

# Seedling Ecology and Evolution

Edited by

Mary Alessio Leck, V. Thomas Parker and Robert L. Simpson



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## Seedling Ecology and Evolution

Seedlings are highly sensitive to their environment. After seeds, seedlings typically suffer the highest mortality rate of any life history stage. This book provides a thoughtful and comprehensive review by leading researchers of the interconnected topics that constitute seedling ecology and ecophysiology, focusing on how and why seedlings are successful. It considers the importance of seedlings in plant communities; environmental factors with special impact on seedlings; the morphological and physiological diversity of seedlings, including mycorrhizae; the relationship of the seedling with other life stages; seedling evolution; and seedlings in human-altered ecosystems, including deserts, tropical rainforests, and habitat-restoration projects. The diversity of seedlings is portrayed by specialized groups, such as orchids, bromeliads, and parasitic and carnivorous plants. This important text sets the stage for future research and is valuable to graduate students and researchers in plant ecology, botany, agriculture, and conservation.

The editors are well known for their work in soil seed-bank ecology. *Mary Alessio Leck*, Emeritus Professor of Biology, Rider University, has worked on seed ecology of tidal freshwater wetland species, and on wetland education for urban youth; *V. Thomas Parker*, Professor of Biology, San Francisco State University, on tidal wetland, chaparral, and mycorrhizal ecology, and *Arctostaphylos* evolution; and *Robert L. Simpson*, Professor of Biology and Environmental Science, University of Michigan – Dearborn, on freshwater wetland ecology and the natural history of Michigan.



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# Seedling Ecology and Evolution

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## Foreword

The properties of seedlings are potentially important to all plant ecologists, whether they be interested chiefly in understanding seminatural indigenous vegetation, invasive plants, or the problems of restoration. In seminatural vegetation, seedling properties may determine the climatic regions occupied on a continental scale and the habitats occupied within a landscape, the ability of one species to coexist with another in a community, and the abundance of one species relative to another at a given time and place. The requirements of seedlings often determine the sites in which potentially invasive species can succeed and whether a given approach to restoration of seminatural vegetation is effective.

During the last 40 years, there has been a steady increase in the amount of research by ecologists on the properties of seedlings as opposed to those of mature plants. Great pioneers such as F. E. Clements and E. J. Salisbury appreciated the importance of studying seedlings, although papers on experimental studies on seedlings were uncommon before the 1960s. Several factors have driven the increase in work on seedlings. Here I emphasize seven.

First, there has been a desire to seek generalizations about seedlings. For example, how does relative growth rate vary with the mass of reserves in the seed, and how does it differ at a given seed-reserve mass between plants of different growth forms (such as tree vs. herb), or species from different kinds of habitat (where the vegetation shows high and low productivity, respectively)? For the mechanistically minded, the key questions become (1) how do seedlings of species with smaller seeds have higher relative growth rates, and (2) how do species of different functional types have different relative growth rates at a given seed-reserve mass? Of course, the answers to these questions have turned out to be related to our increased understanding of the ecophysiology of the vegetative organs of the adult plant, at least of the leaves – there still is much to learn regarding stems and roots.

Second, there has been a realization that differences among species with regard to the requirements of juveniles may play a significant role in making possible long-term coexistence of species in communities. Within a community, the conditions vary more at the scale of the juvenile than of the adult, and juveniles are generally less tolerant of adverse conditions. Here, we are concerned not only with the seedling as defined in a very narrow sense, but also with plants in their first few weeks, months, years, or decades of life – depending on the type of vegetation.

Third, it seemed at one time that a seed number–seedling survival trade-off had considerable potential in explaining the coexistence of species that differ appreciably in seed size but have very

similar requirements for regeneration. In this event, most researchers have concluded that the trade-off by itself is not enough to explain the coexistence of the full range of seed sizes, either where greater survival results from greater competitive ability or where it results from greater tolerance of hazards during establishment.

Fourth, there has been a greatly increased appreciation that seedlings, more often than not, are in symbiosis with a type of micro-organism, most commonly with at least one arbuscular mycorrhizal fungus. Gradually, plant ecologists have come to realize that in one community, some plant species are more dependent on a symbiont than in others, and that symbionts of a given type can have inhibitory as well as stimulatory effects. There have been parallel advances in our knowledge of the seedlings of plants that are partially or wholly parasitic. There remains open the question of how much specialization exists in the relationship between plant species and their symbionts – a question that can now be tackled more satisfactorily as a result of the development of molecular techniques.

Fifth, the development of molecular biology has greatly increased the potential for advances in understanding the physiology of seedlings – particularly their tolerances of shade, drought, low nutrient supply, and excess salt. The same goes for our understanding of seedling development, including the part played by phytohormones.

Sixth, there has been a revolution in our thinking about the kinds of seeds of the most primitive angiosperms and the habitats in which they functioned. Also, there has been renewed attention to the earliest true seeds of gymnosperms and the analogous seed-like structures of certain tree lycophytes.

Seventh, in the last two decades, there has been a surge of interest in the long-standing problem of why some species are much more invasive than others and in the related issue of how to restore vegetation at degraded sites. Some of us feel that it is difficult to extract generalizations in these areas, and, in many cases, the key species are idiosyncratic in their requirements. Nevertheless, the great practical importance of the problems makes it imperative that they be tackled by some of the ablest ecologists. Every stage in a plant's life cycle must be considered, but, in many cases, the seedling stage will turn out to be of critical importance.

With this background, we may welcome a new book that covers the whole range of issues I have outlined. An especially attractive feature of the book is that a good many of the schools of thought that have dominated developments in thinking are represented among the authors and, more specifically, that many of the authors have been among those who have taken leading roles in plant ecology in the last two decades.

Studies on seedlings, despite real advances, are still at an immature stage, and there remain significant disagreements. I cannot accept all of the assertions in this book and, indeed, I have argued in print with some of the authors. However, for me, this does not detract



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from the value of the book. I strongly recommend it to all those who seek thoughtful, up-to-date reviews of the wide range of interconnected topics that constitute seedling ecology and ecophysiology.

Peter J. Grubb  
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June 2007



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## Preface

Interest in developing this multiauthored book grew from our work with seeds and seed-bank ecology. While seed production and seed-bank dynamics are critical stages, what happens to seedlings is also fundamental to explaining field observations of vegetation dynamics and recruitment. Although several recent books discuss seedlings, indicating their importance to plant regeneration (Fenner, 2000) and to seed ecology (Fenner & Thompson, 2005), only one, Swaine (1996), focuses on seedling ecology; it, however, deals exclusively with tropical forest seedlings and is now more than 10 years old. A fourth volume, Forget *et al.* (2005), is primarily about seed predation and dispersal. *Seedling Ecology and Evolution* will complement these works and provide a more all-encompassing discussion. Moreover, it bridges the life-cycle gap following seeds (e.g. Baskin & Baskin, 1998) and seed banks (e.g. Leck *et al.*, 1989). Additional information about regeneration strategies may be found in Harper (1977), Grubb (1977, 1998), and Grime (2001).

We acknowledge the importance of understanding seedling biology in agriculture and horticulture; however, seedlings are well studied in these settings, whereas in natural systems, seedlings are less studied, and the literature is more diffuse. This book explores seedling adaptations and constraints to regeneration in natural and disturbed systems, where a better understanding of seedlings would stimulate study and development of theory regarding this dynamic and often neglected part of the plant life cycle.

After seeds, seedlings typically suffer the highest mortality rate of any life history stage and, therefore, are important in the selection and evolution of species. Seedlings appear to be a “bottleneck” in plant establishment because they are particularly sensitive to the vagaries of the environment. Our purpose is to explore their ecology and evolution and, in the process, bring a diverse literature together for the first time – examining the diverse morphologies and physiologies of seedlings; environmental factors that impact seedlings; driving factors in the evolution of seedlings, including phylogenetic and eco-physiological constraints; seedlings in plant community dynamics, especially how they relate to species and community sustainability; seedling strategies and syndromes, including seedling banks; and the impact of human-generated perturbations, such as invasive species, desertification, and habitat fragmentation and restoration. To accomplish this, contributors were invited to explore a range of topics that are gathered in the book as follows:

- Part I – Introduction. Chapter 1 provides a review of seedling structure, as well as an introduction to the seedling stage of the seed plant life cycle.
- Part II – Seedling diversity. Chapters 2–4 consider aspects of seedling natural history, strategies in stressful habitats where shade,

drought, inundation, and other stressors affect establishment, and strategies of highly specialized plants, including epiphytes, orchids, and parasites.

- Part III – Seedling morphology, evolution, and physiology. Chapters 5–9 examine seedling evolution in the context of embryo evolution and the rise of angiosperm ecological diversity, as well as seedling morphological and developmental changes, phytohormones, maintenance of carbon balance, and the role of symbioses in establishment and survival.
- Part IV – Life history implications. Chapters 10–13 examine the trade-offs of the seedling stage with other stages, and seedlings in population and community contexts, as well as functional groups among and within habitats.
- Part V – Applications. Chapters 14–17 examine seedlings as the advancing front for biological invasions, in deteriorating ecosystems (e.g. deserts), in systems in which they are used for system maintenance (forests), and for restoration.
- Part VI – Synthesis. Chapter 18 considers the multiple perspectives presented by the chapters of this book, presents overarching seedling strategies, and summarizes areas for future study.

## References

- Baskin, C. C. & Baskin, J. M. (1998). *Seed Ecology, Biogeography, and Evolution of Dormancy and Germination*. San Diego: Academic Press.
- Fenner, M., ed. (2000). *Seeds: the Ecology of Regeneration in Plant Communities*. Wallingford: CAB International.
- Fenner, M. and Thompson, K. (2005). *The Ecology of Seeds*. Cambridge: Cambridge University Press.
- Forget, P.-M., Lambert, J. E., Hulme, P. E., & Vander Wall, S. B., ed. (2005). *Seed Fate: Predation, Dispersal and Seedling Establishment*. Wallingford: CAB International.
- Grime, J. P. (2001). *Plant Strategies, Vegetation Processes, and Ecosystem Processes*. Chichester: John Wiley & Sons.
- Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, 52, 107–45.
- Grubb, P. J. (1998). A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives in Plant Ecology, Evolution and Systematics*, 1, 3–31.
- Harper, J. L. (1977). *Population Biology of Plants*. London: Academic Press.
- Leck, M. A., Parker, V. T., & Simpson, R. L., ed. (1989). *Ecology of Soil Seed Banks*. San Diego: Academic Press.
- Swaine, M. D., ed. (1996). *Ecology of Tropical Forest Seedlings, Man and the Biosphere Series, Vol. 17*. Carnforth: UNESCO & The Parthenon Publishing Group.

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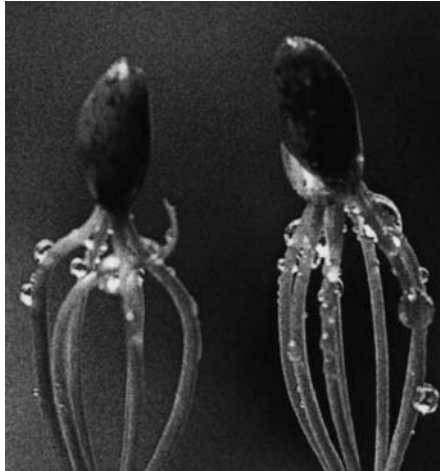
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# Part I

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## Introduction







## Why seedlings?

Mary Alessio Leck, Robert L. Simpson, and  
V. Thomas Parker

It was, as it were, a little green star with many rays, half an inch in diameter, lifted an inch and a half above the ground on a slender stem. What a feeble beginning for so long-lived a tree! By the next year it will be a star of greater magnitude, and in a few years, if not disturbed, these seedlings will alter the face of Nature here.

