Chittaranjan Kole *Editor*

Wild Crop Relatives: Genomic and Breeding Resources

Vegetables

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Chapter 9
Solanum sect. *Lycopersicon*

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9.1 Introduction

Tomatoes belong to the large and diverse family Solanaceae, which includes more than 3,000 species, occupying a wide variety of habitats (Knapp 2002). Recent taxonomic revision of the Solanaceae has reintegrated *Lycopersicon* into the genus *Solanum* with a revised new nomenclature (Peralta and Spooner 2001; Spooner et al. 2005; Peralta et al. 2008). The majority of taxonomists as well as most plant breeders and other users have accepted the reintegration of tomatoes to *Solanum* (e.g., Caicedo and Schaal 2004; Fridman et al. 2004; Schauer et al. 2005; Mueller et al. 2009; see also http://tgrc.ucdavis.edu/key.html).

Morphological characters, phylogenetic relationships, and geographical distribution have demonstrated that tomatoes (*Solanum* sect. *Lycopersicon* (Mill.) Wettst.) and their immediate outgroups in *Solanum* sect. *Lycopersicoides* (A. Child) Peralta and sect. *Juglandifolia* (Rydb.) A. Child form a sister clade to potatoes (sect. *Petota* Dumort.), with *Solanum* sect. *Etuberosum* (Bukasov & Kameraz) A. Child being sister to potatoes + tomatoes (Spooner et al. 1993). Analyses of multiple datasets from a variety of genes unambiguously establish tomatoes to be deeply nested in *Solanum* (Bohs and Olmstead 1997, 1999; Olmstead and Palmer 1997; Olmstead et al. 1999; Bohs 2005). However, tomatoes and their close relatives can be easily distinguished from any other group of *Solanum* species on the basis of shared features such as their bright yellow flowers and pinnatifid, non-prickly leaves.

'The plant group *Solanum* sect. *Lycopersicon* consists of 13 closely related species or subspecies: the cultivated tomato, *Solanum lycopersicum* (formerly *Lycopersicon esculentum*), which includes the domesticated tomato and wild or weedy forms of the cherry tomato (*S. lycopersicum* 'cerasiforme') (Peralta et al. 2008), and the wild species *Solanum arcanum*, *S. cheesmaniae*, *S. chilense*, *S. chmielewskii*, *S. corneliomulleri*, *S. galapagense*, *S. habrochaites*, *S. huaylasense*, *S. neorickii*, *S. pennellii*, *S. peruvianum*, *S. pimpinellifolium*) (Tables 9.1 and 9.2; Peralta et al. 2005; Spooner et al. 2005). Four species have been segregated from the green-fruited species *S. peruvianum* sensu lato (s.l.); two of them *S. arcanum* and *S. huaylasense* have been described as new species (Peralta et al. 2005) from Peru, while the other two *S. peruvianum* and *S. corneliomulleri* had already been named by Linnaeus (1753) and MacBride (1962), respectively. In addition, *S. galapagense*, another yellow-to orange-fruited species, was segregated from *S. cheesmaniae*; both species are endemic to the Galápagos Islands (Darwin et al. 2003; Knapp and Darwin 2007). All members of sect. *Lycopersicon* are closely related diploid species ($2n = 24$) (Peralta and Spooner 2001; Nesbitt and Tanksley 2002) and are characterized by a high degree of genomic synteny (Chetelat and Ji 2007; Stack et al. 2009) and are to some degree intercrossable (Taylor 1986). The group *Solanum* sect. *Juglandifolia* contains the two woody tomato-like nightshades *S. ochranthum* and *S. juglandifolium*. These two species are partially sympatric and they are morphologically similar, both being woody perennials with rampant, liana-like stems up to 30 m in length (Correll 1962; Rick 1988). Based on evidence from molecular sequence data sect. *Juglandifolia* is the

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Table 9.1 Principal ecological, botanical, and reproductive features of the wild tomatoes (*Solanum* sect. *Lycopersicon*) and related *Solanum* species

Species	Geographic distribution	Habitat	Mating system[a]	Crossability to tomato[b]	Distinguishing morphological features[c]
S. lycopersicum "cerasiforme"	Adventive worldwide in the tropics and subtropics (near sea level – 2,400 m); perhaps native in Andean region	Usually mesic sites, often feral or weedy	SC-autogamous	BC	Plants semi-erect to sprawling; fruits red, 1.5–2.5 cm
S. cheesmaniae	Endemic to Galápagos Islands (sea level – 1,500 m)	Arid, rocky slopes, prefers shaded, cooler sites	SC-autogamous	BC	Plants semi-erect to sprawling, flowers very small, pale; fruit purple, greenish-yellow, or orange, 0.5–1.5 cm
S. galapagense	Endemic to Galápagos Islands (sea level – 650 m)	Arid, rocky outcrops and slopes, sometimes near shoreline	SC-autogamous	BC	Plants erect; leaves highly subdivided; internodes short; flowers small, pale, fruit orange (0.5–1 cm)
S. pimpinellifolium	Lowland Ecuador and coastal Peru (sea level – 500 m)	Arid, sandy places, often near sources of water or on the edges of farm fields	SC-facultative	BC	Plants semi-erect to sprawling, flower small-large; fruit red (0.5–1 cm)
S. chmielewskii	Inter-Andean valleys of central and southern Peru (1,600–3,100 m)	Rather moist, well-drained, rocky slopes	SC-facultative	UI	Plant sprawling or trailing; flowers small, pale; fruit green (1–1.5 cm)
S. neorickii	Inter-Andean valleys from Cusco to central Ecuador (1,500–2,500 m)	Rather moist, well-drained, rocky slopes	SC-autogamous	UI	Plants sprawling or trailing; flowers tiny, pale; fruit green; seeds tiny
S. arcanum	Northern Peru, coastal and inter-Andean valleys, middle watershed of Marañon (500–3,000 m)	Varied, but generally dry, rocky slopes	Mostly SI, rarely SC-facultative	UI, EL	Plants erect to prostrate, reduced leaflet no.; flowers mostly straight anther tubes and undivided inflorescences; fruit whitish-green with dark stripe
S. chilense	Southern Peru, northern Chile (50–3,500 m)	Very arid and sometimes saline, rocky slopes or washes	SI	UI, EL	Plants erect; leaves finely pubescent; anthers straight; inflorescences compound; peduncles long; fruit purplish-green
S. peruvianum	Mostly coastal central/southern Peru and northern Chile (sea level – 2,500 m)	Arid, sandy, or rocky dry washes, sometimes near agricultural fields	Mosty SI, rarely SC-facultative	UI, EL	Plants procumbent; anthers bent; inflorescence simple; fruit purplish-green
S. corneliomulleri	Western Andes of central/southern Peru (1,000–3,000 m)	Rocky or sandy slopes and dry washes	SI	UI, EL	Erect to decumbent; leaves glandular pubescent; fruit purplish-green
S. huaylasense	Limited to Callejon de Huaylas, and Río Fortaleza, Peru (1,000–2,900 m)	Rocky slopes and waste places	SI	UI, EL	Spreading, anthers straight, inflorescence compound; fruit purplish-green
S. habrochaites	Northwestern and western central Peru, western and southern Ecuador (40–3,300 m)	Varied, but generally mesic slopes or stream banks	Mostly SI, some SC-facultative	UI	Sprawling shrub or vine; densely pubescent; flowers large; anthers straight; fruit green with dark stripe, hairy
S. pennellii	Coastal valleys of central to southern Peru (near sea level to 1,920 m)	Very arid, sandy or rocky slopes, or dry washes	Mostly SI, some SC-facultative	UI	Spreading shrub; 2 leaves per sympodium[d]; leaflets broad, round; foliage sticky; anthers poricidal; pedicel usually articulated at base

S. juglandifolium	Temperate rainforests of Columbia and Ecuador (1,200–3,100 m)	Mesic slopes and stream banks	SI	UI (no hybrids)	Woody vine or rampant shrub; 8–10 leaves per sympodium[d]; leaves rough, rugose; anthers orange-yellow, poricidal; flowers scented; fruit green (to 2 cm); seeds winged
S. lycopersicoides and *S. ochranthum*	Restricted to narrow range in southern Peru and northern Chile (1,200–3,700 m)	Arid rocky slopes, usually south-facing	SI	UI, EL, HS	Woody, erect to sprawling shrub; anthers white, poricidal; style hooked; flowers scented; fruit green-black (to 1 cm)
	Montane forests of Peru, Ecuador and Colombia (1,200–3,200 m)	Well-watered sites such as riverbanks	SI	UI (no hybrids obtained)	Woody vine, to 15 m height; 6–12 leaves per sympodium[d]; anthers orange-yellow, poricidal; flowers scented; fruit yellowish-green (2–5 cm); seeds winged
S. sitiens	Minor ranges around Calama, northern Chile (2,500–3,500 m)	Hyperarid, rocky slopes, or ravines	SI	UI, EL, HS	Woody, erect shrub; anthers white, poricidal; flowers scented; fruit greenish-brown, dry, and brittle when ripe

[a]SC = self-compatible; SI = Self-incompatible; autogamous = self-pollinating; allogamous = outcrossing; facultative = may self-pollinate or outcross

[b]BC = bilaterally compatible (i.e., no barrier in either direction); UI = unilateral incompatibility (crosses succeed only when cultivated tomato is used as the female parent); EL = embryo lethality (can usually be overcome by embryo culture); HS = hybrid male-sterility; no hybrids = interspecific hybrids with tomato so far not obtained

[c]Except as noted, all spp. are indeterminate, herbaceous shrubs, with 3 leaves per sympodium; flowers have the standard "*Lycopersicon*" morphology – petals yellow; anthers yellow and fused, with a sterile anther appendage, and lateral pollen dehiscence – and lack floral scent

[d]Values based on Charkes Rick's notes at the time of collection, or observations made during regeneration by the TGRC

Table 9.2 Species recognized in *Solanum* section *Lycopersicon* (tomatoes) and allied species and their distribution

Species	Distribution	Previous name in *Lycopersicon*
Solanum arcanum Peralta	Northern Peru, inter-Andean valleys and coastal	*L. peruvianum* (L.) Mill., pro parte
Solanum cheesmaniae (L. Riley) Fosberg	Galápagos Islands	*L. cheesmaniae* L. Riley
Solanum chilense (Dunal) Reiche	Coastal Chile and southern Peru	*L. chilense* Dunal
Solanum chmielewskii (C.M. Rick, Kesicki, Fobes & M. Holle) D.M. Spooner, G.J. Anderson & R.K. Jansen	Southern Peru	*L. chmielewskii* C.M. Rick, Kesicki, Fobes & M. Holle
Solanum corneliomulleri J.F. Macbr.	Southern Peru (Lima southwards), western Andean slopes	*L. peruvianum* (L.) Mill., pro parte
Solanum galapagense S. Darwin & Peralta	Galápagos Islands	*L. cheesmaniae* L. Riley var. *minor* Hook.f.
Solanum habrochaites S. Knapp & D.M. Spooner	Montane Ecuador and Peru	*L. hirsutum* Dunal
Solanum huaylasense Peralta	Callejon de Huaylas, Peru	*L. peruvianum* (L.) Mill., pro parte
Solanum juglandifolium Dunal	Andean Colombia, Ecuador and Peru	–
Solanum lycopersicoides Dunal	Southern Peru and northern Chile	–
Solanum lycopersicum L.	Globally cultivated; native distribution unknown	*L. esculentum* Mill.
Solanum neorickii D.M. Spooner, G.J. Anderson & R.K. Jansen	Ecuador to Peru, inter-Andean valleys	*L. parviflorum* C.M. Rick, Kesicki, Fobes & M. Holle
Solanum ochranthum Dunal	Andean Ecuador and Peru	–
Solanum pennellii Correll	Peru to Chile, coastal and western Andean slopes	*L. pennellii* (Correll) D'Arcy
Solanum peruvianum L.	Coastal Peru to northern Chile	*L. peruvianum* (L.) Mill., pro parte
Solanum pimpinellifolium L.	Coastal Ecuador to Chile	*L. pimpinellifolium* (L.) Mill.
Solanum sitiens I.M. Johnst.	Southern Peru and northern Chile	–

For detailed distribution data, see maps and specimens cited in Peralta et al. (2008). Previous names in the genus *Lycopersicon* are given here for ease in cross-referencing the breeding literature

sister group of *Solanum* sect. *Lycopersicon* (see below). Sister to both groups is *Solanum* sect. *Lycopersicoides* (Child) Peralta, comprising the allopatric sister taxa *S. lycopersicoides* and *S. sitiens* (also previously called *S. rickii*). These four tomato-like nightshade species have in common several morphological features that make them intermediate between tomato and potato (Rick 1988; Stommel 2001; Smith and Peralta 2002). Tomato-like morphological characters that together differentiate them from most of other *Solanum* spp. include yellow corolla, pedicels articulated above the base, pinnately segmented non-prickly leaves, and lack of tubers (Correll 1962; Rick 1988). These four allied outgroup species are diploids ($2n = 24$), however strong reproductive barriers isolate them from the core tomato group (Correll 1962; Rick 1988; Child 1990; Stommel 2001; Smith and Peralta 2002). Overall, crosses between tomato and all but two (*S. ochranthum* and *S. juglandifolium*) of these wild species are possible, although with varying degrees of difficulty (Rick 1979; Rick and Chetelat 1995; Pertuzé et al. 2003).

Peralta et al. (2008) have treated the 13 species belonging to *Solanum* sect. *Lycopersicon*, along with the four closely related species (*S. juglandifolium*, *S. lycopersicoides*, *S. ochranthum*, *S. sitiens*) in the taxonomic series *Systematic Botany Monographs*.

Tomato is an economically important vegetable crop worldwide, which is consumed either fresh or in the form of various processed products (Robertson and Labate 2007). Depending on the type of use, different breeding objectives are pursued, which include improved yield, sensory and nutritional quality, as well as adaptation to biotic and abiotic stresses. As for any other crop, tomato improvement needs to rely on sufficient genetic diversity in order to be able to satisfy current and future breeding challenges. Cultivated tomato germplasm, however, relatively little genetic variation, resulting from its inbreeding mating system associated with severe genetic bottlenecks that are postulated to have occurred prior to, during, and after the domestication process (Rick and Fobes 1975; Rick 1987). In contrast, tomato wild species possess rich genetic variation and are potential sources for the

improvement of many economically important traits (Rick 1987). In fact, despite its relative small size and its recent evolutionary age – the radiation of the tomato clade has been estimated as ca. 7 Mya (Nesbitt and Tanksley 2002) – members of *Solanum* sect. *Lycopersicon*, along with taxa in the related sects. *Juglandifolia* and *Lycopersicoides*, are adapted to a wide variety of environmental conditions, which correspond to a wide range of variation in terms of morphological, physiological, mating system, and biochemical characteristics.

The reduced genetic variation of cultivated tomato can in part explain the slow rate of tomato improvement that was achieved until about 1940, when the first use of wild species as a source of desired traits was reported (Bohn and Tucker 1940). Thereafter, the exploitation of the favorable attributes hidden in tomato wild species via interspecific crosses flourished, resulting in the increased yields observed in the following decades (Rick 1988).

However, despite the wealth of genetic variation and many agriculturally important traits that can be found in the found in the potentially useful tomato wild accessions stored in gene banks, breeders have so far been unable to fully exploit this rich reservoir (Tanksley and McCouch 1997). Most commonly, wild tomato species have been used as a source for major genes for disease and insect resistances, as shown by the numerous resistance genes derived from these wild relatives, which can be found in modern varieties (Plunknett et al. 1987; Robertson and Labate 2007). In contrast, their use for the improvement of complex traits important to agriculture, including yield, quality, and tolerance to biotic and abiotic stresses, has been more limited. Several problems are, in fact, associated with the utilization of wild species, which have in many cases deterred breeders from using them. These include pre- and post-mating barriers, the presence of several undesirable loci that might be transferred along with the traits of interest, a phenomenon known as "linkage drag," the complexity and the time necessary to recover the elite genetic background while selecting for the desired characters, and a generally inferior phenotype of the wild germplasm for many of the traits that breeders would like to improve.

Over the years, the application of various molecular genetic methodologies has provided the necessary tools to overcome some of the above-mentioned limitations to the use of wild species in tomato cultivar improvement, thus accelerating their utilization. The availability of DNA markers and of derived molecular linkage maps has allowed genetic dissection of the loci underlying quantitative traits, as well as gene tagging for monogenic traits. Once markers tightly linked to a target gene or quantitative trait loci (QTL) are identified, marker-assisted selection (MAS) can be used for a more efficient and precise transfer of the gene/QTL into any selected genetic background. The negative effects of linkage drag can also be reduced, since the use of molecular markers allows for more efficient identification of recombinant plants in which close linkages are broken (Tanksley 1993). Using molecular markers, gene banks can be more rationally and efficiently sampled by taking into consideration marker-based estimates of genetic variability within and between accessions. Finally, another important contribution of QTL mapping studies conducted in tomato using interspecific crosses, as well as in other crops, has been the clear demonstration that exotic (wild) germplasm is likely to be a source of agronomically favorable QTL alleles also for traits in which the wild relatives show an inferior phenotype (deVicente and Tanksley 1993; Eshed and Zamir 1995; Tanksley et al. 1996; Tanksley and McCouch 1997; Grandillo et al. 2008). These results suggest that in the wild relatives of our crops there are numerous favorable alleles that were "left behind" by the domestication and breeding processes and that these alleles can now be more efficiently "discovered" and transferred into elite germplasm, using innovative genomic-assisted breeding strategies (Tanksley and McCouch 1997; Zamir 2001; McCouch 2004; Grandillo et al. 2008). This implies that in order to be able to fully exploit the genetic potential of our crops' wild relatives we need to change our selection approaches from phenotype based to allele based (Tanksley and McCouch 1997). In this respect, tomato has once again proven to be a model system in terms of development and application of innovative concepts and breeding approaches that can allow a more efficient and wider utilization of related wild species, and thus lead to an enrichment of the genetic base of this crop and hence to an accelerated rate of genetic improvement.

Approaches based on molecular maps and the integrative power of QTL analysis, such as the "advanced backcross QTL (AB-QTL) mapping strategy" and "exotic libraries" or introgression line (IL) libraries, have allowed the identification of favorable QTL

alleles for numerous traits of agronomical interest, and the development of pre-bred lines that could be used in MAS breeding programs (Tanksley and McCouch 1997; Zamir 2001; Grandillo et al. 2008). The IL concept has proven to be ideal for map-based cloning of QTL, as demonstrated by the first cloning of a QTL (Frary et al. 2000; Fridman et al. 2000), and to explore the genetic basis of heterosis for "real-world" applications, as shown by the development of a new leading hybrid of processing tomato (Lippman et al. 2007).

The numerous genetic and "omics" tools that are available for tomato and that are being developed within the International Solanaceae Genome Project (SOL), including the information derived from the tomato genome sequence (http://solgenomics.net/solanaceae-project/), are expected to further improve the efficiency with which wild tomato relatives will contribute to the improvement of this important crop.

