Chapter 12
Solanum

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12.1 Basic Botany of the Genus *Solanum*

Solanum is a large genus of around 1,500 species with a near-cosmopolitan distribution, and although only one genus of around 90 genera in the Solanaceae family includes almost half of the species in the family. The Solanaceae family sits in the Euasterid I group alongside the Boraginaceae, the Lamiales (e.g., the Lamiaceae and the Oleaceae), and the Gentianales (e.g., Gentianaceae) (Angiosperm Phylogeny Group 2003; Haston et al. 2007). The centers of diversity for the genus are largely tropical, but the adaptability of the group is demonstrated by the occurrence of representatives in cold-temperate environments and at the altitudinal maximum for vegetation around 4,500 m in parts of the Andes for some tuber-bearing *Solanum* species (Hawkes 1990). Life forms in the genus vary from small, high-altitude, rosette-forming species to rambling lianes, arboreal epiphytes, and bushy and woody perennial forms. South America hosts around one third of the worldwide total species in the genus (Hunziker 1979). In a recent molecular phylogenetic study using three chloroplast genes, the established infrageneric structure was found to be inaccurate. It is now suggested that the genus comprises two large clades with around ten subclades, each with informal names pending further investigation (Weese and Bohs 2007).

Solanum species are generally pollinated by bees. Flowers are pentamerous and usually radially symmetrical but sometimes zygomorphic and without floral nectaries, thus providing only a pollen reward for pollinators. Although most members of the genus release pollen through a terminal pore, there are also longitudinal-dehiscent and intermediate types within the genus (García et al. 2008). Limited access to pollen in enclosed anthers is a feature of flowers adapted for buzz pollination by bee species capable of the appropriate behavior. In such flowers, bees access the pollen by vibration of the anther cone and the collection of the resultant flow of pollen from the pores. The robust anther cone associated with such a pollination syndrome appears, from study of the microstructure, to have evolved more than once in the genus (Glover et al. 2004). Corolla color varies from white to purple and occasionally yellow, often with prominent floral guides. Although white flowers are often associated with pollinators flying at night, in a study in a subtropical moist forest in Belize, several white-flowered species opened their flowers only in daylight hours, whereas some species with white or pigmented corollas flowered intermittently at any time (Smith and Knapp 2002).

The genus *Solanum* has contributed several crop species of global standing. The fourth crop in terms of global yield and the most important non-cereal food crop is the potato, *Solanum tuberosum* L. Additional species grown by man include the tomato (*S. lycopersicum* L., reviewed in a separate chapter), the eggplant, aubergine, or brinjal, (*Solanum melongena* L.), the nakati or Ethiopian eggplant (*S. aethiopicum* L.), the naranjilla (*S. quitoense* Lam.), and the invasive tropical shrub the Turkey berry or devil's fig (*Solanum torvum* Sw.).

The potato, as a staple foodstuff, is a crop that supported civilizations in South America over several millennia, rose to a similar status in the western fringes of Europe in the eighteenth and nineteenth centuries,

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and is now lauded as an answer to food insecurity and a means of meeting the Millennium Development Goals in a wide range of developing countries. The localized production and lack of trade as a global commodity insulates consumers of potato from the volatility of global markets, and instead makes price largely determined by local factors (Prakash 2008). Although the majority of production is now processed in North America and some European countries (Kirkman 2007), globally only around 15% of the crop is processed. In the last 20 years, production in the traditional main areas in Europe has suffered a gentle decline, but there has been a large increase in demand and production in Latin America, Africa and Asia, where China and India now produce more than one-third of the global harvest (FAOSTAT 2008).

The cultivated potato was domesticated by the tribes that preceded the Huari and Inca peoples around 8,000 years ago in South-Central Peru. The initial domestication was from species in the *Solanum bukasovii* Juz. complex (Spooner et al. 2005: see Sect. 12.3 for further details) suggesting that cultivation began at around 3,000–4,500 m asl. According to Hawkes (1990) the potato belongs to a group of over 220 tuber-bearing species from section Petota within the genus *Solanum*. Since its initial domestication, the potato has migrated both north and south in the Andes, moved to lower altitudes in the Andes, and found its way to coastal Chile where forms developed which were more suited to temperate agriculture. The initial introductions (of Andean stock) into Europe were made in the 1570s first reaching the Canary Isles. Subsequent spread took the potato as far as China in 1609 and finally the USA in 1719. Potatoes are now grown in 149 countries from latitudes 65°N to 50°S and at altitudes from sea level to over 4,000 m (Hijmans 2001).

The tomato (now *S. lycopersicum*) is also a major world crop with an origin in the Andes of South America (Jenkins 1948; Peralta and Spooner 2007). This crop and its wild relatives will be discussed elsewhere in this book series.