*Henry D. Thoreau (1993), writing in approximately 1862  
about *Pinus rigida* (Pinaceae).*

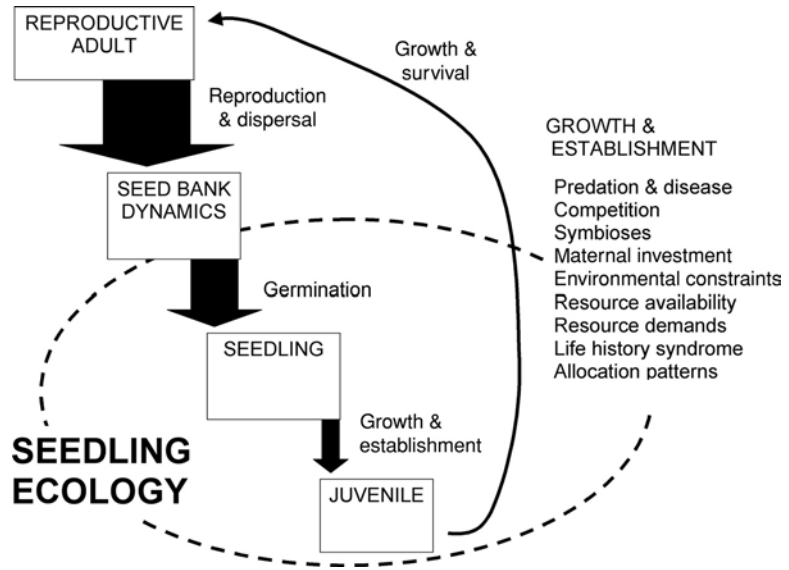
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### I.1 | Seedlings as part of a plant's life cycle

The seedling, the young spermatophyte plant following germination, is but one stage in the continuum of a seed plant's life cycle. For ecological purposes, discussion on the life cycle (illustrated in Fig. 1.1) focuses on the processes involved in replacing the adult and/or colonizing new habitats. A reproductive adult plant produces seeds that, once dispersed, become part of the seed bank (Parker *et al.*, 1989; Simpson *et al.*, 1989). Then, following germination, a seedling faces unpredictable environments and is limited by its particular genetic constraints. However, if successful, it survives to adulthood and reproduction.

Seedlings are highly vulnerable, subject to varied abiotic and biotic factors that affect growth and establishment. Their adversities, although variable in severity – depending on habitat and seedling form – include drought, flooding, herbivory, and lack of resources, such as mycorrhizal associates and light. The probability of a seed producing a successful, established plant is usually quite small (e.g. Simpson *et al.*, 1985; Leck & Simpson, 1994; Bazzaz, 1996; Kitajima,

**Fig. 1.1** Seed plant life cycle continuum. Shown are factors influencing seedling growth and establishment. The change in thickness of arrows from stage to stage suggests amount of attrition. The dotted line encompasses seedling ecology and indicates the scope of this book.



2007). The seedling stage, therefore, is a bottleneck, and selection pressure is assumed to be high (e.g. Grubb, 1977; Harper, 1977; Fenner & Thompson, 2005; Kitajima, 2007). The successful survival of some seedlings of every species is, ultimately, critical because it underlies the development and sustainability of plant communities.

For an individual plant, changes occur in morphological detail as well as in its reproductive ability, as it passes from “seed, to seedling, juvenile, immature, virginile, reproductive (young), mature (old), sub-senile, and senile” stages (Bell, 1991, p. 324). Duration of a particular stage varies with species. Seeds of *Salix* spp. (Salicaceae), for example, germinate within 12–24 hours of dispersal (Young & Young, 1992). Those of other species [e.g. *Verbascum* sp. (Scrophulariaceae)] persist in the soil for more than a century (Telewski & Zeevart, 2002). Similarly, some seedlings, such as those of desert annuals that produce seeds within a few weeks of germination, are not seedlings for long. Conifer seedlings of forests of British Columbia (Canada), in contrast, may be held in the seedling stage for more than 150 years – until light conditions are suitable for continued development (Antos *et al.*, 2005).

Sometimes stages are skipped. For some viviparous species, such as mangroves (e.g. *Bruguiera* spp. Rhizophoraceae; Burger, 1972) and seagrasses (*Thalassia* spp. Hydrocharitaceae; Sculthorpe, 1967), embryo development is continuous and it is not held inactive and dormant within the seed (see Chapter 2). In other cases, plants may proceed directly from seedling to flowering stage. *Chenopodium rubrum* (Chenopodiaceae), *Pharbitis (Ipomoea) nil* (Convolvulaceae), and *Xanthium strumarium* (Asteraceae) have photoperiod sensitive cotyledons, flowering as seedlings following short-day inductive photoperiods; *C. rubrum* produces flowers within six days of initiation of imbibition (Downs & Hellmers, 1975). This precocious behavior is also seen in certain wetland species, including *Lindernia dubia* (Scrophulariaceae) (Leck, pers.

obs.), *Limosella australis* (Scrophulariaceae), and *Myriophyllum variifolium* (Haloragidaceae) (Brock, pers. comm.), that flower within weeks of germination during soil seed-bank experiments. These examples illustrate the plasticity found among plants in the seedling stage of their life cycles.

To become a seedling, the seed must first germinate, often distinguished by the protrusion of the radicle through the seed coat (see Chapter 2). Depending on the species, this process is regulated by dormancy mechanisms interacting with availability of water, quantity and quality of light, (alternating) temperature, levels of oxygen, and/or, in some cases, an external supply of nutrients (see Baskin & Baskin, 1998; Fenner & Thompson, 2005). In a community context, germination is a facet of seed-bank dynamics that are important because what happens to seed banks influences seedlings (Parker *et al.*, 1989; Simpson *et al.*, 1989). Seed banks may be transient or persistent. The relative transience or persistence is related in some habitats to disturbance regime and to seed size, with transient seed-bank species having larger seeds (e.g. Grime, 1989; Leck & Brock, 2000; but see Leishman & Westoby, 1998). Seeds of transient species are present in the soil for <1 year, short-term persistent for >1 year but <5 years, and long-term persistent for >5 years (Fenner & Thompson, 2005). Maintenance of seed banks can involve various mechanisms, including physical, physiological, morphological, and morphophysiological dormancy, and the dormancy level can cycle between dormant and nondormant states (e.g. Baskin & Baskin, 1998). In temperate areas, the larger-seeded transient seed-bank species may germinate at low temperatures (5 °C) and do not require light; their earlier spring germination means that they are in place before later (and smaller) germinators appear (Thompson & Grime, 1979; Leck & Simpson, 1993). Seedling establishment, generally considered to be the process during which a germinated seed achieves independence from maternal reserves (e.g. Fenner & Thompson, 2005), is favored by early germination at least in systems where the environment is predictable. Moreover, seedling establishment requirements of small-seeded persistent species would appear to be different from seedlings of large-seeded transient seed-bank species.

Successful negotiation of stages may vary with species. For example, in tidal freshwater wetland annuals, 91% of *Polygonum punctatum* (Polygonaceae) seeds overwintered to germinate and grow to seedlinghood but less than 1% of *Ambrosia trifida* (Asteraceae) did so (Leck & Simpson, 1994). Survivorship of seedlings varied with species and with location relative to a tidal stream channel (Parker & Leck, 1985). In this tidal freshwater wetland with predictable hydrology and dominated by both annuals and perennials, the later germinating perennials, like *Typha latifolia* (Typhaceae), were not observed to survive in study plots (Parker & Leck, 1985; Leck *et al.*, 1989b; Leck & Simpson, 1995).

Some components of the life cycle are discrete. For example, the seed is an entity, comprised of an embryo, typically with maternally supplied nutrient reserves, within a maternally derived seed coat (e.g.

Baskin & Baskin, 1998). In contrast, the seedling may be more arbitrarily delimited. Although the seedling stage has a defined start when the radicle emerges from the seed coat, its end point is along a growth continuum and is more difficult to recognize (Chapter 2). Furthermore, when a seedling is a seedling may depend on the focus of the viewer. The morphologist considers morphological changes, whereas the physiologist emphasizes the attainment of independence from seed reserves. However, in the case of orchids and parasites, dependence is transferred from maternal resources, if present, to hosts or to mycorrhizal fungi. Thus, it is likely that no one definition, except possibly – *the young spermatophyte plant, following germination* – covers all seedlings.

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## 1.2 | Vulnerabilities and bottlenecks

At each stage of its life cycle, the plant's success is limited by an assortment of intrinsic and extrinsic factors that are to some degree driven by chance. Because of their small size, seedlings have greater susceptibility to resource limitations and other factors that affect establishment and growth (Fig. 1.1). In addition to resource limitations related to size, seedlings may be vulnerable because of low levels of morphological and physiological defenses. Cotyledons of *Toxicodendron pubescens* (Anacardiaceae) suffer herbivory whereas its leaves do not (Miller & Miller, 2005). However, in the case of *Quercus alba*, sprouting causes seeds that are favored by squirrels (*Sciurus carolinensis*) to become less digestible and, under some circumstances, squirrels bite out the embryo, preventing these changes (Steele & Koprowski, 2001). Seeds may present physical barriers that limit granivory; for example, the burs of *Xanthium strumarium* (Asteraceae) are never eaten (N. Good, pers. comm.).

Vulnerability can vary with habitat. As a generalization, dormancy-breaking mechanisms have evolved to increase the probability that germination occurs in a safe site – when and where the likelihood of survival is greatest (e.g. Grubb, 1977; Harper, 1977; Baskin & Baskin, 1998; Fenner & Thompson, 2005). Although a species actually may be able to germinate or live in a range of habitats, it may not find all habitats equally suitable because primary stresses vary. For example, shade-adapted seedlings can slowly acclimate to sunny locations, but survive best inside a forest despite being subject to high levels of herbivory and pathogens; in large gaps, establishment is prevented by competition with fast growing species (see Chapter 8). *Impatiens capensis* (Balsaminaceae) in temperate woodland habitats is more susceptible to white-tailed deer (*Odocoileus virginianus*) herbivory than when growing in a tidal freshwater wetland (Leck, Parker, & Simpson, pers. obs.). Moreover, although germination may occur over a wider range of conditions (along an inundation gradient in a tidal channel), establishment conditions may be narrower (Parker & Leck, 1985; Leck & Simpson, 1994).

Vulnerability varies with phylogeny within a given habitat. Some taxa are more susceptible to an environmental constraint than others. Seedlings of maples (*Acer* spp. Aceraceae) succumb to frost heaving to a greater extent than seedlings of *Carya tomentosa* (Juglandaceae) in successional old fields (New Jersey, USA) (Myster, 1993). Similarly, small seedlings of *Bidens laevis* (Asteraceae), a tidal freshwater wetland dominant, have less predictable establishment than the co-occurring, larger seedlings of *Impatiens capensis* or *Polygonum arifolium* (Leck & Simpson, 1995). In temperate old fields, early spring germinants of *Ambrosia trifida* and *Polygonum* species can tolerate low night temperatures, whereas seedlings of *Abutilon theophrastii* (Malvaceae) and *Ipomoea* cannot; variation in burial depth, resultings in varied emergence time, reduces the intensity of selection (Bazzaz, 1996).

