10.76
number per linear foot	number per linear meter	3.281
degrees Fahrenheit (EF)	degrees Centigrade (°C)	0.55 H (°F - 32)
acres	hectares	0.4047

Glossary

abortive imperfectly or incompletely developed, as abortive seed.

abscission natural separation of leaves, flowers, and fruit from plants generally associated with deterioration of a specialized layer of thin-walled cells.

achene small, dry, indehiscent, 1-seeded fruit with seed attached to ovary wall at only 1 point as in *Cowanina* and *Eriogonum;* or pericarp fused with calyx tube and embryo, completely filling the ovarian cavity as in *Artemesia* and *Chrysothamnus*.

after-ripening biochemical or physical processes occurring in seeds, bulbs, tubers, and fruit after harvesting; often necessary for germination or resumption of growth.

agamospermy a type of apomixis in which seeds develop from female gametophyte tissue without fertilization as in *Amelanchier, Cotoneaster, Crataegus,* and *Rubus*.

aggregate fruit formed from a cluster of ripened ovaries of separate pistils of a single flower, as in *Maclura, Magnolia,* and *Rubus*. (Compare **multiple fruit** and **simple fruit**; *synonym* = **syncarp**).

allele an alternative form of a gene (at a given locus) differing in DNA sequence. If the array contains more than 2 genes, the genes are called multiple alleles. Multiple alleles arise by repeated mutations of a gene, each with different effects. No more than 2 alleles can be present in a given (diploid organism).

ament see **catkin**.

anatropous having an ovule inverted at an early stage of growth, so that the micropyle points toward the funicle, as in *Eriogonum*.

angiosperm member of the group of vascular flowering plants having seeds that develop in a carpellary ovary (compare **gymnosperm**).

anthesis 1. stage of full flower expansion. 2. bursting of pollen sacs with release of pollen.

apomixis any form of reproduction involving generative tissue, but without fertilization (compare **agamospermy**).

apophysis 1. an enlargement or swelling of the surface of an organ. 2. visible portion of a scale in a closed cone.

aril exterior covering of appendage of certain seeds that develops after fertilization as an outgrowth from the point of attachment of the ovule as in *Celastrus* and *Euonymus*.

asexual reproduction reproduction without fertilization; reproduction by purely vegetative means accomplished in woody plants usually by rooting stem cuttings, air-layering, grafting, or budding.

autogamy self-fertilization; pollination of a flower with its own pollen; may occur in *Kalmia,* for example.

berry fleshy indehiscent fruit developed from a single pistil and containing 1 or more seeds as in *Berberis, Diospryros, and Ribes*.

bisexual having functional male and female reproductive organs in the same flower (*synonym = complete flower, perfect flower, hermaphrodite;* compare **unisexual**).

bract 1. modified leaf subtending a flower or flower cluster. 2. modified leaf subtending a scale in female cones.

broadcast sowing scattering seed uniformly over an area (*synonym = broadcast seeding*).

browse 1. any woody vegetation consumed by livestock and wild animals, mainly ungulates. 2. the act of eating such material.

bur prickly or spiny casing around a fruit; the involucre in *Castanea* and *Fagus*.

calyx outermost whorl of floral parts (sepals).

capitulum an aggregation of small flower heads into an unusually dense terminal cluster as in *Gutierrezia*.

capsule dry, dehiscent, usually many-seeded fruit composed of two or more fused carpels as in *Kalmia, Koelreuteria,* and *Populus*.

carpel simple pistil or single member or a compound pistil.

carpellary pertaining to a carpel.

carpellate having carpels.

caruncle a fleshy protuberance at or surrounding the hilum of some seeds as in *Philadelphus*.

catkin spike of unisexual flowers or fruits with imbricated scaly bracts as in *Alnus and Betula*. (*synonym* = **ament**; (compare **strobile**).

cauliflory production of flowers and fruits directly on the trunk or branches of certain trees as in *Cercis*.

certified seed(s) seedlot attested by a designated certifying agency to be from trees of known identity and produced so as to assure that identity (compare **selected seeds** and **source-identified seeds**).

cline a continuous gradient of phenotype or genotype within a species range; usually associated with a gradient in an environmental factor over the range of the population.

clone 1. group of genetically identical plants produced by vegetatively propagating a single plant; 2. a cell line of a single-cell origin (compare **ortet, ramet**).

cold hardiness test a test that estimates physiological condition of a seedling by determining the minimum temperature to which the seedling can be exposed without suffering observable cold injury.

combining ability a statistical value indicating the capacity of a parent to transmit genetic superiority to its offspring.

complete flower see **bisexual**.

cone 1. the dry, woody strobilus of a gymnosperm. A **female cone** consists of a central axis supporting imbricated bracts each of which subtends a scale bearing naked (noncarpellate) seeds. A **male cone** consists of a central axis supporting spirally arranged microsporophylls each of which bears pollen sacs containing pollen grains (synonym= **strobilus**). 2. any seed-bearing structure having conical shape as in *Magnolia* and *Liriodendron*.