Given the value of wild tomato germplasm as a source of favorable alleles necessary to satisfy present and future breeding challenges, there is the need to ensure the availability of this precious resource is preserved for future generations. Therefore, conservation initiatives have to be taken not only for the excellent ex situ collections available worldwide, but also to preserve populations in situ.

9.2 Basic Botany of the Tomato

9.2.1 Agricultural Status

The cultivated tomato (*S. lycopersicum*, previously *Lycopersicon esculentum*, see Table 9.2 for the equivalent names for tomatoes in *Solanum* and *Lycopersicon*) is a popular food and an important source of vitamins and antioxidants. Botanically a fruit but treated as a vegetable, tomatoes are rich in the carotenoids lycopene and β-carotene (provitamin A), which are reported to have anticancer properties. Tomatoes are also an important source of vitamin C – ca. 10% of total dietary intake of vitamin C in the USA (Gerrior and Bente 2002) – due to their use in a wide variety of food products.

While tomato is widely cultivated as an annual vegetable crop throughout the world, its wild relatives are of relatively minor agricultural significance. Fruits of the cherry tomato, *S. lycopersicum* "cerasiforme," are probably consumed more than any other species. These small-fruited tomatoes are common in the eastern foothills of the Peruvian Andes, where they not only apparently grow wild, but are also weedy or feral around cultivated fields and are commonly consumed (Rick and Holle 1990; see also Peralta et al. 2008). The wild "currant" tomato, *S. pimpinellifolium*, is popular with some home gardeners and seeds are available commercially. In the native region, fruits are occasionally picked from wild or weedy plants, but it is not a significant commercial crop. The other wild relatives are only marginally edible and are not consumed in significant quantities. However, there are reports by indigenous people in the Andean region of various medicinal uses of leaves or fruits from wild tomatoes. For example, *S. habrochaites* is reportedly used to treat skin ailments, altitude sickness, and "gas" problems, *S. chilense* for stomach ailments, and *S. ochranthum* as a purgative or as a soap substitute (C. M. Rick and R. T. Chetelat personal communication; http://tgrc.ucdavis.edu).

9.2.2 Geographic Distribution and Ecology

The wild tomatoes (*Solanum* sect. *Lycopersicon*) and allied *Solanum* spp. (sects. *Lycopersicioides* and *Juglandifolia*) are native primarily to the Andean region of South America, principally Peru, Chile, Ecuador (including the Galápagos Islands), and Colombia. Each species has a distinct geographic distribution, often overlapping with other tomato taxa, and reflecting their specific ecological adaptations and habitat preferences (Table 9.1). The western slopes of the Andes in Peru and Chile are extremely arid, and natural populations tend to be limited to the river drainages where there is adequate moisture. Starting at the lowest elevations, *S. pimpinellifolium* and *S. peruvianum* are usually encountered first. At mid elevations, *S. peruvianum* overlaps with or is replaced by *S. corneliomulleri* (formerly part of *L. peruvianum*, see Sect. 9.2), *S. habrochaites,* or *S. pennellii*. The valleys between the Andean cordilleras in the northern part of Peru are home to

S. arcanum and *S. huaylasense* (both formerly part of *L. peruvianum*), *S. chmielewskii, S. neorickii*, and *S. ochranthum.* A similar pattern is seen in Chile and parts of southern Peru, with *S. peruvianum* most common along the coast, and *S. chilense* found at some coastal sites, but mostly at mid to high elevations, where it overlaps with *S. lycopersicoides*, the latter extending to the highest altitudes.

The cherry tomato, *S. lycopersicum* "cerasiforme", is the most widely distributed, having spread out of its original region of distribution into Mesoamerica and beyond. It is now adventive in many subtropical or tropical regions of the world, where it is commonly weedy or feral. In mainland South America, "cerasiforme" is found mostly on the wetter, eastern side of the Andean cordillera. Populations on the western side are usually associated with cultivation. In the Galápagos Islands, "cerasiforme" and the closely related *S. pimpinellifolium* probably escaped from cultivation (Rick 1956) and have in some places become more common than the two native species, *S. cheesmaniae* and *S. galapagense* (Darwin et al. 2003; Nuez et al. 2004). *S. lycopersicum* "cerasiforme" has often been referred to as "var. *cerasiforme*" in the literature, but that name has never been validly published under the rules of botanical naming and thus should not be used (see Peralta et al. 2008). Cherry tomatoes have also been shown to be complex genetic admixtures of *S. lycopersicum* and *S. pimpinellifolium* (Ranc et al. 2008), thus their true native distribution is not known.

The wild currant tomato, *S. pimpinellifolium,* is found along the Pacific coast and at low to mid elevations on the western slopes of the Andes, from southern Peru (Dept. Tacna) to Ecuador (Prov. Esmeraldas). Most populations have been collected below 1,000 m, however many of these have disappeared in the wild due to intensive agriculture and urbanization (see below). A small number (but increasing, see Darwin et al. 2003) of populations are present on the Galápagos Islands, but probably represent recent introductions (note that this does not include the native populations C. M. Rick referred to in early publications as the "*pimpinellifolium* type" – these are now considered part of *S. cheesmaniae*, see Darwin et al. 2003). Often growing as a weed in and around farm fields, *S. pimpinellifolium* has been found in cultivated areas outside the native region. Unlike "cerasiforme," *S. pimpinellifolium* appears to be adapted to the relatively arid conditions of coastal Peru (Nakazato et al. 2008).

The Galápagos endemics *S. cheesmaniae* and *S. galapagense* are each found on several of the islands, although their numbers have been reduced in recent years by goats and other grazers. The more common of the two, *S. galapagense* is found on at least eight of the main islands: Bartolomé, Fernandina, Floreana (including Corona del Diablo and Gardner islets), Isabela, Pinta, Pinzón, Rabida, Santiago, and possibly Santa Cruz. It abounds in the arid, lower life zones, often on rocky outcrops of lava. Occasional populations grow near the shoreline and are tolerant of saline conditions (Rick 1973; Rush and Epstein 1981). Populations from the littoral zone are more common during El Niño years when rainfall is more abundant at lower elevations. For example, the Tomato Genetics Resource Center's (TGRC) sole accession of *S. galapagense* from the tiny Corona del Diablo islet was collected in 1972, an El Niño year – a repeat visit in 1986, a dry year, turned up nothing (R. Bowman personal communication). Most populations of *S. galapagense* are found below 200 m elevation, but on the larger islands may extend into the forested belt up to 650 m on the slopes of the volcanoes. The closely related *S. cheesmaniae* is known from seven islands: Baltra, Fernandina, Isabela, Pinzón, San Cristóbal, Santa Cruz, and Santa Fe. Populations can be found from approximately sea level to 1,500 m, including each of the main life zones, from the littoral to the summits of the volcanoes. Where the two species overlap, *S. cheesmaniae* tends to occupy the cooler, more shady sites, and *S. galapagense* the hotter, drier locations (Rick 1956).

The sister taxa *S. chmielewskii* and *S. neorickii* are concentrated in the inter-Andean valleys of Peru and Ecuador, and no populations of either species are known from the west slopes of the Andes or east of the main cordilleras (Rick et al. 1976). Less widespread, *S. chmielewskii* is found only in southern Peru (Depts. Apurimac, Ayacucho and Cusco) and the adjacent dry Sorata valley of northern Bolivia (Peralta et al. 2008). *S. chmielewskii* overlaps in Peru with *S. neorickii*, the latter extending into southern Ecuador (Provs. Azuay and Loja). Sympatric populations are known from a number of sites (Rick et al. 1976; http://tgrc.ucdavis.edu).

Populations of *S. arcanum* are also concentrated in the inter-Andean valleys – principally the watersheds

Fig. 9.1 Habitats of wild tomatoes and allied *Solanum* species growing in the native region. (**a**) *S. peruvianum* growing in an agricultural field (LA4318, Soro-Molinos, Arica and Parinacota, Chile); (**b**) *S. lycopersicoides* growing on exposed slopes at over 3,600 m (LA4323, Putre, Arica and Parinacota, Chile); (**c**) *S. chilense* growing in a dry wash (LA4334, Quebrada Sicipo, Antofagasta, Chile); (**d**) *S. habrochaites* growing in mesic site along road bank (LA2722, Puente Auco, Río Cañete, Lima, Perú); (**e**) *S. pennellii* on arid, rocky slope (LA1282, Sisacaya, Río Lurin, Lima, Perú); (**f**) *S. juglandifolium* growing in tropical forest (LA2134, Tinajillas, Zamora-Chinchipe, Ecuador); (**g**) *S. arcanum* plant scrambling down rock wall (LA2150, Puente Muyuno, Río Jequetepeque, Cajamarca, Perú). More information is available at http://tgrc.ucdavis.edu [Photos **a**–**c** by CM Jones, **d** and **e** by RT Chetelat, and **f** and **g** by CM Rick.]

of the Río Marañon, Río Chamaya, Río Chotano, and Río Moche – and coastal valleys, especially the Río Jequetepeque (Rick 1986c). In addition, populations of *S. arcanum* extend to the coast, at least in some years, as suggested by the many herbarium specimens collected in the "lomas" (Peralta et al. 2008). The altitudinal range for this species is thus quite broad, from below 500 m to nearly 3,000 m (Fig. 9.1g).

Populations of *S. peruvianum* are widespread in central and southern Peru, extending as far north as Dept. Cajamarca and south into the Regions of Arica/Parinacota and Tarapaca in Chile. Growing

exclusively on the lower western slopes of the Andes and along the coast in lomas habitats, S. peruvianum has a narrow altitudinal range, from approximately sea level to 600 m (Peralta et al. 2008). It often grows in and around agricultural fields (Fig. 9.1a). The distribution of *S. corneliomulleri* is similar and overlapping, from central to southern Peru, but it occurs mostly at mid to high elevations on the western slopes of the Andes. The affiliated species *S. huaylasense* has a much more limited distribution, being found only in the watersheds of the Río Santa (Callejon de Huaylas region) and Río Fortaleza.

The geographic distribution of *S. chilense* extends from southern Peru (Dept. Arequipa) to northern Chile (Antofagasta Region), and from 80 to 3,600 m elevation. Its range overlaps with that of *S. peruvianum*, and the two are sympatric at several sites in Chile. In the drainages where both species are found, *S. chilense* tends to grow to higher elevations and in more arid situations, and generally avoids disturbed sites (Fig. 9.1c). A small number of marginal *S. chilense* populations have been collected as far north as Dept. Ica in Peru (Rick 1990) and are unusual in being polyploid (see below). At the other end of the distribution, the populations around Taltal, Chile, are the southernmost and are morphologically distinctive in several respects (Chetelat et al. 2009); leaves are exceptionally hairy and highly subdivided, and inflorescences are relatively short. Among the populations from coastal Chile, only the Taltal material grows to below 100 m elevation, a trend attributed to more abundant precipitation there than at sites to the north. The easternmost group of populations, located in the drainages to the east of the Salar de Atacama, is also recognizable morphologically from the rest of the species; leaves are glossy (nearly glabrous) green, with broad segments. The Atacama populations grow at higher elevations (up to 3,600 m) and at greater distance from the equator than of any other member of sect. *Lycopersicon* (exceeded only by *S. lycopersicoides*), and thus are a potential source of tolerance to low temperatures. Other abiotic stresses, to which *S. chilense* appears well adapted on the basis of its geographic distribution, include extreme aridity and soil salinity (Chetelat et al. 2009).

The geographic range of *S. habrochaites* extends from southern Ecuador (Prov. Manabi) to southern Peru (Dept. Ayacucho), and from 40 to 3,300 m elevation. In Peru, populations are found mostly at mid to high elevations in the river drainages, generally in less arid situations (Fig. 9.1d) and at higher elevations than *S. peruvianum,* with which it overlaps. In Ecuador, *S. habrochaites* is more broadly distributed (i.e., less restricted to river valleys), and some populations are morphologically distinctive (formerly recognized as *L. hirsutum* f. *glabratum*), with more slender stems, less upright growth, nearly glabrous leaves, and higher levels of anthocyanins compared to the more typical Peruvian material.

Populations of *S. pennellii* are found at relatively low elevations (10–1,940 m) along the coast, in Peru (Depts. Piura to Arequipa), and with a few collections known from northern Chile. This species is found on arid slopes and dry washes (Fig. 9.1e). The extreme drought tolerance of *S. pennellii* has been attributed to several factors: a tighter control of transpiration, increased water use efficiency (WUE), and tolerance of soil salinity (Yu 1972; Mittova et al. 2004; Xu et al. 2008). Populations from the northern margins (Bayovar and El Horador sites) are distinguishable from the rest of the species by their pedicel articulation, which is in the mid, instead of the basal, position. The populations from the vicinity of Nazca (Dept. Ica) differ from the rest of the species by their near absence of hairs on stems and leaves, relatively small leaflets with smooth (entire) margins, and more diminutive stature; on the basis of these traits they were recognized formerly as a subspecies (*L. pennellii* var. *puberulum*).

The sister taxa *S. juglandifolium* and *S. ochranthum* (comprising *Solanum* sect. *Juglandifolia*) are found at mid to high elevations in the valleys between the major cordilleras of the Andes. The natural range of *S. juglandifolium* is from northeastern Columbia (Dept. Santander) to southern Ecuador (Prov. Zamora-Chinchipe), and from ca. 1,200 to 3,100 m elevation (Rick 1988; Peralta et al. 2008). The large number of herbarium specimens collected for this species contrasts with the relatively few ex situ seed collections available – at the TGRC, eight accessions total, only one of which is from Colombia (http://tgrc.ucdavis.edu). Occupying a larger geographic range, *S. ochranthum* can be found from central Colombia to southern Peru (Dept. Apurimac). Its altitudinal range is relatively broad: 1,900–4,100 m, however most populations are in the 2,000–3,200 m range (Smith and Peralta 2002; Peralta et al. 2008). Where these two species occur in the same region, *S. ochranthum* is

generally found at higher elevations than *S. juglandifolium* (Smith and Peralta 2002). The two species grow as rampant bushes or climbing lianas, with stems up to 30 m in length in the case of *S. ochranthum* (Rick 1988). Both prefer relatively mesic sites such as stream beds or tropical forest (Fig. 9.1f). The two have a similar morphology, but *S. juglandifolium* is generally more diminutive in the size of its plant parts, especially leaves, stems, and fruit; leaflets are also fewer in number, though broader in dimensions, and have a rough, scabrous surface texture compared to the softer feel of *S. ochranthum.*

The last two species to be considered herein, *S. lycopersicoides* and *S. sitiens*, form another pair of sister taxa (sect. *Lycopersicoides*). Both have narrow geographic ranges. Growing in no more than six river drainages, *S. lycopersicoides* is confined to deep canyons and slopes around the Chile/Peru frontier. While its altitudinal range is relatively broad (from 1,200 to 3,700 m), it tends to be more common at the higher elevations. This species overlaps with *S. chilense* and *S. peruvianum*, but grows higher – the highest of any tomato species, a likely indicator of low temperature adaptation – and more often on the cooler, less arid south-facing sides of the valleys (Fig. 9.1b). Endemic to Chile, *S. sitiens* grows only within a small part of the Atacama desert, on slopes to the northwest and south of Calama, and in a relatively narrow altitudinal belt of ca. 2,400–3,500 m. Often growing on exposed slopes, or in broad dry washes, *S. sitiens* occupies the most arid sites of any of the wild tomatoes (Chetelat et al. 2009). At many locations, it is the only perennial plant that can survive. Soil tests also point to an ability to tolerate high levels of salinity.

9.2.3 Geographic Distribution of Diversity

Genetic diversity within and between wild tomato populations is often structured in relation to their geographic distribution. Populations may be physically isolated from one another (fragmented) in their native distributions, with gene flow within a species restricted by distance and/or major geographic barriers such as deserts or mountain ranges. In addition, processes of adaptation to local conditions and genetic drift contribute to differentiation of populations. Thus, populations from one part of the geographic distribution – north to south, one river drainage to the next, low to high elevation, etc. – tend to be genetically differentiated from other populations.

The first detailed studies of natural variation in the wild tomatoes were those carried out by C. M. Rick and colleagues in the 1970s and 1980s. Using allozyme markers, they showed that diversity within populations of *S. pimpinellifolium* and *S. habrochaites* is highest in the geographic centers of their respective distributions, and that on the northern and southern margins, genetic variation tends to be depleted. For both species, the centers of highest diversity are in northern Peru. On the geographic margins, populations display changes in flower morphology and/or incompatibility systems that promote inbreeding over outcrossing. For example, the "central" populations of *S. pimpinellifolium* typically have relatively large flowers, with long anthers and exserted stigmas, all traits that in entomophilous flowers tend to increase the rate of outcrossing, and thus maintain diversity (Rick et al. 1977, 1978). The "southern" and "northern" populations on the other hand have relatively small flowers and stigmas that are only slightly exposed to visiting insects. A similar trend is seen in *S. habrochaites*; large flowers, exhibiting self-incompatibility (SI) – and thus strictly allogamous – in the center of the distribution, and smaller, self-compatible (SC) flowers on the margins of the distribution (Rick et al. 1979). Furthermore the northern and southern elements are morphologically distinctive from one another (see above) and show clear genetic differentiation. Crosses between the northern and southern SC races demonstrated that the loss of SI appears to have occurred via independent mutations in each group (Rick and Chetelat 1995).

Similar trends, though less pronounced, of north–south differentiation are seen in some of the other wild tomato species. For example, accessions of *S. pennellii* from the central region show the highest diversity and are strictly allogamous (SI). Self-compatibility (SC) occurs among accessions on the southern margin (Río Atico and Río Majes drainages), which tend to be highly inbred (Rick and Tanksley 1981). One of these, LA0716 from Puerto Atico, Peru, has been widely used for genetic studies in part because it is highly homozygous and polymorphic relative to the cultivated tomato, with which it can be easily hybridized. Accessions from the northern limits of the

distribution, while retaining SI, are morphologically distinctive (see above). In the *S. peruvianum* complex, a highly diverse group recently subdivided to recognize three new species (Peralta et al. 2008), the vast majority of accessions are SI. Rare SC populations are found at or near the southern (LA4125, Río Camiña) and northern (LA2157, Río Chota) limits of the distribution (Rick 1986c; Graham et al. 2003). All populations of *S. chilense, S. lycopersicoides,* and *S. sitiens* are SI, yet in each case the marginal populations show evidence of genetic differentiation from populations in the center of their respective geographic distributions. Two accessions collected at/near the northern margins of *S. lycopersicoides* and *S. sitiens* (LA2387 and LA4114, respectively) are morphologically distinctive; they are the only accessions of either species that exhibit yellow anthers, white or cream colored anthers being the norm for both taxa (Chetelat et al. 2009). Studies of genetic relationships between populations also reveal a strong geographic structure, with northern, central, and southern elements identifiable in both species (Albrecht et al. 2010).

Within *S. chilense,* four geographic races can be readily distinguished morphologically: a northern ("Acari" race), central, southwestern ("Taltal" race), and southeastern ("Atacama") (Graham 2005). Each of the groups is geographically isolated from the others. Experimental hybridization between the northern, central, and southwestern assemblages results in reduced seed set, indicating partial reproductive barriers are developing in this species.