In the Old World, the genus *Solanum* has provided one major crop, the eggplant, aubergine or brinjal, *S. melongena*. This species grows as a perennial shrub a meter or so high in tropical regions, but as a crop in temperate zones it is grown as an annual. China produces more than half of the world harvest of eggplant ahead of India, Egypt and Turkey as other major producers. The main center of diversity of the eggplant is the Indian subcontinent and possibly other parts of Southeast Asia where an exceptionally wide range of fruit types can be found. Vavilov (1928) also considered India as the center of origin for the eggplant, with China as a later secondary center of diversity. Without archeological specimens to date the domestication of the crop, other means of dating domestication have been sought. Recent studies have suggested that the eggplant has been under selection in China since at least 59 BC (Wang et al. 2008). However *Sanskrit* documents take the recorded history of the crop back to at least 800 BC (Daunay and Janick 2007) by which time it was already a popular vegetable fruit in the Indian subcontinent. Most studies indicate that *S. incanum* L. or *S. insanum* L. is the wild progenitor of *S. melongena* (Behera et al. 2006) although an ultimate origin from *S. macrocarpon* L. in Africa cannot be ruled out. The history of the eggplant is further confused by the related African species *Solanum aethiopicum*, known as the Ethiopian eggplant or the nakati. This is a related fruit-bearing species, also used for leaf production to be cooked in a manner similar to spinach, and is thought to have originated from *Solanum anguivi* Lam. (Lester and Niakan 1986). There is a form of the species known as Gilo, now generally considered to be a cultivar group of *S. aethiopicum*. With additional molecular studies of the group, additional clarity on the interrelationships of these species may be forthcoming.

An additional New World *Solanum* species exploited by man is the naranjilla, *Solanum quitoense* Lam. This species is grown for its fruits and is found in Peru, southern Colombia and Ecuador and reaches 2.5 m high, forming a woody shrub when mature. It is found at altitudes between 1,200 and 1,800 m where it prefers humid environments and light shade. As with eggplant, the cultivated form has a greatly reduced complement of spines compared to the wild forms. A further shrubby fruit-bearing species originating in the Andes is *S. betaceum* Cav., until recently placed in the genus *Cyphomandra* (Bohs 1995). This species has entered international trade and is grown for export in Portugal and New Zealand, where it has recently been given the name the tamarillo for marketing purposes.

The basic chromosome number of $x = 12$ for the family is found in almost all *Solanum* species although a reduction to $x = 11$ has been reported for *S. mammosum* L. and *S. platense* Diekmann (Chiarini and

Bernardello 2006). Most species remain diploid, but there are both autopolyploid and allopolyploid species, including the most common form of the cultivated potato, *Solanum tuberosum* L. ($2n = 4x = 48$). Haploid genome sizes in the two major New World crops in the genus, potato and tomato, are 850 and 1,000 Mbp respectively, and the main Old World crop, the aubergine or egg plant, has a genome size of 1,100 Mbp (Arumuganathan and Earle 1991). These values are between six- and eight-fold greater than the *Arabidopsis* genome.

12.2 Conservation Initiatives

With most climate change scenarios predicting major disruption of food production in most regions in the middle decades of the twenty-first century, adapting crops to future climates and other changing pressures has never been more important. The store of diversity available for breeders in the genus *Solanum* is very extensive and represents a source of genes which could make a marked improvement to productivity in different environments and to the ability to resist the pressures from the rapidly changing ranges of pests and pathogens predicted under a changing climate.

A pressing threat to this adaptive and potentially valuable diversity in the wild relatives of *Solanum* crops comes from the habitat loss associated with the change of land use arising from population pressures. The IUCN Red Data list of species (IUCN 2009) includes 45 species from the genus *Solanum*, 11 of them already considered to be endangered or critically endangered. Although only one of the Red Data List *Solanum* species was a tuber-bearing relative of the potato, and it was categorized as of least concern, this masks a much broader concern about the sustainability of many wild potato populations. For example, Coca Morante et al. (2007) surveyed one of the great centers of diversity for tuber-bearing wild potato species, the Department of La Paz, Bolivia (Knapp 2002). In the five provinces in the north of the department visited during the study, habitat loss by encroaching agriculture and direct damage by pests and pathogens from that agriculture such as *Premnotrypes* sp. and *Phytophthora infestans* were threatening populations of wild species and it was considered that the local endemic wild potato species *S. achacachense* Cárd. was now in danger of extinction. Many of the high altitude tuber-bearing *Solanum* species live in scattered populations and little is known of their current status and vulnerabilities.

In some parts of the range of wild potatoes there has been, in the last decade or more, a wholesale conversion of pristine habitat into land with intensive agricultural production. This change in landscape use is on a much broader scale than that threatening *S. achacachense* in the Bolivian highlands and can be readily seen from satellite images and aerial photographs using tools such as Google Earth. For example, CPC 3757 *S. microdontum* Bitt. (http://www.hutton.ac.uk/cpc) is one accession from a locality that is now under intensive agriculture.