Regardless of the cause of vulnerability, small size, limitation in ability to acclimate, habitat suitability, phylogeny, or other constraints, the seedling stage faces hurdles that are exacerbated by stochastic events. Collectively, these contribute to the significance of the seedling stage as a bottleneck in a species' life history. Selection at the seedling stage may produce seedling specialists or generalists. Examples of specialists are the bulb- and corm-forming seedlings of Australian desert perennials (Pate & Dixon, 1982). These specialized seedlings have the ability, because they possess contractile roots and hypocotyls, to place the apical growing point and a storage bulb, corm, or rhizome well below the soil surface, where they can avoid drought and heat during their first growth season. Another group of specialists are diminutive, woody, microstilt Australian perennials that produce heavily lignified, adventitious stilt roots, which allow the plant to survive desiccation and reduce prolonged soil surface heat stress (Pate, 1989). *Ambrosia trifida*, an example of generalist seedlings, can be found in tidal freshwater marshes or as weeds in agricultural fields. Communities may or may not have high seedling competitive ability, depending on the intensity of competition (Lamb & Cahill, 2006). Seedlings may also be conservative or opportunistic in their use of resources (see Chapter 8) or fugitive or stress tolerators (Shipley *et al.*, 1989).

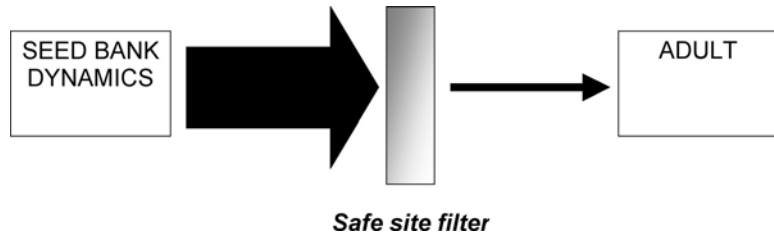
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### 1.3 | Making it: filters, safe sites, and establishment

The idea of the seedling serving as a bottleneck in a species' life history necessitates considering how the individual survives from the seed bank to establishment and, ultimately, to an adult (Fig. 1.2). A location that assures seedling success and that has all the necessary resources for survival may be termed a *safe site* (e.g. Harper, 1977; Fenner & Thompson, 2005). Safe site requirements vary with species, genotype, and time with functionality related to all the factors that influence establishment and growth (Fig. 1.2).

In a particular habitat, the safe-site filters can vary spatially and temporally, resulting in zonation or in cyclic changes in vegetation.

**Fig. 1.2** The importance of safe site filters affecting seedling populations. The thickness of the arrows suggests the impact of the filter(s) on seedling establishment to adult.

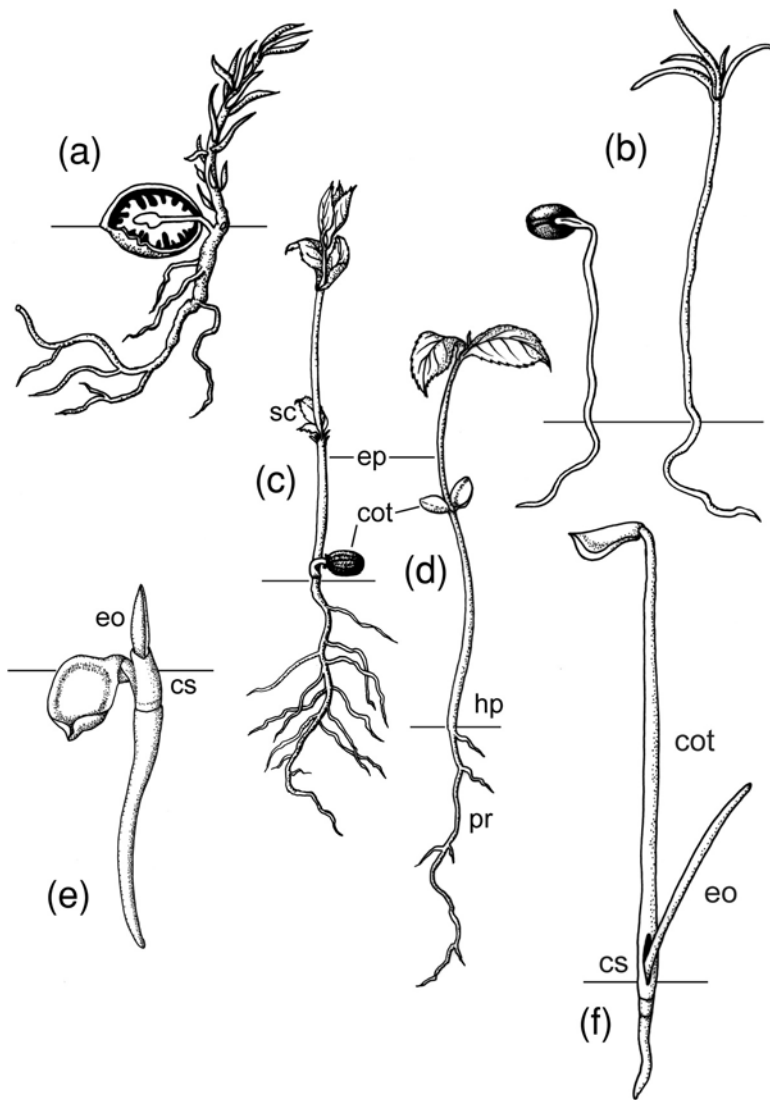


In wetlands, for example, water (inundation) can sort species across depth gradients or produce different communities, depending on drawdown/flooding patterns determined by rainfall (e.g. van der Valk, 1981; Leck & Brock, 2000). In a desert, small-scale habitat differences, such as those caused by porcupine digging or a nurse tree (see Chapter 15), can provide safe sites not available nearby.

The array of factors that can result in a seedling's failure to achieve establishment may act together or separately, and are environmental filters (Fig. 1.2). These factors may be abiotic (light, temperature, drought) and/or biotic in nature (competition, availability of microbial symbionts), and may have varying spatial or temporal impact. Seedling attrition may be huge. Moreover, the behavior of the seedling following germination can be intimately tied to seed characteristics, including dispersibility, size, and dormancy. These characteristics are controlled by genetic as well as by environmental factors during development, maturation, and storage (Gutterman, 1993). Individual traits, such as seed mass, can influence susceptibility of seedlings to drought, depth of burial from which seedlings may emerge, range of microsites suitable for seedling establishment (via gap detection mechanisms; e.g. Dalling, 2005), and tolerances to herbivory (Hoshizaki *et al.*, 1997). Agents of burial, whether biotic (e.g. dung beetles; Andresen & Feer, 2005) or abiotic (e.g. soil cracks; Harper, 1977; Bonnis & Lepart, 1994), influence seed position in the soil. In addition to seed dormancy mechanisms (e.g. Baskin & Baskin, 1998), exogenous influences, such as availability of a dispersal vector or disturbance, that place the seed and, thus, the seedling in a position where chances for survival are optimal, cannot be underestimated.

## 1.4 Seedlings: a primer

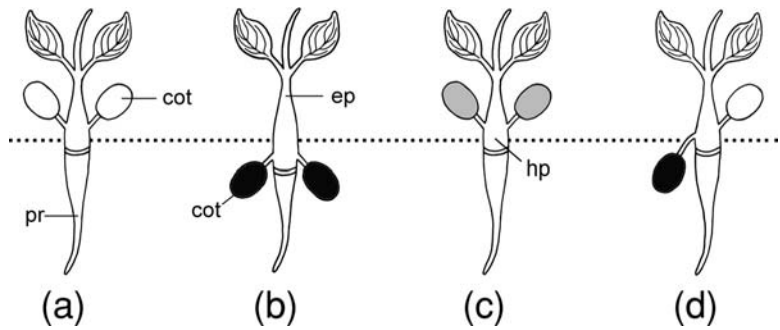
Seedling organs include the *radicle* (or primary root), *cotyledons* (seed leaves), stem, leaves, buds, and surface appendages, such as hairs (Lubbock, 1892; Burger, 1972; de Vogel, 1980). Seed plants include gymnosperms with two to many cotyledons, dicots that typically possess two cotyledons, and monocots with one structure designated as a cotyledon (Fig. 1.3). In each group, major seedling distinctions are based on the position of the cotyledons during germination. When the cotyledons rise above the soil surface, the seedling has *epigeal* germination, and if the cotyledons remain at or below the soil surface,



**Fig. 1.3** Representative seedlings of gymnosperms, dicots, and monocots illustrating hypogeal and epigeal germination types. Gymnosperms are (a) *Torrey myristica* (hypogeal), with part of the seed removed revealing endosperm and one of two cotyledons, and (b) *Taxus baccata* (epigeal) (Taxaceae); dicots are (c) *Prunus americana* (hypogeal) and (d) *P. virginiana* (epigeal) (Rosaceae); and monocots are (e) *Asphodelus lusitanicus* (hypogeal) and (f) *A. tenuifolius* (epigeal) (Asphodelaceae). Not drawn to scale. Abbreviations: cot – cotyledon, cs – cotyledonary sheath, eo – eophyll (the expanded blade part of the cotyledon), ep – epicotyl, hp – hypocotyl, sc – scale leaf, pr – primary root or radicle. Redrawn by A. Hoffenberg: (a) from Chick (1903), (b) Rudolf (1974), (c, d) Grisez (1974), and (e, f) from Tillich (2000) with permission from CSIRO.

germination is *hypogeal*. As the seedling grows, the stem above the cotyledonary node is the *epicotyl* and that below, the *hypocotyl*. The hypocotyl is usually distinct in the embryo of epigeal seedlings; in hypogeal seedlings, it is poorly developed and does not elongate during germination (de Vogel, 1980).

Overall, most gymnosperms and dicots are epigeal and most monocots are hypogeal. Hypogeal germination was once considered advanced (Eames, 1961), but both types can be found within the same taxon (Fig. 1.3). Although this brief description suggests that the seedling form is relatively stereotyped, a particular part, such as the cotyledon, can vary considerably in form and function in both dicots (Fig. 1.4) and monocots (Fig. 1.5). Efforts to correlate structure and function provide other levels of classification (e.g. Garwood, 1996). The greatest number of functional types may be found among tropical



**Fig. 1.4** Dicot seedlings showing cotyledon types: (a) photosynthetic, (b) storage, (c) haustorial (see legend Fig. 1.5), and (d) mixed form where only one cotyledon is photosynthetic. The double line indicates the collet, the transition zone between stem and root. Abbreviations: cot – cotyledon, ep – epicotyl, hp – hypocotyl, pr – primary root or radicle. Redrawn by A. Hoffenberg with permission from Bell (1991), copyright Oxford University Press.