conelet immature female strobilus (cone) of gymnosperms, sometimes described as a flower.

coriaceous leather-like.

corolla inner set of floral leaves consisting of separate or fused petals that surround the carpels.

corymb a flat-topped floral cluster as in *Rhododendron* and *Kalmia*.

cotyledons modified leaves developed in the embryo of a seed. They may contain stored food for the initial growth of the seedling as in *Quercus* or they may become functional leaves after gemination as in *Pinus*.

cryptogeal germination type of seed germination in which the seeds germinate on the surface of the soil, then the cotyledonary stalks elongate, pushing the hypocotyl, plumule, and radicle into the soil as in *Araucaria*. Compare **epigeal** and **hypogeal** germination.

cyme flower cluster having main and secondary axes each terminating in a single flower as in *Sambucus, Viburnum*, and *Sorbus*.

deciduous abscission at the end of the growing season, as deciduous leaves, or at certain stages of development, such as flower petals after fertilization of the ovules, or female cones after seeds are disseminated.

dehiscence splitting open at maturity to discharge contents, as a capsule discharging seeds or an anther discharging pollen (compare **anthesis**).

determinate flowering terminal flowers blooming slightly in advance of their nearest associates (compare **indeterminate flowering**).

dichogamy maturation of male and female organs on the same plant at different times, thus preventing self-pollination. If the staminate (male) flowers appear first, the plant is **protandrous**. If the pistillate (female) flowers appear first, the plant is **protogynous**. If both conditions can occur in a genus, it is said to be **heterodichogamous**, as in *Zuckia*.

dioecious having staminate (male) flowers and pistillate (female) flowers borne on different individual plants as in *Acer, Fraxinus,* and *Ilex* (compare **monoecious**).

diploid having 2 sets of chromosomes (2n), usually 1 set from each parent.

dormancy a physiological state in which a seed predisposed to germinate does not, even in the presence of favorable environmental conditions; also applies to comparable conditions in growth of all plant parts (compare **seedcoat dormancy, embryo dormancy, epicotyl dormancy,** and **double dormancy**).

double dormancy dormancy as a result of two or more primary factors, such as **embryo dormancy** and **seedcoat dormancy**.

drupe fleshy, usually 1-seeded, indehiscent fruit with seed enclosed in a hard, bony endocarp as in *Chionanthus, Cornus,* and *Prunus*.

elaiosome a fleshy appendage of oil-storing tissue around the hilum as in *Ulex*.

ecotype see **race**.

embryo dormancy dormancy maintained by agents or conditions within the mature seed. Compare **internal dormancy**.

endocarp inner layer of the pericarp; e.g., the hard, bony part of the fruit of *Prunus*.

endosperm triploid storage tissue surrounding the embryo in seeds of some angiosperms and consisting of thin-walled cells rich in carbohydrates. The comparable tissue in seeds of gymnosperms is haploid tissue called the **megagametophyte** (often called endosperm by mistake).

epicarp see **exocarp**.

epicotyl portion of the axis of a plant embryo or seedling stem between the cotyledons and the primary leaves. Compare **plumule**.

epicotyl dormancy a condition in which the radicle emerges and develops in the fall, but the epicotyl remains dormant or slightly emerges and becomes dormant again, then develops normally in the spring as in some species of *Aesculus* and *Quercus*.

epigeal type of seed germination in which the cotyledons are forced above the ground by elongation of the hypocotyl (compare **hypogeal** and **cryptogeal germination**).

exocarp outermost layer of pericarp; the skin on fleshy fruits as in *Cornus, Malus,* and *Prunus (synonym = epicarp*).

F_1 first filial generation of offspring from a cross between 2 parents.

F_2 second filial generation of offspring produced by intercrossing or selfing among the F_1 individuals.

fecundity the number of eggs, seeds, or offspring in the first stage of the life cycle produced by an individual.

female cone see **cone**, **strobilus**.

fertilization penetration of a pollen tube through the embryo sac into the ovule (egg cell), discharge of the male nucleus into the ovule, and union of the male nucleus with that of the ovule.

florocane second-year canes in *Rubus* that produce flowers (compare **primocane**).

follicle dry, dehiscent fruit, opening along one line of suture, as in the individual fruits of a *Magnolia* cone and the single fruits *of Zanthoxylum*.

fruit the seed-bearing unit of angiosperms developed after fertilization by a sperm cell from a pollen grain; it is the mature, ripened ovary and all of its associated protective covers, appendages, and su1194pporting structures.

fruit wall outer layer of fruits in which pericarp is not distinguishable from the seedcoat as in the achenes of *Baccharis* (*synonym* = **pericarp**).

full seeds those filled with tissue having a normal appearance as distinguished from empty or partially empty seeds (compare **sound seeds**).

funiculus stalk of an ovule.

fusiform radicles spindle-shaped radicles formed in cryptogeal germination as in *Araucaria*.

