HANDBOOK OF
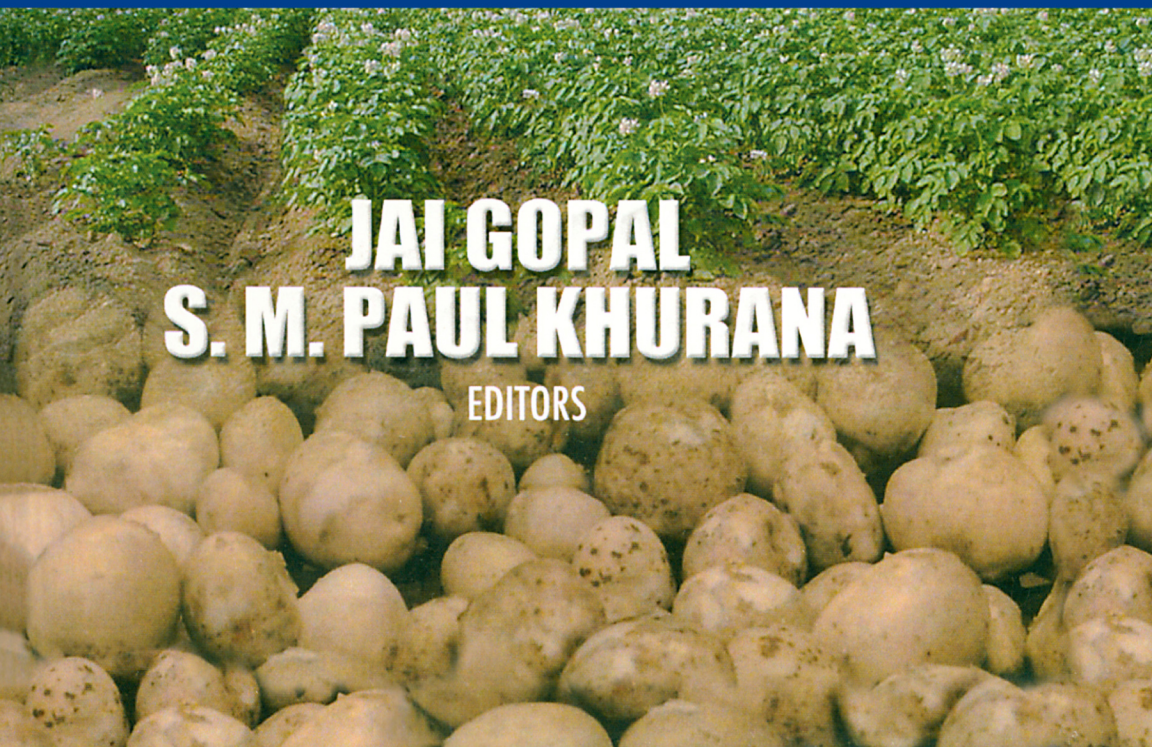# POTATO
PRODUCTION, IMPROVEMENT, AND POSTHARVEST MANAGEMENT

JAI GOPAL
S. M. PAUL KHURANA

EDITORS

Handbook of Potato Production, Improvement, and Postharvest Management

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Jai Gopal, PhD, is Principal Scientist in the Division of Crop Improvement at the Central Potato Research Institute in Shimla, India. His research experience includes nearly three decades in potato genetics, breeding, and biotechnology. He has studied genetics and floral biology of the potato, has bred a number of potato varieties and parental lines, and has developed selection procedures combining in vitro and in vivo approaches. His work has appeared in *Theoretical & Applied Genetics, Plant Breeding, Plant Cell Reports, Euphytica,* and *Potato Research.*

S. M. Paul Khurana, PhD, is Vice-Chancellor at Rani Durgawati University in Jabalpur, India. He was National Coordinator of Potato for ten years and Director of the Central Potato Research Institute for three years. His research experience includes over three decades of work on plant viruses and viroids, and he is an expert in virus detection techniques. He standardized use of ELISA and ISEM for detection of potato viruses and developed simple techniques for screening resistance to potato viruses. His published works have appeared in various international journals. Dr. Khurana has also edited several books, conference proceedings, and journals.

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Foreword

Potato is a significant crop and an important staple food in temperate countries. It is rapidly gaining importance as a major food crop in tropical and subtropical countries, where it is overtaking staple grains in volume of production and consumption. Potato cropping in Asia, Africa, and Latin America has grown rapidly and continues to expand as a result of better varieties, improved access to inputs, integrated crop management, enhanced postharvest handling, and optimum irrigation. Potato is valuable both as a fresh product and as a processed product, and the current trend is for rapid growth in processed forms, mainly chips, French fries, and powder. The area under production is expected to more than double in the future with the increasing demand for fresh and processed potato products arising from the fast-changing food habits in many developing countries.

Accompanying this rapid increase in potato production and consumption, especially in developing countries, is the need to constantly improve varieties and methodologies for higher productivity. Improved postharvest management of potato is vital in terms of total production; conservation systems that make food available after harvest will form a significant requirement. As a semiperishable product, potato needs special care in storage, transport, and processing. It is imperative to acquire specific scientific knowledge to develop and select varieties, to improve the management of inputs and crop protection, and to select efficient methods of storage, handling, and processing.

The *Handbook of Potato Production, Improvement, and Postharvest Management* is a text-cum-reference book covering all aspects of potatoes from biosystematics through breeding, agronomy, diseases, and insect pests to storage, processing, and value addition. Its

publication is particularly timely as potato becomes a significant crop in many tropical and subtropical countries. It collects valuable contributions from renowned scientists associated with potato production and postharvest handling. The well-illustrated chapters provide up-to-date reviews on both basic and applied aspects and include references at the end for readers who want to obtain further details on each topic.

The book is a valuable resource for potato researchers, teachers, and students.

Pamela Anderson, Director General
International Potato Center
Lima, Peru

Preface

Potato is an important component of the human diet in both developed and developing countries. Originally domesticated by Andean farmers, probably in the Lake Titicaca basin, potato is now grown in nearly 150 countries and is the world's fourth most important crop after rice, wheat, and maize. Hence, the production, improvement, and postharvest management of potato are of great interest. Many research institutes and universities, including the International Potato Center (CIP), Lima, Peru, have generated a vast amount of knowledge about potatoes, and in 1978 Professor Paul Harris edited an excellent book entitled *The Potato Crop,* which was revised in 1992. Since then much information has been generated and a few subject- and region-specific compilations have been produced by well-known potato scientists, yet no other comprehensive book on potato has been published.

The *Handbook of Potato Production, Improvement, and Postharvest Management* is a handbook in 15 chapters authored by authorities in their respective fields. It is a text-cum-reference book aiming to provide state-of-the-art information to scientists, students, and industrialists so that it can be effectively used for future research into, and development and utilization of, potato.

The book begins with a contribution from the leading taxonomists and germplasm experts David M. Spooner and Alberto Salas, who provide an introduction to the structure, distribution, and habitats of potato. Their chapter deals critically with the taxonomy of wild and cultivated potatoes and the present taxonomic status, highlighting the problems associated with previous classifications and discussing how these are being resolved.

The second chapter, "Genetics of Agrihorticultural Traits" by John E. Bradshaw, provides comprehensive information on the genetics of flowering, yield and its components, dormancy, tuber shape, pigmentation, and other topics.

"Considerations for Successful Breeding" by Jai Gopal, the third chapter, highlights theoretical and practical strategies for consideration in the selection of superior parents, crosses, and clones from segregating progenies. In addition, it proposes novel and realistic selection procedures based on the combined use of in vitro and in vivo methods.

Chapter 4, "Biotechnology in Potato Improvement" by Gerhard Wenzel, reviews the role of biotechnology in the conservation and characterization of potato germplasm and breeding. It also covers haploids, somatic cell fusion, molecular markers, genetic maps, transgenics, and high-throughput DNA techniques.

In Chapter 5, "Quality Improvement," T. R. Tarn, G. C. C. Tai, and Qiang Liu review the genetics of texture, dry matter, sugar, cold-induced sweetening, starch, proteins, vitamins, antioxidants, flavor, glycoalkaloids, and enzymatic browning from the point of view of the progress being made in improving these characteristics through biotechnology and other methods.

In Chapter 6, "Ecophysiology and Agronomic Management," P. M. Govindakrishnan and A. J. Haverkort analyze the phases of crop growth and the factors important in the development of cultural practices in diverse environments. In addition, in dealing with agro-techniques for optimum resource use, they illustrate how these principles can be embodied into decision support systems.

Under the title "Abiotic Stresses" in Chapter 7 Kazuto Iwama and Junichi Yamaguchi cover the physiobiochemical basis of tuberization and topics relevant to the understanding and management of stresses due to such factors as drought, heat, salinity, frost, and ozone.

The next two chapters deal with fungal and oomycete diseases of potato. Chapter 8 is devoted to late blight disease: G. A. Forbes and J. A. Landeo describe the morphology, taxonomy, origin, and spread of the pathogen and the epidemiology, symptoms, disease cycle, and management through cultural, chemical, and host-mediated resistance. Progress in breeding *R*-gene-free populations and in understanding the molecular aspects of host-pathogen interaction are also

reviewed. H. W. (Bud) Platt and R. D. Peters systematically describe the causal agents, distribution and impact, symptoms, epidemiology, and management aspects of another 14 important fungal and oomycete diseases in Chapter 9.

In Chapter 10, R. Lebecka, E. Zimnoch-Guzowska, and E. Łojkowska describe six bacterial diseases of potato, including the four major ones—bacterial wilt, ring rot, black leg, and common scab. They also provide an extensive review of host resistance and its utilization in developing resistant varieties.

Chapter 11 on "Viruses and Viroids," by Colin Jefferies, H. Barker, and S. M. Paul Khurana, covers the distribution, morphology, nucleic acid types, and mode of transmission of viruses and viroids naturally infecting potato. In addition to detection and management methods, the authors analyze seed certification, phytosanitary regulations, cultural/chemical control measures, and the use of host- and pathogen-derived resistance.

Chapter 12, "Insects, Nematodes, and Integrated Pest Management" by Hanafi Abdelhaq, covers all important pest species, their distribution and the damage they cause, their biology and management, and integrated pest management and biopesticides.

Chapters 13 and 14 address the problems associated with postharvest management of potatoes, which are of great importance to growers and also to industry. Chapter 13, "Storage" by Klaus Gottschalk and R. Ezekiel, addresses both temperate and tropical problems in potato storage, providing information on storage methodology and factors affecting storage as well as mathematical models governing storage conditions. It also reviews the basics of such topics as physiological age and dormancy.

Chapter 14, "Processing and Value Addition" by Xiu-Qing Li, Martin G. Scanlon, Qiang Liu, and Warren K. Coleman, starts with the food value of potatoes, before moving on to review the industrial technology for processed products, including molecular farming and the production of vaccines, pharmaceutical proteins, and so on. This chapter complements the discussion of quality improvement in Chapter 5.

The final chapter is on "True Potato Seed," once a hot research topic. In this chapter, Jai Gopal and R. Ortiz review the past and

present status of TPS and analyze its future prospects. Although these prospects are not very encouraging, the desire to use TPS as an alternative to the traditional method of cropping through seed tubers is not going to die down quickly, as research is continuing to overcome its shortcomings.

The help and support of the authors by way of their contributions is gratefully acknowledged. We hope that this team effort will benefit the cause of the potato. As editors, we have tried to make the presentation comprehensive and error free. Should readers find technical lacunae, we would be happy to be informed of them and also to receive comments for improving future editions.