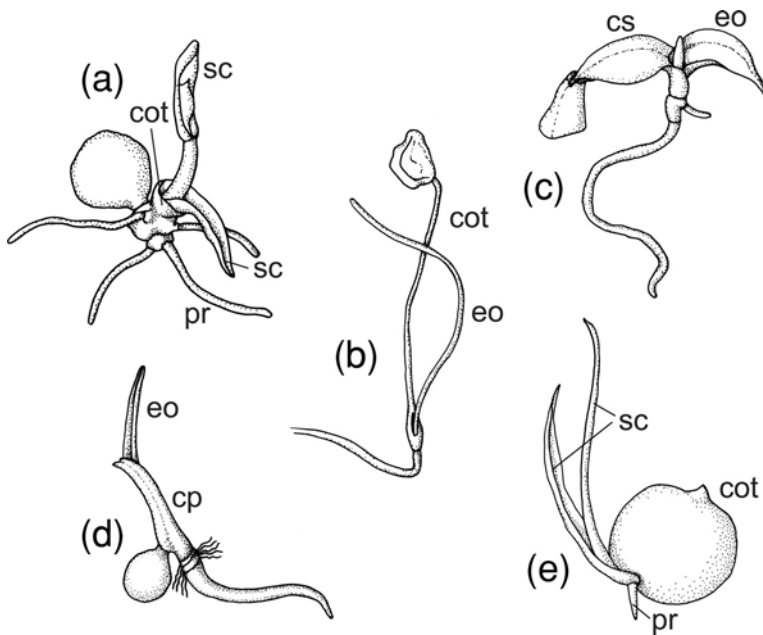
woody dicots (Garwood, 1996) and monocots (e.g. palms; Tomlinson & Estler, 1973; Bell, 1991). Focus has been on function and position of cotyledons, but primary roots may vary in site of origin, architecture, and persistence (Tillich, 2000).

## 1.5 | What seedlings can tell us

Observations from particular environments have relevance across other habitats. For example, Titus and Hoover (1991) observed that in submerged plants, potential challenges to seedling establishment, as well as lack of understanding of the physiology and demography of seed banks and germination, severely limit the predictability of sexual reproductive success in the field. They also note that small seedling size, rapid growth, sparse seed banks, and unfavorable conditions for germination and establishment all contribute to the lack of quantitative data. Garwood (1996) also laments the lack of information about seedlings in reports on germination and other aspects of species biology in tropical environments.

During the past decade, work with *Arabidopsis* (Brassicaceae) mutants has greatly improved understanding of seedling development and physiology (e.g. Leyser & Day, 2003; Achard *et al.*, 2006). Insights have relevance to understanding seedling establishment. For example, *Arabidopsis* studies help explain the basis of etiolation (stem growth in darkness), which raises the cotyledons to the soil surface (Leyser & Day, 2003). Furthermore, understanding seedling requirements may improve the chances for success of restoration projects. In sedge- (Cyperaceae) dominated created wetlands, seedlings may not establish even when high-quality commercial seeds are planted or following transplantation of healthy seedlings (van der Valk *et al.*, 1999). Soil amendments, such as organic matter, are necessary to improve soil moisture and permit establishment (see Chapter 17).





**Fig. 1.5** Monocot seedling types distinguished by Tillich (2000): (a) compact cotyledon, characterized by a low sheath and a completely haustorial hyperphyll\* that is completely imbedded in the seed and not visible (*Bomarea edulis* Alstroemeriaceae); (b) cotyledon with photosynthetic assimilating, elongated, and upright hyperphyll that raises the seed above the soil surface (*Albuca fastigiata* Hyacinthaceae); (c) cotyledon with wide assimilating sheath (*Pitcairnia corallina* Bromeliaceae); (d) cotyledon with a long coleoptile (*Hypoxis hygrometrica* Hypoxidaceae); and (e) storage cotyledon where, due to absence of endosperm, the hyperphyll has storage function (transient seed coat removed) (*Orontium aquaticum* Araceae). Not drawn to scale.

Abbreviations: cot – cotyledon, cp – coleoptile, cs – cotyledonary sheath, eo – eophyll, sc – cataphyll, pr – primary root or radicle.

\*Definitions: *Cataphylls* – first leaves following the cotyledon, sometimes called scale leaves; *coleoptile* – an elongated tubular extension of the sheath above the insertion of the hyperphyll; *eophyll* – first, expanded photosynthetic leaf; *haustorium* – in monocots the leaf blade (or end) of the first leaf, found within the seed, and in gymnosperms and dicots the undifferentiated, colorless suctorial organ that acts as an absorptive organ, transferring nutrients from the endosperm to the growing embryo and developing seedling; *hyperphyll* – part of the cotyledon connecting the haustorium to the sheath, also called the cotyledonary petiole (this may be short in adnate, adjacent germination and long in remote germination); *primary root* – the first root also called the radicle. Redrawn by A. Hoffenberg with permission from Tillich (2000), copyright CSIRO.

Despite numerous studies, literature on seedlings is diffuse and, often, information about seedling ecology is lacking even in species accounts. Also, other stages of the life cycle contribute to seedling success (e.g. Howard & Goldberg, 2001; Chapter 10), including dispersal and maternal investment to seeds. Thus, improved understanding of the roles of seedlings is challenging. Yet, an understanding of plant life cycles underpins the pursuit of knowledge in botanical, ecological, environmental, and agricultural disciplines.

## 1.6 | The scope of *Seedling Ecology and Evolution*

Seedlings, usually the most transitory of life-history stages, provide opportunities to explore novelties, as well as life cycle continuum features and vulnerabilities and trade-offs that, ultimately, are key to population and community dynamics. The purview of this book is illustrated in Fig. 1.1, with text focusing on seeding diversity; seedling morphology, evolution, and physiology; life history implications; and applications; as well as this introduction and a concluding synthesis.

Part II, Chapters 2–4, considers the breadth of seedling diversity. Chapter 2 focuses on the natural history of seedlings, including morphological and physiological diversity, vivipary, longevity, and dispersal of seedlings. Chapters 3 and 4 explore the boundaries and limitations of seedlings. Specialized seedling strategies in stressful environments, such as shade, litter, cold, heat, salinity, and unstable substrates, are discussed in Chapter 3. Other specialized strategies considered in Chapter 4 include orchids, epiphytes, insectivores, and parasites.

Part III, Chapters 5–9, examines seedling morphology, evolution, and physiology. Chapters 5 and 6 discuss extant plant groups and the fossil record. These chapters establish a foundation for examining seedlings from an embryological perspective and provide a broad scope in which to consider seedling evolution and phylogenetic constraints. Chapter 7 considers the relationships between seedling environment, phytohormones, and phenotypic expression, whereas Chapter 8 examines the strategies – opportunistic and conservative – that seedlings use to attain independence from maternal carbon reserves. Nutritional relationships involving symbioses with fungi and bacteria are discussed in Chapter 9.

Part IV, Chapters 10–13, considers life history implications, focusing on seedlings at several levels. The trade-offs between seed production and seedling survival are considered in the context of the entire plant life cycle in Chapter 10. Chapter 11 discusses seedling recruitment and focuses on populations, including recruitment limitation and genetic structure and selection. Chapter 12 discusses seedlings in a community context and considers internal and external forces that influence regeneration niches, recruitment strategies, and assembly rules. Chapter 13 examines the feasibility of delimiting functional seedling groups, how scale relates to seedling processes, and whether spatial, morphologic, and phylogenetic patterns can be successfully elucidated.

Part V, Chapters 14–17, examines seedlings in the context of ecosystems degraded by anthropogenic activities. The varied strategies of seedlings of invasive species are considered in Chapter 14. In arid lands as shown in Chapter 15, understanding seedling requirements is crucial to understanding patch dynamics, in which human (and natural) disturbances are involved in strong, positive feedback relationships leading to degradation and desertification. The effects of

disturbances in forests, which may not be apparent for decades, are related to seed limitation and recruitment; Chapter 16 considers the impact of human disturbances on seedling recruitment, focusing on tropical forests where seedling variation is highest. Worldwide, efforts are being made to restore degraded ecosystems; Chapter 17 explores the factors influencing seedling success in many types of restoration projects. Together, these chapters provide a baseline understanding of regeneration in human-impacted ecosystems.

Part VI, the concluding Chapter 18, provides a synthesis, and explores the trade-offs between phylogeny and recruitment, the significance of safe sites, and the overarching strategies of seedlings. Collectively, these chapters provide insights into the seedling stage and opportunities for fruitful future study.



# Part II

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## Seedling diversity





# Seedling natural history

Mary Alessio Leck and Heather A. Outred

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## 2.1 | Introduction

Consider the following: tidal freshwater marshes along the East Coast of North America in springtime; the deserts near Death Valley, in Africa, and elsewhere following a substantial rainfall; the intermittent wetlands in the arid Australian landscape; and the wheat fields of Europe, North America, and New Zealand. Each landscape is awash with the greens of newly emerged seedlings, each species responding to its particular set of germination cues, each informed by its peculiar evolutionary history. Anyone interested in seed banks and seed germination ecology and physiology, as well as those who garden, are intimately familiar with seedlings. Seedlings are also well known to those who produce seeds for use in agriculture and horticulture and who are concerned with vigor and other seedling attributes (Geneve, 2005; Stephenson & Mari, 2005; Farooq *et al.*, 2006). In this chapter, we explore the diverse and fascinating array of seedlings and seedling natural history. Topics include the seedling stage, morphological and physiological diversity, vivipary, seedling equivalents, seedling longevity and dispersal, and environmental filters and safe sites.

Nomenclature generally follows that of the author and family names (Mabberly, 1997).

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## 2.2 | The seedling stage and fate of seedlings

Contrary to what seems intuitive, the seedling stage is not always easily defined. The success of seedlings is, furthermore, influenced by many environmental factors that determine survival, establishment, and, ultimately, community composition.

### The seedling

*Seedling* is used for a very young individual (Burger, 1972), but problems occur in determining the beginning and end of the stage.

Harper (1977) observed that the ultrastructure of the seed may change within 30 minutes of wetting. Others have suggested the seedling stage to begin with enlargement of the embryo following seed maturation (Tomlinson, 1990), protrusion of the radicle from the seed coat (Wardle, 1984; Kitajima & Fenner, 2000; Fenner & Thompson, 2005), when cotyledons become free of the seed coat (Wardle, 1984), or when cotyledons of epigeal seedlings emerge above ground (Martin & Ogden, 2002).

Plants, however, vary. In *Carex* and *Cyperus* (Cyperaceae), for example, only the cotyledon grows at first; the middle part extends rapidly, pulling the root, which grows later, out of the seed (Lubbock, 1892; Boyd, 1932). In Alismataceae and *Populus* (Salicaceae), the first organ to emerge is the hypocotyl (Lubbock, 1892; Young & Young, 1992). In these, the seedling is initially anchored by rhizoids, which develop from the base of the cotyledon or hypocotyl. Shoot emergence before roots also occurs in aquatics from diverse families (Boyd, 1932; Muenscher, 1944).

Stages of seedling development may differ for epigeal and hypogeal species. For epigeal seedlings, the first stage constitutes growth up to the first leaf; and for hypogeal seedlings, up to the first fully expanded leaf; and the second stage is a plant with almost normal form, young leaves (Burger, 1972).

Before becoming independent, the very young seedling will usually pass through a stage when it is dependent upon stored seed reserves, but like the beginning, the end of the seedling stage also seems difficult to determine. It may coincide with the loss of cotyledons (Philipp, 1992); with the appearance of the first bladed seedling leaf (Tomlinson, 1990) or maturation of the first true foliage leaves, leaving the young plant capable of independent existence (Harper, 1977); or the end of the exponential growth period (Kitajima & Fenner, 2000). The last, however, ignores observations that fluctuating growth spurts often occur (de Vogel, 1980; Chacon & Armesto, 2005). Foresters consider the seedling stage to include young plants to 2.7 m (Whitmore, 1996).