Habitat loss in the Central Andes may, to some extent, be curbed by the extensive protected areas established by national governments. Large areas of the highly diverse eastern Andes have already been deforested, with Yungas forest lost to the extent of 38%, 25% and 15% in three areas of Peru, and deforestation in eastern Bolivia accelerating to about 2,900 km^{-2} per year. The vegetation of the higher Andes is a little more secure with 54% of the area of high Andean vegetation in Peru and Bolivia within protected areas (Young 2007), but even protected and putatively protected areas are not immune to this loss.

In the Old World, there are also wild crop relatives vulnerable to extinction. For example, Prohens et al. (2007) reported on the genetic structure of two endangered eggplant wild relatives found in the Canary Isles, and suggested that measures were established to aid their survival in the wild.

The greatest threat to wild species of *Solanum* may come from the pressures associated with changing climates. The high altitude species of wild potato are under threat just as are many species internationally. Although in some cases they may be able to migrate to an equivalent climatic zone at high altitude, the migration depends on the existence of a suitable habitat as well as an ability to move during the relatively short period that may be available before the original habitat becomes unsuitable. However, given the topography and the habitat fragmentation induced by man, such migrations will, in many cases, not be possible. The likely rates of loss of wild relatives of three crops, groundnut, potato, and *Vigna* bean, were modeled by Jarvis et al. (2008) using standard projections for climate change. Potato wild relatives were found to be at intermediate levels of threat and the modeling suggested that about 7–14% of species (with no or unlimited migration permitted) will go extinct simply due to climate shifts by 2055 under the conditions specified. The modeling also suggested that their range sizes would decrease by between 38% and 69%. It should be stressed that additional pressures of the conversion of land for other use, and the changes in range of pests and pathogens expected from a changing climate, will add further stresses affecting the survival of wild species. Jarvis et al. (2008) suggest that to safeguard important biodiversity for mankind, increased effort should be made on the collection of material in the gene banks.

By the first half of the nineteenth century, wild potatoes had been collected and were established in botanical gardens in Europe. *S. demissum* Lindl. was described in 1848 by Lindley from material in the Royal Horticultural Society gardens in England, sent to him by Udhe in Mexico. One spontaneous hybrid, *S.* × *edinense* Berth., formed at the Royal Botanic Garden in Edinburgh between cultivated potato, *S. tuberosum*, and a Mexican hexaploid species, *S. demissum* and was described by Berthault in Paris in 1911 (Hawkes 1990). The impact of the discovery of late blight resistance in *S. demissum* on potato breeding was great, stimulating the breeding work of Salaman (1931), Black (1943) and others who used *S. demissum* as a source of genes for the breeding of varieties resistant to late blight. The realization of the value of wild species for breeding gave a further impetus to the collection of wild species and fostered a series of collecting expeditions in the early decades of the twentieth century. The first collecting expedition specifically to collect potato germplasm was that of Bukasov in 1925 and again with Juzepczuk, Vavilov, Lekhnovitch, and Kesselbrenner in 1926–1932 (Correll 1962). The Vavilov collection of wild and landrace potatoes has, unfortunately, largely been lost. German, Swedish, and American expeditions were made in the early 1930s. Although the German and Swedish expeditions were relatively unproductive in terms of living material collected, due largely to the unsuitable season, the American expeditions by Russell, Erlanson, and others to Mexico and Chile brought back around 600 accessions, which were used by breeders although not studied systematically at the time. In 1938, EK Balls and JG Hawkes began their collecting expeditions on behalf of the Commonwealth Bureau of Plant Breeding and Genetics in England. In the first expedition, they collected around 1,200 accessions, giving a major boost to the availability of tuber-bearing *Solanum* to breeders and scientists worldwide. Hawkes (2004) published a detailed account of his early collecting expeditions, recounting his preparatory visit to Russia to learn from the prominent taxonomists of the time, and his meeting with Vavilov during his stay. Particularly during the next four decades, many collecting missions visited Central and South America, establishing the main potato wild relative collections in existence today.

The main collections of potato wild species are now found at CIP in Lima, Peru; Sturgeon Bay in Wisconsin, USA; Wageningen, the Netherlands; Dundee, UK; Braunschweig, Germany; and Chile, Argentina, Bolivia, and Peru in South America. A loose grouping of international gene banks was formed under the banner of the Association of Potato Intergenebank Collaboration and has produced a basic combined database built on those accessions in the collections still retaining a single original collector number (Huamán et al. 2000). The extant accessions in the world's potato gene banks numbered 11,819 wild species accessions, 7,112 of which were not duplicates and 5,306 of which retained their original collector's number. Others had lost that identity or were the results of crossing between accessions losing viability due to bottlenecking. Around 30% of the accessions were from Argentina, whereas the major centers of diversity, Peru and Bolivia, contributed only 24% and 20%, respectively. Of the 188 taxa in the collections, 72 were represented by five or fewer accessions and about 70 taxa were not represented in any gene bank.