gametophyte the haploid generation in organisms that alternate haploid *(n)* and diploid *(2n)* generations.

geitonogamy pollination of a flower by pollen from another flower on the same plant.

gene the smallest transmissible unit of genetic material consistently associated with a single primary genetic effect.

genetic diversity the genetic variability within a population or a species.

genetic gain average improvement among progeny over the mean for the parents with respect to the characteristics used in selecting the parents.

genome a complete haploid set of chromosomes as found in a gamete.

genotype 1. an individual's hereditary (genetic) constitution; it interacts with the environment to produce the phenotype. 2. Individual(s) characterized by a certain genetic constitution (compare **phenotype**).

geographic race a race native to a geographic area.

germination resumption of active growth in an embryo which results in its emergence from the seed and the development of structures essential to plant development.

germination percentage see **germinative capacity**.

germination, real percentage of sound seeds that germinate.

germinative capacity proportion of seeds that germinate normally during a period of time when germination is practically complete; usually expressed as a percentage *(synonym* = **germination percentage**).

germinative energy that proportion of germination that has occurred up to the time of peak germination, the time of maximum germination rate, or some other preselected point.

glabrous smooth; without hairs or other projections.

glaucous having a whitish or waxy coating that give a frosted appearance and tends to rub off.

globose approximately or completely spherical; globular.

gymnosperm members of the subdivision of plants having seeds not enclosed in an ovary (naked seeds) borne on the scales of a cone, on the megasporophylls of other types of strobile, or singly with arils as in *Torreya* and *Taxus*.

(compare **angiosperm**).

haploid having 1 complete set of chromosomes per cell.

hardwood cutting cuttings for vegetative propagation that are collected during the dormant period from last season's growth.

head densely packed cluster of stalkless flowers as in *Cornus, Baccharis,* and *Cephalanthus (synonym* = **capitulum**).

hermaphrodite see **bisexual**.

heterodichogamous see **dichogamy**.

heterozygous having 1 or more sets of unlike alleles, e.g., the dominant with the recessive gene. A heterozygote does not generally breed true and is known as a hybrid with respect to the genes in question (compare **homozygous**).

hilum scar on a seed marking the point of attachment to the ovary in angiosperms or to the megasporophyll of gymnosperms.

hip the ripened "false fruit" of *Rosa* species, consisting of a fleshy receptacle that contains many achenes.

homozygous having 1 or more sets of like alleles, e.g., both dominant (AA), or both recessive (aa). A homozygote breeds true when mated with the same genotype (compare **heterozygous**).

husk outside envelope of a fruit, especially if coarse, harsh, or rough as in the involucre of *Carya*.

hypantheum a cup-like receptacle usually derived from the fusion of floral parts as in *Purshia*.

hypocotyl that part of the embryonic axis which is between the cotyledons and the radicle. In seedlings, the juvenile stem which is between the cotyledons and the roots.

hypogeal type of seed germination in which the cotyledons remain below the ground while the epicotyl elongates as in *Juglans, Quercus,* and *Torreya*.

indehiscent refers to dry fruits that normally do not split open at maturity.

indeterminate flowering flowers that open progressively from the base of an inflorescence (compare **determinate flowering**).

inflorescence floral axis with its appendages; flower cluster.

integument(s) in angiosperms, the one or two layers of tissue, often fused, that enclose the nucellus of an ovule and that develop after fertilization into 1 or 2 seedcoats; in gymnosperms, a single layer of tissue that encloses the nucleus of an ovule. In *Pinus,* it develops after fertilization into 3 seedcoats, the outer one of which is usually not distinct in harvested seeds.

internal dormancy see **embryo dormancy**.

involucre 1 or more whorls of bracts situated below and close to a flower cluster; sometimes enclosing the carpels as in *Carya, Castanea,* and *Fagus*.

land race a population of plants, usually exotic, that has become adapted to a specific environment.

legume dry, dehiscent, 1-celled fruit that usually dehisces (splits) along 2 suture lines at maturity as in *Acacia*, *Gleditsia,* and *Lupinus (synonym* = pod).

loculicidal dehiscing lengthwise of a capsule so as to divide each loculus into 2 parts as in *Chimaphila*.

loculus (locule) the cell of a carpel in which the seed is located.

maceration a process for removing the soft, pulpy tissue from fleshy fruits.

male cone see **cone**.

megagametophyte the female gametophyte tissue in the seeds of gymnosperms; often mistakenly labeled as **endosperm**.

mesocarp middle layer of the pericarp; the pulp of drupes and berries.

micropyle minute opening in the integument of an ovule through which the pollen tube normally passes to reach the embryo sac; usually closed in the mature seed to form a superficial scar.

microsporangia in gymnosperms, the pollen sacs on the lower surface of the **microsporophyll**.

microsporophyll in gymnosperms, a scale in the male strobilus.

monoecious having functional staminate and pistillate flowers on the same plant (compare **dioecious**).