Exhaustion of seed reserves may be a reasonable end of the seedling stage, but in some species the young plant uses reserves stored in the hypocotyl, making delineation between a seedling and a juvenile plant difficult (de Vogel, 1980). The end of dependence on cotyledons and stored reserves appears to correlate with a decline in maximum growth rate (RGR) that follows a bell-shaped curve (Fenner & Thompson, 2005). If widely applicable, the RGR could be used to assess the transition of the seedling to the next stage. However, the availability of seed reserves may exceed the time when seedlings become totally dependent on the environment. For example, *Posidonia australis* (Posidoniaceae) seedlings are capable of independence at 9 months, yet 2-year-old seedlings have 20% of the phosphorus and 14% of the nitrogen derived from the parental source (McComb *et al.*, 1981).



### The fate of seedlings

The loss of seedlings in most ecosystems is usually high (e.g. Darwin, 1859; Grubb, 1977; Harper, 1977; Pate & Dixon, 1982; Louda, 1989; Leck & Simpson, 1994; Körner, 2003), their fate determined by many factors that prevent establishment (Chapters 3, 11, 15). Causes of death, whether by biotic or abiotic factors or a combination of both, vary in importance with habitat. In deserts, available moisture, optimal growing season, fire, and grazing determine seedling survival (Pate & Dixon, 1981; Florence, 1981; Gutterman, 1993; Denham & Auld, 2004). In tropical forests, high losses of seedlings may be due to burial under litter and herbivory, washing away by rain, trampling by animals, and starvation due to lack of light or water (e.g. Ng, 1978; Garwood, 1996; Whigham, *et al.*, 1999). In temperate forests, the two major sources of seedling mortality are herbivory and drought (Cook, 1979), but litter and frost heaving may be important, especially for small seedlings (Young & Young, 1992; Myster, 1993; Kostel-Hughes *et al.*, 2005). In alpine tundra, seedlings are susceptible to soil heaving caused by nighttime needle ice and cryogenic processes during winter, as well as drying and heat on bare soil (Körner, 2003).

Wetland habitats provide other challenges. These include anoxic substrates; insufficient aerenchymatous tissue limiting nighttime respiration; unstable substrates, especially where tides and waves occur; light limitations at depths or in shade of established plants; low nutrient availability where competition with neighboring plants occurs or where nutrients are difficult to acquire because of low oxygen or salinity; and susceptibility to pathogens (Titus & Hoover, 1991). To these can be added uprooting, burial or damage to seedlings by litter or flotsam, and, if germination occurs in deep water, lack of resources (energy and time) for survival (Haag, 1983). In brackish and marine habitats (as well as in arid places), salinity offers another level of stress affecting seedling establishment.

Many kinds of organisms can cause death, including differential crab predation in mangrove and coastal terrestrial forests (Lindquist & Carroll, 2004) and rats that reduce establishment of *Pleurophyllum hookeri* (Asteraceae), a subantarctic megaherb (Shaw *et al.*, 2005). Death may also be caused by blight organisms, nematodes, spider mites, grubs, and fungi that cause damping off and root rot (Johnsen & Alexander, 1974). Further, lack of establishment may be due to absence of symbionts required by mycorrhizal and nodulating species (Chapter 9). Where allelopathic compounds that are toxic to mycorrhizal fungi are present, survival of tree seedlings is reduced (Stinson *et al.*, 2006).

Although most seedlings have no special adaptations (de Vogel, 1980), there are differences in vulnerability and ability to repair damage. Young epigeal seedlings are least able to recover because the apical bud is usually lost when cotyledons are eaten. In contrast, seedlings with hypogeal cotyledons have buds that can replace aerial portions, and in certain monocots (e.g. *Cordyline australis* Agavaceae, *Freyinetia banksii* Pandanaceae, *Ripogonum scandens* Smilacaceae), buds

in the axils of (scale) leaves permit regeneration after mechanical damage (Tomlinson & Esler, 1973). In alpine tundra, small-seeded species suffer higher mortality (99%) than larger-seeded ones (50%) over 12 months (Körner, 2003).

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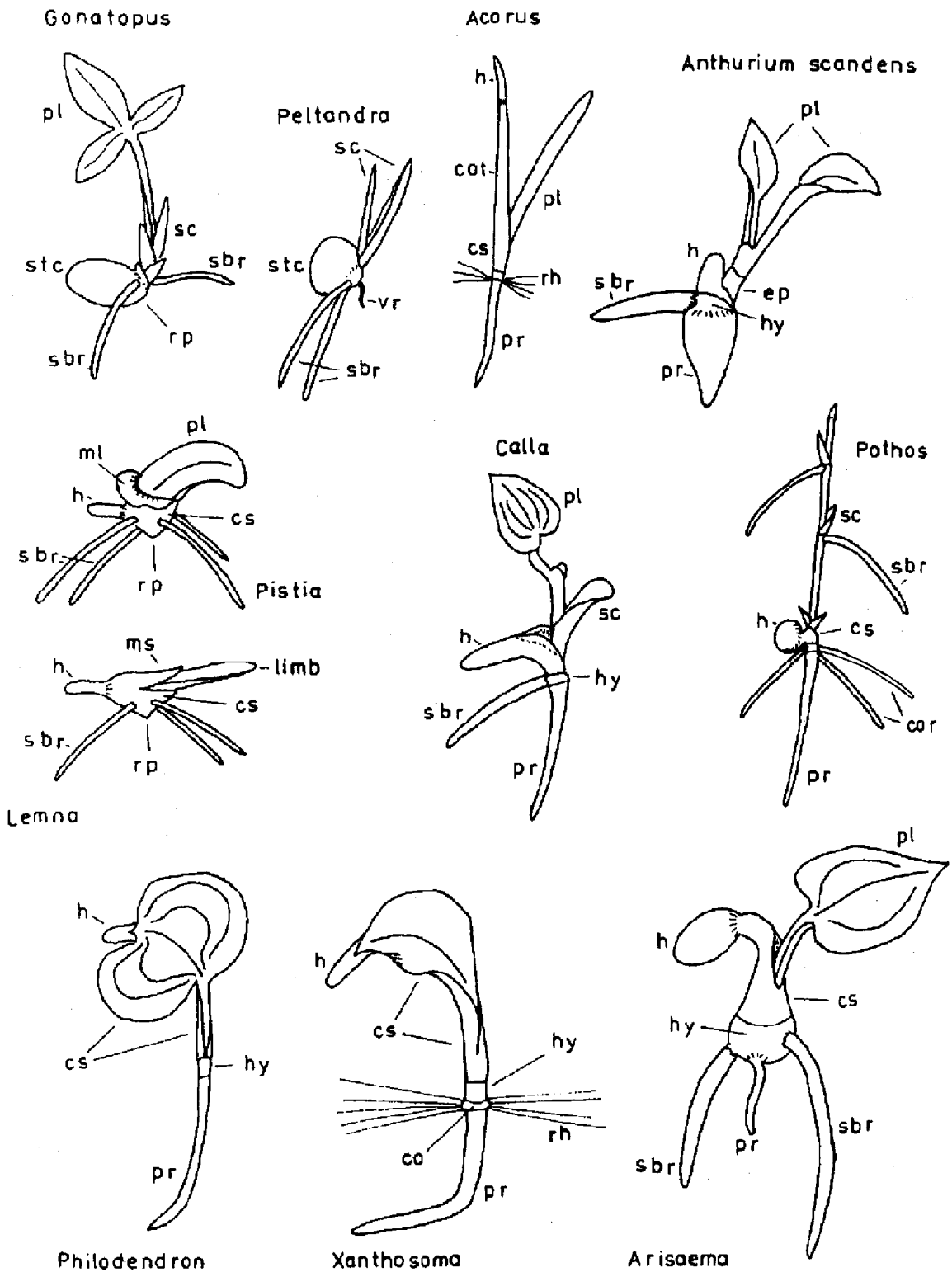
## 2.3 Seedling types

### Monocotyledons

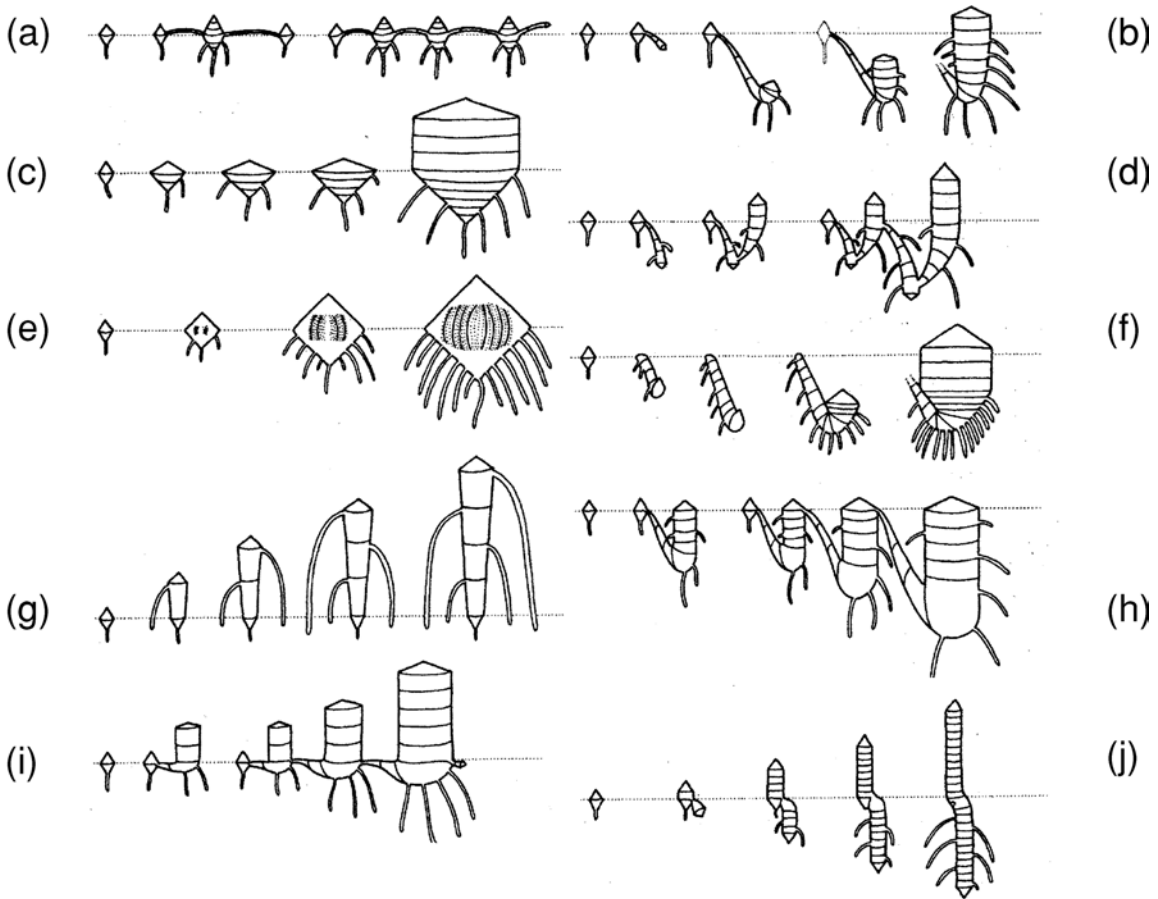
Tillich (1995), who considers seedling structure key to detecting phylogenetic relationships, characterizes monocot seedling organs, standardizes terminology, and illustrates phylogenetic distributions of selected characteristics. His selected characteristics that call attention to functional attributes of monocot seedlings include: (1) the coleoptile: a highly derived structure, which is a tubular elongation of the cotyledonary sheath, is found in some species (e.g. *Elyna myosuroides* Poaceae), but not others (e.g. *Alisma plantago-aquatica* Alismataceae); (2) photosynthetic capacity of the cotyledon: whether green or not, the upper part of the cotyledon (hyperphyll) is primarily a storage organ and only in *Acorus* (Araceae) is it a truly photosynthetic structure; (3) endospermless seeds: nutrients are stored in the embryo itself, either in the cotyledon or the hypocotyl; (4) conspicuous collar: the collar, the transitional zone between the hypocotyl and the primary root, can be very pronounced and can develop dense trichomes or rhizoids; (5) robust and branched primary root: presumably an ancestral condition, and although generally considered atypical for monocots, occurs variably in a number of families (e.g. in Dracaenaceae, it occurs in *Dracaena* but not *Sansiveria*); (6) velvety root hairs: these are very dense, short root hairs that look like velvet and are most conspicuous under laboratory conditions in moist chambers (Convallariaceae, Luzuriagaceae, Philesiaceae); and (7) seedling without a primary root: a highly derived condition with only four families completely lacking primary roots (Eriocaulaceae, Lemnaceae, Poaceae, Zosteraceae). Roots may have a coleorhiza, or root cover, through which the root grows.