The subset of this world assembly of wild potato accessions that is held in Europe is now accessible via a combined database available from the CGN gene bank Web site at Wageningen. Again, the original collector's number is used to provide a unique reference point for combining evaluation data from each collection sharing the accession. More detailed additional information is available from individual gene banks such as the Sturgeon Bay gene bank available through the GRIN system, and the Germinate database of the CPC available at the James Hutton Institute.

Most gene banks preserve material as true seed in cold, dehumidified stores according to protocols close to IBPGR standards (Hanson 1985). In some rare cases, particularly when individual clones have been well characterized, it would be beneficial to maintain clonal material in a safe form, but so far cryopreservation and the use of slow growth medium has been successfully applied only to clonal material of cultivated varieties, breeder's lines and mapping populations as the benefit for this type of material is clear (Foroughi-Wehr et al. 1977; Schäfer-Menuhr et al. 1996). However, true seed of *Solanum* species generally retains a high viability when stored both dried and cold, and practical experience has shown that seed stored in a reasonable condition retains its viability for at least 30 years.

The in situ conservation route through the development of protected areas and by implication the species within the habits that exist there has already been mentioned. In Peru, there are also specific initiatives focused on the potato, the most important of which is the Potato Park in Pisac, Peru. This groundbreaking initiative by local community groups sought to repatriate genetic resources and maintain them for the benefit of local communities. Although the main focus is on the native cultivated biodiversity, the park sits in the center of the area of the original domestication of the potato and includes the wealth of diversity available in the wild potatoes of the area. The sympathetic management of the area of 9,300 ha by the participants in the initiative will afford protection for some of the wild potato species found there.

Eggplant and its wild relatives do not have the same well-developed international network charged with the preservation of genetic resources. However, an EU project on eggplant germplasm resources built a Europe-wide database of 3,500 accessions of eggplant and its wild relatives (van der Weerden and Barendse 2007), which has since grown to around 6,000 accessions under the auspices of the ECP/GR program (http://www.bgard.science.ru.nl/WWW-IPGRI/eggplant.html). About one quarter of the total European holdings of eggplant are thought to be wild relatives of the eggplant species. A further major repository is the National Bureau for Genetic Resources in Pusa, Delhi, where around 2,500 accessions of eggplant are held, many of them indigenous cultivated landraces. The USDA network of gene banks in the GRIN system holds about 760 eggplant accessions and 860 taxa in the genus *Solanum*, although the numbers of unique species held will be somewhat lower.

12.3 Role of Wild *Solanum* Species in Elucidation of Origin and Evolution of Allied Crop Plants

Competing claims to be the source of the cultivated potato have been made by Chile, Bolivia and Peru, encouraged by a confused literature on the topic. There is no simple answer to the question of the origin of the cultivated potato, and to a degree all three countries mentioned above and others can claim a part in the story. One remarkable aspect of the story of the cultivated potato was the discovery by Hosaka (2003, 2004) that the Chilean potato carried the chloroplast type found today only in an Argentinean and Bolivian white starry-flowered species with a covering of glandular hairs, *S. tarijense* Hawkes. Subsequent work has shown that the landraces of potato in the Andes mostly carry the chloroplast signature of the species of the *S. bukasovii* group from Peru, with which all potatoes have a strong affinity at the nuclear DNA level, and also a Bolivian group of species once thought to be better candidates as ultimate ancestors than the Peruvian species (Sukhotu et al. 2006). The signature of *S. tarijense* has not been detected in the nuclear DNA of cultivated potato, yet the clear implication of this work is that an Andean stock of potato hybridized with this species, which has a natural range today in Bolivia and northern Argentina, and that derivatives of that event, backcrossed to Andean stock, made the journey south to coastal Chile where Chilean potatoes became adapted to conditions very different from their home in the Andes. Ames and Spooner (2008) have used the chloroplast DNA deletion characteristic of Chilean potato to survey European potatoes and confirm that potatoes in Europe largely carry Chilean cytoplasm, though prior to the late blight epidemic of the mid-1840s a wider diversity of chloroplast types were found.