mucro a small, short abrupt tip of a scale as in *Cupressus*.

multiple fruit fruit formed from several flowers whose coalesced ripened ovaries are inserted on a common receptacle as in *Morus* and *Platanus*. (compare **aggregate fruit and simple fruit**).

nucellus mass of thin-walled cells that composes the central and main part of the body of an ovule and that contains the embryo sac and is surrounded by 1 or more integuments (compare **perisperm**).

nucleus the component of a cell that is made up chiefly of chromosomes.

nut dry, indehiscent, 1-seeded fruit with a woody or leathery pericarp, as in *Quercus*, or generally partially or wholly encased in an involucre or husk, as in *Carya* and *Corylus*.

nutlet small nut, often with accessary parts such as bracts or husks, as in *Betula* and *Fagus*.

obovoid inversely egg shaped; ovoid with the broad end toward the apex.

open pollination pollination in which a mixture of related and unrelated pollen is delivered by wind, insects, etc. and is usually not directly influenced by humans.

ortet original plant from which a vegetatively propagated clone has been derived (compare **ramet**).

outcrossing mating unrelated individuals.

ovary in angiosperms, the basal portion of a pistil that bears the ovules.

ovoid egg shaped with the broad end toward the point of attachment.

ovule egg-containing structure in seed plants that develops into a seed after fertilization.

panicle a branched flower cluster as in *Aesculus, Chionanthus,* and *Fraxinus*.

papilionaceous descriptive of flowers of many Fabaceae that have irregular corollas shaped like a butterfly as in *Colutea*.

pappus a tuft of delicate fibers or bristles that form a feathery appendage of an achene as in *Baccharis* and *Chrysothamnus*.

parthenogenesis reproduction from an unfertilized ovule; embryo may be either haploid or diploid. See **apomixis**.

parthenocarpy development of fruit without fertilization.

pedicel stalk of a single flower within a flower cluster.

peduncle stalk that bears a single flower or a flower cluster.

peltate a foliage characteristic in which the petiole of a leaf blade is attached to the lower surface instead of to the base.

perfect flower see **bisexual**.

perianth the envelope of a flower; calyx, corolla, or both.

pericarp wall of a ripened ovary that is homogeneous in some genera and in others is composed of three distinct layers: **exocarp, mesocarp,** and **endocarp** *(synonym* = **fruit wall**).

perigynous having stamens and petals arranged on the edge of a cup-like receptacle around the pistil as in *Heteromeles*.

perisperm nutritive tissue of a seed derived from the nucellus and deposited external to the embryo sac; diploid in contrast to **endosperm**, which is triploid.

phenology study of relations between climatic changes and periodic biological phenomena such as dormancy, growth, flowering, and fruiting of plants.

phenotype 1. the observed state, description, or degree of expression of a character or trait; 2. the product of the interaction of the genes of an organism with the environment.

pinna a leaflet on a pinnate leaf.

pinnate leaf a compound leaf bearing leaflets (pinnae) on opposite sides of the rachis.

pistil ovule-bearing organ of an angiosperm flower, composed of ovary, style, and stigma.

pistillate having pistils, but lacking functional stamens (compare **staminate**).

placenta the interior of the ovary where ovules are borne.

planting zone area of reasonably uniform growing conditions in which plants from 1 or more **seed sources** are well adapted.

plumule the stem apex of the seed embryo from which the primary plant shoot develops.

pollination deposition of pollen on the receptive part of the female flower or strobilus.

polyembryony the production of more than 1 embryo from 1 egg as in some *Acer.*

polygamo-dioecious species that are functionally dioecious, but have a few bisexual flowers on some of the male-flowering plants as well as on some of the female-flowering plants.

polygamo-monoecious species that are functionally monoecious, but have a few bisexual flowers on some individual plants that also bear unisexual flowers of both sexes.

polygamo-trioecious species that may exhibit dioecious, monoecious, and bisexual flowering habits as in *Ceratonia*.

polygamous bearing both bisexual and unisexual flowers on the same plant or on different plants of the same species; pertains to species having mostly bisexual flowers.

pome a fleshy fruit resulting from a compound ovary with seeds encased in a papery inner wall, as in *Crataegus* and *Malus*.

prechilling practice of exposing imbibed seeds to cool (5 to 10 °C) temperatures for a few days prior to germination [contraction of the correct phrase, **pre-germination chilling**]. Prechilling is the same as **stratification**, but the term is more commonly used in seed testing, whereas stratification is more commonly used in nursery operations.

primocane first-year canes in *Rubus* that are solely vegetative (compare **florocane**).

prophyll the first bud of an inflorescence in certain plants (see *Serenoa*).

propagule any part of a plant, such as bud, tuber, root, shoot, or spore, that may be used to propagate an individual or vegetatively.

protandrous see **dichogamy**.

protogynous see **dichogamy.**

provenance the original geographic source of seed**.**

pruinose having a frost-like "bloom" or powdery secretion as in *Berberis*.