Jai Gopal
S. M. Paul Khurana

Chapter 1

Structure, Biosystematics, and Genetic Resources

David M. Spooner
Alberto Salas

The potato is one of the world's most important food crops and the world's most important vegetable crop. Potato produces more carbohydrate per acre per year than any other crop except sugarcane. It has a higher quality protein than any other vegetable, and only soybean yields more protein per acre (Rhoades, 1982; Anonymous, 1984; Ortiz, 1998). Cultivated and wild potatoes are both tuber-bearing members of the genus *Solanum*. The only difference in the designation of a potato as "cultivated" or "wild" is cultural, that is, whether it is intentionally grown for food or is growing naturally. The "modern" cultivated potatoes of world commerce are collectively designated under the name *S. tuberosum*. L. Potato has a rich gene pool of nearly 200 tuber-bearing species that represent a huge and only partially explored reservoir of germplasm useful for potato breeding. Wild species of potato have known desirable traits such as resistance to heat and frost, fungi, bacteria, viruses, nematodes, and insects. Most of these species are cross-compatible with the cultivated potato either directly or through the use of $2n$ gametes.

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This chapter provides an introduction to the structure, distribution, habitats, and taxonomy of wild and cultivated potatoes. It also discusses the collection, conservation, and use of potato genetic resources. Potato continues to be the focus of intense collection and taxonomic research; hence our understanding of the number of species and their interrelationships continues to change. Therefore an effort has been made to give the latest taxonomic summary of wild and cultivated potatoes.

STRUCTURE

One of the earliest descriptions of the potato was by Gerard (1597), who briefly outlined the outward morphology of the plant. In stark contrast, Cutter (1992) provided a 97-page treatise on both the external morphology and internal anatomy of potato and stated, "it is clear that the structure and development of the potato, admittedly a very complex plant, are by no means fully understood" (p. 65). This chapter covers the basic details of the external morphology of potato.

In potato, the stems arise at the beginning of each growing season from a tuber of the previous year, referred to as the mother tuber (shown at the base of the stem in Figure 1.1). A potato tuber is a modified underground stem, not a swollen root. The "eyes" of potato tubers are stem buds, similar to buds on the nodes of a stem. Each potato tuber has several eyes, and each eye is capable of producing a separate stem.

The young plant draws its initial nutrition from the mother tuber, which soon withers. This plant produces (1) roots that develop from the base of the plant, (2) aerial stems, and (3) underground horizontal stolons originating above the roots near the base of the aerial stems. As the plant grows, the stolons thicken at their ends, or in some wild species thicken like beads on a string along their length (see section "*Solanum* series *Piurana*"), and produce new tubers.

A tuber is a starch storage organ that perpetuates the plant into the next year by nonsexual means, also called vegetative propagation. In contrast, plants can also arise from "sexual" or "true" seeds produced from the flowers (see Chapter 15, "True Potato Seed"). Tubers of various cultivars/genotypes vary considerably in skin and flesh color,
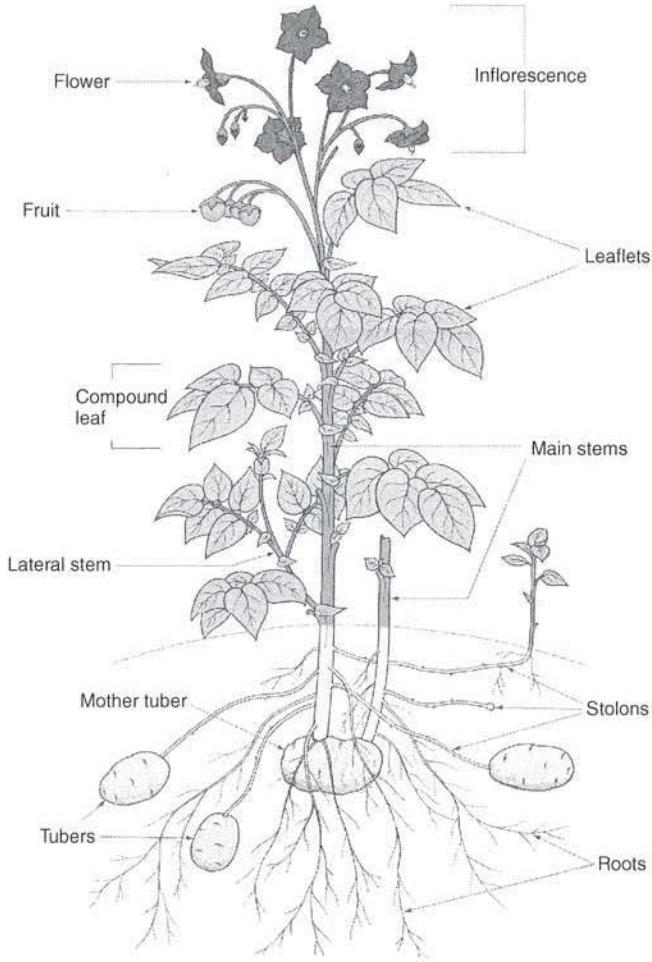
FIGURE 1.1. Stylized illustration of a cultivated potato plant. Drawing courtesy of the International Potato Center. See Plate 1.1 in the color gallery.

shape, and size. In modern cultivars skin colors vary from white to yellow to red to tan, but most have white tubers (some cream to yellow). Tuber shapes vary from round to elongate, and tuber skin surface varies from smooth to netted (russets) (Hils and Pieterse, 2005). These colors and shapes are commonly grouped into
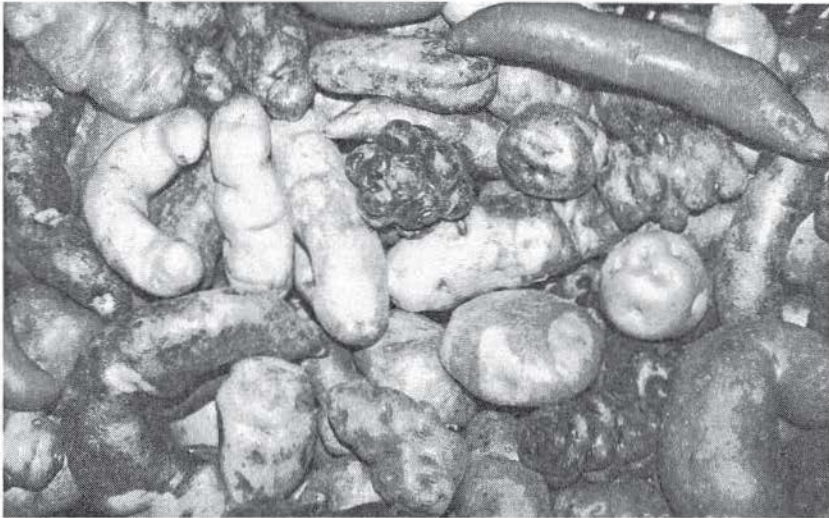
FIGURE 1.2. Tuber variation in potato land races (indigenous cultivars) from South America. See Plate 1.2 in the color gallery.

convenient market classes. For instance, the U.S. Potato Board (http://www.healthypotato.com/nutrition/varieties.asp) groups potatoes by the market classes russets, round whites, long whites, long reds, yellow flesh, and blue and purple flesh. Modern cultivars have been bred for relative uniformity in shape and color, but tuber variation is greater in land races (indigenous cultivars) from South America, which exhibit a much wider array of shapes and colors (Figure 1.2).

Stems can be green to purple or mottled mixtures of these colors and may have "wings" (ridges of tissue growing outward from the stem). Compound leaves arise in a spiral pattern on the aerial stems. In the angle between the stems and leaves (the leaf axil), branches or flower clusters (inflorescences) are produced. Typically, at the base of the leaves, flaps of tissue called "pseudostipular leaflets" are produced (Figure 1.3A). Sometimes these fall off or are not produced at all.

Leaves of cultivated and wild potatoes vary tremendously in relative degree of dissection and shape. Figure 1.3A (one leaf form of *S. tuberosum*) illustrates parts of a potato leaf. Except that secondary lateral leaflets are not very common, the leaf in Figure 1.3A looks
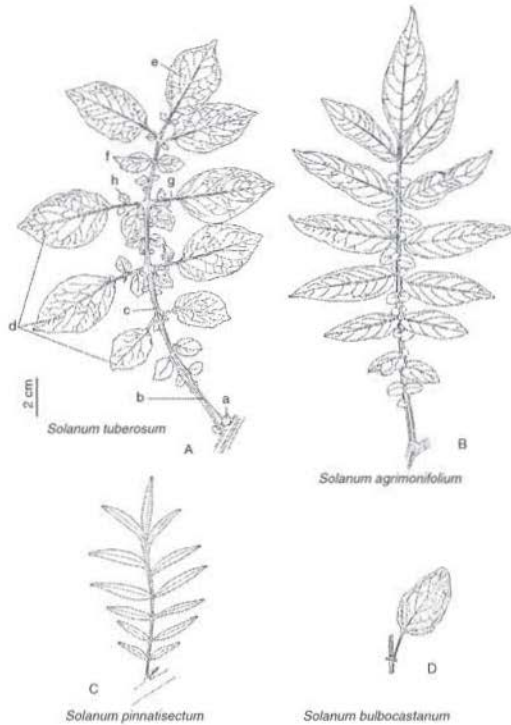
FIGURE 1.3. Variation in leaf morphology in wild and cultivated potatoes *(Solanum* section *Petota). (A)* The most dissected leaf type is illustrated in a collection of *S. tuberosum,* showing *a.* pseudostipular leaflets, here appearing as ovate flaps but sometimes shaped as half-moons (lunate); *b.* petiole (base of the leaf lacking lateral leaflets); *c.* rachis; *d.* lateral leaflets; *e.* apical leaflet; *f.* interjected leaflets; *g.* petiolule (base of the lateral and apical leaflets without leaf tissue); *h.* secondary lateral leaflets (separate leaf tissue arising on the petiolule). The designation of the small structures near the base of the leaf axis as interjected leaflets or small lateral leaflets is open to interpretation. *(B) Solanum agrimonifolium* shows a leaf type more characteristic of a group of approximately 40 wild potatoes in *Solanum* series *Conicibaccata* with leaves having a somewhat parallel-sided morphology, with leaflet pairs more subequal or diminishing gradually toward the base. *(C) Solanum pinnatisectum* and only one other species *(S. jamesii)* have pseudostipular leaflets that are not ovate or lunate but pinnate; this species, and a few others, such as *S. infundibuliforme,* have narrow lateral and terminal leaflets without petiolules and no interjected leaflets. *(D) Solanum bulbocastanum* and a few other species have entire leaves; this species has lunate pseudostipules. There is a wide range of variation among these types.

similar to the leaves of most wild and cultivated species. *Solanum agrimonifolium* (Figure 1.3B) illustrates another leaf type with somewhat parallel sides typical of most members of *Solanum* series *Conicibaccata* Bitter (series are described in the section "Genus *Solanum*"). Some species, such as *S. pinnatisectum* (Figure 1.3C), lack interjected leaflets. *Solanum pinnatisectum* and the related species *S. jamesii* also have atypical dissected pseudostipules shaped like diminutive leaves. *Solanum bulbocastanum* (Figure 1.3D) has nondissected or entire leaves, a rare type in wild potatoes.

Colors and shapes of corollas also vary. A group of species showing characteristics of the probable earliest ancestors of potato have corollas that are star-shaped (stellate) and generally white, or white tinged with blue or purple (Figure 1.4A). Corolla colors are more typically blue to purple (Figure 1.4B), and in the cultivated species sometimes pink (Figure 1.4C), a corolla color rarely seen in the wild species. Shapes also vary from pentagonal (Figure 1.4C, D) to more circular or rotate in outline (Figure 1.4B).