Genetic diversity within the cherry tomato, *S. lycopersicum* "cerasiforme," follows a different geographic pattern. Early studies with allozyme markers indicated that within the Andean region, the greatest diversity is found in the San Martín and Ayacucho areas (Rick and Holle 1990). Diversity decreased to the north and south. High levels of diversity within the Tarapoto (Dept. San Martín) region suggested the possibility of hybridization and introgression with cultivars. Subsequent studies with DNA-based markers provided further evidence for hybridization with introduced cultivars (Williams and St. Clair 1993), and supported the suggestion that the Andean region was the primary center of diversity for "cerasiforme" (Villand et al. 1998).

The preceding information related to geographic trends derives primarily from herbarium records and notes from plant collectors. These records provide a historical view of each species broadest natural range, and thus do not reflect recent changes, notably those caused by human influences. Wild tomatoes are threatened in their native area by a variety of anthropogenic factors, including loss of habitat, agricultural development, overgrazing, mining, and other aspects of urban expansion and economic development. In the coastal river valleys of Peru, modern agricultural practices appear to have contributed to the loss of many populations known from earlier collections. Wild tomatoes have largely disappeared from the lower stretches of river valleys and around cities. On the Galápagos Islands, the endemic tomato species have become rare – goats are a likely culprit – while nonnative cherry and currant tomatoes are now common (Darwin et al. 2003; Nuez et al. 2004). Similar changes are occurring throughout the Andean region. Many populations known from herbarium specimens or genebank collections no longer exist in situ.

9.2.4 Morphology

Only a summary of morphological characters need be presented here, as a detailed description is available elsewhere (Peralta et al. 2008). The wild tomatoes and affiliated *Solanum* species have in common several basic morphological characteristics. Most grow as short-lived, herbaceous perennials in the native environment. It is common to find evidence of several years of growth. The base of plants often becomes woody, and some species appear to be capable of generating new shoots at or below the soil level. Most noteworthy in this regard is *S. sitiens*, plants of which are sometimes comprised mostly of dead branches, with only a few green shoots emerging from the crown (Chetelat et al. 2009).

Shoot growth is normally indeterminate, with each branch consisting of a repeating sequence of two or more leaves and an inflorescence, which together comprise a sympodium. At the base of each leaf, an axillary shoot is normally present. Growth of each sympodium terminates with the inflorescence, the next sympodium being produced by outgrowth of what would otherwise be an axillary meristem. The number of leaves between successive inflorescences – the sympodial index – is generally constant, once flowering begins in earnest. The sympodial index is

2–3 in species of sect. *Lycopersicon*; in the remaining species the alternation of leaves and flowers is less regular, and all tend to produce more leaves and fewer flowers. Plants of *S. ochranthum* and *S. juglandifolium* produce many leaves between inflorescences Peralta et al. (2008).

Plant habit also varies significantly among the species. A sprawling, decumbent growth habit is the most common (e.g., *S. pimpinellifolium, S. peruvianum,* and others). A more bushy, erect form of growth is seen in *S. lycopersicoides, S. sitiens, S. chilense,* and *S. galapagense*. A climbing vine-like growth habit is exhibited by *S. ochranthum* and *S. juglandifolium*; individual shoots of the former species can grow to 15 m or more, often clambering into or over trees and shrubs (Rick 1988).

Leaves are pinnately compound, with the number, size, shape, and relative dimensions of leaflets varying considerably between and within species. Leaflets may be further subdivided into secondary leaflets. Leaflets are connected, via petiolules, to the leaf rachis generally in pairs of primary lateral leaflets, with smaller interstitial leaflets in between. A petiole connects each leaf to the stem. Stipules or pseudostipular leaves are present at the base of the petiole in some species. Leaf surfaces are densely pubescent with several types of unbranched trichomes – unicellular, multicellular, and glandular – the density and types of hairs varying between and within species. Both *S. habrochaites* and *S. pennellii* are densely pubescent, yet each includes populations – previously recognized taxonomically as *L. hirsutum* f. *glabratum* and *L. pennellii* var. *puberulum* – that are much less hairy or nearly glabrous. Leaves of *S. juglandifolium* are rough textured and scabrous, with a prominent network of veins.

Flowers are born on cymose inflorescences, which may be simple (single cyme) or compound (more than one cyme), in the latter case with a variable number of dichotomous branch points. In some species, floral bracts are present at the base of the inflorescence and sometimes at each branch point within the inflorescence. Branched inflorescences are seen in *S. chilense, S. habrochaites, S. huaylasense, S. pennellii*, *S. peruvianum*, sect. *Juglandifolia,* and sect. *Lycopersicoides*. The other species more commonly produce unbranched inflorescences. Flowers are attached to the inflorescence by a pedicel that is articulated (i.e., position of the abscission zone) more or less midway between flower and inflorescence. Pedicel articulation in *S. pennellii* is strongly basal on the inflorescence, although some populations from the northern margin of its distribution are articulated in the middle. In the species of sect. *Lycopersicoides* and some *S. habrochaites* accessions, the pedicel joint is closer to the flower than the inflorescence rhachis.

The flower structure of the wild tomatoes resembles the typical *Solanum* flower in many respects. Flowers are composed of four whorls of organs: carpels, stamens, petals, and sepals. The innermost whorl normally consists of two carpels (the number may vary) fused together to form the pistil consisting of ovary, style, and stigma. The remaining whorls are generally five-parted, though this number also varies. The stamen whorl consists of stamens, which in *Solanum* sect. *Lycopersicon* are generally attached via interlocking hairs. Pollen is released through ovoid pores that quickly lengthen to longitudinal slits in the anthers. The tips of anthers are sterile (i.e., contain no pollen) except in *S. pennellii*. Anthers are various shades of yellow, and mostly straight or recurved downwards, as in *S. peruvianum* and *S. pennellii*. Style length and morphology vary considerably. In the outcrossing SI species, styles are longer that the anthers and stigmas are exserted several millimeter beyond the end of the anther cone. In the SC inbreeding species, stigmas are flush with the anther cone or slightly exserted. Styles are essentially straight in most species, but in *S. pennellii, S. lycopersicoides,* and *S. sitiens* styles are prominently bent or recurved where they protrude past the anthers. Petals and sepals are each fused to form a radially symmetrical (regular) corolla and calyx. No noticeable scent or nectar is produced.

A striking exception to this typical "Lycopersicon" flower structure is presented by *S. pennellii,* wherein anthers lack the sterile appendage and pollen grains are shed via terminal anther pores. Flowers are slightly irregular (zygomorphic), with the upper corolla segments being enlarged relative to the lower ones. Flowers of sect. *Lycopersicoides* and sect. *Juglandifolia* show additional structural differences. Pollen is shed via terminal pores which extend laterally. Anthers in sect. *Lycopersicoides* are white or cream colored, with occasional yellow variants in some populations. In sect. *Juglandifolia,* anthers are orange-yellow. Flowers of all four species are noticeably scented, the odor varying from species to species.

9.2.5 Cytology and Karyotype

The species considered herein are virtually all diploids, with $2n = 2x = 24$ chromosomes, like most other *Solanum* spp. The only reported exceptions are two cases of naturally occurring tetraploidy, both in *S. chilense* (Rick 1990). These appear to be marginal populations; one is from the northernmost locality for this species (LA1917, Llauta, Río Palpa, Dept. Ica, Peru), and is relatively infertile. Polyploidy is thus uncommon in the wild tomatoes.

Eleven of the 12 chromosome pairs are submetacentric. Chromosome 2 (the chromosomes are numbered 1–12 from longest to shortest at pachytene) is acrocentric, containing only a very short and heterochromatic short arm, which contains the nucleolus organizing region (NOR). At the pachytene stage of meiosis, each of the 12 chromosomes can be identified by the position of the centromere, the relative lengths of long and short arms, and the lengths of heterochromatic and euchromatic regions (Khush 1963; Sherman and Stack 1995).

The classical studies of chromosome morphology, based on light microscopy, revealed relatively little structural variation among the wild species. For example, hybrids between cultivated tomato and *S. pennellii*, two of the most distantly related species in sect. *Lycopersicon*, showed relatively few differences in chromosome structure at pachytene by light microscopy, and these were limited to the number and positions of heterochromatic knobs on certain chromosomes (Khush and Rick 1963). Other interspecific hybrids within the tomato clade gave a similar impression of overall colinearity in the early cytological work (reviewed by Chetelat and Ji 2007). However, this view is beginning to change, as new evidence of rearrangements and structural differences has emerged from higher resolution genetic and physical maps, and from improved cytological methods.

Comparative genetic linkage maps of the *S. lycopersicoides* and *S. sitiens* genomes show they differ from tomato by a paracentric inversion of the long arm of chromosome 10 (Pertuzé et al. 2002). This finding is consistent with the occasional inversion loops seen in *S. lycopersicum* × *S. lycopersicoides* hybrids (Menzel 1962), and the strongly suppressed recombination seen in this region (Chetelat et al. 2000). Surprisingly, this inversion was not seen with bacterial artificial chromosome-fluorescence in situ hybridization (BAC-FISH) (Szinay 2010). Assuming it is real, the 10L inversion must have occurred within the lineage leading to tomato, since the ancestral arrangement is found in all other Solanaceae examined to date (Livingstone et al. 1999; Doganlar et al. 2002a), but prior to divergence of the tomato species since their genomes appear to be collinear in this region. Interestingly, both *S. ochranthum* and *S. juglandifolium* have the inverted (i.e., tomato) orientation of chromosome 10L, suggesting they are more closely related to the tomatoes (Albrecht and Chetelat 2009) than are members of sect. *Lycopersicoides*. This interpretation is consistent with recent molecular phylogenies (Peralta et al. 2008, and see below), but contrasts with the evidence from crossing relationships, which point instead to sect. *Lycopersicoides* as being more tomato-like.

Short, proximal inversions were detected on chromosome 6S in *S. peruvianum* (Seah et al. 2004), chromosome 7S in *S. pennellii* (van der Knaap et al. 2004), and chromosome 12S in *S. chilense* (Szinay 2010), relative to cultivated tomato. A reciprocal whole arm translocation involving chromosomes 8 and 12 occurred in either *S. ochranthum* or *S. juglandifolium* (Albrecht and Chetelat 2009).

By studying the synaptonemal complexes of several interspecific tomato hybrids using electron microscopy, Stack et al. (2009) revealed a series of chromosome rearrangements, including inversions, translocations, length differences, and mismatched kinetochores. The number of structural rearrangements was generally consistent with phylogenetic expectations; *S. lycopersicum* × *S. pimpinellifolium* hybrids showed fewer structural changes than *S. lycopersicum* × *S. pennellii* hybrids, for instance. However, the *S. chmielewskii* hybrid revealed a greater than expected number of changes. Despite these examples of genome changes, overall gene order amongst the wild tomatoes and related *Solanum* is highly conserved, a fact that in large part explains their great practical usefulness.

9.2.6 Genome Size and Composition

Genome sizes have not been determined for all of the wild tomato species, but the data available are

sufficient to indicate considerable variation. Estimates of the DNA content for the cultivated tomato, *S. lycopersicum,* vary from 1.88 to 2.07 pg/2C for a sample of six cultivars and 1.83 pg/2C for the closely related *S. cheesmaniae* (Arumuganathan and Earle 1991). The basal taxon in the core tomato clade, *S. pennellii*, has a larger genome size (2.47–2.77 pg/2C), while *S. peruvianum* is intermediate (2.27 pg/2C) (Arumuganathan and Earle 1991). Two other species, *S. habrochaites* and *S. pimpinellifolium*, have slightly smaller genomes (1.85 and 1.77 pg/2C, respectively) (Bennett and Smith 1976). The genome sizes of the sect. *Juglandifolia* species (1.75–1.96 pg/2C) are similar to the more compact tomato genomes, whereas those of the sect. *Lycopersicoides* group (2.43–2.69 pg/2C) are about 25% larger (Chetelat 2009).

In map units, the genome size of the tomatoes is approximately 1,200–1,400 centiMorgans (cM) (Tanksley et al. 1992; Frary et al. 2005). These values are based on recombination in F_1 interspecific *S. lycopersicum* × *S. pennellii* hybrids, and thus might be biased by sequence divergence or selection. Recombination rates in intraspecific maps appear to be similar, but a little lower (the lower marker polymorphism rate may be a contributing factor); a map for *S. peruvianum* contained 1,073 cM (van Ooijen et al. 1994), and one for *S. lycopersicum* only 965 cM (Saliba-Colombani et al. 2000).

The tomato genome is comprised of approximately 75% heterochromatin, most of which is located in the pericentromeric regions (Peterson et al. 1996). The remaining 25% of the genome is euchromatin and located in segments distal to the pericentromeric heterochromatin on each chromosome arm. The majority of expressed genes are thought to be located in the euchromatin fraction, an inference supported by several lines of evidence. Mapping of induced deletions to pachytene chromosomes showed that most mutant loci are in euchromatin (Khush and Rick 1968). Sequencing of BACs found a much higher gene density per unit DNA length in inserts from euchromatin than heterochromatin (van der Hoeven et al. 2002; Wang et al. 2006). Finally, recombination is generally higher in gene rich regions, whereas tomato heterochromatin is recombinationally inert. Mapping of recombination nodules on synaptonemal complexes showed that the pericentromeric heterochromatin portion of each chromosome is nearly devoid of crossovers (Sherman and Stack 1995), a result consistent with genetic evidence of crossover suppression around centromeres (Tanksley et al. 1992).

9.3 Evolutionary Relationships of *Solanum* Section *Lycopersicon* (Tomatoes) and Allied Species

9.3.1 The Generic Position of Tomatoes and Wild Relatives

Wild tomatoes (sensu stricto) traditionally were treated as members of the genus *Lycopersicon* Mill., mainly based on the anther morphology (D'Arcy 1972; Hunziker 2001). In the past decade, several molecular phylogenetic studies of the Solanaceae have unambiguously showed tomatoes to be deeply nested within *Solanum* (Spooner et al. 1993, 2005; Bohs and Olmstead 1997, 1999; Olmstead and Palmer 1997; Olmstead et al. 1999; Peralta and Spooner 2001; Bohs 2005). Data from chloroplast DNA (cpDNA) sequences strongly support a monophyletic *Solanum* (Bohs 2005; Weese and Bohs 2007) with the inclusion of all traditional segregate genera; *Cyphomandra* Mart. ex Sendtn. (Bohs 1995), *Lycopersicon* Mill. (Spooner et al. 1993), *Normania* Lowe, and *Triguera* Cav. (Bohs and Olmstead 2001). Some workers (e.g., Hunziker 2001) continue to maintain these taxa as distinct genera. The monophyletic *Solanum* is one of the ten most species-rich genera of angiosperms (Frodin 2004; see also Solanaceae Source, http://www.solanaceae-source.org), and contains several crops of economic importance such as the tomato (*S. lycopersicum*), the potato (*S. tuberosum* L.) and the aubergine or eggplant (*S. melongena* L.), as well as other minor crops (naranjilla, *S. quitoense* Lam.; tamarillo, *S. betaceum* Cav. and pepino, *S. muricatum* Aiton).

The tomatoes and their close relatives are easily distinguished from any other group of *Solanum* species by their bright yellow flowers and pinnatifid, non-spiny leaves; the only other species in the genus with yellow flowers is *S. rostratum* Dunal, a member of sect. *Androceras* (Nutt.) Whalen (1979). The tomatoes are most closely related to the potatoes and form a distinct clade (the Potato clade, sensu Bohs 2005; Weese and Bohs 2007) with relatively high (80%)

bootstrap support (Bohs 2005). Peralta et al. (2008) presented a phylogenetic classification of the group that simply states the hypothesis that tomatoes have more "predictivity" under *Solanum*; they also apply a Linnaean nomenclatural system (hierarchical) to provide the valid names of wild species under *Solanum*. Here we provide a short discussion on the history of generic classification of the tomatoes and their wild relatives in sects. *Lycopersicoides* and *Juglandifolia*, and discuss in detail both traditional taxonomic schemes for species-level relationships and modern statistically based studies of these relationships.

9.3.2 History of the Generic Classification of Tomatoes and Wild Relatives

In his first edition of *The Gardener's Dictionary* (Miller 1731) Philip Miller, the English botanist and curator of the Chelsea Physic Garden, used the generic name *Lycopersicon* and included a number of taxa with multilocular fruits ("roundish, soft, fleshy Fruit, which is divided into several Cells, wherein are contained many flat Seeds"), all color variants of the cultivated tomato (*S. lycopersicum*). In this same work, he also recognized *Solanum*, and included within it the eggplant as "*Solanum Americanum, spinosum, foliis Melongenae, fructu mammoro*" and the potato as "*Solanum tuberosum, esculentum*" (Miller 1731). His definition of *Lycopersicon* was confined to plants we would today recognize as cultivars of *S. lycopersicum*, the cultivated tomato.

In *Species Plantarum*, Linnaeus (1753) classified tomatoes in the genus *Solanum*, and described *S. lycopersicum* and *S. peruvianum*. Jussieu (1789), in his classification, also included tomatoes in *Solanum*. Miller (1754), however, continued to use both the generic name *Lycopersicon* and polynomial nomenclature in the abridged 4th edition of *The Gardener's Dictionary*. He expanded his definition of *Lycopersicon* by including "*Lycopersicon radice tuberose, esculentum*" (the potato) within it, using the following reasoning (Miller 1754): "This Plant was always ranged in the Genus of *Solanum*, or Nightshade, and is now brought under that Title by *Dr. Linnaeus*; but as *Lycopersicon* has now been established as a distinct Genus, on account of the Fruit being divided into several Cells, by intermediate Partitions, and as the Fruit of this Plant [the potato] exactly agrees with the Characters of the other species of this Genus, I have inserted it here." The editor of the posthumously published edition of *The Gardener's and Botanist's Dictionary* (Miller 1807), Thomas Martyn, merged *Lycopersicon* and *Solanum*, and recognized all Miller's species as members of *Solanum*. A number of classical and modern authors have recognized the genus *Lycopersicon* (e.g., Dunal 1813, 1852; Bentham and Hooker 1873; Müller 1940; Luckwill 1943; Correll 1958; D'Arcy 1972, 1987, 1991; Hunziker 1979, 2001; Rick 1979, 1988; Child 1990; Rick et al. 1990; Symon 1981, 1985; Taylor 1986; Warnock 1988; Hawkes 1990), but others continued to recognize the tomatoes as members of the genus *Solanum* (MacBride 1962; Seithe 1962; Heine 1976; Fosberg 1987).

9.3.3 Relationships of the Species of Tomatoes and Their Wild Relatives

The species of tomatoes have been treated quite differently by different authors, both in terms of species identity (current species recognized in the group and their distributions are presented in Table 9.2) and in terms of group membership and relationships. Figure 9.2 shows the chronology of the differing classifications through the twentieth century and compares them to the classification of Peralta et al. (2008) that is used here.