pubescence covered with down or short fine hairs.

purity percentage of clean, intact seed, by weight in a seed lot.

pyrene individual seed of a drupe as in *Ilex, Prunus, and Rubus*.

pyriform pear-shaped.

race a population that exists within a species and exhibits general characteristics discontinuous and distinct from other populations (synonym = *ecotype*; compare **strain,** variety).

raceme an unbranched inflorescence with flowers on stalks of equal length arising from a main axis as in *Amelanchier* and *Prunus*.

rachis 1. the elongated axis of an inflorescence. 2. the axis of a compound leaf bearing leaflets.

radicle the root of a seed embryo from which the primary root develops.

ramet individual member of a **clone** vegetatively propagated from an **ortet**.

raphe external ridge on a seed developed from an inverted ovule formed by the part of the funiculus adnate to the ovule.

receptacle end of a flower stalk on which the floral organs are borne.

root growth potential test a test that estimates the physiological condition of seedlings by their ability to produce new roots when growing in an ideal environment.

roguing systematic removal of individuals not desired for perpetuation of a population.

samara dry, indehiscent, winged fruit; 1-seeded as in *Fraxinus* and *Ulmus,* or sometimes with 2 samaras fused together as in *Acer*.

scarification pregerminative disruption of seedcoats, usually by mechanical abrasion or by brief treatment in a strong acid, to increase their permeability to water and gases, or to lower their mechanical resistance.

seed matured ovule containing an embryo and nutritive tissue enclosed in layers of protective tissue (seedcoat).

seed certification guaranty of seed identity and quality by a recognized agency, usually evidenced by a certificate including such information as certification category, species and variety, year of collection, origin, purity, soundness, and germinative capacity. See also **certified seeds, selected seeds, source-identified seeds**.

seedcoat protective outer layer of a seed derived from the integuments of the ovule. When 2 coats are present, the thick, tough outer coat is the testa and the thin, delicate inner coat is the tegmen.

seedcoat dormancy dormancy as a result of seedcoat conditions: impermeability to water or gas exchange or mechanical restrictions.

seed zone a designated area having defined boundaries and altitudinal limits within which soil and climate are sufficiently uniform to indicate high probability for maintaining a relatively uniform genetic composition as determined by progeny-testing various seed sources.

seedlot a specified quantity of seeds having reasonably uniform quality. It may comprise seeds from a specific location or a single seed collection zone, all collected in the same year.

seed orchard a plantation of clones or seedlings from selected trees for early and abundant production of seed and to promote balanced, random mating.

seed-production area an existing stand that is usually upgraded and opened by removal of phenotypically undesirable trees and then cultured for early and abundant seed production.

seed source the locality where a seedlot was collected (compare **provenance**).

selected seed a seedlot derived from clearly defined and carefully chosen natural stands or plantations that conform to specified standards and have been approved and registered by a designated authority.

serotinous 1. flowering or fruiting late in the growing season. 2. pertaining to cones that remain closed on a tree for several months or years after maturity and are therefore late in dispersing seeds.

shrub perennial woody plant branching close to the ground and with no major central stem (compare **tree**).

simple fruit formed from a single ovary and sometimes including other flower parts; the most common type of fruit (compare **aggregate frui**t and **multiple fruit**).

softwood cuttings cuttings for vegetative propagation that are collected from soft, succulent new shoots that have just begun to harden; normally in the spring, but also at any time of the year in plants that have multiple flushes of shoot growth.

sound seeds seeds that contain in viable condition the tissues necessary for germination.

source-identified seed a seedlot attested by a designated authority as being derived from a defined **seed source**.

species category of taxonomic classification into which genera are subdivided, comprising a group of similar interbreeding individuals sharing a common morphology, physiology, and reproductive process.

spike elongated inflorescence with sessile flowers on a main axis as in *Amorpha* and in pistillate flowers of *Carya* and *Juglans*.

stamen pollen-bearing organ of a flower in angiosperms consisting of a filament and an anther.

staminate having pollen-bearing organs (stamens) but no pistils.

staminode a sterile or abortive stamen as seen in flowers of *Diospyros*.

steckling a plant propagule grown from rooting cuttings; a plantable rooted cutting.

stigma the part of the pistil, usually the tip, often sticky, which receives the pollen and on which the pollen germinates.

stone the hard, bony part of a drupe that consists of the seed within the hard endocarp, as in *Cornus* and *Prunus*.

strain a group of organisms related by common descent but different in some respect from the main body of the species.

stratification pregermination treatment to overcome dormancy in seeds and to promote rapid and uniform germination; accomplished by keeping seeds in cold, moist conditions for a specified time, sometimes with a preceding exposure to moisture at room temperature (See **prechilling**).

striate marked with parallel grooves, lines, or ridges.

strobile (*plural* **strobile**s) dry, conelike fruits that develop from pistillate catkins as in *Alnus* and *Betula*.