Hawkes (1990), without the benefit of the detailed molecular data that was to follow over a decade later, considered that the origin of the potato could be somewhere in the center of diversity of the wild potato, from central Peru to the Lake Titicaca region and in particular northern Bolivia. Although earlier Russian researchers were inclined to place the origin of the potato in Peru, as Hawkes had been earlier in his career, he considered that as the most wild-looking biotypes of landrace Stenotomum potatoes (then given specific rank but now considered a group within *S. tuberosum*) were to be found in Bolivia then it was likely that potatoes were descended from Bolivian ancestors. *S. leptophyes* Bitt. seemed to fit most closely due to its occurrence in the same phytogeographical region and at a similar altitude to Stenotomum potatoes, the living representatives of the earliest domesticated types. This was at variance with some of the early molecular data appearing in print at the time, including the study of Debener et al. (1990), which placed Stenotomum and Andigena accessions close to *S. canasense* Hawkes and not the Bolivian and Argentinean group of species, which included *S. gourlayi* Hawkes, a close ally of *S. leptophyes*. This arrangement of species agrees with the position of Bukasov (1966) who placed the origin of the cultivated potato in the Peruvian group to which *S. canasense* (part of *S. bukasovii sensu lato*) belongs.

Spooner et al. (2005) published a large-scale study using amplified fragment length polymorphism (AFLP) markers. A total of 438 AFLP polymorphisms were assayed on 362 wild and 98 landrace accessions of potato from the Commonwealth Potato Collection and the USDA Potato Genebank at Sturgeon Bay. Cladograms were presented using Wagner parsimony methods, and these demonstrated a clustering of the majority of the accessions in the study into two clades representing the northern and southern *S. brevicaule* complexes, the main groups of species found in Peru and Bolivia plus Argentina, respectively. All the landrace accessions in the study clustered with the northern group and in particular a group of species from southern Peru. This group from the northern Brevicaule complex is regarded by some as one broad species with the earliest name *S. bukasovii*, and by others as several distinct species *S. ambosinum* Ochoa, *S. bukasovii* Juz. *sensu stricto, S. candolleanum* Berth., *S. canasense, S. marinasense* Vargas, and *S. multidissectum* Hawkes. Later exploration of the data using principal coordinate analysis suggested that within this group the accessions labeled *S. canasense* demonstrated the greatest overlap with cultivated landraces, although other species are also candidates for involvement in the ancestry of the cultivated potato.

Together, these studies indicate that the original domestication event took place in central or southern Peru at an altitude of around 3,000–4,300 m, that the original domesticates formed hybrids with other Andean wild species after migration under domestication, and that backcrossing has yielded new combinations of mostly Peruvian nuclear DNA with a range of different cytoplasms, including a relatively distant event to generate the nuclear–cytoplasmic combination found in most Chilean and European potatoes. There is also no indication of a hybridization event with *S. sparsipilum* (Bitt.) Juz. et Buk. to form tetraploid landraces as suggested by Hawkes (1990), but instead the move to tetraploidy seems more likely to have been directly from diploid landraces.

No comparable study exists which clarifies the origin of the eggplant using DNA techniques. With a number of possible contributors to the diversity found in cultivated species, and the ability shown by other members of the genus to achieve introgression from a number of related species, the story of the origin of the eggplant may be complex.

12.4 Role in Development of Cytogenetic and Genetic Stocks

Cultivated potato, *S. tuberosum*, is most commonly grown in the tetraploid form, although diploid forms are also frequent, particularly in the Andes. Also in the Andes are forms of cultivated potato, which have arisen by interspecific hybridization with *S. megistacrolobum* Bitt. or *S. acaule* Bitt. These forms, *S.* × *ajanhuiri* Juz. et Buk. and *S.* × *juzepczukii* Buk., respectively, give frost tolerance to domesticated potato at the expense of reintroducing high levels of tuber glycoalkaloids bred out by the original people domesticating the potato. These high-altitude forms are grown for the production of the ancient food, chuño, a dried product produced with a long soaking period, which de-bitters previously freeze-dried whole small tubers.

With no appreciable differentiation at the DNA level between the traditional diploid and tetraploid taxa of domesticated potato, there is a general acceptance that the material previously given specific rank, for example in Hawkes (1990), should be classified as groups arising under domestication. Dodds (1962) described a system of classification entirely consistent with these modern ideas on the limits of *S. tuberosum*, and his classification is used here. He placed five groups under *S. tuberosum*: Stenotomum, Phureja (both diploid), Andigena, Tuberosum (both tetraploid), and Chaucha (crosses between a diploid and Andigena). In addition, *S.* × *juzepczukii* (*S. tuberosum* group Stenotomum × *S. acaule*, 3×) and *S.* × *curtilobum* Juz. et Buk. (*S. tuberosum* group Andigena *S.* × *juzepczukii*) retained specific rank thanks to their origin as interspecific hybrids, and the position of *S.* × *ajanhuiri* as an interspecific hybrid between *S. tuberosum* Group Stenotomum and *S. megistacrolobum* was clarified by Johns et al. (1987). Some recent authors have used the more recent system proposed by Huamán and Spooner (2002), but we consider that the similar system of Dodds (1962), retained specific epithets for known interspecific hybrids, to be preferable.