Fruits of most wild and cultivated species are globose (Figure 1.5A), but some are conical (Figure 1.5D), with intermediate shapes that are ovoid (Figure 1.5B, C). They can be green or purple or almost
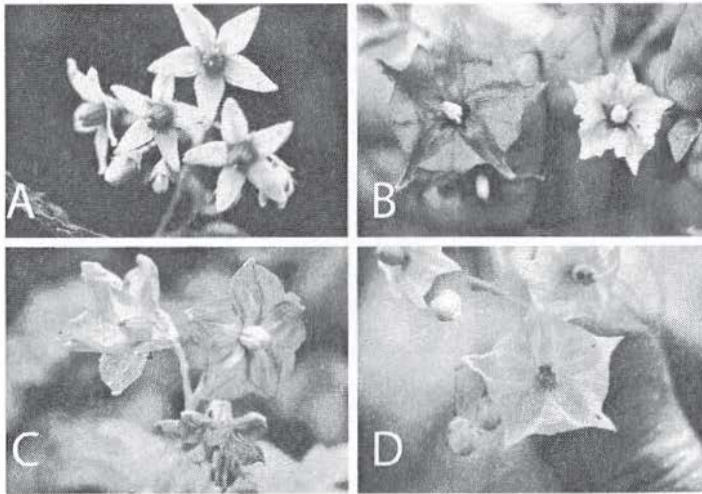
FIGURE 1.4. Wild and cultivated potato flowers. See Plate 1.4 in the color gallery.
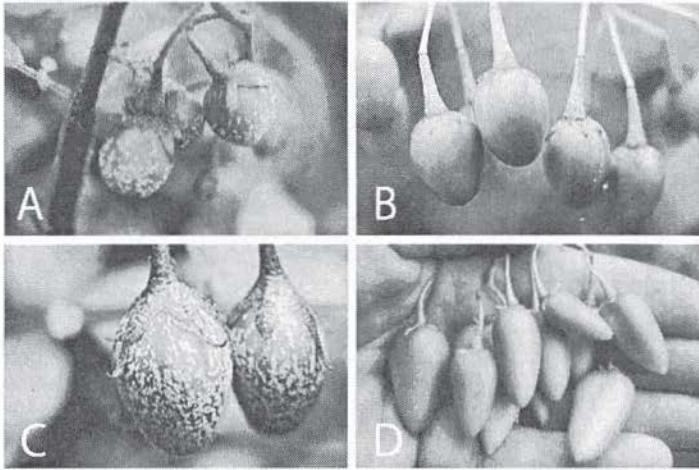
FIGURE 1.5. Wild potato fruits. See Plate 1.5 in the color gallery.

white or have mottled or dotted combinations of these colors (Figure 1.5A, C).

ORIGIN, SPREAD, AND HABITAT

The cultivated potato was believed to have originated somewhere in the Andes; different ideas were advanced for its wild species progenitors and specific place of origin. Spooner et al. (2005) supported a single origin of potato from a wild species progenitor in the *S. brevicaule* complex in southern Peru. The Spaniards found cultivated potatoes in Peru at the time of their conquest beginning in 1536 (Hawkes, 1990), and records exist of potatoes crated for shipment from Chile to Europe in 1587 (Glendinning, 1983). Cultivated potato first appeared outside South America in the Canary Islands (Spain) in 1567 (Hawkes and Francisco-Ortega, 1992). Between 1650 and 1840 potatoes had become a vital part of the basic food supply in Ireland. When late blight disease wiped out the crop in the 1840s, famine forced many Irish people to immigrate to America. Because of its early food use and importance in Ireland, the potato plant is some-

times called the Irish potato. From Europe, potato soon became established as a popular and cheap food crop worldwide (Hawkes, 1990).

Wild potatoes grow in 16 countries, from the southwestern United States to central coastal Chile and adjacent Argentina. Most of the 188 species of wild potatoes (see section "Taxonomy of section *Petota*") are rare and narrowly endemic. In general, they occur between 38°N and 41°S, with more species in the Southern Hemisphere. High species richness occurs in northern Argentina, central Bolivia, central Ecuador, central Mexico, and south and north-central Peru. Wild potatoes grow from sea level to 4,300 m but typically between 2,000 and 4,000 m altitudes (Hijmans and Spooner, 2001). They grow in an amazing variety of habitats from very seasonal wet/dry climates (e.g., *S. bulbocastanum,* Figure 1.6A) to high-altitude grasslands (e.g., *S. colombianum,* Figure 1.6B), to beach margins (e.g., *S. tuberosum,* Figure 1.6C), to upland rain forests (e.g., *S. candolleanum,* Figure 1.6D).

Native cultivated potatoes, or "land race" cultivars, grow throughout the Andes from Venezuela to northern Argentina, and then again in
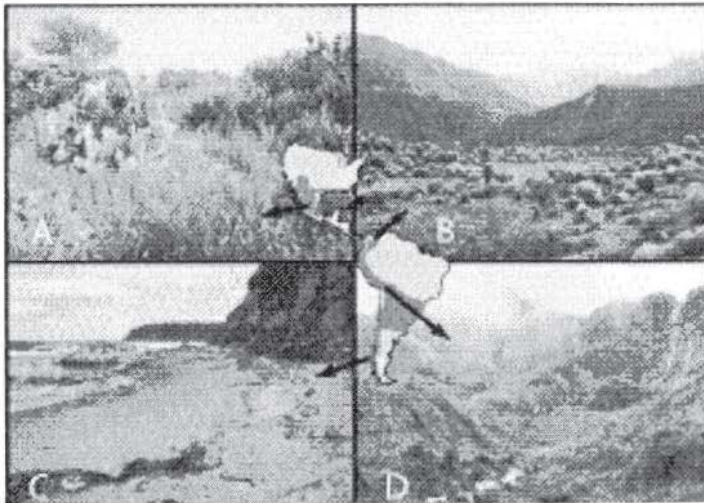
FIGURE 1.6. Wild potato habitats. See Plate 1.6 in the color gallery.

central Chile (in the Chonos Archipelago). No formal distributional analysis like that for the wild species exists for the cultivated species, but most populations in the Andes are planted in mid (2,000 m) to high elevations (4,000 m), and in Chile in low elevations near sea level.

The origin of "modern" cultivated potatoes has been very controversial. Juzepczuk and Bukasov (1929) proposed that modern potatoes originated from the tetraploid land races from Chile (Chilotanum Group), whereas Salaman and Hawkes (1949), Salaman (1946, 1954), and Hawkes and Francisco-Ortega (1992) suggested an initial origin from tetraploid land races from the Andes (Andigenum Group). The different arguments relate to day-length adaptation of these types in Europe, morphology of early herbarium specimens, shipping records, and times when the early cultivars were grown in Europe. For example, the Chilean introduction hypothesis rests on the fact that Chilean land races form tubers under long days, but potatoes from the Andes form tubers only in the short days in the tropics and thus would form tubers only very late in the year or not at all in Europe. The Andean introduction hypothesis argues that early cultivated herbarium specimens from Europe show a form similar to members of the Andigenum Group, the first cultivated potatoes in Europe were harvested late in the year, as expected for this short-day crop, and potatoes from Chile would not survive the long transport time to Europe.

Whatever the source of the early introductions to Europe, modern cultivars were later bred with Andean and Chilean land races and wild species. Hosaka et al. (1988) showed that tetraploid Chilean land races are primarily distinguished from most populations of tetraploid Andean land races and other cultivated and wild species by an approximately 400 base pair deletion in chloroplast DNA (cpDNA). Chloroplast DNA restriction site data documented five chloroplast genotypes (A, C, S, T, W types) in *S. tuberosum* (including the Andigenum Group and the Chilotanum Group). Subspecies *andigenum* has all five types, and the Chilotanum Group had three types, A, T, and W (Hosaka and Hanneman, 1988). The most frequently observed type in the Chilotanum Group is T, which was more precisely found to have a 241 base pair deletion, not a 400 base pair deletion (Kawagoe and Kikuta, 1991).

Hosaka (1995) further studied the origin of the cultivated tetraploid potato species using cpDNA restriction site data. He studied 132 accessions of the diploid Stenotomum Group and of six related diploid wild species. He showed extensive cpDNA polymorphism in all taxa except *S. brevicaule* and concluded that Andean diploid land races were domesticated many times from the wild species, followed by sexual polyploidization to form Andean land races. However, a recent study by Spooner et al. (2005) supported a single origin of cultivated potato. Hosaka (1995) also concluded that Chilean land races were selected from a limited subset of the Andean tetraploid land races somewhere near the Bolivian and Argentinean border. Hosaka (2003) showed an identical cpDNA deletion in some populations of the wild species *S. tarijense* and suggested that the Chilean populations arose from a history of hybridization with this species.

On the basis of cytoplasmic sterility factors, geographical isolation, and ecological differences, Grun (1990) suggested that the Chilotanum Group was distinct from the Andigenum Group. Hawkes (1990) distinguished these two Groups by the Chilotanum Group having fewer stems, with foliage aligned at a broad angle to the stem, and having less-dissected leaves with wider leaflets and thicker pedicels. Huamán and Spooner (2002) corroborated Hawkes's conclusion of morphological differences between the potatoes from these two regions but showed that they could be distinguished only with great difficulty by using many characters that individually were not always diagnostic (polythetic support).

GENUS SOLANUM

Solanum L. is one of the largest genera of flowering plants, including perhaps 1,500 species of herbs, shrubs, vines, and trees. It is one of the world's most economically important genera, including potato (*S. tuberosum* L.), tomato (*S. lycopersicum* L.), eggplant (*S. melongena* L.), and minor tropical fruits such as pepino (*S. muricatum* Aiton). The inclusion of tomato in *Solanum* (rather than in the genus *Lycopersicon* Miller) is novel to some, but it is well supported by many modern morphological and molecular studies.

Dunal (1852) wrote the first species-level worldwide monograph on *Solanum*. Later, Seithe (1962) and Danert (1970) attempted to use selected characters such as hair morphology and branching patterns to infer relationships within *Solanum*. D'Arcy (1972, 1991) divided *Solanum* into seven subgenera. Hunziker (2001) modified D'Arcy's (1972) system slightly and provided descriptions, nomenclature, and commentary for each of D'Arcy's sections. D'Arcy (1972, 1991) and Hunziker (2001) recognized potatoes in the subgenus *Potatoe* (G. Don), containing various sections, including the section *Petota* Dumort (covering all the wild and cultivated potatoes). A species-level revision of the genus *Solanum* is currently being undertaken by Solanaceae colleagues Lynn Bohs, Sandra Knapp, Michael Nee, and David Spooner.

Until Hawkes's (1990) classification, most classifications of wild and cultivated potatoes used overall similarity (phenetics) to delimit species and to infer their interrelationships. Sections and series are taxonomic ranks below genus that group related species (section is the higher rank and contains various series). Hawkes (1990) divided section *Petota* into subsection *Potatoe* Hawkes, with 19 tuber-bearing series, and subsection *Estolonifera* Hawkes, with 2 non-tuber-bearing series: *Etuberosa* Buk. and Kameraz and *Juglandifolia* (Rydb.) Hawkes.