strobilus (plural strobili) conelike male or female fruiting bodies, composed of compact bracts or scales, of the conifers.

style neck of the pistil which connects the stigma with the ovary.

sub-shrub a shrub, usually small, the woody parts of which normally die back at least partially during winter.

suture the line of dehiscence on fruits that opens naturally to disperse seeds.

syncarp see **aggregate fruit**.

target seedling a seedling ideally suited to planting for a specific management objective on a particular site. Production of such seedlings is a major management goal in nurseries, and requires matching genetic characteristics, environmental factors of the intended planting site, and cultural practices in the nursery.

tegmen the inner seedcoat, usually thin and delicate.

testa the outer seedcoat, usually thick and tough.

tree a woody perennial plant, typically large, and with a well-defined central stem or stems with branches forming a more or less definite crown (compare **shrub**).

tree percent number of trees in a nursery bed at time of lifting expressed as a percentage of the number of viable seeds sown.

trichome an outgrowth of the epidermis, as a hair or scale, which is variable in shape, size, and function.

triploid having 3 times (3*n*) the haploid (*n*) number of chromosomes.

umbel a flat-topped inflorescence with flower stalks arising from a common point, as in *Rhamnus caroliniana*; frequently compound as in the paniculate umbels of *Aralia spinosa*.

unisexual individual flowers of 1 sex, either **staminate** or **pistillate** (compare **bisexual**).

unitegmic having only 1 integument as the ovules of the composite family.

utricle a bladdery, 1-seeded, usually indehiscent fruit, consisting of an achene surrounded by bracts, as in *Eurotia* and *Grayia*.

variety a category usually intermediate between species (or subspecies) and forma, given a Latin name preceded by "var." based on fewer correlated characters than are used to differentiate species or subspecies, and having a more restricted geographical occurrence.

viability the state of being capable of germination and subsequent growth and development of the seedling.

viscid fruits covered with sticky secretions as in *Ceanothus*.

List of Families and Genera

A

Aceraceae—Maple family
- *Acer* L.

Agavaceae—Century-plant family
- *Yucca* L.

Anacardiaceae—Sumac family
- *Cotinus* P. Mill.
- *Rhus* L.

Annonaceae—Custard-apple family
- *Asimina* Adans.

Aquifoliaceae—Holly family
- *Ilex* L.
- *Nemopanthus* Raf.

Araliaceae—Ginseng family
- *Aralia* L.
- *Kalopanax* Miq.

Araucariaceae—Araucaria family
- *Araucaria* Juss.

Arecaceae —Palm family
- *Roystonea* O.F. Cook
- *Sabal* Adans.
- *Serenoa* Hook. f.
- *Washingtonia* H. Wendl.

Asteraceae—Aster family
- *Ambrosia* L.
- *Artemisia* L.
- *Baccharis* L.
- *Chrysothamnus* Nutt.
- *Encelia* Adans.
- *Ericameria* Nutt.
- *Gutierrezia* Lag.
- *Tetradymia* DC.

B

Berberidaceae—Barberry family
- *Berberis* L.
- *Mahonia* Nutt.
- *Nandina* Thunb.

Betulaceae—Birch family
- *Alnus* P. Mill.
- *Betula* L.
- *Carpinus* L.
- *Corylus* L.
- *Ostrya* Scop.

Bignoniaceae—Trumpet-creeper family
- *Campsis* Lour.
- *Catalpa* Scop.
- *Chilopsis* D. Don
- *Spathodea* Beauv.

C

Cactaceae—Cactus family
- *Carnegiea* Britt. & Rose

Caprifoliaceae—Honeysuckle family
- *Lonicera* L.
- *Sambucus* L.
- *Symphoricarpos* Duham.
- *Viburnum* L.

Casuarinaceae—Casuarina family
- *Casuarina* Rumph. ex L.

Celastraceae—Bittersweet (Staff-tree) family
- *Celastrus* L.
- *Euonymus* L.

Chenopodiaceae—Goosefoot family
- *Atriplex* L.
- *Grayia* Hook. & Arn.
- *Kochia* Roth
- *Krascheninnikovia* Guldenstaedt
- *Sarcobatus* Nees
- *Zuckia* Standl.

Clethraceae—Clethra (White alder) family
- *Clethra* L.

Cornaceae—Dogwood family
- *Cornus* L.

Cupressaceae—Cypress family
- *Calocedrus* Kurz
- *Chamaecyparis* Spach
- *Cupressus* L.
- *Juniperus* L.
- *Platycladus* Spach
- *Thuja* L.

E

Ebenaceae—Ebony family
- *Diospyros* L.

Elaeagnaceae—Oleaster (Elaeagnus) family
- *Elaeagnus* L.
- *Hippophae* L.
- *Shepherdia* Nutt.

Ephedraceae—Ephedra (Mormon-tea) family
- *Ephedra* L.