There has been a great deal of research performed on the means of moving from one ploidy level in potato to another. Some of this work has used wild relatives of potato, for example to introduce the embryo spot marker to permit the identification of true hybrids rather than the desired dihaploids (Hermsen and Verdeniu 1973). The two processes involved in breeding across ploidy level are the spontaneous doubling of the chromosome complement during gamete formation (Ross and Langton 1974) (or the artificial doubling of chromosome number with chemical agents), and the reduction of chromosome number through a failed pollination, often using the Phureja lines with an introgressed gene for nodal pigmentation (e.g., Uijtewaal et al. 1987), or anther culture. To be able to move between ploidy levels opens up new possibilities for approaches to breeding and in particular allows the breeder the possibility of the benefit of selection at the diploid level and the recreation of productive tetraploid genotypes from such diploid lines (Peloquin et al. 1989). Clulow and Rousselle-Bourgeois (1997) challenged the assumption of parthenogenesis following fertilization and provided evidence for direct introgression of Phureja DNA into the derived dihaploids from incomplete fertilization or from the loss of chromatin soon after fertilization. Although this may provide a means of more rapidly introgressing DNA from wild species into cultivated potato, its use for this purpose has yet to be demonstrated. Furthermore, recent studies have questioned the evidence for direct introgression from Phureja, suggesting that dihaploid induction does generally operate via parthenogenesis (Samitsu and Hosaka 2002; Straadt and Rasmussen 2003).

The ability to inbreed germplasm opens up possibilities to expose recessive alleles, prepare for hybrid true seed production, provide an alternative to monoploids for near-homozygous DNA isolation, and develop material to investigate heterosis. Much of this is best achieved at the diploid level. Although in general self-compatibility is lost when moving from tetraploidy to diploidy in cultivated potato, there are rare genotypes that maintain self-compatibility in the diploid state. Wild species have contributed to the development of inbred lines. Cappadocia et al. (1986) described self-compatibility arising from anther culture doubled haploids of the wild potato *S. chacoense* Bitt. Hosaka and Hanneman (1998) described a gene from *S. chacoense, Sli*, which suppresses the self-incompatibility system normally functioning in diploid potatoes, that this has now been exploited to generate inbred lines as far as the S_5 (Phumichai et al. 2005).

Aneuploids have been recorded several times during the introgression of traits from wild species to the cultivated potato. Observations of aneuploidy in derivatives of *S. demissum* × *S. tuberosum* were made by Cooper and Howard (1952). More recently Wilkinson (1992) observed aneuploidy in aerial parts of cv. Toridon and aneusomaty in the roots. However, such aneuploidy has been recorded as a product of interspecific breeding but not explicitly exploited as a genetic tool in its own right.

12.5 Role in Classical and Molecular Genetic Studies

As an outbreeding tetraploid, potato has not been an attractive subject for classical genetic studies. Such studies in potato have burgeoned since the advent of quantitative trait loci (QTL) mapping based on molecular marker maps, often using parents bearing wild species introgressions (Meyer et al. 2005; Bradshaw et al. 2008; Ritter et al. 2009). As a direct result of this mapping effort potato has become a model for the development of autotetraploid mapping (Luo et al. 2001; Hackett et al. 2003). Some of these gene mapping studies have been performed in hybrids between wild species prior to transfer of the genes to cultivated stock (Danan et al. 2009). However, unlike its close relative tomato, most of the effort has been directed to existing cultivated germplasm rather than using wild relatives directly, although that cultivated stock usually carries uncharacterized introgressions from wild species. These uncharacterized wild species introgressions have often been from species donating pest and disease resistance into cultivated breeding lines. As such they will have encountered few rounds of meiotic recombination since their introduction and may suffer inherently less frequent recombination in any case. The relatively large distances over which linkage disequilibrium occurs in the first published studies of association genetics in potato (Gebhardt et al. 2004; Simko 2004; Simko et al. 2006) may be due to this special nature of introgressed segments originating from wild potato species.

12.6 Role in Crop Improvement Through Traditional and Advanced Tools

Potato, unlike the other major bulk food crops as the cereals, can and has benefited from the extensive use of wild relatives in breeding. The value contributed globally by the wild relatives of the potato is likely to exceed than that of those of any other crop. Prakash (2008) estimated the global value of international trade in potato at US$6 billion and, as much potato production is not traded across international boundaries, the true value must be several-fold higher. As most potato varieties have genetic contributions from deliberate breeding using wild species, the contribution to the global economy from the protection offered by these genes can be seen to be immense.