Spooner et al. (1993) used cpDNA restriction site data and morphological data to investigate the relationships between members of potatoes (section *Petota*) and *Solanum* and other genera (including the genus *Lycopersicon*) of the Solanaceae. Their results confirmed placement of all members of Hawkes's (1990) tuber-bearing species into section *Petota*. However, the non-tuber-bearing species that Hawkes (1990) had placed into section *Petota* (series *Juglandifolia* and series *Etuberosa*) were excluded from the group. Members of series *Juglandifolia* were related to tomatoes, and, quite surprisingly, the branch of the phylogenetic tree that included tomatoes and series *Juglandifolia* was most closely related to the branch that included potatoes (i.e., they were sister clades). Members of series *Etuberosa* formed a sister clade to the combined tomato and potato clade, showing a need to modify Hawkes's (1990) classification of section *Petota* to exclude series *Juglandifolia* and series *Etuberosa* (Figure 1.7).
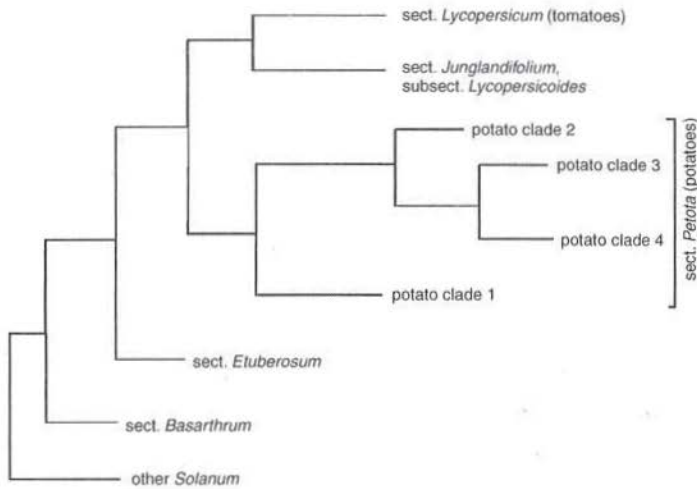
FIGURE 1.7. Cladogram of potato *(Solanum* section *Petota)* and immediate outgroups (see text).

On the basis of cpDNA and morphological data and a classification method that relied on phylogenetic relationships (cladistics, in contrast to phenetics), Spooner et al. (1993) placed tomatoes in the genus *Solanum* (not *Lycopersicon*), and Contreras and Spooner (1999) recognized Hawkes's series *Etuberosa* at the sectional level as section *Etuberosum* (Buk. and Kameraz) Child, at the same taxonomic rank as potatoes.

Recent molecular studies (Spooner et al., 1993; Olmstead and Palmer, 1997; Bohs and Olmstead, 2001; Bohs, 2005) have clarified the definition of *Solanum* and led to new insights into infrageneric classification. These studies established more natural groups, based on branches of a phylogenetic tree (monophyletic "clades") of *Solanum* that includes the previously segregate genera *Lycopersicon, Cyphomandra, Normania,* and *Triguera* (recognized as separate genera by D'Arcy and Hunziker). Bohs (2005) analyzed cpDNA sequence data from more than 100 species of *Solanum* representing the majority of infrageneric groups recognized by previous workers as well as a number of taxa thought to represent distinct clades based on morphology. She recognized 12 major clades within *Solanum,* gave

them unranked informal clade designations, and speculated on potential nonmolecular characters that might be used to identify the major clades. She placed potatoes in the "potato" clade that included tomatoes and their relatives, a treatment distinctly different from those of D'Arcy (1972, 1991) and Hunziker (2001) and providing a more natural classification.

RELATIONSHIPS WITHIN SOLANUM *SECTION* PETOTA

Wild potatoes constitute approximately 10 percent of the total species diversity of *Solanum*. Hosaka et al. (1984) analyzed 37 species of section *Petota*, including members of section *Etuberosum* and tomatoes. They used cpDNA, digested with eight endonucleases, and analyzed the data by comparing the banding patterns of the entire cpDNA molecule. They interpreted four clades: (1) the South American species, Mexican polyploids, and *S. verrucosum;* (2) the Mexican diploids (including *S. bulbocastanum* and *S. cardiophyllum*); (3) *S. etuberosum* (section *Etuberosum*); and (4) tomatoes. (The authors of potato species are mentioned in Table 1.A1 at the end this chapter.)

This cpDNA study was extended by Spooner and Sytsma (1992) and Spooner and Castillo (1997). They used 19 cloned cpDNA probes and 22 restriction endonucleases with 86 species representing 17 of the 19 tuber-bearing series of Hawkes (1990; germplasm of series *Cuneoalata* Hawkes and *Olmosiana* Ochoa was not available). These studies defined four exclusively tuber-bearing clades in section *Petota:* (1) the U.S., Mexican, and Central American diploid species, exclusive of *S. bulbocastanum, S. cardiophyllum,* and *S. verrucosum;* (2) *S. bulbocastanum,* and *S. cardiophyllum;* (3) all examined members of the South American series *Piurana* and some South American species classified to other series; and (4) all remaining South American species and the U.S., Mexican, and Central American polyploid species (Figure 1.7). These studies redefined our understanding of outgroup relationships through the definition of *S. bulbocastanum* and *S. cardiophyllum* as a distinct clade and by the definition of a distinct *Piurana* clade.

The separation of *S. bulbocastanum* and *S. cardiophyllum* (clade 2) from the other species of clade 1 was unexpected based on all prior

taxonomic interpretations. Rodríguez and Spooner (1997) studied many accessions of all subspecies of these two species and showed that *S. cardiophyllum* subsp. *ehrenbergii* fell in clade 1, while all other subspecies fell in clade 2. These results suggested mis-classification of subspecies *ehrenbergii* or introgressive hybridiza-tion with members of this clade. Spooner et al. (2004) used these results to justify separate species status for *S. cardiophyllum* subsp. *ehrenbergii* (Tables 1.1 and 1.A1). Because cpDNA is predominately or entirely maternally inherited in *Solanum* (Corriveau and Coleman, 1988), the interpretation of cpDNA "gene trees" into "species trees" awaits confirmation from biparentally inherited nuclear markers (Wendel and Doyle, 1998).

Nuclear markers were used for phylogenetic reconstruction in sec-tion *Petota* by Debener et al. (1990; nuclear restriction fragment length polymorphisms [RFLPs]), Bonierbale et al. (1990; nuclear RFLPs), Kardolus et al. (1998; amplified fragment length poly-morphisms [AFLPs] that included nuclear and organellar markers), and Volkov et al. (2003; external transcribed spacer regions of ribo-somal DNA). The first three studies corroborated the cpDNA studies above in placing the outgroups (*Etuberosa* and/or tomatoes) sister to the Mexican diploids but did not include representatives of cpDNA clade 2 *(S. bulbocastanum* and *S. cardiophyllum)* or clade 3 (series *Piurana* clade) to corroborate the cpDNA results. Volkov et al. (2003) included representatives *S. bulbocastanum* of clade 2 but not *S. cardiophyllum* subsp. *cardiophyllum* to address this relationship, and they did not include members of clade 3. Their results failed to support section *Etuberosum* as an outgroup. The results of Bonierbale et al. (1990) and Volkov et al. (2003) are significant in that unlike the cpDNA results, they grouped a representative of series *Circaeifolia* sister to the Mexican diploids found in clade 1, not with members of clade 4 as expected. Species in series *Circaeifolia* are atypical in that they are South American species with white stellate corollas like the Mexican diploid species. This striking discordance of organellar and nuclear datasets is well documented in other groups (Rieseberg and Soltis, 1991) and suggests a history of hybridization in the evolution of this species. Clearly, a well-supported phylogeny

TABLE 1.1. New determinations of synonymy, new combinations, and newly res-urrected names in wild and cultivated potato species *(Solanum* section *Petota)* subsequent to Hijmans and Spooner (2001).

Huamán and Spooner (2002)

Solanum tuberosum L.

  S. ajanhuiri Juz. and Bukasov (Ajanhuiri Group, diploid)

  S. chaucha Juz. and Bukasov (Chaucha Group, triploid)

  S. curtilobum Juz. and Bukasov (Curtilobum Group, pentaploid)

  S. juzepczukii Bukasov (Juzepczukii Group, triploid)

  S. phureja Juz. and Bukasov

    subsp. *hygrothermicum* (not understood well enough yet to assign to a Group)

    subsp. *phureja* (Phureja Group, diploid)

  S. stenotomum Juz. and Bukasov

    subsp. *goniocalyx* (Juz. and Bukasov) Hawkes (Stenotomum Group, diploid)

    subsp. *stenotomum* (Stenotomum Group, diploid)

  S. tuberosum L.

    subsp. *andigenum* (Juz. and Bukasov) Hawkes (Andigenum Group, tetraploid)

    subsp. *tuberosum* (Chilotanum Group—the Chilean land races only; the modern cultivars have yet to be assigned Groups, tetraploid)

Spooner et al. (2004)

S. bulbocastanum

  S. bulbocastanum subsp. *bulbocastanum*

  S. bulbocastanum subsp. *dolichophyllum* (Bitter) Hawkes

  S. bulbocastanum subsp. *partitum* (Correll) Hawkes

S. cardiophyllum Bitter

  S. cardiophyllum subsp. *cardiophyllum*

  S. cardiophyllum subsp. *lanceolatum* (P. Berthault) Bitter

S. demissum Lindley

  S. ×*semidemissum* Juz.

S. ×*edinense* P. Berthault

  S. edinense subsp. *edinense* Hawkes

  S. edinense subsp. *salamanii* (Hawkes) Hawkes

S. ehrenbergii (Bitter) Rydberg

  S. cardiophyllum subsp. *ehrenbergii* Bitter

S. hjertingii Hawkes

  S. hjertingii var. *hjertingii*

  S. fendleri var. *physaloides* Correll

  S. matehualae Hjerting & T. R. Tarn

TABLE 1.1 *(continued)*

S. iopetalum (Bitter) Hawkes
   S. brachycarpum (Correll) Correll
S. stenophyllidium Bitter
   S. brachistotrichium (Bitter) Rydberg
   S. nayaritense (Bitter) Rydberg
S. stoloniferum
   S. fendleri A. Gray
     S. fendleri subsp. *arizonicum* Hawkes
     S. fendleri subsp. *fendleri*
   S. leptosepalum Correll
   S. papita Rydberg
   S. polytrichon Rydberg
   S. stoloniferum subsp. *moreliae* Hawkes
   S. stoloniferum subsp. *stoloniferum*
S. verrucosum Schlechtendal
   S. macropilosum Correll

Note: The listed name is the new one proposed by the authors in the heading, and the indented names are the old, superseded (synonymized) taxa.

of section *Petota* awaits the use of more classes of molecular markers and further morphological studies with a wider range of species.

TAXONOMY OF SECTION PETOTA

Taxonomic research is partly justified on its ability to be used as a predictive tool (Rollins, 1965; Daly et al., 2001). For plant breeders, prediction means that germplasm can be chosen or avoided based on the past positive or negative evaluations of related species. Germplasm evaluations for resistance or agronomic traits, organized taxonomically, are common in the literature. For example, species-specific statements about the breeding value of wild potato germplasm are found in Ross (1986), Hawkes (1990), and Ruiz de Galerreta et al. (1998). Clearly, not all accessions of a species will share all traits, but when one lacks prior evaluation data, taxonomy should provide a useful guide for making inferences about unevaluated germplasm based on

present knowledge. For this reason, potato has been the subject of intensive taxonomic research.

The taxonomy of wild and cultivated potatoes continues to be notoriously difficult. Many potato species, sometimes even those that look very different, maintain the ability to hybridize when they come into contact, which further blurs species boundaries. In addition, different taxonomists have applied different taxonomic concepts to recognize and to group species (Spooner and Van den Berg, 1992a). Most accepted species are distinguished from similar ones by a "polythetic morphological species concept"; that is, species are defined by the greatest number of shared features, no single one of which is essential for group membership or sufficient to make an organism a member of a group (Stuessy, 1990). Stated otherwise, species are distinguished only by a complex of morphological features, all or most of which overlap in extent with other species. A wide range of molecular markers continue to be applied to questions of the validity and interrelationships of potato species, and their taxonomic interpretation surely will be modified.