Müller (1940) and Luckwill (1943) produced the two most complete taxonomic treatments of wild tomatoes based on morphological concepts, and treated them under *Lycopersicon*. Müller (1940) divided *Lycopersicon* into two subgenera: subg. *Eulycopersicon* possessing glabrous, and red- to orange- to yellow-colored fruits, flat, obovate, and silky pubescent seeds, ebracteate inflorescences, and leaves without pseudostipules; subg. *Eriópersicon* with pubescent or hirsute green or greenish white to yellowish and purple-tinged fruits, frequently with a dark green, lavender, or purple stripe, thick, oblanceolate glabrous (pilose only at the apex) seeds, bracteate inflorescences, and leaves usually with pseudostipules. Luckwill (1943) hypothesized that the two subgenera might

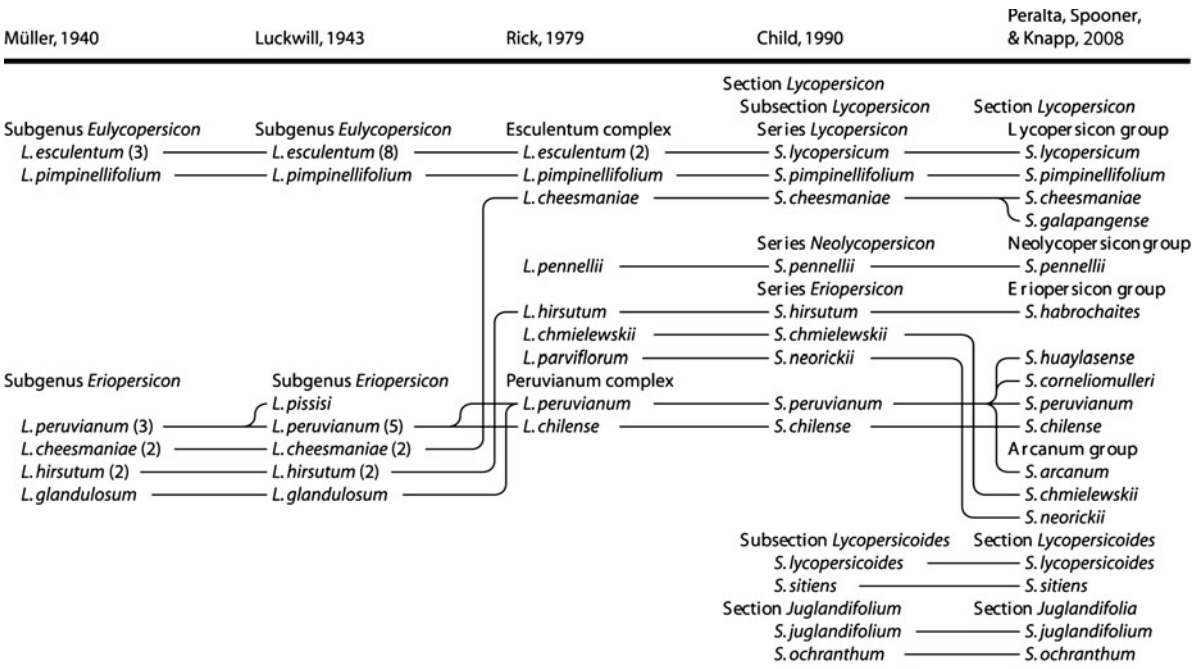

Fig. 9.2 Chronological flow chart of hypotheses of species boundaries and relationships of *Solanum* section *Lycopersicon*, section *Juglandifolia*, and section *Lycopersicoides* recognized by Müller (1940), Luckwill (1943), Child (1990), and Peralta et al. (2008). The *numbers* in *parentheses* represent the number of infraspecific taxa recognized by these authors. Modified and reproduced with permission from Syst Bot Monogr 84: 13, Fig 5 (2008)

have evolved from a simple ancestral form characterized by imparipinnate leaves with 5–7 entire leaflets, few interjected leaflets, probably no secondary leaflets, unbranched inflorescences, and undeveloped pseudostipules. He suggested that two lineages diverged from this ancestral form, one characterized by fruits with carotenoid pigments and the other by green fruits with anthocyanin pigments.

Rick (1979) recognized two "complexes" based on crossing relationships, the "Esculentum complex" and "Pervianum complex" (see Fig. 9.2). Rick (1986a) hypothesized that the races of his "*L. peruvianum*" found in the Río Marañón drainage in northern Peru were ancestral to all other wild tomatoes (*Solanum* sect. *Lycopersicon* as defined here), and that speciation and differentiation took place with migration to the south. Rick (1963) suggested that this distribution pattern pointed to a single origin of his broadly defined "*L. peruvianum*" with subsequent spread before or during the uplift of the central Andes.

Recent cladistic and phenetic studies of species boundaries and relationships within the tomatoes and wild relatives have used a combination of molecular and morphological data. Figure 9.3 shows abstracted summary trees based on cpDNA restriction sites (Palmer and Zamir 1982; Fig. 9.3a; Spooner et al. 1993; Fig. 9.3d), mitochondrial DNA (mtDNA) restriction sites (McClean and Hanson 1986; Fig. 9.3b), nuclear restriction fragment length polymorphisms (RFLPs) (Miller and Tanksley 1990; Fig. 9.3c), isozymes (Bretó et al. 1993; Fig. 9.3e), internal transcribed spacer (ITS) region of nuclear ribosomal DNA gene sequences (Marshall et al. 2001; Fig. 9.3f), nuclear DNA microsatellites (Alvarez et al. 2001; Fig. 9.3g), and morphology-based cladistics (Peralta and Spooner 2005; Fig. 9.3h). These phenetic and cladistic studies detailed below used a variety of statistical techniques and programs, the reader is referred to the primary literature for further details of specific algorithms used and parameters set.

The name *S. peruvianum* is used in three ways in the discussion of species relationships here. Firstly, *S. peruvianum* s.l. refers to the broadly circumscribed species complex prior to recognition of four species within it (Peralta et al. 2005). Second, *S. peruvianum* "north" and "south" refers to the geographic

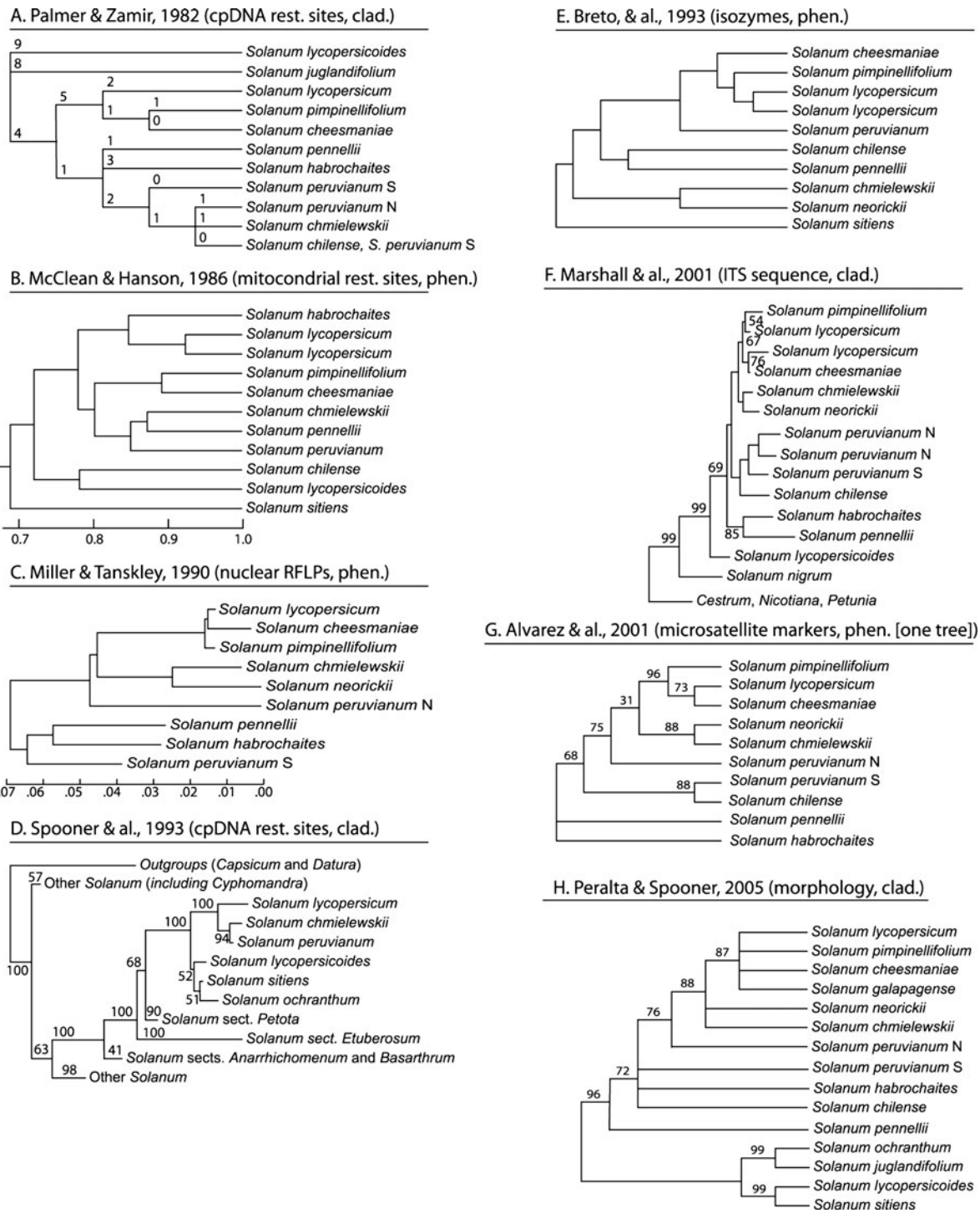

Fig. 9.3 An abstracted summary of cladistic (clad.) and phenetic (phen.) studies of tomatoes and outgroups using morphological, isozyme, and molecular data, including similarity coefficients (*lines below trees*, **b**, **c**) restriction sites supporting each branch (**a**), or bootstrap values over 50% (**d**, **f**, **g**, **h**); the study in **e** showed no statistics to support the *tree*. *Trees* are shortened when necessary to show summary results and use the *Solanum* equivalents of *Lycopersicon* names (see Table 9.2). The letters *N* and *S* following *S. peruvianum* indicate northern (N) and southern (S) accessions of that species corresponding to the companion GBSSI sequence study (Peralta and Spooner 2001), morphological study (Peralta and Spooner 2005) and AFLP study (Spooner et al. 2005) of tomatoes and outgroups (see text). Reproduced with permission from Taxon 54: 46, Fig. 2 (2005)

partitioning of *S. peruvianum* s.l. into two groups with the use of granule-bound starch synthase (GBSSI) (Peralta and Spooner 2001), morphological (Peralta and Spooner 2005), and amplified fragment length polymorphism (AFLP) data (Spooner et al. 2005). Third, in Peralta et al. (2008), based on the results of these three investigations and our examination of hundreds of additional herbarium specimens, *S. peruvianum* "north" was divided into *S. arcanum* and *S. huaylasense*, and *S. peruvianum* "south" into *S. corneliomulleri* and *S. peruvianum* s.str. (Peralta et al. 2005, 2008).

9.3.3.1 Chloroplast DNA Restriction Site Data

The cpDNA restriction site phylogenetic study of Palmer and Zamir (1982; Fig. 9.3a) was one of the first studies using this technique, and stimulated the use of chloroplast DNA in scores of other plant groups. The technique was soon refined to the use of heterologous probes, rather than total chloroplast banding patterns, to assess polymorphisms more accurately. Palmer and Zamir's (1982) study, using 25 restriction endonucleases, placed *S. lycopersicoides* (*Solanum* sect. *Lycopersicoides*) and *S. juglandifolium* (*Solanum* sect. *Juglandifolia*) as sister to tomatoes, and supported the monophyly of the red- to orange- to yellow-fruited species (*S. cheesmaniae*, *S. lycopersicum*, and *S. pimpinellifolium*). Palmer and Zamir's (1982) study was not able to place into separate clades the northern and southern populations of *S. peruvianum* or to solve the relationships of *S. chilense* and *S. chmielewskii*.

Spooner et al. (1993; Fig. 9.3d) examined cpDNA polymorphism of representatives of tomato, potato, other species of *Solanum*, and outgroups in *Capsicum* L. and *Datura* L. with a focus on examining outgroup relationships of tomato and potato. Their study showed tomatoes and their immediate outgroups in *Solanum* sect. *Lycopersicoides* and sect. *Juglandifolia* to form a sister clade to potatoes (sect. *Petota*), with *Solanum* sect. *Etuberosum* as the sister to all the above. These results stimulated the taxonomic recognition of all tomatoes in *Solanum*, which was also supported by other cpDNA restriction site and sequence data (Bohs and Olmstead 1997, 1999; Olmstead and Palmer 1997; Olmstead et al. 1999; Bohs 2005). These multiple datasets from a variety of genes unambiguously established tomatoes to be deeply nested in *Solanum*, and Spooner et al. (1993) made the necessary nomenclatural transfers. Treating tomatoes as members of *Solanum* is accepted by the majority of taxonomists as well as by most plant breeders and other users (e.g., Caicedo and Schaal 2004; Fridman et al. 2004; Schauer et al. 2005; Mueller et al. 2009; see also http://tgrc.ucdavis.edu/key.html).

9.3.3.2 GBSSI Sequence Data

Peralta and Spooner (2001) provided a GBSSI (granule-bound starch synthase, also often referred to as "waxy") gene sequence phylogeny of 79 accessions of tomatoes and outgroups, concentrating on the most geographically widespread and polymorphic species *S. peruvianum* s.l. These results (see Fig. 5 in Peralta and Spooner 2001) supported sect. *Juglandifolia* as sister to tomatoes; sect. *Lycopersicoides* as sister to tomatoes + sect. *Juglandifolia*; potatoes (sect. *Petota*) sister to tomatoes + sect. *Juglandifolia* + sect. *Lycopersicoides;* and sect. *Etuberosum* as sister to tomatoes + sect. *Juglandifolia* + sect. *Lycopersicoides* + sect. *Petota*. Within sect. *Lycopersicon*, there was a polytomy composed of *S. chilense*, *S. habrochaites*, and *S. pennellii*, and the central-southern Peruvian to northern Chilean populations of *S. peruvianum*. A sister clade contained the northern Peruvian populations of *S. chmielewskii, S. neorickii*, and *S. peruvianum*, and a monophyletic group composed of the SC and brightly colored (red- to orange- to yellow-fruited) species *S. cheesmaniae* (including accessions now recognized as *S. galapagense*), *S. lycopersicum*, and *S. pimpinellifolium*.

9.3.3.3 Internal Transcribed Spacer Region of Nuclear Ribosomal DNA Gene Sequences

Marshall et al. (2001) analyzed phylogenetic relationships of wild tomatoes with DNA sequences of the ITS region of nuclear ribosomal DNA (Fig. 9.3f). *Solanum lycopersicoides* was supported as sister to tomatoes (members of sect. *Juglandifolia* were not included in this study). *Solanum chilense* and S. *habrochaites* were supported as sister to all other tomatoes. *Solanum chilense* and northern and southern populations of

S. peruvianum formed a clade sister to *S. chilense* and *S. habrochaites*. *Solanum chmielewskii* and *S. neorickii* formed the next clade, followed by a clade of brightly colored-fruited species.

9.3.3.4 Morphological Phenetics and Cladistics

The phenetic morphological study of Peralta and Spooner (2005) used many of the same accessions as the GBSSI study described earlier. In total, 66 characters (50 quantitative and 16 qualitative) were measured for six individuals of 66 accessions, and averages of all six plants were taken as representative of the accession. Similarity matrices for the 61 characters found to be significantly different between at least two species were generated with various algorithms, and dendrograms were constructed with the unweighted pair group method (UPGMA) (see Figs. 6 and 7 in Peralta and Spooner 2005). The morphological distance phenogram had the best fit of the similarity matrix to the tree as determined by a cophenetic correlation coefficient (0.93), while the correlation matrix had a lower value (0.75). The distance phenogram defined four main groups. The outgroups, *S. lycopersicoides* and *S. sitiens*, cluster as the external branch (group D), followed by *S. galapagense*, and then a group of all three accessions of *S. pennellii* (group C). The SC, red- to orange- to yellow-fruited species (*S. lycopersicum*, *S. cheesmaniae*, and *S. pimpinellifolium*) form a third cluster (group A), but with the exclusion of the distinctive *S. galapagense*. The fourth group (B) includes the remaining species. Within group B, *S. neorickii* and two accessions of *S. chmielewskii* cluster together, to the exclusion of one accession of *S. chmielewskii* (LA1306) that grouped with all accessions of *S. arcanum*. All accessions of *S. chilense* formed a group that also contained one accession of *S. huaylasense* (LA1982). The three accessions of *S. habrochaites* formed a separate group. Two major groups were recognized within former *S. peruvianum*; the "northern" and the "southern." The "northern" *S. peruvianum* accessions are now recognized as the distinct species *S. arcanum* and *S. huaylasense*, and the "southern" ones as *S. peruvianum* s. str. and *S. corneliomulleri*.

The correlation UPGMA dendrogram had a lower cophenetic correlation (0.75; vs. distance, 0.93), but it placed *S. galapagense* with the other SC, red- to orange- to yellow-fruited species, and better grouped the former north and south populations of *S. peruvianum*. Unlike the distance phenogram, it placed the two outgroups, *S. lycopersicoides* and *S. sitiens*, as an internal branch with one of two main clusters (A). The three accessions of *S. habrochaites* formed a separate group, and also the three *S. pennellii* accessions clustered together. The other main branch (B) includes *S. arcanum*, *S. chilense*, *S. chmielewskii*, *S. corneliomulleri*, *S. huaylasense*, *S. neorickii*, and *S. peruvianum* s. str. This dendrogram, unlike the distance phenogram, shows better clustering of the former northern and southern *S. peruvianum* groups. Like the distance phenogram, *S. huaylasense* clustered with *S. chilense*, as part of a larger cluster that includes *S. corneliomulleri* and *S. peruvianum*. *S. arcanum, S. chmielewskii,* and *S. neorickii* cluster together.

Approximately one third of the morphological characters (24/66) could be scored as discrete for use in cladistic studies. A cladistic analysis of these characters in tomato and outgroups in sect. *Juglandifolia* and sect. *Lycopersicoides* supported *S. pennellii* as sister to all tomato species (see Fig. 8 in Peralta and Spooner 2005). The relationships among the self-incompatible (SI) species *Solanum chilense*, *S. habrochaites*, and *S. peruvianum* "southern" were not resolved. *Solanum peruvianum* "northern" appeared as sister to *S. chmielewskii* and *S. neorickii*. *Solanum chmielewskii* and *S. neorickii* always were sister to each other and these two sister to the monophyletic group formed by *S. cheesmaniae*, *S. galapagense*, *S. lycopersicum,* and *S. pimpinellifolium*.