Potato late blight was the first major crop disease tackled by the exploitation of resistance in wild relatives. The promise of resistance in *S. demissum* and its hybrid derivatives was noted by Salaman in 1909 (Hawkes 1958), and the outputs of breeding with these lines were reported by Salaman (1931) and Black (1943). Today, resistance genes, many of them now overcome by new strains of the pathogen, are found in most modern cultivars of the potato. This unprecedented scale of penetration of wild germplasm into the cultivated types still does not mean that the pathogen has been defeated. The disease still poses a threat to crop production and food security across the world, and new forms of the disease repeatedly appear and pose a new threat to the food security of the region (Drenth et al. 1994; Montarry et al. 2010). In response, the breeders and geneticists have resorted to explore the diversity of resistance genes available in the wild relatives of potato and have reported high frequencies of useful resistance in species from the northern and southern parts of the range of tuber-bearing species, with very few naturally blight resistant species from Peru (Colon and Budding 1988; Ramsay et al. 1999).

One source of promising new resistance genes thought to confer broad-spectrum and possibly more durable resistance to late blight is *S. bulbocastanum*. As this Mexican species does not readily cross with cultivated potato, three different approaches have been taken to overcome this difficulty – bridging crosses (Hermsen and Ramanna 1973), protoplast fusion (Helgeson et al. 1998), and gene isolation for genetic transformation (Song et al. 2003). Both the bridging cross approach and the genetic modification (GM) route have yielded commercializable varieties. This work has stimulated further searches for novel R-genes, using approaches that target *avr* genes in the pathogen (Hein et al. 2007; Vleeshouwers et al. 2008).

Further exploitation of wild tuber-bearing species has focused on the next most important global pathogen of the potato, the potato cyst nematode (PCN). At Dundee, the wild species *S. vernei* Bitt. et Wittm. has been used for PCN resistance, taking 28–30 years to achieve the 5–6 backcrossing cycles required to introgress resistance genes but remove undesirable traits from *S. vernei* (Bradshaw et al. 1995). The successful introduction of pest and disease resistance traits into potato cultivars comes from a relatively small number of wild species. *S. demissum* and *S. stoloniferum* Schltdl. et Bché. have donated late blight resistance and resistance to viruses, additional virus resistance has come from *S. chacoense* and *S. acaule*, whereas both *S. vernei* and *S. spegazzinii* Bitt. have donated resistance to PCN (see for review Bradshaw et al. 2005).

By contrast, eggplant has benefited on only a small scale from the use of wild species in breeding due to difficulties in making fertile interspecific crosses (Sękara et al. 2007) and the wealth of diversity in the crop species. However, wild species are seen as potential sources of pest and disease resistance traits, and various biotechnological approaches have been made to access this variation (Kashyap et al. 2003).

12.7 Genomics Resources Developed

For the entire *Solanum* genus, entries lodged in the CBI databases for nucleotides and expressed sequence tags (ESTs) at the end of 2009 amounted to about 144k nucleotide database sequences and 727k EST sequences. The majority of these sequences were for tomato and the immediate wild relatives of tomato. For the wild relatives of potato, eggplant, and other minor *Solanum* species, the nucleotide entry counts were between 200 and 400 for *S. demissum*, *S. bulbocastanum* Dun., *S. melongena*, and *S. quitoense*, and around 100 for *S. chacoense* and *S. nigrum* L. The only wild *Solanum* species outside the tomato group with any significant number of EST sequences was *S. chacoense* with 7.7k sequences.

This resource is meager compared to the full genome sequence of the potato, which was made available in draft form in September 2009. By the end of 2010, it is intended to have the sequence fully aligned and annotated. The specific goals of the project include the presentation of the genome sequence with >95% of genes together with the regulatory regions, to have >95% of known potato ESTs located on the genome and to anchor at least 50% of the genome and 80% of the genes to chromosomes. The consortium is also committed to public access to the data, and to as full annotation as is practicable (Visser et al. 2009).

Although at this stage no sequencing of wild potatoes is envisaged, the current genome scaffolds and the expected full sequence provide an excellent starting point for comparative sequencing of the genomes of related species, and this is expected to be a major result of the publication of the sequence.

Unlike in tomato and its wild relatives, potato, eggplant, and their wild relatives do not have organized lists and collections of mutants, although some provisional mutagensis has been attempted in the self-compatible diploid potato relative, *S. verrucosum*.