Taxonomic changes of wild and cultivated potatoes are the subject of a continuing series of reviews (Grun, 1990; Spooner and Van den Berg, 1992a; Hawkes, 1997; Hijmans and Spooner, 2001). The last review (Hijmans and Spooner, 2001) updated the taxonomy of Hawkes (1990) through publications from the period 1990-2000. The present review updates Hijmans and Spooner (2001) through changes in the taxonomy of the cultivated species by Huamán and Spooner (2002) and changes in the taxonomy of the North and Central American species by Spooner et al. (2004). Relative to the account in Spooner and Hijmans (2001), the papers by Huamán and Spooner (2002) and Spooner et al. (2004) account for a net loss of 6 species and 6 subspecies for the cultivated potatoes and 9 species, 12 subspecies, and 2 varieties for the wild species. Updated species diversity estimates are 188 wild and 1 cultivated species for section *Petota,* plus 3 species in section *Etuberosa.* The present review also provides speculation on future taxonomic changes through literature research and field collections. Species in Table 1.A1 are indicated as "stable" (likely to be maintained by future work) or placed into groups where future work is needed.

Descriptions of the groups mentioned in Table 1.A1 follow. Because of unresolved questions, and because of the many species involved, designation of species in Table 1.A1 as *S. brevicaule* complex north or south, series *Conicibaccata*, or series *Piurana* is based on the publications mentioned here. For the species not yet studied in these publications, designation of a species to a group is based on speculation from original species descriptions, the excellent descriptions and illustrations in Ochoa (1999), or inferences based on geography for the *S. brevicaule* north and south subsets. Table 1.A1 is bibliographic in nature and should *not* be construed as final acceptance of names or groups, but rather as a working hypothesis. The series are used purely to connect these names to the literature; they do not imply acceptance of these ranks.

Solanum brevicaule *Complex*

The *S. brevicaule* complex represents a group of approximately 20 morphologically similar species, distributed from the south of Peru to Argentina, that are difficult to distinguish from some land races of *S. tuberosum*. All members of the *S. brevicaule* complex

1. have pinnately dissected leaves
2. have round fruits
3. have rotate to rotate-pentagonal corollas
4. are largely sexually compatible
5. are hypothesized to form occasional natural hybrid swarms
6. have endosperm balance numbers (a phenomenon of sexual compatibility based on ratios of maternal/paternal genomes in the endosperm) matching their ploidy levels
7. are frequently confused in the literature, herbarium, and germplasm collections regarding identifications

They vary in ploidy from diploid ($2n = 2x = 24$), through tetraploid ($2n = 4x = 48$), to hexaploid ($2n = 6x = 72$) (Van den Berg et al., 1998).

The species boundaries were studied using morphological phenetics by Van den Berg et al. (1998), and species boundaries and

relationships with molecular marker data by Miller and Spooner (1999). All data were concordant in showing the following:

1. No species-specific morphological characters existed, and any species that may be valid would be distinguished only by use of a complex of widely overlapping traits (polythetic support).
2. At best, two "species" were defined with a north-south geographical partitioning, one from Peru and northwestern Bolivia and another from northwestern Bolivia to northern Argentina. AFLP data (Kardolus et al., 1998; Spooner et al., 2005) further confirmed the north-south split of the two geographical groups of the *S. brevicaule* complex.
3. Within these two geographical groups were contained morphologically distinct species that were not previously considered to be part of the complex, suggesting that the complex was "unnatural" in a taxonomic philosophy that relied on relationships to define and group species.
4. Morphological similarity was not always a good indicator of phylogenetic relationships.
5. The cultivated accessions fell into the north *S. brevicaule* clade.

These results suggest that some of the species in the complex will eventually be placed into synonymy, further reducing the number of names in sect. *Petota*.

Solanum *Series* Circaeifolia

Solanum series *Circaeifolia* has been treated as containing three species and two subspecies (Hawkes, 1990) or two species and two subspecies (Ochoa, 1990). Despite this confusion at the species and subspecies level, all taxa in series *Circaeifolia* are clearly related based on morphological and molecular data. All species of the series have white stellate corollas, entire to little-dissected leaves, and narrow elliptic-lanceolate fruits unlike any other in section *Petota*. Van den Berg and Groendijk-Wilders (1999) analyzed morphological phenetics for the four taxa of series *Circaeifolia* and showed difficulty in distinguishing *S. capsicibaccatum* and *S. circaeifolium* subsp. *quimense*. Van den Berg et al. (2001), however, showed that all

four taxa of this series were well distinguished by AFLP data, suggesting that the taxa were valid at some rank (species or subspecies). Further studies are needed to resolve these discrepancies and make final decisions on the species status.

Solanum *Series* Conicibaccata

Many species of *Solanum* series *Conicibaccata* usually are easily grouped morphologically by leaves with a somewhat parallel-sided morphology and narrowly ovate to elliptical leaflets (Figure 1.3B) and by conical fruits (Figure 1.5D). Most grow in rich organic soil of rain forests. However, the leaf and fruit characters are not consistently distinctive as the leaf morphology can intergrade with those of members from other groups. Some members of the series have fruits only slightly elongate (elliptical), and some apparently unrelated species also have conical fruits (e.g., *S. hintonii, S. iopetalum*).

Castillo and Spooner (1997) examined species status and phylogenetic relationships of 23 out of 40 species of series *Conicibaccata* (as determined by Hawkes, 1990) using cpDNA restriction site variation and morphology. The results defined three main groups within the series: (1) polyploids from central Mexico to southern Ecuador, (2) diploids from northern Peru to Bolivia, and (3) diploids and tetraploids cladistically related to members of series *Piurana* and suggesting misclassification in series *Conicibaccata*. Some species within these ploidy groups were not clearly distinct from others within the group based on morphology. These results suggest that either prior designations of the series were not correct or some species may have to be regarded as synonymous.

Solanum *Series* Piurana

Solanum series *Piurana* includes 15 species, distributed from southern Ecuador to central Peru (Hawkes, 1990). It contains some of the morphologically most diverse species in section *Petota,* but what constitutes a species remains controversial. The most distinctive features of series *Piurana,* used by all major taxonomists of section *Petota* (Correll, 1962; Hawkes, 1990; Ochoa, 1999), are the combination of globose to ovoid fruits and coriaceous glossy leaves.

The problem is that this fruit shape and coriaceous and shiny leaves are present in species placed in other series, and it is difficult to clearly decide what to include in series *Piurana*. All of the above authors have expressed doubt as to the limits of the series, but perhaps the clearest statement of this difficulty was made by Correll (1962, p. 139): "This series, more than any of the others, may be considered a catchall. Paradoxically, its component species are held together not so much by their similarity as by their differences."

The cpDNA restriction site phylogenetic studies of section *Petota* by Spooner and Castillo (1997) and Castillo and Spooner (1997) defined only four clades, with all members of series *Piurana* in a well-defined clade (Figure 1.7, but this clade also included species placed in series *Conicibaccata, Megistacroloba, Yungasensia,* and *Tuberosa*). Field studies in Peru (Salas et al., 2001), combined with insights into tuber morphology from Ochoa (1999), suggested a third character defining the series: many members possess "moniliform" tubers, or tubers arranged like beads along the stolons, unlike the more typical arrangement of single tubers placed at stolon ends. However, this trait is present in some species in series *Conicibaccata* (e.g., *S. irosinum*), so even this trait is difficult to use to absolutely define series.

TAXONOMY OF CULTIVATED POTATO

Hawkes (1990) recognized seven cultivated species and seven subspecies: *S. ajanhuiri, S. chaucha, S. curtilobum, S. juzepczukii, S. phureja* subsp. *phureja, S. phureja* subsp. *estradae, S. phureja* subsp. *hygrothermicum, S. stenotomum* subsp. *stenotomum, S. stenotomum* subsp. *goniocalyx, S. tuberosum* subsp. *andigenum,* and *S. tuberosum* subsp. *tuberosum.* However, this seven cultivated species taxonomy is not universally accepted (Spooner and Van den Berg, 1992a). For example, the Russian potato taxonomists Bukasov (1971) and Lechnovich (1971) recognized 21 species, including separate species status for *S. tuberosum* subsp. *andigenum* (as *S. andigenum* Juz. and Bukasov) and subsp. *tuberosum* (as *S. tuberosum*). Ochoa (1990, 1999) recognized nine species and 141

infraspecific taxa (subspecies, varieties, and forms, including his unlisted autonyms) for the Bolivian cultivated species alone.

Dodds (1962) had a radically different view of cultivated potato taxonomy. He contended that the morphological characters used by Hawkes (1956) to separate the cultivated species exaggerated the consistency of qualitative and quantitative characters. He also showed that Andean farmers grow land races of all ploidy levels together in the same field and that these can all potentially hybridize. He showed no genetic differentiation of the cultivated diploids (Dodds and Paxman, 1962). In contrast to the above treatments of potatoes as distinct "species," named by nomenclature rules governed by the International Code of Botanical Nomenclature (ICBN; Greuter et al., 2000), Dodds (1962) treated the cultivated species as three species, *S.* ×*curtilobum, S.* ×*juzepczukii,* and *S. tuberosum,* with five "Groups" recognized in the latter. Groups are taxonomic categories used by the International Code of Nomenclature for Cultivated Plants (ICNCP; Brickell et al., 2004) solely to associate cultivated plants with traits that are of use to agriculturists, not to group phylogenetically related organisms. The ICNCP recognizes the complex hybrid origins of most crops and focuses on a classification of convenience to users and the nomenclature stability needed for trade (Hetterscheid and Brandenburg, 1995).

Huamán and Spooner (2002) studied morphological differences of all land race potato species (i.e., all cultivated potatoes except the modern cultivars) in a field plot in Peru. Their results showed some degree of morphological support for *S. ajanhuiri, S. chaucha, S. curtilobum, S. juzepczukii,* and *S. tuberosum* subsp. *tuberosum,* but little for *S. phureja* subsp. *phureja, S. stenotomum* subsp. *goniocalyx, S. stenotomum* subsp. *stenotomum,* and *S. tuberosum* subsp. *andigenum.* Most characters overlapped extensively with those of other species (polythetic support). These results led Huamán and Spooner (2002) to recognize all land race populations of cultivated potatoes as a single species, *S. tuberosum,* with the eight Groups: Ajanhuiri Group, Andigenum Group, Chaucha Group, Chilotanum Group, Curtilobum Group, Juzepczukii Group, Phureja Group, and Stenotomum Group.

Some phenetic support means that a reasonable argument could be made to recognize *S. ajanhuiri, S. chaucha, S. curtilobum, S. juzepczukii,* and *S. tuberosum* subsp. *tuberosum* as separate species or subspecies and all the other taxa as Groups under a separate cultivated species *S. andigenum*. Support for a separate taxon treatment was provided by Raker and Spooner (2002), who demonstrated that most of the land race populations of *S. tuberosum* subsp. *tuberosum* can be distinguished with microsatellite data from most populations of *S. tuberosum* subsp. *andigenum*, and we expect that molecular support will be provided for *S. ajanhuiri, S. curtilobum,* and *S. juzepczukii*. No final "correct" taxonomic treatment exists in such situations, and Huamán and Spooner (2002) used the Group classification for cultivated potatoes because of predominant polythetic morphological support, reticulate origins (Huamán et al., 1982, 1983; Schmiediche et al., 1982; Cribb and Hawkes, 1986; Hawkes, 1990), evolutionary dynamics or continuing hybridization, and their classification philosophy of the appropriateness of the ICNCP for cultivated species.

COLLECTION, CONSERVATION, AND USE OF GERMPLASM

Wild and cultivated potato genetic resources have proven value in breeding programs for disease resistance, environmental tolerances, and other agronomic traits of interest (Ross, 1986; Plaisted and Hoopes, 1989; Hawkes, 1990; Spooner and Bamberg, 1994; Ruiz de Galerreta et al., 1998; Jansky, 2000). Plaisted and Hoopes (1989) documented the parentage of North American cultivars, citing the importance of both wild species and the *S. tuberosum* Phureja Group, Andigenum Group, and Tuberosum Group. The following 14 wild species have entered into the parentage of European and North American cultivars: *S. acaule, S. chacoense, S. commersonii, S. demissum, S. kurtzianum, S. maglia, S. microdontum, S. raphanifolium, S. sparsipilum, S. spegazzinni, S. stoloniferum, S. megistacrolobum* subsp. *toralapanum, S. vernei,* and *S. verrucosum. Solanum demissum,* a hexaploid Mexican species with late blight resistance, has been most widely used, but the other wild species have conferred resistance to a variety of viral, fungal, and bacterial diseases as well as nematode and insect pests of potatoes. Wild species

and primitive cultivars have improved agronomic traits such as yield, specific gravity, chipping quality, and suppression of enzymatic browning. Current research is discovering the disease resistance and improved horticultural traits present in many other wild species, and this list is sure to increase.