9.3.3.5 AFLP Cladistics

Spooner et al. (2005) used four AFLP primer combinations to study the phylogenetic relationships of 65 accessions of tomato and outgroups, including most of the accessions corresponding to the GBSSI (Peralta and Spooner 2001) and morphological studies (Peralta and Spooner 2005) described earlier. A strict consensus tree of these 296 AFLP trees (see Fig. 7 in Spooner et al. 2005) support tomatoes (*Solanum* sect. *Lycopersicon*) and their immediate outgroup relatives in sect. *Juglandifolia* and sect. *Lycopersicoides* to form a sister clade to potatoes (sect. *Petota*) and further outgroups in sect. *Etuberosum*. *Solanum pennellii* and

S. habrochaites were part of a polytomy in sect. *Lycopersicon*. All red- or orange-fruited, SC species (*S. cheesmaniae*, *S. galapagense*, *S. lycopersicum*, *S. pimpinellifolium*) formed a well-supported clade. *Solanum chmielewskii*, *S. neorickii*, and four accessions of the SI *S. arcanum* from the Río Marañón drainage formed a clade. AFLP data, like the GBSSI and morphological data, show a clear separation of the northern and southern groups of *S. peruvianum* s. l., which includes *S. corneliomulleri* and *S. peruvianum* s. str. Only one accession from northern Peru (LA1984) grouped with the southern *S. peruvianum*. Interestingly, Rick (1986c) thought that this accession represented a "crossing bridge" between northern and southern populations of *S. peruvianum*. AFLP data, unlike morphological data, grouped *S. arcanum* with *S. huaylasense* instead of *S. chilense*.

9.3.3.6 Congruence Tests Among AFLP, cpDNA, GBSSI, ITS, and Morphological Studies

Spooner et al. (2005) tested congruence among AFLP, cpDNA (Palmer and Zamir 1982), GBSSI (Peralta and Spooner 2001), ITS (Marshall et al. 2001), and morphology (Peralta and Spooner 2005) datasets through three methods: (1) distance matrix-based comparisons (the Mantel test), (2) character-based comparisons (the incongruence length difference test (ILD), also called the partition homogeneity test of data partition congruence, of Farris et al. 1995), and (3) visual qualitative comparison of trees. Two comparative datasets were used: (1) A dataset containing 47 identical tomato accessions from AFLP and GBSSI studies and with one accession of *S. etuberosum* Lindl. as outgroup. (2) A smaller comparative dataset contained only 10 accessions that were common to all studies cited earlier (all tomato species were included except *S. neorickii* which was lacking from the cpDNA dataset; the northern and southern accessions of *S. peruvianum* were included as separate taxa; *S. lycopersicoides* was the common outgroup).

The distance-matrix test showed that all pairs of compared matrices were statistically correlated at $\alpha = 0.05$ except for GBSSI/ITS, GBSSI/morphology phenetics, and ITS/cpDNA. The matrix correlation coefficients of all comparisons varied greatly with AFLP/GBSSI the highest, and ITS/cpDNA the lowest. The character-based test showed the ITS/cpDNA, AFLP/GBSSI (both 10 and 48 taxon comparisons), the GBSSI/morphology, AFLP/ITS, GBSSI/ITS, AFLP/cpDNA, ITS/morphology, and AFLP/morphology datasets to be congruent. The other comparisons (cpDNA/morphology, cpDNA/GBSSI) proved to be incongruent.

9.3.3.7 Total Evidence Analysis of Chloroplast DNA, ITS, AFLP, and GBSSI

A combined AFLP and GBSSI Fitch tree (Spooner et al. 2005), consisting of 48 taxa and constructed with 1,652 characters, produced 34 most parsimonious 994-step trees with a consistency index of 0.35 and a retention index of 0.56. A strict consensus tree of these 34 trees (not shown) presented a topology very similar to that of the AFLP strict consensus tree (see Fig. 7 in Spooner et al. 2005; Peralta et al. 2008), including showing the relationship *S. chmielewskii*, *S. neorickii*, and four accessions of *S. arcanum*. A combined AFLP, GBSSI, cpDNA, ITS tree, and morphology analysis (10 taxa; 2,301 characters of which 148 were parsimony informative) produced two most-parsimonious 577-step trees with a consistency index of 0.816 and a retention index of 0.603. A strict consensus tree (Fig. 9.4) of these two trees showed (1) the brightly colored-fruited species as monophyletic, (2) *S. chmielewskii* and *S. arcanum* to be a sister clade to the above, (3) *S. chilense* and *S. peruvianum* s.s. and *S. corneliomulleri* to be a sister clade of the species above, (4) *S. habrochaites* and *S. pennellii* to be a well supported clade, but forming a polytomy. *Solanum lycopersicoides* was sister to tomatoes (sect. *Lycopersicon*). Members of sect. *Juglandifolia* were not included in this analysis.

9.3.4 Summary

The tomatoes and their wild relatives (sects. *Lycopersicoides*, *Juglandifolia* and *Lycopersicon*) are clearly monophyletic and sister to the potatoes (sect. *Petota*), with sect. *Etuberosum* clearly monophyletic and sister to potatoes + tomatoes s.l. Sect. *Lycopersicoides* (formerly recognized as a subsection of sect. *Lycopersicon*) is clearly monophyletic and sister to sect.

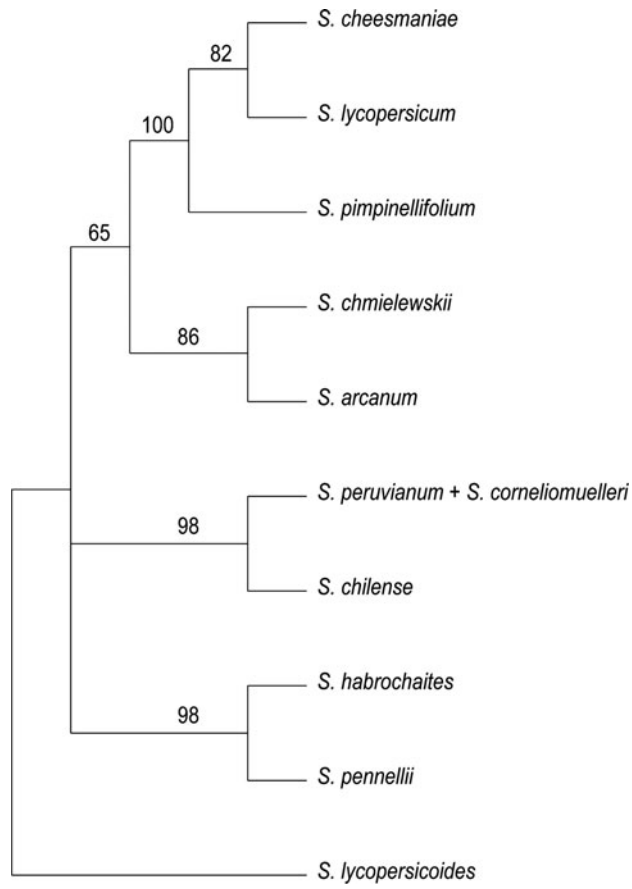

Fig. 9.4 The single combined AFLP, GBSSI, cpDNA, and ITS 530-step Fitch tree (10 taxa; 2,275 characters). The *numbers above* each *branch* represent bootstrap values over 50% (from Spooner et al. 2005). Modified and reproduced with permission from Syst Bot Monogr 84: 52, Fig. 18 (2008)

Juglandifolia + sect. *Lycopersicon*, and sect. *Juglandifolia* is clearly monophyletic and sister to sect. *Lycopersicon*.

Within sect. *Lycopersicon*, *S. pennellii* in most cases appears at the base of the trees as a polytomy with *S. habrochaites*, or sometimes forms a clade with this species. This relationship was considered unresolved by Peralta et al. (2008), although morphological data suggest that *S. pennellii* is sister to the rest of the tomatoes s.str. (sect. *Lycopersicon*); it is the only species in that group lacking the sterile anther appendage, the presence of which is a morphological synapomorphy of *S. habrochaites* and the rest of the core tomato clade. *S. pennellii* was placed by Peralta et al. (2008) in its own "group." Relationships within sect. *Lycopersicon* have been presented by Peralta et al. (2008) as informal species groups as given in Table 9.3. Such informal group systems of classification have been widely applied to *Solanum* by Whalen (1984), Knapp (1991, 2000, 2002), Bohs (1994, 2005), and Spooner et al. (2004). They are not intended to represent formal classification and are provisional names representing most highly supported ideas of relationships that are still unresolved.

Solanum huaylasense (a "northern" segregate of *S. peruvianum* s.l.) is grouped with *S. chilense*, *S. habrochaites*, *S. corneliomulleri* (a segregate of "southern" *S. peruvianum* s.l.), and *S. peruvianum* s. str. in the "Eriopersicon" species group (see Peralta et al. 2008). The SC green-fruited species *S. chmielewskii* and *S. neorickii* are related to *S. arcanum* (another northern segregate of *S. peruvianum* s.l.) as supported in almost all datasets and are recognized by Peralta et al. (2008) as the "Arcanum" species group. The four species with brightly colored fruits (*S. cheesmaniae*, *S. galapagense*, *S. lycopersicum*, *S. pimpinellifolium*) unambiguously form a closely related monophyletic group and are the closest relatives of the cultivated crop. These species with red to orange fruits could be recognized as a formal taxonomic group (as a series, for example), but this formal classification has not been taken up at present because of

Table 9.3 Classification of *Solanum* section *Lycopersicon* (tomatoes) and allied species (Peralta et al. 2008)

Section	Species group	Species
Section *Lycopersicoides*	–	*Solanum lycopersicoides*
–	–	*Solanum sitiens*
Section *Juglandifolia*	–	*Solanum juglandifolium*
–	–	*Solanum ochranthum*
Section *Lycopersicon*	"Neolycopersicon"	*Solanum pennellii*
–	"Eriopersicon"	*Solanum chilense*
–	–	*Solanum corneliomulleri*
–	–	*Solanum habrochaites*
–	–	*Solanum huaylasense*
–	–	*Solanum peruvianum*
–	"Arcanum"	*Solanum arcanum*
–	–	*Solanum chmielewskii*
–	–	*Solanum neorickii*
–	"Lycopersicon"	*Solanum cheesmaniae*
–	–	*Solanum galapagense*
–	–	*Solanum lycopersicum*
–	–	*Solanum pimpinellifolium*

Species within each group are in alphabetical order

ambiguity in the other species groups in sect. *Lycopersicon*.

9.4 Role in Development of Cytogenetic Stocks and Their Utility

The wild relatives of cultivated tomato have been used to develop several types of cytogenetic stocks. Of particular relevance here are the chromosome substitution and addition stocks. Other types of pre-breds, including ILs and backcross inbred lines (BILs), are not considered herein as they have been thoroughly covered in other recent reviews (Zamir and Eshed 1998a, b; Zamir 2001; Labate et al. 2007; Lippman et al. 2007; Grandillo et al. 2008).

Alien substitution lines and monosomic alien addition lines contain intact wild species' chromosomes in the genetic background of a standard tomato variety. The monosomic additions are trisomics ($2n + 1$), i.e., the foreign chromosome is added to a diploid tomato genome. In the substitution lines, the foreign chromosome replaces one or both of the corresponding tomato chromosomes (homeologs), and thus they are diploids. Monosomics ($2n - 1$) and other types of deficiency or deletion stocks are not commonly used in tomato because gametes carrying the deficient chromosomes generally fail to transmit through meiosis and gametogenesis (Khush and Rick 1966, 1968).

The first alien substitution lines in tomato contained chromosomes of *S. pennellii* in the background of *S. lycopersicum* (Rick 1969, 1971). They were obtained by backcrossing the wild parent to multiple marker stocks containing two or more morphological mutations, usually seedling expressed, located on a single chromosome. The *pennellii* chromosomes carried the wild type (dominant) alleles at each locus. Thus, selection for the non-mutant phenotype over several generations resulted in the replacement of one tomato chromosome by the homeologous chromosome of *S. pennellii*, as well as the progressive elimination of all other wild species chromosomes. After five or more backcross (BC) generations, homozygous substitutions were obtained by self-pollination. The method was rapid and inexpensive, but was limited by incomplete and uneven coverage of the chromosomes with convenient visual markers and dominance of the wild species alleles. For example, the chromosome 6 substitution was heterozygous; use of DNA-based markers (vastly more abundant) allowed isolation of the desired homozygous stock, and demonstrated a recombination event near the end of the chromosome that was not detected with the visual markers (Weide et al. 1993). A few alien substitution lines were also synthesized for *S. lycopersicoides* (Canady et al. 2005).

A complete set of monosomic alien addition lines in tomato was synthesized for *S. lycopersicoides*

(Chetelat et al. 1998) and a small number for *S. sitiens* (Pertuzé et al. 2003). These lines are relatively stable, because the extra wild species chromosomes tend to recombine at relatively low rates (Ji and Chetelat 2003). However, they are also relatively infertile and thus easily lost through poor seed set. The morphology of each monosomic addition is strikingly similar to the corresponding tomato trisomic. This observation is consistent with the observed colinearity of genetic maps for tomato and its wild relatives, including *S. lycopersicoides* (Pertuzé et al. 2002), suggesting a similar gene content of each chromosome.

Monosomic addition and substitution lines are potentially useful for a variety of genetic studies and breeding applications. In tomato, these stocks have been particularly useful for studies of genetic recombination between the alien chromosomes and their tomato homeologs. For example, in progeny of the *pennellii* substitution lines, recombination frequency was higher in early BC generations than in later ones, and higher in progeny of female than male meioses (Rick 1969, 1971). Similar trends were observed with the *lycopersicoides* substitution lines, which recombined at higher rates than either the monosomic additions or shorter, segmental introgressions, which recombined at only 0–10% of normal rates (Ji and Chetelat 2003; Canady et al. 2006). The low rates of genetic exchange between homeologous chromosomes may be due to competition by recombination within *homologous* chromosomes or chromosomal regions, a process that occurs in monosomic additions and segmental introgressions, but not heterozygous substitutions. Examination of chromosome pairing by genomic in situ hybridization (GISH) cytology indicated that the degree of pairing failure, as indicated by the formation of univalents, is correlated with the severity of recombination suppression. Pairing in the monosomic additions was more disrupted than the substitutions. Lines containing chromosome 10 of *S. lycopersicoides,* which carries a paracentric whole arm inversion relative to cultivated tomato, presented the most irregular pairing behavior. These results indicate that for future breeding purposes, substitution lines provide the best starting material for obtaining recombination events around a gene of interest.

9.5 Conservation Initiatives

9.5.1 Germplasm Collections

Tomato breeding and research can rely on a wide range of germplasm resources, which include extensive collections of wild forms and their derivatives (see recent reviews by Chetelat and Ji 2007; Ji and Scott 2007; Robertson and Labate 2007). The first collections of wild tomato species began in the eighteenth century in the region of their native distribution, which extends from northern Chile to southern Columbia and from the Pacific Ocean coast to the eastern foothills of the Andes, and the collection of this valuable material continues to this day.

Overall, there are more than 75,000 accessions of *Solanum* sect. *Lycopersicon* germplasm maintained in gene banks in more than 120 countries all around the world (for detail see review by Robertson and Labate 2007). The largest collections are hold at (1) the Asian Vegetable Research and Development Center (AVRDC), now referred to as The World Vegetable Center, located in Tainan, Taiwan; (2) the C. M. Rick Tomato Genetics Resource Center (TGRC), at the University of California-Davis; (3) the United States Department of Agriculture, Agricultural Research Service (USDA-ARS) Plant Genetic Resources Unit (PGRU) in Geneva, NY (Table 9.4).

The AVRDC was founded in 1971 with the mandate to increase vegetable production in the Asian tropics and is an international center affiliated with the Consultative Group of International Agricultural Resources (CGIAR). The first of the five research themes of the Center is “germplasm conservation, evaluation, and gene discovery”. The AVRDC stores large amounts of germplasm including a vast collection of tomato, numbering ca. 7,500 accessions. Apart from the cultivated types (more than 6,000 accessions), the Center stores a collection of 725 accessions of wild tomato species (Table 9.4). *Solanum pimpinellifolium* and *S. peruvianum* are the most represented with 325 and 135 accessions, respectively. In addition, there are also almost 600 accessions of unidentified wild material, listed as *Lycopersicon* sp., and a few hundreds lines deriving from interspecific crosses (Ebert AW, pers. comm.). The Center has a very

Table 9.4 *Solanum* section *Lycopersicon* (tomatoes) and allied species genetic stocks maintained by The World Vegetable Center (AVRDC), the Tomato Genetic Resource Center (TGRC), and the USDA at Geneva, NY (USDA)

Species[a]	AVRDC[b]	TGRC	USDA
S. arcanum	3	44	4
S. cheesmaniae	17	44	7
S. chilense	47	112	1
S. chmielewskii	11	37	7
S. corneliomulleri	11	52	13
S. galapagense	17	29	5
S. habrochaites	82	120	63
S. huaylasense	0	14	0
S. neorickii	12	59	1
S. pennellii	65	65	10
S. peruvianum	135	78	122
S. pimpinellifolium	325	309	231
S. juglandifolium	0	8	0
S. lycopersicoides	0	23	0
S. ochranthum	0	9	0
S. sitiens	0	13	0
Subtotal	**725**	**1,016**	**464**
sp.	**595**	**0**	**0**
S. lycopersicum	6,067	2,349	5,884
S. lycopersicum "cerasiforme"	125	338	272
Subtotal	**6,192**	**2,687**	**6,156**
Total	**7,512**	**3,703**	**6,620**

[a]Previous names in the genus *Lycopersicon* are given in Table 9.2
[b]Erbert AW, pers. comm

useful web interface, with an information system (The AVRDC Vegetable Genetic Resources Information System or AVGRIS) for searching the data available for germplasm conserved at AVRDC's Genetic Resources and Seed Unit. A web version of AVGRIS is accessible at the URL http://203.64.245.173/avgris/ and provides all users a direct access to the stored germplasm data. Through this facility, it is possible to search for the accessions present in the gene bank and to have also access to a characterization data sheet per each accession.

Another excellent collection of wild tomato genetic resources is held by the C. M. Rick TGRC. The TGRC has been named in memory and honor of Dr. Charles M. Rick (1915–2002), Professor Emeritus of Vegetable Crops at the University of California, Davis, USA, who had originally built up much of the collection through his research and plant collecting activities (Rick 1979, 1986a, b). Dr. Rick had first recognized the potential value of wild germplasm as a useful reservoir of genes for the improvement of tomato. He undertook 15 expeditions to South America, between 1948 and 1995, in the Andean regions of Peru, Ecuador, and Chile and to the Galápagos Islands, establishing a first collection of some 700 samples of sect. *Lycopersicon* and related wild species of *Solanum*.

The TGRC is hosted by the Department of Plant Sciences of the University of California at Davis, and is integrated with the National Plant Germplasm System (NPGS), the latter 'storing backup seed samples of the TGRC collection and only very few samples that are not stored at the TGRC.

As regards the wild tomato germplasm, the TGRC maintains over 1,000 accessions of wild relatives that represent 13 species in *Solanum* sect. *Lycopersicon*, and the four related *Solanum* species *S. lycopersicoides*, *S. sitiens*, *S. juglandifolium,* and *S. ochranthum* (Chetelat 2006; Table 9.4). All the entries are reported with the *Lycopersicon* and the equivalent *Solanum* species name. This Center maintains a series of special purpose collections of selected wild and cultivated accessions with known or inferred tolerances to various environmental (abiotic and biotic) stresses that have been extensively utilized in tomato crop improvement (for detail see review by Robertson and Labate 2007; http://tgrc.ucdavis.edu/). A nice interface allows mapping of TGRC accession collection sites worldwide. The TGRC has a very useful website at the URL http://tgrc.ucdavis.edu/index.aspx, which is worth a visit.