12.8 Scope for Domestication and Commercialization

Solanum species provide a huge reservoir of bioactive compounds. Ethnobotanical reports suggest widespread use of members of the genus for a diversity of therapeutic and other purposes. Applications include the use of a decoction taken as a drink of *S. americanum* Mill. used to treat hypertension by traditional healers in Côte-d'Ivoire (N'guessan et al. 2009). In Mexico, *S. chrysotrichum* Schltdl. is used to control skin fungal infections (Lozoya et al. 1992). The roots of *S. virginianum* L. are used in a mixture of extracts to treat tuberculosis in Bangladesh (Mahabub Nawaz et al. 2009). The juice of crushed fruits of *S. erianthum* D. Don is applied to exposed skin by the Paliyar tribes, an indigenous people of Tamil Nadu, India, to repel leeches during visits to the forest (Ignacimuthu et al. 2006). Other studies show a wide diversity of uses; for example, *S. nigrum* and *S. surattense* Burm. are used for treating heart disease, rheumatism, fever, and chest complaints in northern Pakistan (Wali Khan and Khatoon 2008), and a review of all uses of *Solanum* extracts in India has been published by Amir and Kumar (2004).

Among the most promising uses of *Solanum* extracts is its use for the treatment of cancer. *S. aculeastrum* Dunal is used to make a decoction to treat cancer and is the most commonly used plant for this purpose in South Africa's Eastern Cape, administered daily until symptoms disappear (Koduru et al. 2007). Glycoalkaloids from *S. linnaenum* Hepper & P.-M.L. Jaeger (previously *S. sodomaeum*) have been identified to have antitumor effects (Cham et al. 1987; Cham and Meares 1987). These solasodine rhamnosyl glycosides specifically bind cancer cell receptors and induce cell death so effectively that farmers in Australia apply crushed leaves to retard the progress of ocular squamous cell carcinomas in cattle. The mix of solasodine glycosides from this plant has now been shown to be effective against a range of cancers and is now available in the form of a topical cream for the treatment of malignant and non-malignant skin cancers (Cham 2007).

12.9 Some Dark Sides and Their Addressing

There are several *Solanum* species considered as noxious weeds in some parts of their range. Some are considered to be useful species in one situation and harmful in another. For example, *S. torvum* is widely planted in some countries for its fruit and is used as a bacterial wilt resistant rootstock for the grafting of eggplant (Rahman et al. 2002). In Hawaii and Papua New Guinea, it is an invasive species, particularly in pasture.

Solanum elaeagnifolium Cav., the silverleaf nightshade, is one of several species widely regarded as a noxious weed. It is a native of northeast Mexico and the southwest of USA but has spread to many US states, Morocco, around the Mediterranean basin, in South Africa, and in Australia. Its aggressive growth from deep rootstocks makes it difficult to control, and long-dormant seeds make it liable to recur even when cleared from sites (Anonymous 2007).

12.10 Recommendations for Future Actions

There are a number of crucial issues for the future effective conservation and use of wild *Solanum* germplasm. It is very clear that even in potato, which has a long history of the use of wild germplasm for improvement of the crop, the useful germplasm used in breeding is a very small fraction of the available diversity. To be able to use that diversity effectively to help safeguard food production in the future, the following requirements exist:

- Appropriate understanding of the diversity available and the uses which can be made of that diversity
- Appropriate access to that biodiversity, bearing in mind that countries donating germplasm to collections now rightly expect to share in the benefits of its exploitation
- Conservation of that diversity in situ and ex situ so that it is readily available to researchers now and preserved for uses in the future
- Means of identifying the genes responsible for traits within a realistic timescale
- Societal permission to use technologies, including GM, that can ensure the transfer of traits without the need for very many rounds of recombination to recover properly adapted mixes of genes

Technology and politics combine to intervene in many of these areas. For example, genetic techniques to identify and understand useful genes have been continually improving, making it possible to isolate the full gene sequence for many traits by a variety of techniques. The availability of the full genome sequence of potato will make this task much easier in the future, although for complex traits such as resistance to abiotic stress the lack of a full understanding of the biology of the trait will hinder the identification of the relevant genes. In some parts of the world, significant resistance remains to moving these genes into cultivars by the most efficient route, and so much longer traditional sexual introgression may be required. There is clearly much yet to be done to reduce the public's mistrust of such technologies and to gain acceptance of their use.

The International Treaty for Plant Genetic Resources for Food and Agriculture (http://www.planttreaty.org/) provides a framework for the sustainable use of plant genetic resources and aims to provide a mechanism that returns benefit to the countries donating useful germplasm to the world community. For this to succeed, it is necessary that the mechanisms function well and that such benefit is seen as commensurate with the benefits obtained by the countries using the germplasm. At present, not all countries holding significant *Solanum* genetic resources are permitting internationally based collecting of genetic resources in their countries. However, as much of the wealth of genetic resources found in the wild are coming under increasing risk from various pressures including the rapid shifting of climate zones, there is a greater need than ever to safeguard useful crop relative biodiversity for the future of mankind.

To summarize, the actions required include the continual improvement of the understanding of the important traits for the sustainability of crop production, the integration of this work with genome science, actions to reduce societal reluctance to embrace new technology and enhance global cooperation relating to genetic resources, and an increased effort to bring invaluable crop-related genetic resources into well-managed facilities to make them available to the international community.

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