The economic value of genetic resources has stimulated more than 40 potato-collecting expeditions over the past 40 years by various international organizations. Correll (1962), Hawkes and Hjerting (1969, 1989), Ochoa (1990), and Spooner et al. (2004) have summarized accounts of these potato collections. Further germplasm needs to be collected, particularly from Peru.

Seeds and tubers of these collections have been sent to potato genebanks worldwide. The major genebanks for potatoes are Instituto Nacional de Tecnología Agropecuaria, Balcarce, Argentina; Universidad Austral de Chile, Valdivia, Chile; Colección Central Colombiana, Bogotá, Colombia; Institüt fur Pflanzenbau und Pflanzenzüchtung, Germany; Landwirtschaftswissenschaften, Gross-Lüsewitz, Germany; International Potato Center, Lima, Peru; Commonwealth Potato Collection, Dundee, United Kingdom; The United States Potato Genebank, Sturgeon Bay, United States; and N.I. Vavilov Research Institute of Plant Industry, Leningrad, Russia (Hawkes, 1990). An intergenebank catalogue documents common and unique holdings of these collections (Huamán et al., 2000).

Most potato germplasm accessions are preserved as botanical seeds. Seeds are easier to maintain in a disease-free state, require less labor and materials for storage and shipping, contain greater genetic diversity, and have much greater longevity than vegetative propagules (tubers and in vitro shoot tips). Clonal stocks are maintained for collections that cannot be increased sexually, for cultivated collections where the genotype must be maintained, and for certain mapping populations.

In conclusion, wild and cultivated potatoes represent an amazing diversity of forms of great use for potato improvement. The taxonomy of wild and cultivated potatoes is complex, owing in part to the ability of many species to easily hybridize. Taxonomic research is continuing to refine our understanding of what constitutes a species and how these species are interrelated, to aid in the organization and planned use of these genetic resources by potato breeders.

TABLE 1.A1. Wild and cultivated potato species *(Solanum* section *Petota)* and wild species of close outgroup relatives in section *Etuberosa (S. etuberosum, S. fernandezianum, S. palustre).*

Taxon (putative hybrid origins)[a]	Code[b]	Country[c]	Ploidy and (EBN)[d]	Status of name[e]
Wild species				
Solanum acaule Bitter	acl	ARG, BOL, PER	4x (2EBN)	A
subsp. *acaule*				A
f. *acaule*				
f. *incuyo* Ochoa	inc	PER	4x	
subsp. *aemulans* (Bitter and Wittm.) Hawkes and Hjert.	aem	ARG	4x (2EBN)	A
subsp. *palmirense* J. Kardolus	pal	ECU	6x	A
subsp. *punae* (Juz.) Hawkes and Hjert.	pne	PER	4x (2EBN)	A
S. achacachense Cárdenas	ach	BOL	2x	B
S. acroglossum Juz.	acg	PER	2x (2EBN)	D
S. acroscopicum Ochoa	acs	PER	2x	B
S. agrimonifolium Rydb.	agf	GUA, HON, MEX	4x (2EBN)	E, H
S. alandiae Cárdenas	aln	BOL	2x	
S. albicans (Ochoa) Ochoa	alb	ECU, PER	6x (4EBN)	A
S. albornozii Correll	abz	ECU	2x (2EBN)	D
S. amayanum Ochoa	amy	PER	2x (2EBN)	B
S. ambosinum Ochoa	amb	PER	2x (2EBN)	B
S. anamatophilum Ochoa	amp	PER	2x (2EBN)	D
S. ancophilum (Correll) Ochoa	acp	PER	2x (2EBN)	I
S. ancoripae Ochoa	anp	PER	2n	B
S. andreanum Baker	adr	COL, ECU	2x (2EBN)	D
S. × *arahuayum* Ochoa (med × wtm)	ara	PER	2x	
S. ariduphilum Ochoa	adp	PER	2x (2EBN)	D
S. arnezii Cárdenas	arz	BOL		
S. augustii Ochoa	agu	PER	2x (1EBN)	D
S. avilesii Hawkes and Hjert.	avl	BOL	2x	C
S. ayacuchense Ochoa	ayc	*PER*	*2x (2EBN)*	E
S. aymaraesense Ochoa	aym	PER	2x	B
S. berthaultii Hawkes	ber	BOL	2x (2EBN)	F
S. bill-hookeri Ochoa	bhk	PER	2x	B
S. × *blanco-galdosii* Ochoa (amp × plq)	blg	PER	2x (2EBN)	D

TABLE 1.A1 *(continued)*

Taxon (putative hybrid origins)[a]	Code[b]	Country[c]	Ploidy and (EBN)[d]	Status of name[e]
S. boliviense Dunal	blv	BOL	2*x* (2EBN)	G
subsp. *astleyi* (Hawkes and Hjert.) D. M. Spooner, M. Ugarte, and P. M. Skroch	ast	BOL	2*x* (2EBN)	G
subsp. *boliviense*				G
S. bombycinum Ochoa	bmb	BOL	4*x*	E
S. brevicaule Bitter	brc	BOL	2*x* (2EBN)	C
S. ×*bruecheri* Correll (*S. gourlayi* [= lph by Ochoa, 1990] × inf)	bru	ARG		
S. buesii Vargas	bue	PER	2*x* (2EBN)	E
S. bukasovii Juz.	buk	PER	2*x* (2EBN)	B
f. *bukasovii*				B
f. *multidissectum* (Hawkes) Ochoa	mlt	PER	2*x* (2EBN)	B
S. bulbocastanum Dunal	blb	MEX, GUA, HON	2*x* (1EBN)	H
S. burkartii Ochoa	brk	PER	2*x*	E
S. burtonii Ochoa	brt	ECU	3*x*	
S. cajamarquense Ochoa	cjm	PER	2*x* (1EBN)	D
S. calacalinum Ochoa	cln	ECU	2*x*	E
S. calvescens Bitter	clv	BRA	3*x*	
S. candolleanum P. Berthault	cnd	BOL, PER	2*x* (2EBN)	C
S. cantense Ochoa	cnt	PER	2*x* (2EBN)	D
S. cardiophyllum Lindl.	cph	MEX	2*x* (1EBN), 3*x*	H
S. chacoense Bitter	chc	ARG, BOL, PAR, URU	2*x* (2EBN)	I (species only)
subsp. *chacoense*	chc			
subsp. *muelleri* (Bitter) Hawkes and Hjert.	mue	ARG, BRA	2*x* (2EBN)	
S. chancayense Ochoa	chn	PER	2*x* (1EBN)	D
S. chilliasense Ochoa	chl	ECU	2*x* (2EBN)	D
S. chillonanum Ochoa	chi	PER	2*x*	B
S. chiquidenum Ochoa	chq	PER	2*x* (2EBN)	D
var. *chiquidenum*	chq	PER		D
f. *amazonense* Ochoa	ama	PER	2*x*	D
f. *chiquidenum*	chq			D
var. *gracile* Ochoa	gra	PER	2*x*	D

TABLE 1.A1 *(continued)*

Taxon (putative hybrid origins)[a]	Code[b]	Country[c]	Ploidy and (EBN)[d]	Status of name[e]
var. *robustum* Ochoa	rob	PER	2x	D
S. chomatophilum Bitter	chm			D (species only)
var. *chomatophilum*	chm	ECU, PER	2x (2EBN)	
f. *angustifolium* Correll	ang	ECU		
f. *chomatophilum*	chm	PER		
f. *sausianense* Ochoa	sau	PER		
var. *subnivale* Ochoa	sbn	PER	2x	
S. circaeifolium Bitter	crc	BOL	2x (1EBN)	J
var. *capsicibaccatum* (Cárdenas) Ochoa	cap	BOL	2x (1EBN)	J
var. *circaeifolium*	crc			J
S. clarum Correll	clr	MEX, GUA	2x	H
S. coelestipetalum Vargas	cop	PER	2x (2EBN)	B
S. colombianum Bitter	col	COL, ECU, VEN	4x (2EBN)	E
S. commersonii Dunal	cmm	ARG, BRA, URU	2x (1EBN)	I (species only)
subsp. *commersonii*	cmm			
subsp. *malmeanum* (Bitter) Hawkes and Hjert.	mlm	ARG, BRA, PAR, URU	2x (1EBN)	
S. contumazaense Ochoa	ctz		2x (2EBN)	
S. demissum Lindl.	dms	GUA, MEX	6x (4EBN)	H
S. × *doddsii* Correll (aln × chc)	dds	BOL	2x (2EBN)	
S. dolichocremastrum Bitter	dcm	PER	2x (1EBN)	D?
S. donachui (Ochoa) Ochoa	dnc	COL		E
S. × *edinense* P. Berthault	edn	MEX	5x	H
S. ehrenbergii (Bitter) Rydb.	ehr	MEX	2x (1EBN)	H
S. etuberosum Lindl.	etb	CHL	2x (1EBN)	K
S. fernandezianum Phil.	frn	CHL	2x (1EBN)	K
S. flahaultii Bitter	flh	COL	4x	E
S. flavoviridens Ochoa	flv	BOL		
S. gandarillasii Cárdenas	gnd	BOL	2x (2EBN)	I
S. garcia-barrigae Ochoa	gab	COL		E
S. gracilifrons Bitter	grc	PER	2x	
S. guerreroense Correll	grr	MEX	6x (4EBN)	H
S. guzmanguense Whalen and Sagást.	gzm	PER	2x (1EBN)	I
S. hastiforme Correll	hsf	PER	2x (2EBN)	I
S. hintonii Correll	hnt	MEX		H
S. hjertingii Hawkes	hjt	MEX	4x (2EBN)	H

TABLE 1.A1 *(continued)*

Taxon (putative hybrid origins)[a]	Code[b]	Country[c]	Ploidy and (EBN)[d]	Status of name[e]
S. hoopesii Hawkes and K. A. Okada	hps	BOL	4*x*	C
S. hougasii Correll	hou	MEX	6*x* (4EBN)	H
S. huancabambense Ochoa	hcb	PER	2*x* (2EBN)	
S. huancavelicae Ochoa	hcv	PER	2*x* (2EBN)	B
S. huarochiriense Ochoa	hro	PER	2*x* (2EBN)	D
S. humectophilum Ochoa	hmp	PER	2*x* (1EBN)	D
S. hypacrarthrum Bitter	hcr	PER	2*x* (1EBN)	D
S. immite Dunal	imt	PER	2*x* (1EBN), 3*x*	D
var. *immite*				
var. *vernale* Correll	vrl	PER		
S. incahuasinum Ochoa	inh	PER	2*x* (1EBN)	
S. incamayoense K. A. Okada and A. M. Clausen	inm	ARG	2*x*	C
S. incasicum Ochoa	ins	PER	2*x* (2EBN)	I
S. ×indunii K. A. Okada and A. M. Clausen (acl × mga)	ind	ARG	36	
S. infundibuliforme Phil.	ifd	ARG, BOL	2*x* (2EBN)	I
S. ingifolium Ochoa	igf	PER	2*x* (1EBN)	D?
S. iopetalum (Bitter) Hawkes	iop	MEX	6*x* (4EBN)	H
S. irosinum Ochoa	irs	PER	2*x* (2EBN)	D or E
var. *irosinum*	irs			
var. *tarrosum* Ochoa	trr	PER	2*x*	
S. jaenense Ochoa	jnn	PER	6*x* (4EBN)	D or E
S. jalcae Ochoa	jlc	PER	2*x* (2EBN)	D
var. *jalcae*				
var. *pubescens* Correll	pub	PER		
S. jamesii Torr.	jam	MEX, USA	2*x* (1EBN)	H
S. kurtzianum Bitter and Wittm.	ktz	ARG	2*x* (2EBN)	I
S. laxissimum Bitter	lxs	PER	2*x* (2EBN)	E
S. leptophyes Bitter	lph	BOL, PER	2*x* (2EBN) 4*x* (4EBN)	C
S. lesteri Hawkes and Hjert.	les	MEX	2*x*	H
S. lignicaule Vargas	lgl	PER	2*x* (1EBN)	I
S. limbaniense Ochoa	lmb	PER	2*x* (2EBN)	E
S. ×litusinum Ochoa (ber × tar)	lit	BOL	2*x* (2EBN)	F
S. lobbianum Bitter	lbb	COL	4*x* (2EBN)	E
S. longiconicum Bitter	lgc	CRI, PAN	4*x*	E, H
S. longiusculus Ochoa	lgs	PER	2*x*	B
S. lopez-camarenae Ochoa	lpc	PER	2*x* (1EBN)	D
S. maglia Schltdl.	mag	CHL	2*x*, 3*x*	I