In addition to wild tomato species the TGRC also stores over 1,000 monogenic mutants, including spontaneous and induced mutations affecting many aspects of plant development and morphology, disease resistance genes, and protein marker stocks (Labate et al. 2007). In addition, the collection contains hundreds of miscellaneous genetic and cytogenetic stocks such as trisomics, tetraploids, and translocations, as well as derivatives of wild species such as pre-bred stocks that are very valuable for mapping and breeding purposes. The pre-bred stocks include ILs, BILs, alien substitution lines, and alien addition lines. The IL populations originated from *S. pennellii* LA0716 (Eshed and Zamir 1995; Liu and Zamir 1999), *S. habrochaites* LA1777 (Monforte and Tanksley 2000a), and *S. lycopersicoides* LA2951 (Canady et al. 2005); the BILs were derived from the cross *S. lycopersicum* × *S. pimpinellifolium* LA1589

(Doganlar et al. 2002a). Moreover, the center stores a few alien substitution lines representing seven of the 12 *S. pennellii* LA0716 chromosomes (Rick 1969; Weide et al. 1993); four *S. lycopersicoides* (LA2951) chromosomes (Chetelat and Meglic 2000; Ji and Chetelat 2003); and ten alien addition lines, each containing one extra chromosome from *S. lycopersicoides* LA1964 added to the tomato genome (Chetelat et al. 1998).

The USDA-PGRU germplasm collection focuses on *S. lycopersicum* accessions, which constitute ca. 90% of the more than 6,600 accessions held by this center for tomato, including a large number of modern, vintage, and primitive cultivars along with breeding lines. The collection also contains 464 accessions of wild species, the majority of which are *S. peruvianum* s.l. (see Sect. 9.3) and *S. pimpinellifolium* (http://www.ars.usda.gov). Also the USDA-PGRU collection is duplicated in the National Center for Genetic Resources Preservation (NCGRP) located at Fort Collins, Colorado.

9.5.2 Modes of Preservation and Maintenance

Conservation of genetic resources requires several steps including germplasm collection, maintenance, distribution, characterization, and evaluation. In order to avoid loss of genetic diversity (or genetic erosion) within any given collection and to maintain genetic identity of accessions conserved therein, it is necessary to develop standard methodologies during all these steps, and large numbers of plants or seed are needed. Deployment of these methodologies mainly depends on the breeding system of the species, with cross-pollinated species requiring larger samples. The cultivated tomato is self-pollinated, while the other taxa can vary from self-pollinated to obligately cross-pollinated, showing different rates of outcrossing (Table 9.1). In most gene banks, *S. lycopersicum* is maintained by regenerants from relatively few (e.g 6–24) plants, with accessions usually planted in the field without pollination control. This allows the production of a sufficiently large amount of seed for storage, which can significantly reduce the chances of cross-pollination, or mix-ups, by increasing the time between regenerations. In contrast, for the cross-pollinated species such as most wild taxa, prevention of genetic drift and contamination requires the use of larger samples and controlled pollination. Generally, up to 50 plants are used for regeneration to obtain a representative sample by reducing the effects of genetic drift and selection during the regeneration process (Robertson and Labate 2007).

Seed production must be monitored in order to ensure sufficient production of quality, disease-free seed for maintenance and distribution. For long-term storage of species with orthodox seed, such as tomato, a temperature of $-20°C$ and at a moisture content of $5 \pm 1\%$ is suggested (Robertson and Labate 2007). In some cases, the use of cryopreservation (conservation using liquid nitrogen) of seed for long-term genetic conservation has been suggested, although additional studies are necessary in order to determine whether there is any advantage to this for orthodox seed (Robertson and Labate 2007).

9.5.3 In Situ Conservation

The wild species of tomato are well preserved ex situ through national gene banks, but there is an urgent need to preserve threatened populations in situ as well. Throughout the native region, wild tomatoes are impacted in various ways by human activities. In the highlands, grazing by goats, sheep, and other herbivores is a constant threat. At low elevations, intensive agricultural development and urbanization have had a dramatic impact. A recent trip to Peru organized by one of the authors (RTC) provided clear evidence of genetic erosion via the loss or displacement of local populations.

During this expedition, conducted in April–May 2009, several river valleys (Pisco, Cañete, Lurin, Rimac, Chillon, Pativilca, and Jequetepeque) were explored. In the lower stretches of the valleys, intensive agriculture and urban development are common. With increasing elevation, the environment becomes more rural and agricultural systems more traditional and less intensive. As might be expected, the wild species growing predominantly at low elevations were more severely impacted than those growing at the higher, less disturbed sites.

Of particular concern, populations of *S. pimpinellifolium* have virtually disappeared from low elevation

sites. Only two populations of this species were found below 1,000 m, whereas at least 25 populations were previously collected from the same river valleys. This represents a loss of up to 23 populations of this species in only seven valleys surveyed. The drainages around Lima (Ríos Rimac, Lurin, and Cañete) were most severely affected, due to urbanization and development. Similar trends are occurring around the other major cities in coastal Peru. North of Lima, intensive, modern agricultural practices, including sugarcane cultivation and the widespread use of herbicides, has resulted in the elimination of many local populations of wild tomatoes known from earlier collections. Wild tomatoes are also threatened by climate change. In three valleys (Cañete, Chillon, and Lurin), *S. pimpinellifolium* was found growing above 1,000 m elevation for the first time.

These examples of genetic erosion in *S. pimpinellifolium* are troubling for several reasons. First, this species is closely related to the cultivated tomato – its fruit are edible and sometimes consumed – and has served as a source of disease resistances and other desired traits used by plant breeders to develop improved varieties. The first disease resistance genes bred into the cultivated tomato, *Verticillium* and *Fusarium* wilt resistances, originated in *S. pimpinellifolium,* and it continues to be an important source of such genes. Secondly, the area in which the loss of *S. pimpinellifolium* populations seems most severe, the northern half of Peru, is/was the center of genetic diversity for this species. Accessions collected in the north have/had larger flowers with exserted stigmas, traits which tend to promote cross pollination and maintenance of genetic diversity (Rick et al. 1977).

Although excellent ex situ collections are available to support future breeding and research on tomato, they are subject to their own long-term risks, such as unstable funding, catastrophic loss, and genetic changes (inbreeding depression, artificial selection, etc.). For this reason, there will always be a need to preserve populations in situ. The appropriate authorities in national governments of the countries of origin – mainly Ecuador, Peru, and Chile – should be helped to take steps to protect their native tomatoes from further loss. International organizations, such as the CGIAR, are urged to get involved to initiate and/or support such conservation efforts. Without action, the wealth of wild germplasm in the tomato relatives may not be available to future generations.

9.6 Role in Classical and Molecular Genetic Studies

9.6.1 Genetic Variation

The cultivated tomato (*S. lycopersicum*) is highly autogamous and, despite its wide range of fruit shape, size, and color diversity, its genetic diversity is so reduced that it lacks many genes required for breeding purposes (Rick 1976). Genetic erosion of this crop has resulted from repeated genetic bottlenecks (due to a combination of natural self-pollination, reproduction in small populations, and natural and artificial selection), associated with the domestication process, the early history of improvement in Europe and North America, and modern breeding practices (Rick 1986a).

The level of genetic erosion of the primary tomato gene pool has been measured using different types of markers including allozymes (Rick and Fobes 1975) and RFLPs (Helentjaris et al. 1985; Miller and Tanksley 1990). The study conducted by Miller and Tanksley (1990), estimated that the level of genetic variation of cultivated varieties can be lower than 5% of that available in nature (Miller and Tanksley 1990). Due to this lack of genetic diversity, it is very difficult to identify polymorphisms within the cultivated tomato gene pool, even using sensitive molecular marker techniques (García-Martínez et al. 2006 and references therein).

In contrast, higher levels of variability exist in primitive cultivars of the native area and even more in the wild species, with particularly large genetic diversity observed within the SI species like *S. chilense* and *S. peruvianum* s.l. (Rick 1982, 1988). Interestingly, more genetic variation has been found within a single accession of the SI species than in all accessions of any of the SC species (Miller and Tanksley 1990; Städler et al. 2005). Given the low level of polymorphism among autogamous species, the study of their relationships necessitates the use of more variable molecular markers, such as microsatellites and single nucleotide polymorphisms (SNP) (Alvarez et al. 2001; Yang et al. 2004).

Wild tomato species in sect. *Lycopersicon* occupy a wide variety of habitats ranging from sea level to above 3,000 m in altitude, and from temperate deserts to wet tropical rainforests (see Sect. 9.2.2). Accordingly, these wild species span a broad variation in

terms of morphology, physiology, mating system, and biochemistry, which is of potential value for the improvement of cultivated tomato. In addition, in spite of the severe crossing barriers that separate the four tomato-like nightshade taxa in sects. *Juglandifolia* and *Lycopersicoides* from tomatoes (*Solanum* sect. *Lycopersicon*), these allied species are considered very promising to broaden the genetic variability available for tomato improvement (Rick 1988). In fact, even though they have not been thoroughly tested, the specificity of their habitats suggests that they might harbor novel traits that are lacking in the sect. *Lycopersicon* species (see Sect. 9.2.2). These include tolerance to extreme aridity, excessive moisture and freezing temperatures, as well as resistance to certain diseases and insects (Rick 1988; Rick and Yoder 1988).

9.6.2 Wide Hybridizations

The use of wild species as sources of traits of interest can be hindered by blocks to hybridization and hybrid sterility that might occur at the beginning of the breeding program. These limitations can vary enormously and generally are more severe as the phylogenetic distance between the parental species of the cross increases. Thus, while there are no problems for crosses between *S. lycopersicum* and the closely related wild species *S. cheesmaniae*, *S. galapagense,* and *S. pimpinellifolium*, at the other extreme, crosses with *S. chilense* or *S. peruvianum* s.l., are more difficult and require some type of embryo or ovule rescue; intermediate situations characterize the crosses with *S. chmielewskii*, *S. habrochaites*, *S. pennellii*, and others (Rick and Chetelat 1995). On the other hand, the exploitation of the genetic variability stored in the tomato-like nightshades *S. juglandifolium*, *S. lycopersicoides*, *S. ochranthum,* and *S. sitiens* has been more limited, as severe reproductive barriers isolate them from the core tomato group (Rick 1988; Child 1990; Stommel 2001; Smith and Peralta 2002). Within the group of the four tomato-like nightshades, the only successful cross is the one between *S. lycopersicoides* and *S. sitiens*. In this case, the easily synthesized F_1 hybrids display normal meiotic behavior and high fertility (Pertuzé et al. 2002; Ji et al. 2004). Of the four species, only *S. lycopersicoides* is cross-compatible with *S. lycopersicum* (Rick 1951, 1979; Pertuzé et al. 2002); F_1 hybrids are readily obtained using embryo culture, although they are generally infertile due to meiotic abnormalities (Menzel 1962). *Solanum lycopersicoides* has also been hybridized unilaterally with other taxa of sect. *Lycopersicon*, including *S. cheesmaniae*, *S. chilense,* and *S. pimpinellifolium*. In contrast, *S. sitiens* does not cross directly to tomato in either direction (Rick 1979, 1988), but it can be indirectly hybridized with cultivated tomato using polyploid and bridging line methods (e.g., by using *S. lycopersicum* × *S. lycopersicoide*s derivatives as bridge) (DeVerna et al. 1990; Pertuzé et al. 2003). As a result, it has been possible to introgress to varying degrees chromosomes or chromosome segments from *S. lycopersicoides* and *S. sitiens* into the tomato genome (Chetelat and Meglic 2000; Ji and Chetelat 2003; Pertuzé et al. 2003; Canady et al. 2005). For *S. lycopersicoides* a complete set of monosomic alien addition lines in tomato was synthesized by Chetelat et al. (1998), and a set of ILs are now available (Chetelat and Meglic 2000; Canady et al. 2005); gene transfer from *S. sitiens* to *S. lycopersicum* has been obtained through chromosome addition, substitution, and recombination in the progeny of complex aneuploid hybrids (Pertuzé et al. 2003). In contrast, the other two tomato-like nightshades, *S. ochranthum* and *S. juglandifolium* appear to be sexually incompatible with cultivated tomato in all combinations tested (Rick 1988); although somatic hybrids between *S. lycopersicum* and *S. ochranthum* have been obtained by protoplast fusion, they are highly sterile and have not, so far, provided a means for gene transfer (Stommel 2001).

In spite of these difficulties, recent comparative genetic linkage maps based on an interspecific F_2 *S. ochranthum* × *S. juglandifolium* population obtained via embryo culture indicate that, consistent with the status of the sect. *Juglandifolia* as the nearest outgroup to the tomatoes, these two taxa are more closely related to cultivated tomato than predicted from crossing relationships (Peralta et al. 2008; Albrecht and Chetelat 2009). These results are encouraging from the standpoint of tomato breeding, as they suggest that with further attempts at hybridization

there might be more opportunity for germplasm introgression with cultivated tomato than previously assumed (Albrecht and Chetelat 2009).

9.6.3 Development of Classical and Molecular Genetic Linkage Maps

High-density molecular linkage maps provide useful tools for genome studies, gene/QTL mapping and cloning, varietal development, and many other potential applications.

The analysis of linked genes in tomato began in the early 1900s, when Jones (1917) interpreted the results of Hedrick and Booth (1907) as linkage between *dwarfness* (*d*) and fruit shape. At the beginning, genetic linkage analysis of tomato was slow, but accelerated with the availability of seedling mutants, advanced mapping stocks, and a complete set of trisomics; these cytogenetic stocks have been extremely valuable in the assignment of genes to chromosomes and chromosome arms, or even to restricted regions in the arms (Stevens and Rick 1986; Rick and Yoder 1988). As a result, by mid-1970s, a total of 258 morphological and physiological markers had been assigned to tomato chromosomes (Linkage Committee 1973; Rick 1975). Subsequently, isozyme markers started to be used, and in 1980 Tanksley and Rick published an isozyme linkage map comprising 22 loci mapped on nine of the 12 tomato chromosomes. Isozyme mapping in tomato was accomplished using interspecific F_2 and BC populations along with the trisomic technique. In the late 1980s, the last comprehensive "classical" linkage map of tomato was published, which included ~400 morphological, physiological, isozyme, and disease resistance genes mapped onto the 12 tomato chromosomes (Stevens and Rick 1986; Mutschler et al. 1987). In mid-1980s, DNA-based RFLP markers were starting to be mapped also in tomato (Bernatzky and Tanksley 1986; Tanksley and Bernstzky 1987), and by the 1990s, this species had become one of the first plants for which RFLPs were used to generate a high-density linkage map (Tanksley et al. 1992). The map was based on a *S. lycopersicum* cv. "VF36-*Tm2a*" × *S. pennellii* (LA0716) F_2 population of 67 plants and comprised 1,030 RFLP markers. This map, referred to as the Tomato-EXPEN 1992, has been updated periodically and includes DNA markers, isozyme markers, and some morphological markers (Pillen et al. 1996b; http://solgenomics.net/). Although *S. pennellii* is not closely related to the cultivated tomato, the presence of the SC accession (LA0716) has favored its use as a parental line for many mapping studies (Tables 9.5–9.8).

Over the years numerous molecular linkage maps have been developed using different mapping populations, and, due to the limited genetic variation inherent in domesticated tomato, most of them derived from interspecific crosses between the cultivated tomato and most of the tomato wild species belonging to sect. *Lycopersicon,* with recent examples involving also the allied wild species *S. lycopersicoides* (Table 9.5). Other maps have been developed using crosses between species belonging to sect. *Lycopersicoides* (*S. sitiens* × *S. lycopersicoides*; Pertuzé et al. 2002) and sect. *Juglandifolia* (*S. ochranthum* × *S. juglandifolium*; Albrecht and Chetelat 2009).

For some interspecific crosses, particularly those between the cultivated tomato and the closely related wild species *S. pimpinellifolium*, *S. cheesmaniae,* and *S. galapagense*, identification of a sufficient number of polymorphic markers has been a serious limitation; however, albeit with more difficulties, genetic maps have been developed (Table 9.5). In addition, despite the low level of genetic variation found within *S. lycopersicum,* molecular linkage maps have been constructed also using intraspecific crosses (Table 9.5).

Several of these maps were developed with the objective of mapping genes/QTLs for traits of interest, and in many cases polymerase chain reaction (PCR)-based markers, including random amplified polymorphic DNAs (RAPDs), AFLPs, simple sequence repeats (SSRs), sequence characterized amplified regions (SCARs), and cleaved amplified polymorphic sequences (CAPSs), were developed and integrated with the RFLP maps (Table 9.5; see also reviews by Ji and Scott 2007; Labate et al. 2007). For some tomato chromosomes, the integration of the molecular map with classical maps has been accomplished using interspecific progenies that segregated for morphological and molecular markers (short arm of chromosome 1: Balint-Kurti et al. 1995; chromosome 3: van der Biezen et al. 1994; chromosome 6: Weide et al. 1993, Van-Wordragen et al. 1996; chromosome 7: Schumacher et al. 1995; chromosome 11: Wing et al. 1994).