Among the monocots, the Araceae contains the greatest number of seedling types (Fig. 2.1; Tillisch, 1995). The primary root, found in most examples, is lacking in *Pistia* and *Lemna*, indicating a close relationship between these genera. The seedling axis also shows considerable modification, varying from the tuberous corm of *Arisaema* to the elongated internodes of *Pothos*, a liana. Lack of information about seedlings of many subgroups precludes full understanding of relationships and determining probable ancestral types beyond reductionary evolution from a robust, long-lived, branched primary root, ultimately, to total reduction.

In addition to epigeal or hypogeal germination, the cotyledonary axis of monocotyledons may be either extended (remote) or not (adjacent) (Boyd, 1932; Tomlinson, 1990; Bell, 1991). In the latter, the cotyledonary part of the embryo barely extrudes, causing the seedling to



**Fig. 2.1** Seedlings as found in the order Arales that have the greatest familial seedling diversity among monocots (Acoraceae, Lemna Lemnaceae; others Araceae). Abbreviations: co – collar, cor – collar root, cot – unifacial, assimilating hyperphyll (upper leaf part of cotyledon), cs – cotyledonary sheath, ep – epicotyl, h – haustorium, hy – hypocotyl, in – internode, ml – median sheath lobe, ms – median sheath lobe of *Lemna* cotyledon, pl – primary leaf, pr – primary root, rh – rhizoids, rp – root pole, sbr – shoot-borne root, sc – scale leaf, stc – storage cotyledon, vr – vestigial primary root. Seedlings are not drawn to scale. From Tillich (1995), reproduced with permission, copyright The Board of Trustees of the Royal Botanic Gardens, Kew.



**Fig. 2.2** Establishment growth of monocots (see Bell 1991 for details). (a) Stolon production, (b) production of successively larger, short-lived sympodial units, (c) increase in width of successive nodes, internodes short, (d) increase in size of sympodial units that alternate growth direction, (e) increase in width from cambial activity, (f) initial vertical growth, similar to 'c,' (g) prop roots supporting initial vertical growth, internodes long, (h) increase in size and depth of successive long-lived sympodial units, (i) increase in size of successive sympodial units, and (j) production of single downward growing side shoot. From Bell (1991), reproduced with permission, copyright Oxford University Press.

develop next to the seed. In contrast, during remote germination where the plumule develops away from the seed, the extended cotyledon buries the plumule, promoting rooting. In *Lodoicea maldivica* (the massive double coconut, Palmae), the cotyledonary axis, developing over 3–4 years, may extend horizontally for greater than 4 m, assisting dispersal.

In woody monocotyledons, establishment involves various growth behaviors (Fig. 2.2; Tomlinson & Esler, 1973). Because of the lack of secondary growth in arborescent monocotyledons, radicles of fixed diameter would not be able to supply adequate water to a growing aerial shoot; in palms, this problem is circumvented by the production of many adventitious roots (Tomlinson, 1990). Establishment growth also involves increase in diameter of successive internodes, which for the largest palms involves increase from 1 mm to 1 m in adults.

Tomlinson also notes a number of seedling features. First, internode length is typically short and nodes close together. Successive internodes increase in diameter. The transition to the adult phase, characterized by long internodes, is often abrupt. Stilt palms, with consistently long internodes, are an exception. Second, leaves become progressively larger and more elaborate. The leafy crown, as it expands in size, remains at the soil surface. Third, adventitious roots progressively increase in number and diameter. Finally, the vascular bundles of the stem increase in number, increasing the water-carrying capacity of the stem. For additional discussion of monocotyledon seedlings, see Boyd (1932), Eames (1961), Tomlinson (1990), Bell (1991), Tillich (1995, 2000), and Henderson (2006).

## Dicotyledons

Examination of a temperate seedling flora (e.g. Muller, 1978; Young & Young, 1992) would suggest that most dicot seedlings are epigeous (96.7% and 94.5%, respectively). Virtually all herbaceous dicot crop and weed seedlings are epigeous (e.g. Kummer, 1951; Reilly, 1978; Uva *et al.*, 1997), with only *Lathyrus*, *Pisum*, and *Vicia* (Leguminosae) being hypogeal. In contrast, an examination of, for example, Burger (1972), de Vogel (1980), and Garwood (1996) who describe tropical tree seedlings, would indicate that both epigeous and hypogeous seedlings are important. Five seedling functional types for tropical forest trees based on exposure, texture, and position of the cotyledons have been identified (Miquel, 1987; Garwood, 1996). These types vary in importance: with planerocotylar\*–epigeal–foliaceous ranging from 33 to 56% of tropical forest tree species (eight sites; three continents); followed by planerocotylar–epigeal–reserve, 16–43%; cryptocotylar\*–hypogeal–reserve, 7–28%; planerocotylar–hypogeal–reserve, 6–14%; and cryptocotylar–epigeal–reserve, 1–8% (Garwood, 1996; see also Ibarra-Manríquez *et al.*, 2001). Analysis of Malaysian woody plants by de Vogel (1980) showed  $\approx$ 13% of genera and 46% of families having more than 1 seedling type (of 16); Leguminosae, with both Caesalpinaceae and Papilionaceae; and Myrsinaceae, each having 5 to 6 types. Germination of *Citrus aurantifolia* (Rutaceae) and *Durio zibethinus* (Bombacaceae) may be either hypogeal or epigeal, which in the latter is determined by the orientation of the micropylar end (Enoch, 1980).

In temperate woody plants described by Young & Young (1992), only *Prunus* (Rosaceae) had both epigeal (*P. virginiana*) and hypogeal (*P. americana*) germination types. Seedling type, at least for tropical woody species, is considered a conservative evolutionary trait (Ibarra-Manríquez *et al.*, 2001). Garwood (1996) notes several problems with attempting to relate seedling classification schemes based on morphology to the ecology of (tropical tree) seedlings. Among the points she makes are these: (1) Focus, primarily on the cotyledon, is too narrow because other functions, such as water and nutrient uptake and

\*Planerocotylar – cotyledons become entirely exposed and are free from the fruit wall and testa; cryptocotylar – cotyledons remain enveloped in a persistent fruit wall and/or testa and, if it is present, also in the endosperm; de Vogel, 1980.

anchorage, are also important in establishment. (2) The five types may not be good functional groups. Seedlings with photosynthetic cotyledons may in some species have no stored reserves while in others reserves are stored in endosperm. (3) Focus on only one stage may obscure the functional morphology that is necessary to understand seedling development and establishment. (4) To understand functional morphology, it would be important to focus on how functions change through development and establishment. [See Garwood (1996) for a comprehensive discussion of functional seedling morphology.]

No overall seedling classification scheme with a functional perspective exists. Classification schemes for tropical tree seedlings do not include gymnosperms or monocots, even arborescent kinds that have distinctive establishment strategies (Fig. 2.2) (Tomlinson & Esler, 1973; Tomlinson, 1990; Bell, 1991). Also, there is no inclusion of root architecture, despite the observation that roots are as diverse as shoots (Robinson *et al.*, 2003; but see Tillich, 1995, 2000). Functional types in other habitats, including aquatic and wetland species, may be more obscure. Seedlings of parasitic plants, those with specialized morphologies (e.g. bulbs and vines), and viviparous species, although considered by de Vogel (1980) and Bell (1991), are needed to develop a unified view of functional seedling types. Ibarra-Manríquez *et al.* (2001) further note, that for improved understanding of functional morphology, it is necessary to determine variation and role of seedling traits, including size, quantity, and quality of maternal reserves; growth rate; allocation of resources among organs; and the relationship between morphology and function of seedling organs.

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## 2.4 Seedling diversity – morphology

What appear to be inconsequential aspects of seedling morphology may have great adaptive importance in determination of safe sites and, thus, successful establishment (Cook, 1979). The range of morphological features exhibited by seedlings, while not exhaustive, is described in Appendixes 2.1 and 2.2. Examples can be found in which one or more of the typical seedling organs are missing. In some cases, structure mirrors the morphology of the parent, but in others, differences are developmental. Variable attributes reflect evolutionary forces working in diverse habitats. A brief consideration of seedling diversity is given below. For more extensive discussions, see Lubbock (Vol. 1, 1892), Boyd (1932), de Vogel (1980), Tomlinson (1990), Tillich (1995, 2000), Garwood (1996), and Henderson (2006). Kummer (1951) and Uva *et al.* (1997) also provide descriptions of seedlings.

### Seedling organs

#### Cotyledons

Cotyledons, usually synonymous with seed leaves or seed lobes, are of three types: food-storing, haustorial, and photosynthetic (de Vogel,

1980; Chapter 1). The undifferentiated haustorial cotyledons transfer nutrients from the endosperm to growing regions of the embryo and seedling; they may not be easily distinguished from food-storing ones. Muller (1978) uses cotyledon for the first two, and *seed leaves* for photosynthetic ones. For our purposes, cotyledon will encompass all three (reflecting our temperate biases). Usually cotyledons are of one type, but in certain *Peperomia* (Piperaceae) species, one cotyledon maintains haustorial function and remains within the seed coat, while the other becomes exposed (Hill, 1906, cited in de Vogel, 1980; Bell, 1991) and presumably photosynthetic. Generally, cotyledons occur in constant numbers within a taxon, but numbers can vary (Appendix 2.1).

In most epigeous species, cotyledons are sessile when borne above ground by hypocotyl growth, but petiolate when close to the ground (Lubbock, 1892). In other species, the cotyledons are aerial because of elongated petioles that in *Polygonum bistortoides* and *P. bistorta* (Polygonaceae) form a tube through which the first leaf passes (Alessio, 1967; Muller, 1978).