Ericaceae—Heath family
- *Arbutus* L.
- *Arctostaphylos* Adans.
- *Epigaea* L.
- *Gaultheria* L.
- *Gaylussacia* Kunth
- *Kalmia* L.
- *Ledum* L.
- *Leucothoe* D. Don
- *Oxydendrum* DC.
- *Pieris* D. Don
- *Rhododendron* L.
- *Vaccinium* L.

Euphorbiaceae—Spurge family
- *Aleurites* J.R. & G. Forst.
- *Triadica* Lour.
- *Vernicia* Lour

F

Fabaceae—Pea family
- *Acacia* L.
- *Adenanthera* L.
- *Albizia* Durz.
- *Amorpha* L.
- *Bauhinia* L.
- *Caragana* Fabr.
- *Ceratonia* L.
- *Cercis* L.
- *Cladrastis* Raf.
- *Colutea* L.
- *Cytisus* Desf.
- *Delonix* Raf.
- *Ebenopsis* Britt. & Rose
- *Enterolobium* Mart.
- *Gleditsia* L.
- *Gymnocladus* Lam.
- *Hymenaea* L.
- *Laburnum* Medik.
- *Lespedeza* Michx.
- *Leucaena* Benth.
- *Lupinus* L.
- *Olneya* Gray
- *Paraserianthes* I. Nielsen
- *Pithecellobium* Mart.
- *Prosopis* L.

Psorothamnus Rydb.
Pterocarpus Jacq.
Robinia L.
Senna P. Mill.
Sophora L.
Ulex L.
Fagaceae—Beech family
Castanea P. Mill.
Chrysolepis Hjelmquist
Fagus L.
Lithocarpus Blume
Quercus L.

G
Garryaceae—Silk tassel family
Garrya Dougl. ex Lindl.
Ginkgoaceae—Ginkgo family
Ginkgo L.
Grossulariaceae—Currant family
Ribes L.

H
Hamamelidaceae—Witch-hazel family
Hamamelis L.
Liquidambar L.
Hippocastanaceae—Horsechestnut family
Aesculus L.
Hydrangeaceae—Hydrangea family
Carpenteria Torr.
Philadelphus L.
Hydrophyllaceae—Waterleaf family
Nama L.

J
Juglandaceae — Walnut family
Carya Nutt.
Juglans L.

L
Lamiaceae—Mint family
Salvia L.
Lauraceae—Laurel family
Lindera Thunb.
Persea P. Mill.
Sassafras Nees & Eberm.
Umbellularia (Nees) Nutt.
Lythraceae—Loosestrife family
Lagerstroemia L.

M
Magnoliaceae—Magnolia family
Liriodendron L.
Magnolia L.
Malvaceae—Mallow family
Thespesia Soland. ex Correa
Meliaceae—Mahogany family
Melia L.
Swietenia Jacq.
Toona (Endl.) Roemer
Menispermaceae—Moonseed family
Menispermum L.
Moraceae—Mulberry family
Maclura Nutt.
Morus L.
Myricaceae—Bayberry (Wax-myrtle) family
Myrica L.
Morella Lour.
Myrtaceae—Myrtle family
Eucalyptus L'Her.
Lophostemon Schott

N
Nyssaceae—Sour gum family
Nyssa L.

O
Oleaceae—Olive family
Chionanthus L.
Fraxinus L.
Ligustrum L.
Menodora Bonpl.
Olea L.
Syringa L.

P
Papaveraceae—Poppy family
Dendromecon Benth.
Pinaceae—Pine family
Abies P. Mill.
Cedrus Trew
Larix P. Mill.
Picea A. Dietr.
Pinus L.
Pseudotsuga Carr.
Tsuga Carr.
Platanaceae—Plane-tree (Sycamore) family
Platanus L.
Polygonaceae—Buckwheat family
Eriogonum Michx.
Proteaceae—Protea family
Grevillea R. Br. ex Knight
Pyrolaceae—Shinleaf family
Chimaphila Pursh

R
Ranunculaceae—Buttercup family
Clematis L.
Rhamnaceae—Buckthorn family
Ceanothus L.
Frangula P. Mill.
Rhamnus L.
Ziziphus P. Mill.
Rosaceae—Rose family
Amelanchier Medik.
Aronia Medik.
Cercocarpus Kunth
Chamaebatia Benth.
Chamaebatiaria (Porter) Maxim.
Coleogyne Torr.
Cotoneaster Medik.
Crataegus L.
Fallugia Endl.
Heteromeles M. Roemer
Holodiscus (K. Koch) Maxim.
Malus P. Mill.
Oemleria Reichenb.
Peraphyllum Nutt.
Physocarpus (Camb.) Raf.
Prunus L.
Purshia DC. ex Poir.
Pyrus L.
Rhodotypos Sieb. & Zucc.
Rosa L.
Rubus L.
Sorbaria (Ser. ex DC.) A. Braun
Sorbus L.
Spiraea L.
Rubiaceae—Madder family
Cephalanthus L.
Mitchella L.
Rutaceae—Rue family
Flindersia R. Br.
Phellodendron Rupr.
Ptelea L.
Zanthoxylum L.