Table 9.5 Summary of molecular linkage maps developed in *Solanum* sect. *Lycopersicon* and allied species

Initial cross	Mapping population[a]	Population size[b]	Type of markers[c]	No. of markers[d]	Online[e]	Reference[f]
S. lycopersicum × *S. arcanum*						
E6203 × LA1708	BC_3	241	RFLP, PCR	174 (171; 3)		Fulton et al. (1997)
S. lycopersicum × *S. chmielewskii*						
UC82B × LA1028	BC_1	237	RFLP, ISO, MO	70 (63; 5; 2)	NCBI	Paterson et al. (1988)
CH6047 × LE777	F_2	149	AFLP, CAPS/SCAR/ CG*FL*, SSR	255 (136; 81; 38)	SGN	Jiménez-Gómez et al. (2007)
S. lycopersicum × *S. galapagense*						
UC204B × LA0483	F_2	350	RFLP	71		Paterson et al. (1991)
UC204B × LA0483	F_7-RIL	97	RFLP, MO, ISO	135 (132; 2; 1)		Paran et al. (1995)
S. lycopersicum × *S. habrochaites*						
E6203 × LA1777	BC_1	149	RFLP	135	SGN, NCBI	Bernacchi and Tanksley (1997)
E6203 × LA1777	NIL, BIL	111	RFLP	95		Monforte and Tanksley (2000a)
T5 × LA1778	BC_1	196	RFLP	89		Truco et al. (2000)
Hunt 100 × LA0407	BC_2S_5- BIL	64	RFLP, PCR	63 (58; 5)		Kabelka et al. (2002)*
NC84173 × PI 126445	BC_1	145	RFLP, PCR/RGA[g]	171 (142; 29)		Zhang et al. (2002)
NC84173 × PI-126445	BC_1 (SGe)	76	RFLP, PCR/RGA[g]	179 (145; 34)		Zhang et al. (2003b)
Moneymaker × LYC4	F_2	174	AFLP, CAPS	269 (218; 51)		Finkers et al. (2007a)
Moneymaker × LYC4	IL	30	AFLP, CAPS	491 (457; 34)		Finkers et al. (2007b)
Ferum × PI 247087	BC_2S_1	130	AFLP, RFLP, SSR, CAPS, MO	217 (138; 36; 26; 15; 2)		Stevens et al. (2007)*
S. lycopersicum × *S. lycopersicoides*						
VF36 × LA2951	BC_1	84	RFLP, ISO, MO	93 (71; 20; 2)	NCBI	Chetelat et al. (2000)
VF36 × LA2951	BIL	311	RFLP, ISO, MO	139 (110; 22; 7)		Chetelat and Meglic (2000)
S. lycopersicum × *S. neorickii*						
E6203 × LA2133	BC_2	170	RFLP, PCR, MO	133 (131; 1; 1)		Fulton et al. (2000)
S. lycopersicum × *S. pennellii*						
LA1500 × LA0716	BC_1, F_2	46; 46[h]	RFLP, ISO	112 (76; 36)	NCBI	Bernatzky and Tanksley (1986)
VF36-*Tm2a* × LA0716 (high-density map of tomato; Tomato-EXPEN 1992)	F_2	67	RFLP, ISO, MO,	1,030; 1,050[i]	SGN, NCBI	Tanksley et al. (1992), Pillen et al. (1996b)
VF36-*Tm2a* × LA0716	F_2	67 (42)	SSR	11		Broun and Tanksley (1996)
VF36-*Tm2a* × LA0716	F_2	67 (42)	AFLP	909		Haanstra et al. (1999b)
VF36-*Tm2a* × LA0716	F_2	67	SSR	19; 20[i]		Areshchenkova and Ganal (1999, 2002)
Vendor *Tm2a* × LA0716	two rec. BC_1	78; 115[h]	RFLP	85		deVicente and Tanksley (1991)
Vendor *Tm2a* × LA0716	F_2	432	RFLP	98		deVicente and Tanksley (1993)
Allround × LA0716	F_2	84 (44)	RFLP, SSR	74 (51; 23)		Arens et al. (1995)
Allround × LA0716	F_2	84 (80)	RFLP, AFLP	707		Haanstra et al. (1999b)
M82 × LA0716	IL	50	RFLP	375	SGN	Eshed and Zamir (1995)

(*continued*)

Table 9.5 (continued)

Initial cross	Mapping population[a]	Population size[b]	Type of markers[c]	No. of markers[d]	Online[e]	Reference[f]
M82 × LA0716	IL	75	RFLP, t-NBS[g]	~665 (~590;75)		Pan et al. (2000)
M82 × LA0716	IL	72	AFLP, SSR, SNP	218 (159; 52; 7)		Suliman-Pollatschek et al. (2002)
M82 × LA0716	IL	52	T-DNA	140		Gidoni et al. (2003)
M82 × LA0716	IL	75	RFLP, CG*CB*	637 (614; 23)		Liu et al. (2003)
M82 × LA0716	IL	75	RFLP, CG*FSC*	~669 (~590; 79)		Causse et al. (2004)
M82 × LA0716	IL	50	SNP	20		Yang et al. (2004)
M82 × LA0716	IL	50	SSR, CAPS	122 (63; 59)		Frary et al. (2005)
M82 × LA0716	IL	75	CG*AA*	13		Stevens et al. (2007)
E6203 × LA1657	BC_2	175	RFLP	150		Frary et al. (2004a)
LA0925 × LA0716 (Tomato-EXPEN 2000)	F_2	83	RFLP, CAPS/COS/COSII, SSR, SNP	2,506	SGN, NCBI	Fulton et al. (2002b); http://solgenomics.net/
LA0925 × LA0716	F_2	83	SSR, CAPS	152 (76; 76)		Frary et al. (2005)
LA0925 × LA0716	F_2	83	RFLP, CAPS, SSR/TES/TGS, TEI	2,116	KAZUSA	Shirasawa et al. (2010)
S. lycopersicum × *S. pimpinellifolium*						
M82 × LA1589	BC_1	257	RFLP, RAPD, SSR, MO	120 (115; 53; 6; 2)	SGN	Grandillo and Tanksley (1996b)
NC84173 × LA0722	BC_1	119	RFLP	151		Chen and Foolad (1999)
Yellow Pear × LA1589	F_2	82	RFLP	82		Ku et al. (1999)
Giant Heirloom × LA1589	F_2	200 (114)	RFLP, CAPS	90		Lippman and Tanksley (2001)
Sun 1642 × LA1589	F_2	100	RFLP, SNP	108 (106; 2)	TMRD	van der Knaap and Tanksley (2001), Yang et al. (2004)
E6203 × LA1589	BC_2F_6-BIL	196	RFLP, MO	127 (126;1)	SGN	Doganlar et al. (2002b)
Long John × LA1589	F_2	85	RFLP	97		van der Knaap et al. (2002)**
Yellow Stuffer × LA1589	F_2	200	RFLP	93		van der Knaap and Tanksley (2003)
Banana Legs(BL), Howard German (HG) × LA1589	BLF_2, HGF_2, $HGBC_1$	99; 130; 100[h]	RFLP, PCR	111; 111; 108[h]		Brewer et al. (2007)***
Rio Grande × LA1589	F_2	94	SSR, RFLP, CAPS	181 (77; 68; 36)	SGN	Gonzalo and van der Knaap (2008)*
NCEBR-1 × LA2093	F_2	172	RFLP, CR-EST, RGA[g]	250 (115; 94; 41)		Sharma et al. (2008)
NCEBR-1 × LA2093	F_7-RIL	170	RFLP, CR-EST, CAPS, SSR[g, j]	294 (132; 132; 16; 14)		Ashrafi et al. (2009)
S. lycopersicum "cerasiforme" × *S. cheesmaniae*						
E9 × L3	F_6-RIL	115	SCAR, SSR	114		Villalta et al. (2005)
S. lycopersicum "cerasiforme" × *S. pimpinellifolium*						
E9 × L5	F_6-RIL	142	SCAR, SSR	132		Villalta et al. (2005)
S. ochranthum × *S. juglandifolium*						
LA3650 × LA2788	Pseudo-F_2	66	COS/COSII, RFLP, SSR	132 (96; 19; 17)		Albrecht and Chetelat (2009)

S. sitiens × *S. lycopersicoides*						
LA1974 × LA2951	F_2	82	RFLP	101		Pertuzé et al. (2002)
S. lycopersicum "cerasiforme" × *S. lycopersicum*						
Cervil × Levovil	F_7-RIL	153	AFLP, RFLP, RAPD, MO	377 (211; 132; 33; 1)		Saliba-Colombani et al. (2000)
S. arcanum × *S. arcanum*						
LA2157 × LA2172	BC_1	268	RFLP	94	NCBI	Van Ooijen et al. (1994)
S. pimpinellifolium × *S. pimpinellifolium*						
LA1237 × LA1581	F_2	147	RFLP	47		Georgiady et al. (2002)

Maps developed for specific chromosomes are not included (see also review by Labate et al. 2007)

[a] *IL* introgression line; *BIL* backcross inbred line; *RIL* recombinant inbred line; *SGe* selective genotyping

[b] In parenthesis: no. of genotyped plants

[c] *AFLP* amplified fragment length polymorphism; *CAPS* cleaved amplified polymorphic sequence; *COS* Conserved Ortholog Set; *COSII* Conserved Ortholog Set II; *ISO* isozyme; *MO* morphological; *PCR* PCR-based, not specified; *RAPD* random amplified polymorphic DNA; *RFLP* restriction fragment length polymorphism; *RGA* resistance gene analog; *SCAR* sequence characterized amplified region; *SNP* single nucleotide polymorphism; *TES* tomato EST-derived SSR; *TGS* tomato genome-derived SSR; *TEI* tomato EST-derived intronic polymorphism; *CGAA* candidate genes associated with ascorbic acid biosynthesis; *CGC* candidate carotenoid genes; *CGFL* candidate genes for flowering; *CGFSC* candidate genes for fruit size and composition; *CR-EST* candidate resistance/defense-response EST; *t-NBS* tomato-nucleotide binding site-leucine rich repeat (NBS-LRR) sequences

[d] In parenthesis: no. of markers per marker type

[e] *SGN* www.sgn.cornell.edu/cview; *NCBI* www.ncbi.nlm.nih.gov/mapview; *TMRD* (Tomato Mapping Resources Database) www.tomatomap.net; *KAZUSA* http://www.kazusa.or.jp/tomato/

[f] *Linkage map not shown; **Linkage maps shown only for four chromosomes; ***A composite map shown for the two F_2 populations

[g] The approximate locations of disease resistance genes (R genes) and QTL are shown

[h] Per population

[i] Per study

[j] The approximate locations of fruit quality-related genes are shown

Table 9.6 Summary of disease resistance genes and QTLs mapped in *Solanum* sect. *Lycopersicon* and allied species, using molecular markers

Source of resistance/tolerance	Disease	Pathogen	Gene/QTL[a]	Chrom. location[b]	Mapping population[c]	Marker type[d]	References
S. arcanum LA2157	Bacterial canker	*Clavibacter michiganensis* ssp. *michiganensis*	5 (Q)	1, 6–8, 10	(three) BC_1	RFLP	Sandbrink et al. (1995)
S. arcanum LA2157	Bacterial canker	*C. michiganensis* ssp. *michiganensis*	3 (Q)	5, 7, 9	F_2	RFLP, SCAR	Van Heusden et al. (1999)
S. arcanum LA2157	Early blight	*Alternaria solani*	6 (Q)	1, 2, 5–7, 9	F_2, F_3	AFLP, SSR, SNP	Chaerani et al. (2007)
S. arcanum LA2172	Powdery mildew	*Oidium neolycopersici*	*Ol-4*	6	pseudo-F_2, BC_2S_1	AFLP, PCR	Bai et al. (2004, 2005)
S. arcanum LA2157	Nematode (root-knot)	*Meloydogine* spp.	*Mi-9*	6S	F_2, F_3	RFLP, PCR	Veremis et al. (1999), Veremis and Roberts (2000), Ammiraju et al. (2003), Jablonska et al. (2007)
S. cheesmaniae LA0422	Blackmold	*Alternaria alternata*	5(Q)*: Bm-2a, 2c, 3, 9, 12*	2 (two), 3, 9, 12	BC_1S_1, BC_1S_2	RFLP, CAPS	Cassol and St. Clair (1994), Robert et al. 2001
S. chilense LA0458	Cucumber mosaic	Cucumber mosaic virus (CMV)	*Cmr*	12	BC_1-inbreds	ISO, RFLP	Stamova and Chetelat (2000)
S. chilense LA1969	Tomato yellow leaf curl	Tomato yellow leaf curl virus (TYLCV)	*Ty-1*	6S	BC_1S_1, NIL	RFLP, ISO	Zamir et al. (1994), Ji et al. (2007a)
S. chilense LA1932, LA2779, LA1938	Tomato yellow leaf curl, tomato mottle virus	TYLCV, tomato mottle virus (ToMoV)	3 (Q)	6	(three) F_2	RAPD	Griffiths and Scott (2001), Ji and Scott (2005), Agrama and Scott (2006), Ji et al. (2007a)
S. chilense LA2779, LA1932	Tomato yellow leaf curl, tomato mottle	TYLCV, ToMoV	*Ty-3*	6L	F_2, ABLs	RAPD/SCAR, CAPS	Ji et al. (2007a), Jensen (2007)
S. chilense LA1932	Tomato yellow leaf curl, tomato mottle	TYLCV	*Ty-4*	3L	ABLs	PCR	Ji et al. (2009a)
S. chilense LA0458	Powdery mildew	*Leveillula taurica*	*Lv*	12C	(two)F_2, BC_1	RAPD, RFLP	Chungwongse et al. (1994, 1997)
S. habrochaites PI 134417	Alfalfa mosaic	Alfalfa mosaic virus (AMV)	*Am*	6S	F_2, rec. BC_1	RFLP, AFLP	Parrella et al. (2004)
S. habrochaites PI 247087	Potyviruses	*Potato virus Y* (PVY) and *tobacco etch virus* (TEV)	*pot-1*	3S	F_2/F_3, BC_1	AFLP, RFLP	Parrella et al. (2002), Ruffel et al. (2005)
S. habrochaites PI 126445	Tobacco/tomato mosaic	Tobacco/tomato mosaic virus (TMV/ToMV)	*Tm-1*	2C	F_2 NILs	RAPD, SCAR	Holmes (1957), Levesque et al. (1990), Tanksley et al. (1992), Ohmori et al. (1996), Ishibashi et al. (2007)

S. habrochaites B6013	Tomato yellow leaf curl	TYLCV	*Ty-2*	11L	F_2, F_3 from H24 line	RFLP	Hanson et al. (2000, 2006), Kalloo and Banerjee (2000), Ji et al. (2007b, 2009b)
S. habrochaites LA0407	Bacterial canker	*Clavibacter michiganensis* ssp. *michiganensis*	2 (Q)*: Rcm2.0, Rcm5.1*	2, 5	BC_2S_5-BILs F_2 from BIL	RFLP, PCR	Kabelka et al. (2002), Coaker and Francis (2004)
S. habrochaites PI 126445	Early blight	*Alternaria solani*	7-13 (Q): *EBR1.1-12.2*	1–6, 8–12	BC_1, BC_1S_1	RFLP, RGA	Foolad et al. (2002), Zhang et al. (2002, 2003b)
S. habrochaites LYC4	Gray mold	*Botrytis cinerea*	3, 10 (Q): *Rbcq1,2,4, 6,9,11,12*	1–3, 4 (two), 6, 9 (two), 11, 12	F_2, ILs	AFLP, CAPS, SCAR	Finkers et al. (2007a, b)
S. habrochaites LA1033	Late blight	*Phytophthora infestans*	4–9 (Q)	ns[f]	F_2, BC_1F_1	AFLP	Lough (2003)
S. habrochaites LA2099	Late blight	*Phytophthora infestans*	13, 18 (Q): *lb1a-lb12b*	All	rec. BC_1, NIL, sub-NILs	RFLP	Brouwer et al. (2004), Brouwer and St Clair (2004)
S. habrochaites PI 370085	Leaf mold	*Cladosporium fulvum* (syn. *Passalora fulva*)	*Cf-4*	1S – *MW* locus	F_2 from NILs	RFLP	Jones et al. (1993), Balint-Kurti et al. (1994), Parniske et al. (1997), Thomas et al. (1997)[e], Rivas and Thomas (2005)
S. habrochaites G1.1560	Powdery mildew	*Oidium neolycopersici*	*Ol-1*	6L	F_2, BC_1S_1, BC_1S_2	RFLP, RAPD, SCAR	Van der Beek et al. (1994), Huang et al. (2000a, b), Bai et al. (2005)
S. habrochaites G1.1290	Powdery mildew	*Oidium neolycopersici*	*Ol-3*	6L	ABL	RFLP, SCAR	Huang et al. (2000b), Bai et al. (2005)
S. habrochaites PI 247087	Powdery mildew	*Oidium neolycopersici*	*Ol-5*	6L	BC_2, BC_2S_1 from ABL	PCR	Bai et al. (2005)
S. lycopersicoides LA2951	Gray mold	*Botrytis cinerea*	7 (Q): 5 R + 2 Su	1–5, 9, 11	ILs	CAPS, RFLP	Davis et al. (2009)
S. lycopersicum cv. 'Hawaii 7998'	Bacterial spot	*Xanthomonas campestris* pv. *vesicatoria*	*rx-1*, *rx-2*, *rx-3*	1S, 1L, 5	BC_1	ISO, RFLP	Yu et al. (1995)
S. lycopersicum cv. MoneyMaker	Bacterial spot	*Xanthomonas campestris* pv. *vesicatoria* (avrBs4-expressing strain)	*Bs4*	5S	F_2	AFLP. RFLP, STS	Ballvora et al. (2001), Schornack et al. (2004)[e]

(*continued*)

Table 9.6 (continued)

Source of resistance/tolerance	Disease	Pathogen	Gene/QTL[a]	Chrom. location[b]	Mapping population[c]	Marker type[d]	References
S. lycopersicum cv. "Hawaii 7996"	Bacterial wilt	*Ralstonia solanacearum* race 1	several (Q)	3, 4 (two), 6 (two), 8, 10, 11	F_2, F_{2-3}, F_3	RFLP, RAPD	Thoquet et al (1996a, b), Mangin et al. (1999)
S. lycopersicum cv. "Hawaii 7996"	Bacterial wilt	*Ralstonia solanacearum* race 3	4 (Q): *Bwr-3, Bwr-4, Bwr-6, Bwr-8*	3, 4, 6, 8	$F_{2:3}$, F_8-RIL	RFLP	Carmeille et al. (2006)
S. lycopersicum	Antracnose ripe rot	*Colletotrichum coccodes*	6 (Q)	Various	F_2	RAPD, AFLP	Stommel and Zhang (1998, 2001)
S. lycopersicum	Leaf mold	*Cladosporium fulvum*	*Cf-1*	1S – *MW*	ns[f]	ns[f]	Langford (1937), Kerr and Bailey (1964), Jones et al. (1993), Rivas and Thomas (2005)
S. lycopersicum 'Peru Wild'	Verticillium wilt	*Verticillium dahliae* race 1	*Ve1, Ve2*	9S	$F_{2:3}$, RIL, IL	RAPD, RFLP	Kawchuk et al. (1998), Diwan et al. (1999), Kawchuk et al. (2001)[e]
S. lycopersicum "cerasiforme" L285	Bacterial wilt	*Ralstonia solanacearum*	3 (Q)	6, 7, 10	F_2, F_3	RFLP, RAPD	Danesh et al. (1994)
S. lycopersicum "cerasiforme": PI 187002	Leaf mold	*Cladosporium fulvum* (syn. *Passalora fulva*)	*Cf-5*	6S	F_2 from NILs	RAPD, RFLP	Jones et al. (1993), Dickinson et al. (1993), Dixon et al. (1998)[e], Rivas and Thomas (2005)
S. lycopersicum "cerasiforme" LA1230	Powdery mildew	*Oidium neolycopersici*	*ol-2*	4C	F_2	AFLP, RAPD, SCAR	De Giovanni et al. (2004), Bai et al. (2008)
S. neorickii G1.1601	Gray mold	*Botrytis cinerea*	3 (Q): *pQTL3, pQTL4, pQTL9*	3, 4, 9	F_3, BC_3S_1, BC_3S_2	AFLP, CAPS, SCAR	Finkers et al. (2008)
S. neorickii G1.1601	Powdery mildew	*Oidium neolycopersici*	3 (Q): *Ol-qtl1, -qtl2, -qtl3*	6L, 12 (two)	F_2, F_3	AFLP, CAPS, SCAR	Bai et al. (2003)
S. pennellii LA0716	Bacterial spot	*Xanthomonas campestris pv. vesicatoria* (race T3)	*Xv4*	3	F_2, IL	RFLP, CAPS	Astua-Monge et al. (2000)
S. pennellii LA0716	*Alternaria* stem canker	*Alternaria alternata* f. sp. *lycopersici*	*Asc*	3L	F_2, BC_1	RFLP	Van der Biezen et al. (1995), Mesbah et al. (1999), Brandwagt et al. (2000)
S. pennellii LA0716	Fusarium wilt	*Fusarium oxysporum f. sp. lycopersici* (race 1)	*I-1*	7	BC_1	RFLP	Sarfatti et al. (1991), Scott et al. (2004)