For certain hypogeous species, cotyledon burial may be accomplished during germination. Extension of the cotyledonary stalk of certain palms pushes the embryo into the ground a considerable distance (Tomlinson, 1990). Except for *Nypa fruticans*, a mangrove species, and *Ravenea musicalis*, the river palm of Madagascar, that are viviparous/cryptoviviparous, burial is necessary to provide support for the trunk; lacking this, support is provided by stilt roots or a broad root-bearing surface below the soil surface (Tomlinson & Esler, 1973; Hallé *et al.*, 1978; Tomlinson, 1990; Beentji, 1993). In temperate and tropical oaks (*Quercus* spp. Fagaceae), seeds are pushed belowground during germination (Ng, 1978).

Typically, hypogenous cotyledons are large, nonphotosynthetic, and lack stomates (Lubbock, 1892; de Vogel, 1980). However, cotyledons of certain hypogeous species (e.g. *Lucuma* sp. Sapotaceae) may turn green when exposed to light at the soil surface. In *Quercus ilex*, if an acorn is deeply buried, the first leaves are scale-like, but if shallow and in light, they become green and foliaceous. In the epigeal peanut (*Arachis hypogaea* Leguminosae), cotyledons, although carried up into the air, never become green (Brown, 1935).

During seedling growth, cotyledons can change (Appendix 2.1; e.g. Lubbock, 1892; Burger, 1972; Muller, 1978; de Vogel, 1980). Opposite cotyledons may become alternate by unequal growth of the stem, sessile cotyledons may become petiolate, shape may change, or one cotyledon may grow while the other does not.

### Stems, leaves, and surface features

Seedlings may develop a variety of surface features, including hairs, pores, and secretory structures, as well as odors, colors, and specialized functions (Appendix 2.2). These, as suggested by Fahn (1979) for secretory plant tissues *per se*, appear to be ecological adaptations of two types, mediating either edaphic/climatic conditions or surrounding animal populations. Hydathodes and salt glands are of the first

type, permitting loss of water when moisture conditions reduce transpiration or removal of salt for species in saline habitats. High tannin content, odors, and the myrosin cells of Brassicaceae, as well as color variegation (*Byttneria aculeata* Sterculiaceae) (Lee, 2007), provide defense against animals. Special secretory tissues permit the production and accumulation of poisonous substances.

Form may be quite variable (e.g. de Vogel, 1980; Young & Young, 1992). First leaves are usually simpler than those that follow, but this generalization is reversed in species from arid habitats (Lubbock, 1892). Certain gymnosperm seedlings, including *Chamaecyparis lawsoniana* (Cupressaceae), *Cryptomeria* spp. (Taxodiaceae), and *Juniperus* spp. (Cupressaceae), have both juvenile needle-like leaves and appressed adult scale leaves. Cycad seedlings have a shoot apex that produces scale leaves for several years and single foliage leaves at intervals. Over time, the number of foliage leaves increases until crowns of leaves alternate with scale leaves (Chamberlain, 1935). Dicots may have simple leaves followed by compound leaves (e.g. *Aegle marmelos* Rutaceae, *Vitex pubescens* Verbenaceae) and, less frequently, compound leaves followed by simple ones (e.g. *Acacia oraria* Leguminosae). In palms, where leaf form changes following the first green bladed leaf, Tomlinson (1990) distinguishes six transition types. Finally, red-tipped seedlings of *Eusideroxylon zwageri* (Lauraceae), growing from one of the largest seeds in the world (12 cm long × 4 cm wide), exceed 1 m in height before producing leaves (Veever-Carter, 1991).

### Roots

There are three broad groups of root types (Lauenroth & Gill, 2003), conifers and woody dicots, herbaceous dicots with roots organized around a primary (tap) root, and herbaceous monocots with roots not organized around a primary root. However, generalizations are difficult because the tap root of many dicots is augmented by adventitious roots (Kummer, 1951) and some monocots have a primary root (Fig. 2.1; Tillich, 1995, 2000). Root architecture responds to environmental factors, including nutrient and water availability, herbivory, and soil microbes. Root form, in turn, may influence function. The herringbone type (main axis and few laterals), although requiring more resources to construct than those with dichotomous architecture, is more efficient at exploiting resources such as phosphate. In *Picea sitchensis* (Pinaceae), roots growing on the windward site of young seedlings are thicker, longer, and more branched than on the leeward side providing resistance to wind throw (Robinson *et al.*, 2003).

Another feature is root exudates (Inderjit & Weston, 2003). Seedling roots may produce a variety of compounds, including in the case of wheat (*Triticum* sp. Poaceae) phenolic acids and *Sorghum bicolor* (Poaceae) root hair droplets containing a mixture of long-chain hydroquinones. In these crops, the amount of exudate varies with cultivar. Exudates have a variety of roles, including inhibiting seedling growth of other plant species, enhancing inorganic nutrient availability in nutrient-limited habitats, inhibiting nematodes, stimulating nodule



and mycorrhizal symbioses, and providing a favorable environment for growth of a beneficial rhizosphere community. They can also stimulate germination and haustorial growth of parasites like *Orobancha ramosa* (Orobanchaceae) and *Striga* species (Scrophulariaceae).

We know little about seedling root characteristics (but see Tillich, 1995, 2000). For example, we do not understand the significance of the lack of nodules on *Mora megistoperma* seedlings, although characteristic of many Leguminosae (adults appear to be mycorrhizal) (Janzen, 1983); the lack of root hairs on most hypogeal seedlings (de Vogel, 1980); or the adherence of, for example, *Pilea pumila* (Urticaceae), roots to filter paper (Leck, Outred pers. obs.).

### Specialized storage structures

Modified stems, such as bulbs, tubers, and rhizomes, as well as storage roots (Appendix 2.1), are adaptations that provide storage and survival function. In fire-adapted and nutrient-limited communities, lignotubers (woody storage structures) provide protection from fire and aridity (Hallé *et al.*, 1978; Florence, 1981; Boucher, 1983). An interesting example of lignotuber formation occurs in *Quercus oleoides* where the seedling must transfer resources to an underground tuber to win the race against seed consumption with a moth larva, the egg of which was laid just as germination began. The larva begins to eat the inside of the acorn; tuber formation must take place before shoot development can occur (Hallé *et al.*, 1978). In the case of *Ginkgo biloba* (Ginkgoaceae), lignotubers originate from cotyledonary buds that become imbedded in the stem cortex, and, then, following a traumatic event, grow downward to form the lignotuber (Del Tredici, 1997).

Contractile roots or hypocotyls bury bulbs, corms, or other structures (Appendix 2.1) (Pate & Dixon, 1982). Contraction occurs by widening and shortening of cells or by their total collapse (Bell, 1991). In alpine tundra plants, contractile roots gradually pull the shoot apex of young *Lepidium* (Brassicaceae) several centimeters below the surface, an adaptation to withstand the vertical forces associated with freezing when protective snow cover is missing (Körner, 2003). Contractile roots also occur in the grass trees *Kingia australis* (Dasypogonaceae) and *Xanthorrhoea australis* (Xanthorrhoeaceae), where stem apices of seedlings are several cm below the soil surface and production of an aerial stem is delayed many years to protect against fire (Staff & Waterhouse, 1981). The hypocotyl is contractile in *Asclepias tuberosa* (Asclepiadaceae), placing the apical meristem (and tuber formation) belowground (Kummer, 1951). If the hypocotyl takes part in the formation of a storage organ, then both roots and hypocotyls may be contractile [e.g. *Chloraea membranaceae* (Orchidaceae); Skene, 1959].

In certain cases however, burial involves growth rather than contraction. Asymmetrical growth of the present year's corm carries the new *Colchicum autumnale* (Liliaceae) corm deeper into the soil (Boyd, 1932). In *Tulipa* (Liliaceae), the cotyledon base forms a hollow, blunt tube, which penetrates the soil, and as it grows downward, carries the plumule into the ground (Lubbock, 1892; Boyd, 1932). Both the

cotyledon and base of the plumule form the first bulb that is buried in the soil. In *Marah* (Cucurbitaceae), burial is accomplished by elongation of the fused cotyledonary petioles that can be 20 cm long and that push the radicle and plumule into the soil (Schlising, 1969). Dropper roots, as occur on seedlings of *Dichopogon strictus* (Anthericaceae), place the storage root well below the soil surface (Pate & Dixon, 1982). In seedlings of *Pinus rigida* and *P. echinata* (Pinaceae), basal crooks develop, forcing dormant basal buds into mineral soil where they are protected from fire (Good *et al.*, 1979). Similarly, the hypocotyl of *Eupatorium perfoliatum* (Asteraceae) bends and reclines, bringing the crown to the soil surface (Kummer, 1951).

### Plasticity

Varied seedling responses can occur depending on environment, including inundation, crowding, light, and soil conditions like salinity and compaction. An *Eichhornia crassipes* (Pontederiaceae) seedling germinated in water develops an elongated hypocotyl and a basal ring of rhizoids, but on soil the hypocotyl does not elongate and adventitious roots are produced (Muenscher, 1944). Shoots appear first when seeds of wetland species (e.g. *Peltandra virginica* Araceae, *Phalaris arundinacea* Poaceae) germinate underwater; the leaves of submerged *P. arundinacea* seedlings may have conspicuous oxygen bubbles at their tips (Leck, 1996). The shoot of *Zizania* (Poaceae) seedlings may grow 50–100 cm to reach a lighted position in the water column where photosynthesis can replace stored reserves (Aiken, 1986). In *Mimulus lutea* (Scrophulariaceae), the primary internodes do not develop unless seedlings are crowded, resulting in elongation (Lubbock, 1892). *Dactylis glomerata* and *D. polygama* (Poaceae), in response to reduced light (20–30% full sunlight), double or triple leaf area and allocation to roots, but do not reduce root length, nitrogen uptake, or plant growth (Ryser & Eek, 2000). These examples suggest that phenotypic plasticity appears to maximize resource acquisition and growth for the short term; for shade-tolerant species, higher tissue-mass density and longer leaf-life spans provide long-term adaptations.

Varied soil conditions may contribute to seedling plasticity. *Taxodium distichum* (Taxodiaceae) seedlings respond to increased salinity (0–4 g l<sup>-1</sup>) by increasing partitioning of biomass to roots, thereby increasing the surface area for water uptake and increasing the possibility of reaching zones lower in salinity (Allen *et al.*, 1997). Dwarf and nondwarf home site differences can cause striking phenotypic differences between reciprocal seedlings transplants of *Pinus rigida* (Pinaceae) (Fang *et al.*, 2006). Additionally, the mechanical resistance of soil, due to surface crusts or compaction, can cause seedlings (e.g. *Lycopersicon esculentum* Solanaceae) to develop thicker hypocotyls, thereby providing greater emergence force (Liptay & Geier, 1983). The greatest compression regime caused the greatest increase in hypocotyl diameter and increased time to emergence. Other types of plastic responses occur. Hypocotyl growth can be significantly reduced by pricking or rubbing cotyledons (e.g. *Bidens pilosus*, *B. dioica* Asteraceae), implicating the rapid transmission of a signal from the cotyledon to

the hypocotyl with the underlying mechanisms involving auxin activity and lignification by peroxidases on elongating cells (Desbiez & Boyer, 1981). The *Trapa natans* (Trapaceae) seedling initially has a negatively geotropic hypocotyl and may produce both positively and negatively geotropic roots (Sculthorpe, 1967). In addition, plasticity attributes may change with seedling age. Shade-tolerant woody species, for example, may lose the ability to modify architecture to capture limited light as investment to mechanical structure increases, and shade-tolerant and shade-intolerant species converge to become less shade tolerant with age (Kneeshaw *et al.*, 2006). Behavior of seedling parts may vary. For example, the shoot of *Hedera helix* (Araliaceae), a vine, is photophobic and grows toward dark forms, while the leaves are positively phototropic (Metcalfe, 2005).