S

Salicaceae—Willow family
- *Populus* L.
- *Salix* L.

Sapindaceae—Soapberry family
- *Koelreuteria* Laxm.
- *Sapindus* L.

Sapotaceae—Sapodilla (Sapote) family
- *Sideroxylon* L.

Scrophulariaceae—Figwort family
- *Paulownia* Sieb. & Zucc.
- *Penstemon* Schmidel

Simaroubaceae—Quassia (Ailanthus) family
- *Ailanthus* Desf.

Simmondsiaceae—Jojoba family
- *Simmondsia* Nutt.

Solanaceae — Potato (Nightshade) family
- *Lycium* L.
- *Solanum* L.

Sterculiaceae—Cacao (Sterculia) family
- *Fremontodendron* Coville

Styracaceae—Storax (Snowball) family
- *Halesia* Ellis ex L.
- *Styrax* L.

T

Tamaricaceae—Tamarix family
- *Tamarix* L.

Taxaceae—Yew family
- *Taxus* L.
- *Torreya* Arn.

Taxodiaceae—Redwood family
- *Cryptomeria* D. Don
- *Metasequoia* Miki ex Hu & W.C. Cheng
- *Sciadopitys* Siebold & Zucc.
- *Sequoia* Endl.
- *Sequoiadendron* Buchh.
- *Taxodium* L.C. Rich.

Theaceae—Tea family
- *Franklinia* Bartr. ex Marsh.
- *Gordonia* Ellis

Thymelaeaceae—Mezereum family
- *Dirca* L.

Tiliaceae—Linden family
- *Tilia* L.

U

Ulmaceae—Elm family
- *Celtis* L.
- *Ulmus* L.

V

Verbenaceae—Verbena family
- *Callicarpa* L.
- *Tectona* L. f.
- *Vitex* L.

Vitaceae — Grape family
- *Parthenocissus* Planch.
- Vitis L.

Z

Zamiaceae—Sago-palm family
- *Zamia* L.

Zygophyllaceae—Creosote-bush (Caltrop) family
- *Larrea* Cav.

Index of Authors

Index of Common Names

Preferred common names are listed in boldface type and other common names are in lightface roman type. The scientific name of the genus in italics follows each primary entry. Since genus units are arranged in alphabetical order of the scientific name, and each page is tabbed with the genus name, readers can locate a particular genus without referring to page numbers.

C

snow
Syrian
Ussuri
wild European
willow-leaf
pecan, *Carya*
bitter
sweet
pecky cedar, *Calocedrus*
pegwood, *Cornus*
pencil cedar, *Calocedrus*
penstemon, *Penstemon*
Bridges
bush
crevice
Leonard
littlecup
moth
shrubby
sidehill
toadflax
pepperbark, *Zanthoxylum*
pepperidge, *Nyssa*
pepperwood, *Umbellularia*
peronias, *Adenanthera*
persimmon, *Diospyros*
black
common
eastern
Japanesse
Texas
petty morrel, *Aralia*
pignut, *Carya*
pinabete, Abies
pine, *Pinus*
Aleppo
Apache
Arizona
Arizona longleaf
Arizona ponderosa
Arizona yellow
Arkansas
Armand
arolla
Austrian
Balfour
Balkan
banksiana
bay
beach
Benguet
Bhutan
big-cone
bishop
black
blackjack
blue
Bolander
border limber
Bosnian
bottom white
bristlecone
bull
Calabrian
Canary
Canary Island
Caribbean
cedar
cembrian
Chiapas white
Chihuahua
chilgoza
Chir
cluster
coast
Coulter
Del Mar
Digger
dwarf mountain
dwarf Siberian
eastern white
European black
foxtail
Gerard
gray
graybark
Greek stone
hard
Heldreich
hickory
Himalayan
Honduras
Hudson Bay
Idaho white
Italian stone
jack
Japanese black
Japanese red
Japanese stone
Japanese white
Jeffrey
Jersey
Jerusalem
Khasi
knobcone
Korean
limber
loblolly
lodgepole
longleaf
longleaf Indian
longstraw
Macedonian
maritime
marsh
Merkus
Mexican weeping
Mexican white
Monterey
mountain
Muhgo
North Carolina
northern white
Norway
nut
oldfield
Pacific ponderosa
pinaster
piñyon
pitch
pocosin
pond
prickle-cone
prickly
radiata
red
rock
Rocky Mountain lodgepole
Rocky Mountain ponderosa
Rocky Mountain white
sand
Santa Cruz Island
Scots
Scotch
scrub
shore
shortleaf
Siberian stone
Sierra Nevada lodgepole
silver
slash
soft white
Soledad
South Florida slash
southern
southern yellow
southwestern white
spruce
stone
sugar
swamp
Swiss mountain
Swiss stone
Table Mountain
tamarack
Tenasserim
Torrey
umbrella
Virginia
Washoe
whitebark