TABLE 1.A1 *(continued)*

Taxon (putative hybrid origins)[a]	Code[b]	Country[c]	Ploidy and (EBN)[d]	Status of name[e]
S. marinasense Vargas	mrn	PER	2x (2EBN)	B
S. medians Bitter	med	PER	2x (2EBN), 3x	I (species only)
var. *autumnale* Correll	aut	PER	2x (2EBN)	
var. *medians*	med	PER		
S. megistacrolobum Bitter	mga	ARG, PER, BOL	2x (2EBN)	L
subsp. *megistacrolobum*	mga			L
f. *megistacrolobum*	mga			
f. *purpureum* Ochoa	prp	PER	2x	
subsp. *toralapanum* (Cárdenas and Hawkes) R. B. Giannattasio and D. M. Spooner	tor	ARG, PER, BOL	2x (2EBN)	L
S. ×*michoacanum* (Bitter) Rydb. (blb × pnt)	mch	MEX	2x	H
S. microdontum Bitter	mcd	ARG, BOL	2x (2EBN), 3x	M (species only)
var. *microdontum*	mcd			
var. *montepuncoense* Ochoa (mcd × vio)	mon	BOL	2x	
S. minutifoliolum Correll	min	ECU	2x (1EBN)	I
S. mochiquense Ochoa	mcq	PER	2x (1EBN)	I
S. morelliforme Bitter and G. Muench	mrl	MEX, GUA, HON	2x	H
S. moscopanum Hawkes	msp	COL	6x (4EBN)	E
S. multiinterruptum Bitter	mtp	PER	2x (2EBN)	B
var. *machaytambinum* Ochoa	mac	PER		
var. *multiinterruptum*	mtp			
f. *albiflorum* Ochoa	alf	PER	2x	
f. *multiinterruptum*	mtp			
S. nemorosum Ochoa	nmr	PER	6x (4EBN)	E
S. neocardenasii Hawkes and Hjert.	ncd	BOL	2x	I
S. neorosii Hawkes and Hjert.	nrs	ARG	2x	
S. neovalenzuelae L. López	nvz	COL	4x	E
S. neovargasii Ochoa	nvg	PER	2x	
S. neovavilovii Ochoa	nvv	PER	2x (2EBN)	
S. ×*neoweberbaueri* Wittm. (med × chc)	nwb	PER	3x	
S. nubicola Ochoa	nub	PER	4x (2EBN)	E
S. okadae Hawkes and Hjert.	oka	ARG, BOL	2x	C
S. olmosense Ochoa	olm	ECU, PER	2x (2EBN)	D?

TABLE 1.A1 *(continued)*

Taxon (putative hybrid origins)[a]	Code[b]	Country[c]	Ploidy and (EBN)[d]	Status of name[e]
S. oplocense Hawkes	opl	ARG, BOL	2x (2EBN) 4x (4EBN) 6x (4EBN)	N
S. orocense Ochoa	oro	COL		E
S. orophilum Correll	orp	PER	2x (2EBN)	B
S. ortegae Ochoa	ort	PER	2x	B
S. otites Dunal	oti	COL, VEN		E
S. oxycarpum Schiede	oxc	MEX	4x (2EBN)	E, H
S. palustre Poepp.	pls	ARG, CHL	2x (1EBN)	K
S. pampasense Hawkes	pam	PER	2x (2EBN)	B
S. pamplonense L. López	ppl	COL	4x	E
S. pascoense Ochoa	psc	PER	2x	D
S. paucijugum Bitter	pcj	ECU	4x (2EBN)	D
S. paucissectum Ochoa	pcs	PER	2x (2EBN)	D
S. peloquinianum Ochoa	plq	PER	2x (2EBN)	D
S. pillahuatense Vargas	pll	PER	2x (2EBN)	E
S. pinnatisectum Dunal	pnt	MEX	2x (1EBN)	H
S. piurae Bitter	pur	PER	2x (2EBN)	D
S. polyadenium Greenm.	pld	MEX	2x	H
S. puchupuchense Ochoa	pch	BOL, PER	2x	B
S. raphanifolium Cárdenas and Hawkes	rap	PER	2x (2EBN)	O
S. raquialatum Ochoa	raq	PER	2x (1EBN)	D
S. ×rechei Hawkes and Hjert. (ktz × mcd)	rch	ARG	2x, 3x	P
S. regularifolium Correll	rgf	ECU	2x	
S. rhomboideilanceolatum Ochoa	rhl	PER	2x (2EBN)	
S. ×ruiz-lealii Brücher (chc × ktz)	rzl	ARG		
S. salasianum Ochoa	sls	PER	2x	E
S. ×sambucinum Rydb. (ehr × pnt)	smb	MEX	2x	H
S. sanctae-rosae Hawkes	sct	ARG	2x (2EBN)	I
S. sandemanii Hawkes	snd	PER	2x (2EBN)	I
S. santolallae Vargas	san	PER	2x (2EBN)	E
S. sarasarae Ochoa	srs	PER	2x (2EBN)	B
S. sawyeri Ochoa	swy	PER	2x (2EBN)	B
S. saxatilis Ochoa	sax	PER	2x (2EBN)	B
S. scabrifolium Ochoa	scb	PER	2x	
S. schenckii Bitter	snk	MEX	6x (4EBN)	H
S. ×setulosistylum Bitter (chc ×spg)	stl	ARG	2x	
S. simplicissimum Ochoa	smp	PER	2x (1EBN)	D

TABLE 1.A1 *(continued)*

Taxon (putative hybrid origins)[a]	Code[b]	Country[c]	Ploidy and (EBN)[d]	Status of name[e]
S. soestii Hawkes and Hjert.	sst	BOL	2x	J
S. sogarandinum Ochoa	sgr	PER	2x (2EBN)	I
S. solisii Hawkes	sol	ECU		D
S. sparsipilum (Bitter) Juz. and Bukasov	spl	BOL, PER	2x (2EBN)	C
S. spegazzinii Bitter	spg	ARG	2x (2EBN)	I
S. stenophyllidium Bitter	sph	MEX	2x (1EBN)	H
S. stoloniferum Schltdl. and Bouchet	sto	MEX, USA	4x (2EBN)	H
S. subpanduratum Ochoa	sup	VEN	4x	E
S. × *sucrense* Hawkes (adg × opl)	scr	BOL	4x (4EBN)	
S. sucubunense Ochoa	suc	COL		E
S. tacnaense Ochoa	tcn	PER	2x (2EBN)	
f. *decurrentialanum* (Ochoa) Correll	dec	PER	2x	
f. *tacnaense*	tcn			
S. tapojense Ochoa	tpj	PER	2x (2EBN)	B
S. tarapatanum Ochoa	trp	PER	2x	I
S. tarijense Hawkes	tar	ARG, BOL	2x (2EBN)	F
S. tarnii Hawkes and Hjert.	trn	MEX	2x	H
S. taulisense Ochoa	tau	PER	2x (2EBN)	
S. trifidum Correll	trf	MEX	2x (1EBN)	H
S. trinitense Ochoa	trt	PER	2x (1EBN)	I
S. tundalomense Ochoa	tnd	ECU	6x (4EBN)	E
S. tuquerrense Hawkes	tuq	COL, ECU	4x (2EBN)	D
S. ugentii Hawkes and K. A. Okada	ugt	BOL	4x	C
S. urubambae Juz.	uru	PER	2x (2EBN)	
f. *chakchabambense* Ochoa	chk	PER	2x	
f. *urubambae*				
f. *velutinum* (Correll) Ochoa	vel	PER		
S. × *vallis-mexici* Juz. (sto × ver)	vll	MEX	3x	H
S. velardei Ochoa	vlr	PER	2x	B
S. venturii Hawkes and Hjert.	vnt	ARG	2x (2EBN)	
S. vernei Bitter and Wittm.	vrn			I
subsp. *ballsii* (Hawkes) Hawkes and Hjert.	bal	ARG	2x (2EBN)	
subsp. *vernei*	vrn	ARG	2x (2EBN)	
S. verrucosum Schltdl.	ver		2x (2EBN)	H
S. vidaurrei Cárdenas	vid	ARG, BOL	2x (2EBN)	I
S. × *viirsoii* K. A. Okada and A. M. Clausen (acl × ifd)	vrs	ARG	3x	

TABLE 1.A1 *(continued)*

Taxon (putative hybrid origins)[a]	Code[b]	Country[c]	Ploidy and (EBN)[d]	Status of name[e]
S. violaceimarmoratum Bitter	vio	BOL	2x (2EBN)	
S. virgultorum (Bitter) Cárdenas and Hawkes	vrg	BOL	2x	
S. wittmackii Bitter	wtm	PER	2x (1EBN)	I
S. woodsonii Correll	wds	PAN		E, H
S. yamobambense Ochoa	ymb	PER	2x	D
S. yungasense Hawkes	yun	BOL, PER	2x (2EBN)	I
Cultivated species				
S. tuberosum L., a single cultivated species with eight Groups				
Ajanhuiri Group	ajh	BOL, PER	2x	
Andigenum Group	adg	widespread in the Andes	4x (4EBN)	
Chaucha Group	cha	BOL, PER	3x	
Chilotanum Group (the Chilean land races only; the modern cultivars traditionally classified as *S. tuberosum* subsp. *tuberosum* have yet to be assigned Groups)	chl	CHL	4x (4EBN)	
Curtilobum Group	cur	BOL, PER	4x (4EBN), most 5x	
Juzepczukii Group	juz	BOL, PER	3x	
Phureja Group	phu	widespread in the Andes	2x (2EBN)	
Stenotomum Group	stn	BOL, PER	2x (2EBN)	

Source: Based on Spooner and Hijmans (2001), with subsequent changes as outlined in Table 1.1.

Note: The country code, EBN, and ploidy are listed only at the species level in the case of autonyms.

[a]Author abbreviations are as standardized by Brummitt and Powell (1992). Putative hybrid origins are from Hawkes (1990) and from Ochoa (1999) for *S. ×arahuayum, S. ×blanco-galdosii,* and *S. ×neoweberbaueri.*

[b]Species and subspecies codes follow Spooner and Hijmans (2001).

[c]Country abbreviations are ARG, Argentina; BOL, Bolivia; BRA, Brazil; CHL, Chile; COL, Colombia; CRI, Costa Rica; ECU, Ecuador; GUA, Guatemala; HON, Honduras; MEX, Mexico; PAN, Panama; PER, Peru; URU, Uruguay; USA, United States; VEN, Venezuela.