Regeneration from cotyledons has been observed in *Gustavia superba* (Lecythidaceae) (Harms *et al.*, 1997) and in *Idiospermum australiense* (Calycanthaceae), in which any of the two to six cotyledons can produce independent seedlings (Edwards *et al.*, 2001). Detached cotyledons of *Bidens laevis* (Asteraceae) can form roots (Leck, pers. obs.).

### Polymorphism

Seedlings of a given cohort may exhibit little (e.g. agricultural crops) or much variability in form, depending on genetic and environmental factors. The seedlings of *Geranium sessifolium* (Geraniaceae) may be brown, green, or intermediate (Philipp, 1992). The brown ones have the highest survival rates due to the higher cyanidin-6-glucoside content that protects seedling and juvenile leaves from ultra-violet (UV) light and/or predators (Mooney *et al.*, 1983; Drumm-Herrel & Mohr, 1985). Certain other species produce more than one kind of seed, resulting in marked seedling differences. When large seeds of *Taraxacum hamatifforme* (Asteraceae) germinate, the radicle tends to emerge first, but cotyledons tend to emerge first from small seeds (Mogie *et al.*, 1990). The adaptive value of this is not known. The offspring of amphicarpic species with dimorphic seeds vary in size and other characteristics. For example, *Amphicarpum purshii* (Poaceae) seedlings from aerial seeds were shorter than those from subterranean ones ( $7.9 \pm 0.4$  vs.  $18.1 \pm 0.8$  cm), fewer in number ( $48.4 \pm 13.3$  vs.  $112.4 \pm 22.6$  m<sup>-2</sup>), and weighed less ( $5.1 \pm 0.6$  vs.  $50.8 \pm 4.3$  mg) (Cheplick, 1982; Cheplick & Quinn, 1988). In *Cardamine chenopodifolia* (Brassicaceae), seedlings from subterranean seeds, which were 6 times heavier than aerial ones, had more rapid root elongation, greater dry weight accumulation, and larger cotyledons and first leaves (Cheplick, 1983). The seedlings of subterranean seeds, because of their faster growth, greater vigor, and earlier reproduction, have selective advantage in temporary unpredictable habitats. For desert species such as *Gymnarrhena micrantha* (Asteraceae) and *Emex spinosa* (Polygonaceae), seedlings from subterranean propagules are more tolerant of water stress (see Gutterman, 1993).

Chasmogamy/cleistogamy and fruit/seed dimorphism are more widespread than amphicarpy and also represent responses to a variable, heterogeneous environment (Cheplick, 1998). In *Impatiens*

*capensis* (Balsaminaceae), cleistogamous flowers, produced in shade, yield fewer and smaller seeds than chasmogamous flowers (Simpson *et al.*, 1985); seedlings from chasmogamous flowers have a greater chance of surviving (Waller, 1984).

In contrast, seed heteromorphism is conspicuous in certain Asteraceae. While important for dispersal, Venable *et al.* (1995) found that seedlings from disk, ray, and intermediate achenes of *Heterosperma pinnatum* did not differ in size, growth, or competitive ability, and embryo biomass at maturity was also similar. In the case of *Polygonum hydropiper* (Polygonaceae), however, polymorphism is related to cross-generation effects; with the seed's architectural position (terminal vs. axial inflorescence) on the parent plant influencing the rate of development and other seedling traits (Lundgren & Sultan, 2005). Responses also varied with plants grown in shade versus full sun.

Other forms of polymorphism occur. Species with polyembryony may produce seedlings of varying form and sizes (e.g. *Citrus aurantifolia* Rutaceae, Enoch, 1980). In *Macfadyena unguis-cati* (Bignoniaceae), a dry forest liana of Costa Rica, two distinct juvenile forms occur (Gentry, 1983). Initially, the seedling is erect with largish opposite, simple leaves; it then develops into a wiry vine with tiny bifoliate leaves having a trifid tendril with hooked tips. The second stage is photophobic and grows toward the closest dark, light-blocking form, usually a tree trunk that it climbs with its cat's claw tendrils. The juvenile may persist for several years.

For dioecious species, the sex of seedlings is not discernable without using histological techniques/DNA markers for species with sex chromosomes (J. Consolloy & J. Quinn, pers. comm.). There are, however, some morphological differences in male and female laboratory-grown *Cannabis sativa* (Cannabaceae) by the time plants are about three weeks old (S. Datwyler, pers. comm.).

### Interesting oddities

Seedlings of a number of species defy categorization (Bell, 1991). Those of *Streptocarpus* (Gesneriaceae), which begin apparently as normal dicots, have one cotyledon that enlarges to form a 30- to 90-cm-long and 23- to 50-cm-wide phyllomorph (a leaf-like structure) (Lubbock, 1892; Bell, 1991; Rauh & Basile, 2000; Mantegazza *et al.*, 2007). The plants of Podostemaceae and Tristichaceae, found in fast-flowing streams, superficially resemble algae. Germinating seeds do not produce radicles, and adventitious roots may be produced by the hypocotyl. Roots may elaborate to form a hapteron, a holdfast-like structure, which attaches the plant to the rock surface (Bell, 1991). The young thallus may develop as a lateral outgrowth from the hypocotyl and less often from the cotyledons and plumular leaves (Arber, 1920; Sehgal *et al.*, 1993). Attachment may occur via rhizoids, and a cyanobacterial film on the immobile substrate appears necessary for attachment (Philbrick & Novelo, 2004). The Lemnaceae also do not fit common morphological interpretation (Bell, 1991). Seedlings are exceedingly small (e.g.  $\approx 1.2$  mm, *Lemna minor*, Muencher, 1944)

and lack differentiation, except in the development of two meristematic areas (usually one in *Wolffia*) that are each in a sunken pocket (but see Tillich, 1995). New fronds on the developing seedling occur in these pockets.

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## 2.5 | Seedling diversity – ecophysiology

### Growth patterns

Growth patterns of the seedling, and subsequently of the mature plant, may involve the loss of meristems. In certain temperate tree seedlings, abscission of the terminal bud occurs at the end of the first year followed by substitution of a lateral bud that functions for a year (e.g. *Ulmus effusa* Ulmaceae), but in tropical trees, growth periodicity is not necessarily annual (Hallé *et al.*, 1978). The fate of the meristem influences the subsequent architectural model (Hallé *et al.*, 1978). Moreover, behavior appears related to the amount of food reserve in the seed. Severing the seed from the hypogeous seedling may reduce the length of the orthotropic (vertical) phase; seedlings with little or no reserves quickly become plagiotropic (oblique or horizontal); and in *Sida carpinifolia* (Malvaceae), the orthotropic phase may be extended by growing the seedlings in a very rich medium (Hallé *et al.*, 1978). In some trees, the length of the epicotyledonary axis determines the length of the trunk (e.g. *Aloe* spp. Liliaceae, *Senecio johnstonii* ssp. *johnstonii* Asteraceae). The distribution of carbohydrate appears to trigger lignotuber development in *Ginkgo biloba*, with formation in 50% of horizontal seedlings compared to 0% in vertical ones (Del Tredici, 1997). *Welwitschia mirabilis* (Welwitschiaceae) displays a unique developmental pattern. Following formation of two permanent leaf primordia and so-called scaly bodies (foliar appendages) that persist for 30–40 years, precocious death of the terminal meristem occurs. This is unique among vascular plants because further growth is restricted to the edge and leads to increased girth; the elliptical apex becomes a crater-like depression (Sporne, 1967).

### Dormancy/interrupted growth

Once germination has begun, growth of seedlings may not be continuous. Stem growth of woody species may be interrupted with pulses of inactivity (Lubbock, 1892; de Vogel, 1980). How development proceeds, especially the occurrence of resting phases, may be an especially important clue to seedling identification (de Vogel, 1980). Resting stages may be short or long or growth may occur in flushes with several internodes produced during each. In *Embelia viridiflora* (Myrsinaceae), four distinct growth intervals appear in a short period of time during which the primary axis grows the initial 10 cm. Growth may also be interrupted, as seen in *Jacquinia ruscifolia* (Theophrastaceae), and when growth ceases, the bud is protected by small scales. There is a long interval before growth resumes in seedlings of *Mangifera indica*

(Anacardiaceae) following the initial growth phase during which the epicotyl reaches approximately 30 cm and the first leaves have matured (Enoch, 1980). The seedlings of *Mora megistosperma* (Leguminosae) grow 1–2 m in the first 2–4 months and then remain at that height for more than 3 years (Janzen, 1983). In some Burseraceae and Leguminosae, dormancy begins after the unfolding of the primary leaves (van der Pijl, 1982). The tuberous swollen hypocotyl of some *Araucaria* species (Araucariaceae) rests for several months, a feature that enabled the transport of the first specimens of *Araucaria araucana* from Chile to Europe in 1795 (Dallimore & Jackson, 1966).

Root growth may also be interrupted. De Vogel (1980) notes that branching and formation of lateral roots in hypogenous seedlings of tropical species may be delayed and also that elongation of the primary root is delayed in some herbaceous temperate seedlings (e.g. *Downingia pulchella* Campanulaceae). Roots of cacti, with sympodial, determinate growth, cease growing when experiencing water deficits (Dubrovsky, 1997a).

Interrupted germination and, consequently, interrupted seedling growth have been reported for a number of herbaceous species from temperate regions. Some exhibit epicotyl (defined to include apical meristem or bud) and/or radicle dormancy. During germination, the epicotyl and/or radicle require specific dormancy-breaking conditions. See Baskin & Baskin (1998) for a detailed discussion; only two examples will be considered here.

In species with epicotyl dormancy like *Hydrophyllum* species (Hydrophyllaceae), radicle emergence typically begins in autumn and the root system develops slowly, becoming 4–7 cm long depending on species; then in early spring when temperatures are high enough for leaf growth, the cotyledons emerge. In other species, both the epicotyl and radicle may be dormant. This double dormancy was first described for *Trillium grandiflorum* (Liliaceae). Such species require at least two winters and one summer for complete seedling emergence. Moist seeds of *T. grandiflorum* require 3 months at 5–10 °C (1st winter) to break radicle dormancy, followed by 3 months at 20–30 °C (spring and summer) to allow radicle emergence, development of the root system and bud, and finally, 4 months at 4 °C (2nd winter) to break bud (epicotyl) dormancy (Barton, 1944; cited in Baskin & Baskin, 1998).

Young seedlings of a variety of temperate woodland herbs, such as *Arisaema triphyllum* (Araceae), *Lilium superbum* (Liliaceae), and *Mertensia virginiana* (Boraginaceae), become dormant well before the end of the growing season (Phillips, 1985), as do the ephemeral adults. Finally, seedlings of winter annuals may also show interrupted growth. *Chaerophyllum procumbens* var. *shortii* (Apiaceae) of deciduous forests overwinters with cotyledons and one or two leaves (Baskin *et al.*, 2004). Germination in late summer permits establishment of seedlings because deciduous trees lose leaves during autumn, creating canopy gaps.

Likewise, adaptations of wetland seedlings (e.g. Topa & McLeod, 1986; Koňcalová, 1990; Al-Hamdani & Francko, 1992; de Oliveira Wittmann *et al.*, 2007) permit establishment in various kinds of