[d]See Spooner and Hijmans (2001) for references to ploidy and EBN determinations.

[e]This column represents, through the publications cited below or through literature research, field collections, and our speculation, the future taxonomic status of most wild and cultivated species in this list. The status of some of these names will change in rank (from species to sub-

species or subspecies to species), or more likely some names will be placed in synonymy with other species. The status of some names is speculated to be stable; that is, they will remain as a good species (e.g., G, H, I, K, L, M, N, O, P). In other cases putative group relationships are provided (e.g., B, C, D, E, F, J), and some reductions in names within these groups is possible. For other names we do not know enough to speculate about species status or relationships and leave these cells empty.

A. The phenetic analysis of Kardolus (1999) suggested that these names are stable, although we find it very difficult to distinguish *S. acaule* subsp. *acaule* from subsp. *punae*, and subsp. *acaule* f. *incuyo* needs evaluation.
B. Possible member of *S. brevicaule* complex north (see text).
C. Possible member of *S. brevicaule* complex south (see text).
D. Possible member of *Solanum* series *Piurana* (see text).
E. Possible member of *Solanum* series *Conicibaccata* (see text).
F. The morphological phenetic analysis of Spooner and Van den Berg (1992b) suggests that the names *S. berthaultii*, *S. litusinum*, and *S. tarijense* may need to be combined into one.
G. The RAPD analysis of Spooner et al. (1997) suggests these names are stable.
H. Species from North and Central America have been well researched in different phenetic and molecular studies (Spooner and Hijmans, 2001), were recently documented in a monograph (Spooner et al., 2004) and are likely to remain stable.
I. A phenetically very distinctive species from South America that likely will remain as a good species.
J. Member of *Solanum* series *Circaeifolia* (see text).
K. The three species in *Solanum* section *Etuberosum* were studied using field and herbarium collections by Contreras and Spooner (1999) and likely will remain stable.
L. The two subspecies in *S. megistacrolobum* were studied using morphological and molecular marker data by Giannattasio and Spooner (1994a,b) and likely will remain stable.
M. The species *S. microdontum* was studied using morphological phenetics by Van den Berg and Spooner (1992) and likely will remain stable.
N. *Solanum oplocense* was shown to be a well-defined species using morphological phenetics by Van den Berg et al. (1998) and using molecular marker data by Miller and Spooner (1999), but it was not defined in the AFLP study of Spooner et al (2005).
O. *Solanum raphanifolium* is a phenetically well-defined species and well characterized by cpDNA data (Spooner et al., 1991; Spooner and Castillo, 1997) and likely will remain stable. Clausen and Spooner (1998) supported the orgin of *S.* × *rechi* from *S. kurtzianum* and *S. mlcrodontum*.
P. *Solanum* × *rechei* is of clear hybrid origin between *S. kurtzianum* and *S. microdontum* (Clausen and Spooner, 1998). Although it may be hard to distinguish from them it is clearly worthy of its hybrid designation and likely will remain stable.

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Chapter 2

Genetics of Agrihorticultural Traits

John E. Bradshaw

Today, potatoes are grown in 149 countries from latitudes 65°N to 47°S and from sea level to altitudes of approximately 4,000 m (Hijmans, 2001). Plant breeders are continuing their efforts for the better adaptation of the potato to a wide range of environments while seeking cultivars that meet current consumer preferences and the demanding quality requirements of processors and supermarkets. To achieve these goals, they need an increasing amount of genetic knowledge, as well as a wealth of germplasm and modern molecular breeding techniques.

Cultivated potato *Solanum tuberosum* L. is a tetraploid, displays tetrasomic inheritance, and comprises highly heterozygous individuals, which suffer inbreeding depression on selfing. Hence, in potato genetics, it has not been possible to achieve the same degree of sophistication as in the genetic analysis of crosses between true-breeding inbred lines that display disomic inheritance. In this chapter, genetic methods applicable to potato are briefly considered before reviewing the genetics of flowering, yield and its components, maturity, dormancy, tuber shape, eye depth, and pigmentation.

GENETIC METHODS

Traits are either qualitative or quantitative in nature. For qualitative traits (e.g., flower and tuber color and presence or absence of molecular markers), individuals can be classified into distinct categories and the number of individuals in each category can be counted. One can look for simple Mendelian ratios in order to understand the inheritance of the trait, whether in diploid or tetraploid potatoes. Furthermore, one can look for associations between traits and build up linkage maps of the underlying genes. For example, Jacobs et al. (1995) used a diploid backcross population to construct a genetic map of the 12 chromosomes of potato integrating molecular and classical markers. The total length of the combined female and male maps was 1120 cM.

For quantitative traits, measurements are made and individual genes cannot be recognized by Mendelian analysis because discrete classes cannot be discerned. Nevertheless, genetic information can be inferred from measurements on related individuals on the supposition of Mendelian inheritance. Biometrical methods have been developed and refined to undertake genetic analyses of quantitative traits (for potatoes see reviews by Bradshaw, 1994; Ortiz and Peloquin, 1994).

A statistically significant offspring-midparent regression is evidence of heritable variation, and the slope of the regression line is a measure of heritability. A detailed genetic analysis can be performed and an explanation of heritability provided when both full-sib and half-sib families (a group of full-sib families with a common parent) are produced in a hierarchical, factorial, or diallel set of crosses. Combining-ability analysis has become popular in both diploid and tetraploid potatoes because no random mating population in equilibrium has to be assumed. The general combining ability (GCA) of a parental clone provides an assessment of its genetic output, as judged by the mean performance of its progenies from crosses with other clones. In order to make valid inferences, these latter clones should be either all those of interest or a random sample of them. Two types of factorial crossing design are commonly used to determine combining abilities. In the first, one set of clones is crossed with another set

that complements it for desirable traits. In the second, a diallel set of crosses is made among clones showing a range of values for the trait(s) of interest. Where possible, reciprocal crosses should be made and, ideally, the subsequent progenies assessed in more than one environment in order to study genotype-environment interactions. The departure of a progeny mean from that expected on the basis of the GCAs of its parents is called specific combining ability (SCA). Hence, the progeny mean of the cross between parents i and j, as a departure from the population mean μ, is

$$\text{progeny}_{ij} - \mu = \text{GCA}_i + \text{GCA}_j + \text{SCA}_{ij}$$

The total genetic variation between families for a factorial design is

$$\sigma_G^2 = \sigma_{GCA}^2(\text{set 1}) + \sigma_{GCA}^2(\text{set 2}) + \sigma_{SCA}^2$$

and for a diallel design it is

$$\sigma_G^2 = 2\sigma_{GCA}^2 + \sigma_{SCA}^2$$

Should the parents come from a random mating population in equilibrium, the total genetic variation can be partitioned into uncorrelated components that are attributable to different causes and can be used to determine the covariance of relatives (FS: full-sib, HS: half-sib) and to predict the response to selection.

$$\sigma_{GCA}^2 = \text{cov(HS)}$$

$$\sigma_{SCA}^2 = \text{cov(FS)} - 2\,\text{cov(HS)}$$

In the absence of epistasis (non-allelic interactions)

In diploids: $\quad$ cov(HS) $\qquad\qquad\qquad = \tfrac{1}{4}\sigma_A^2$

$\qquad\qquad\qquad$ cov(FS) $- 2$ cov(HS) $= \tfrac{1}{4}\sigma_D^2$

$\qquad\qquad\qquad$ cov(parent-offspring) $= \tfrac{1}{2}\sigma_A^2$

In tetraploids: $\quad$ cov(HS) $\qquad\qquad\qquad = \tfrac{1}{4}\sigma_A^2 + \tfrac{1}{36}\sigma_D^2$

$$\text{cov(FS)} - 2 \text{ cov(HS)} = \tfrac{1}{6}\sigma_D^2 + \tfrac{1}{12}\sigma_T^2 + \tfrac{1}{36}\sigma_Q^2$$
$$\text{cov(parent-offspring)} = \tfrac{1}{2}\sigma_A^2 + \tfrac{1}{6}\sigma_D^2$$

where σ_A^2 and σ_D^2 are the additive and dominance (diallelic interactions) components of variance and σ_T^2 and σ_Q^2 are those for triallelic and tetra-allelic interactions in tetraploids. However, it must be remembered that we are dealing with gene and genotype frequencies in populations and that diallelic interactions (and triallelic and tetra-allelic ones in tetraploids) can contribute to the additive genetic variance. A few examples exist of variance component analysis in potato. Thompson and Mendoza (1984), for example, used 4cov(HS) and 6[cov(FS) − 2cov(HS)] to estimate $\sigma_A^2 + \tfrac{1}{9}\sigma_D^2$ and $\sigma_D^2 + \tfrac{1}{2}\sigma_T^2 + \tfrac{1}{6}\sigma_Q^2$, respectively, for 11 traits including yield in a heterogeneous potato population propagated from true seed. More recently, Ortiz and Golmirzaie (2002) compared hierarchical and factorial mating designs (also known as North Carolina mating designs I and II, respectively) for the quantitative genetic analysis of tuber yield in tetraploid potato. They recommended the hierarchical design because of the ease of generating the families and sampling a large number of parents, but they conceded that the design does not allow a direct and precise estimate of σ_D^2. A decrease in population mean on selfing is further evidence of nonadditive gene action, but the situation in tetraploids is more complex than that in diploids (Bradshaw, 1994).

Although biometrical genetic analyses provide valuable information about the variation present in a breeding program for traits displaying continuous variation, they do not provide any clues as to the number of genes segregating, their chromosomal locations, or the magnitude of their effects. More detailed genetic analyses of quantitative trait loci (QTLs) can now be performed through their linkage to molecular markers. A recent summary of the potato genetic maps developed using diploid populations and of the gene mapping and genetic analyses performed using molecular markers can be found in the review by Ortiz (1998). Schäfer-Pregl et al. (1996) developed a model for interval mapping of QTLs in offspring of noninbred diploid parents. Hackett et al. (2001) have published a method for QTL interval mapping in autotetraploid species for a full-sib family derived by crossing two parents. QTL mapping provides information on

the minimum number and approximate genomic positions of the factors controlling a quantitative trait but does not identify their molecular basis.

For quantitative and qualitative traits, the ultimate goal is to understand the gene function at the biochemical level and to know how this relates to the observed phenotype. Genetic and biochemical information is available on metabolic pathways for carbohydrates, anthocyanins, and carotenoids in potatoes. Candidate genes for QTLs can be postulated and hypotheses tested, as described in later sections of this chapter. Furthermore, large "gene catalogs" now exist for many species in the form of expressed sequence tag (EST) databases. An EST is a partial cDNA (complementary or copy DNA) molecule that has been sequenced. As the cDNA is synthesized from messenger RNA, an EST represents a gene being expressed in the target cells of interest. By 2005, there were 236,717 potato ESTs in GenBank (http://www.ncbi.nlm.nih.gov), a public database that includes potato and tomato. Their value will increase as they are located on physical maps, which in turn are integrated with genetic maps. Further, ESTs will be more useful as the extent of the colinearity of different genomes is established and exploited for comparative genomics, where known gene position and function in one genome are used to draw inferences for other genomes (e.g., from tomato to potato, pepper, and eggplant in the Solanaceae).

Finally, as the potato can be transformed with relative ease using *Agrobacterium*-mediated systems, the advent of "targeted" gene transfer technology has resulted in the use of transgenic potato to manipulate biochemical pathways by antisense suppression or by overexpression of key genes and to provide proof of function of cloned genes at the molecular level.

FLOWERING

Though breeding new cultivars and genetic experiments are both dependent upon making successful crosses, little is known about the genetics of flowering in potato. However, summaries of reproduction biology can be found in Tarn et al. (1992) and in Chapter 3 "Considerations for Successful Breeding."