S. pennellii LA0716 and PI 414773	Fusarium wilt	*Fusarium oxysporum f. sp. lycopersici* (race 3)	*I-3*	7L	BC_1, IL	RFLP, RGA, AFLP, SCAR, CAPS	Bournival et al. (1989, 1990), Scott and Jones (1989), Sarfatti et al. (1991), Tanksley and Costello (1991), Sela-Buurlage et al. (2001), Hemming et al. (2004), Scott et al. (2004), Lim et al. (2008)
S. pennellii LA0716	Fusarium wilt	*Fusarium oxysporum f. sp. lycopersici* (race 2)	*I-5, I-6*	2, 10	IL	RFLP	Sela-Buurlage et al. (2001)
S. peruvianum PI 128650	Tobacco mosaic	Tobacco Mosaic Virus (TMV)	*Tm-2a* (*Tm-2*^{2}) and *Tm-2*	9C	F_2, NILs	RFLP	Young et al. (1988), Pillen et al. (1996a), Lanfermeijer et al. (2003, 2005)[e]
S. peruvianum s.l. (ns)[f,g]	Tomato spotted wilt	Tomato Spotted Wilt (TSWV)	*Sw-5*	9L	NIL, NIL-BC, F_2	RFLP, RAPD	Stevens et al. (1995), Brommonschenkel and Tanksley (1997), Brommonschenkel et al. (2000)[e]
S. peruvianum s.l. (ns)[g]	Tomato yellow leaf curl	TYLCV	5(Q): *Ty-5* (major) + 4 (minor)	1, 4 (major), 7, 9, 11	F_2	PCR	Anbinder et al. (2009)
S. peruvianum s.l. (ns)[g]	Corky root rot	*Pyrenochaeta lycopersici*	*py-1*	3S	NIL, F_2	RAPD, RFLP	Doganlar et al. (1998)
S. peruvianum s.l. (ns)[g]	Fusarium crown and root rot	*Fusarium oxysporum* f. sp. *radici-lycopersici*	*Frl*	9	F_2	NA	Vakalounakis et al. (1997)
S. peruvianum PI 128657	Nematode (root knot) and potato aphid	*Meloidogyne* spp. and *Macrosiphum euphorbiae*	*Mi-1* (*Meu-1*)	6S	NILs, (four) F_2	RFLP, ISO	Medina-Filho (1980), Klein-Lankhorst et al. (1991), Messeguer et al. (1991), Milligan et al. (1998)[e], Rossi et al. (1998), Vos et al. (1998)
S. peruvianum PI 126443-1MH	Nematode (root knot)	*Meloidogyne* spp	*Mi-3, Mi-5*	12S	BC, F_2	RAPD, RFLP	Yaghoobi et al. (1995), Veremis and Roberts (1996a, b)
S. pimpinellifolium "hirsute INRA"	Tomato yellow leaf curl	TYLCV	1 (Q)	6	F_4	RAPD	Chaguè et al. (1997)
S. pimpinellifolium (ns)	Bacterial speck	*Pseudomonas syringae* pv. 'tomato'	*Pto* + *Prf*	5S	NIL, F_2	RFLP, RAPD	Martin et al. (1991, 1993)[e], Salmeron et al. (1996)
S. pimpinellifolium PI 79532	Fusarium wilt	*Fusarium oxysporum* f. sp. *lycopersici* (race 1)	*I*	11S	BC_1	RFLP	Paddock (1950), Sela-Buurlage et al. (2001), Scott et al. (2004)

(*continued*)

Table 9.6 (continued)

Source of resistance/tolerance	Disease	Pathogen	Gene/QTL[a]	Chrom. location[b]	Mapping population[c]	Marker type[d]	References
S. pimpinellifolium PI 126915	Fusarium wilt	*Fusarium oxysporum* f. sp. *lycopersici* (race 2)	*I-2* complex locus (*I2C* gene family)	11L	NIL, F_2	MO, RFLP,	Laterrot (1976), Sarfatti et al. (1989), Segal et al. (1992), Ori et al. (1997), Simons et al. (1998)[e], Sela-Buurlage et al. (2001)
S. pimpinellifolium PI 79532	Gray leaf spot	*Stemphyllium spp.*	*Sm*	11	F_2	RFLP	Dennett (1950), Behare et al. (1991)
S. pimpinellifolium L3708	Late blight	*Phytophtora infestans*	2 (Q)	6, 8	F_2	RFLP	Frary et al. (1998)
S. pimpinellifolium WVa700	Late blight	*Phytophtora infestans*	*Ph-2*	10L	Several	AFLP, RFLP	Moreau et al. (1998)
S. pimpinellifolium L3708	Late blight	*Phytophtora infestans*	*Ph-3*	9L	F_2	AFLP, RFLP	Chungwongse et al. (2002)
S. pimpinellifolium (ns)[f]	Leaf mold	*Cladosporium fulvum* (syn. *Passalora fulva*)	*Cf-2*	6S	ns[f]	ns[f]	
S. pimpinellifolium PI 126915	Leaf mold	*Cladosporium fulvum* (syn. *Passalora fulva*)	*Cf-9*	1S – *MW*	F_2, NIL, BC_1	RFLP	van der Beek et al. (1992), Jones et al. (1993, 1994), Balint-Kurti et al. (1994), Parniske et al. (1997), Rivas and Thomas (2005)
S. pimpinellifolium PI 126947	Leaf mold	*Cladosporium fulvum* (syn. *Passalora fulva*)	*Cf-ECP2, Cf-ECP3*	1S – *OR*	F_2	CAPS	Haanstra et al. (1999a), Yuan et al. (2002)
S. pimpinellifolium CGN15529	Leaf mold	*Cladosporium fulvum* (syn. *Passalora fulva*)	*Cf-ECP5*	1S – *AU*	TC, F_3	CAPS	Haanstra et al. (2000)
S. pimpinellifolium LA1547, LA1683	Leaf mold	*Cladosporium fulvum* (syn. *Passalora fulva*)	*Cf-ECP1, Cf-ECP4*	1S – *MW*	NILs, F_2	PCR	Soumpourou et al. (2007)
S. pimpinellifolium LA0121	Potato cyst nematode	*Globodera restochiensis*	*Hero*	4S	NIL, F_2	RAPD, RFLP	Ganal et al. (1995), Ernst et al. (2002)[e]

[a]*(Q)* QTL; *R* resistant, *Su* susceptible; for the approximate locations of some of the listed disease resistance genes (R genes) and QTLs see Pan et al. (2000); Zhang et al. (2002, 2003a); Ashrafi et al. (2009)

[b]*L* long arm of chromosome; *S* short arm of chromosome; *C* centromeric region; *MW Milky Way* locus; *OR Orion* locus; *AU Aurora* locus

[c]*ABL* advanced breeding lines; *TC* testcross; *rec*. reciprocal

[d]*STS* sequence tagged site; for other markers abbreviations see legend to Table 9.5

[e]Studies reporting the cloning of the corresponding gene(s)

[f]*ns* accession number, or other data, not specified

[g]Not being available the accession number, these genotypes have been referred to as *S. peruvianum* s.l

Table 9.7 Summary of QTL mapping studies conducted in *Solanum* sect. *Lycopersicon* for morphological, yield-, fruit quality- and reproductive-related traits

Wild or donor parent	Main traits analyzed	No. traits evaluated[a]	No. QTL[b]	Mapping population (pop. size)[c]	Marker type[d]	No. Markers	References[e]
S. arcanum LA1708	Yield, fruit quality, horticultural	35 (29)	166	BC_3/BC_4 (200)	RFLP, PCR, MO	174	Fulton et al. (1997)
S. arcanum LA1708	Biochemical related to flavor	15	103	BC_3/BC_4 (200)	RFLP, PCR, MO	174	Fulton et al. (2002a)
S. chmielewskii LA1028	Fruit weight, brix, pH	3	15	BC_1 (237)	RFLP, ISO, MO	70	Paterson et al. (1988, 1990), Frary et al. (2003)
S. chmielewskii LA1028	Brix	1	ns[f]	LA1563 (BC_5S_5), derived F_2	RFLP	60	Osborn et al. (1987)
S. chmielewskii LA1028	Yield, brix, pH	6	ns	LA1500-LA1503, LA1563 (BC_5S_5), derived F_2/F_3	RFLP, ISO	132	Tanksley and Hewitt (1988)
S. chmielewskii LA1028	Yield, brix, fruit quality	13	ns	LA1500-LA1503, LA1563 (BC_5S_5), BILs	RFLP	9	Azanza et al. (1994)
S. chmielewskii CH6047	Flowering time	2	8	F_2 (149)	AFLP, CAPS/SCAR/CG, SSR	225	Jiménez-Gómez et al. (2007)
S. chmielewskii LA1840	Fruit weight and composition	16 (14)	103	ILs (20)	COSII, SSR	133	Prudent et al. (2009)
S. galapagense LA0483	Frui size, brix, pH	3	29	F_2/F_3 (350)	RFLP	71	Paterson et al. (1991)
S. galapagense LA0483	Fruit quality	3	73*	F_8 RILs (97)	RFLP, MO, ISO	135	Goldman et al. (1995)
S. galapagense LA0483	Morphological	7	41*	F_8 RILs (97)	RFLP, MO, ISO	135	Paran et al. (1997)
S. habrochaites LA1777	Sexual compatibility factors and floral morphology	9	23	BC_1 (149)	RFLP	135	Bernacchi and Tanksley (1997), Chen and Tanksley (2004), Chen et al. (2007)
S. habrochaites LA1777	Yield, fruit quality, horticultural	19	121	BC_2/BC_3 (315/200)	RFLP	122	Bernacchi et al. (1998a)
S. habrochaites LA1777 and *S. pimpinellifolium* LA1589	Yield, fruit quality, horticultural	12	22	NILs	RFLP	ns[f]	Bernacchi et al. (1998b), Monforte and Tanksley (2000b), Monforte et al. (2001), Yates et al. (2004)
S. habrochaites LA1777	Biochemical related to flavor	15	34	BC_2/BC_3 (315/200)	RFLP	122	Fulton et al. (2002a)
S. habrochaites LA1777	Aroma volatiles	40 (27)	30	ILs, BILs (89)	RFLP	95	Mathieu et al. (2009)
S. habrochaites LA1777	Hybrid incompatibility, floral morphology	25	22	ILs, BILs (71)	RFLP	95	Moyle and Graham (2005), Moyle (2007)
S. habrochaites LA0407	Stem vascular morphology	5	1	BILs (BC_2S_5), $F_{2:3}$ (64)	RFLP, PCR	67	Coaker et al. (2002)
S. habrochaites LA0407	Fruit color	3	13	BILs (BC_2S_5)/F_3, F_4 (64)	RFLP, PCR	63; 394	Kabelka et al. (2004)
S. habrochaites PI-247087	Ascorbic acid	2	5	BC_2/BC_2S_1 (130/79,68)	AFLP, RFLP, SSR, MO, CG*AA*	217	Stevens et al. (2007)

(*continued*)

Table 9.7 (continued)

Wild or donor parent	Main traits analyzed	No. traits evaluated[a]	No. QTL[b]	Mapping population (pop. size)[c]	Marker type[d]	No. Markers	References[e]
S. habrochaites LYC4 (IL5-1 and IL5-2 lines) and *S. habrochaites* (IVT-line 1)	Parthenocrapy, stigma exsertion	2	5	(two) BC_5S_1, F_2	CAPS, COS, SSR	34	Gorguet et al. (2008)
S. lycopersicum "cerasiforme" Cervil inbred line	Aroma volatiles (18), fruit quality	32 (26)	81	F_7-RILs (144)	RFLP, AFLP, RAPD, MO	103	Saliba-Colombani et al. (2001), Causse et al (2002, 2007), Lecomte et al. (2004a, b), Chaïb et al. (2006)
S. lycopersicum "cerasiforme" Cervil inbred line	Sensory attributes (12)	12	49	F_7-RILs (144)	RFLP, AFLP, RAPD, MO	103	Causse et al. (2001, 2002, 2007), Lecomte et al. (2004a, b), Chaïb et al. (2006)
S. lycopersicum "cerasiforme" Cervil inbred line	Ascorbic acid	2	6	F_7-RILs (144)	RFLP, AFLP, RAPD, MO	103	Stevens et al. (2007)
S. neorickii LA2133	Yield, fruit quality, horticultural	30	199	BC_2/BC_3 (170)	RFLP, PCR, MO	133	Fulton et al. (2000)
S. neorickii LA2133	Biochemical related to flavor	15	52	BC_2/BC_3 (170)	RFLP, PCR, MO	133	Fulton et al. (2002a)
S. pennellii LA0716	Fruit weight, seed weight, stigma exsertion, leaflet shape	4	21	BC_1 (400)	ISO	12	Tanksley et al. (1982)
S. pennellii LA0716	Morphological (plant, flower, leaf)	11	74	F_2 (432)	RFLP	98	deVicente and Tanksley (1993)
S. pennellii LA0716	Yield, fruit quality	6	104	ILs/HILs/ILs × Tester (49/50/50)	RFLP	375	Eshed and Zamir (1995, 1996), Alpert et al. (1995), Eshed et al. (1996), Gur and Zamir (2004)
S. pennelli LA0716	Fruit shape	2	1	F_2 from IL2-5 (60)	RFLP	15	Ku et al. (1999)
S. pennellii LA0716	Sensory attributes , aroma volatiles	ns	1	ILS (4)	RFLP	ns	Tadmor et al. (2002)
S. pennellii LA0716	Leaf morphology and size	8	30	ILS (58)	RFLP	375	Holtan and Hake (2003)
S. pennellii LA0716	Fruit color, carotenoids	6	50	ILs (75)	RFLP, CG	637 (614, 23)	Liu et al. (2003)
S. pennellii LA0716 and *S. pimpinellifolium* LA1589	Locule number	2	4	Several F_2	ns	ns	Barrero and Tanksley (2004)
S. pennellii LA0716	Fruit size and composition	9	81	ILs (70)	RFLP, CG	671 (592,79)	Causse et al. (2004)
S. pennellii LA0716	Leaf and flower morphology	22 (18)	36	F_2 (83)	RFLP, SSR, COS	391, (350, 10, 31)	Frary et al. (2004b)

S. pennellii LA0716	Fruit quality, transcriptomic analysis	6	ns	ILs (6)	RFLP	ns	Baxter et al. (2005)
S. pennellii LA0716	Fruit antioxidants	5	20	ILs (76)	RFLP	~600	Rousseaux et al. (2005)
S. pennelli LA0716	Primary metabolites (74), yield related	83	889, 326[g]	ILs (76)	RFLP	~600	Schauer et al. (2006)
S. pennelli LA0716	Yield fitness	35	841	ILs, ILHs (76; 76)	RFLP	~600	Semel et al. (2006)
S. pennelli LA0716	Aroma volatiles (23), organic acids	25 (24)	29	ILs (74)	RFLP	~600	Tieman et al. (2006)
S. pennellii LA0716	Ascorbic acid	1	12	ILs (71)	RFLP	~600	Stevens et al. (2007, 2008)
S. pennelli LA0716	Hybrid incompatibility	4	19	ILs (71)	RFLP	~600	Moyle and Nakazato (2008)
S. pennelli LA0716	Primary metabolites (74)	74	332	ILs, ILHs (68;68)	RFLP	~600	Schauer et al. (2008)
S. pennellii LA1657	Yield, fruit quality, horticultural	25	84	BC_2/BC_2F_1 (175)	RFLP	150	Frary et al. (2004a)
S. pimpinellifolium CIAS27	Fruit quality, horticultural	18	85	F_2 (1,700)	MO, ISO	6, 4	Weller et al. (1988)
S. pimpinellifolium LA1589	Fruit quality, flower morphology, flowering and ripening time	19	54	BC_1 (257)	MO, RAPD, RFLP	120	Grandillo and Tanksley (1996a), Alpert et al. (1995), Grandillo et al. (1996), Ku et al. (2000)
S. pimpinellifolium LA1589	Yield, fruit quality, horticultural	21 (18)	87	$BC_2/BC_2F_1/BC_3$ (~170/170)	MO, RAPD, CAPS, RFLP	121	Tanksley et al. (1996)
S. pimpinellifolium LA0722	Fruit quality, lycopene	7	59	BC_1/BC_1S_1 (119)	RFLP	151	Chen et al. (1999)
S. pimpinellifolium LA1589	Fruit shape	2	2	F_2 (82)	RFLP	82	Ku et al. (1999)
S. pimpinellifolium LA1589	Fruit size and shape	7	30	F_2 (114)	RFLP, CAPS	90	Lippman and Tanskley (2001)
S. pimpinellifolium LA1589	Fruit and ovary shape	2	1	F_2 (100)	RFLP, SNP	108	van der Knaap and Tanksley (2001)
S. pimpinellifolium LA1589	Fruit quality, horticultural	22	71	BC_2F_6 – BILs (196)	RFLP, MO	127	Doganlar et al. (2002b)
S. pimpinellifolium LA1589	Biochemical related to flavor	15	33	$BC_2/BC_2F_1/BC_3$ (~170)	MO, RAPD, CAPS, RFLP	121	Fulton et al. (2002a)
S. pimpinellifolium LA1589	Fruit shape	3	4	F_2 (85)	RFLP	97	van der Knaap et al. (2002)
S. pimpinellifolium LA1589	Fruit shape and size	10	50	F_2 (200)	RFLP	93	van der Knaap and Tanksley (2003)
S. pimpinellifolium LA1589	Fruit shape	15	36, 32, 27[h]	(two) F_2, BC_1 27(99; 130; 100)[h]	RFLP, PCR	111, 111, 108[h]	Brewer et al. (2007)
S. pimpinellifolium LA1589	Fruit shape	14	20, 23, 20[h]	(three) F_2 (130;106; 94)	RFLP, PCR	111, 96, 97	Gonzalo and van der Knaap (2008)

(*continued*)

Table 9.7 (continued)

Wild or donor parent	Main traits analyzed	No. traits evaluated[a]	No. QTL[b]	Mapping population (pop. size)[c]	Marker type[d]	No. Markers	References[e]
S. lycopersicum IVT KTl (breeding line containing S. pimpinellifolium and S. neorickii introgressions)	Fruit size, flowering and ripening time	6	3	F_2, F_3 (292)	RFLP	45	Lindhout et al. (1994c)
S. pimpinellifolium LA1237 (the "selfer") and LA1581 (the "outcrosser")	Flower morphology and number	6 (4)	5	F_2 (147)	RFLP	48	Georgiady et al. (2002)

[a]The number of traits for which QTLs were identified is indicated in parenthesis
[b]An "*" indicates the number of significant markers × traits associations
[c]*ILH* Introgression line hybrid
[d]For markers abbreviations see legends to Tables 9.5 and 9.6
[e]Some of the related and/or follow-up studies are also listed
[f]*ns* not specified
[g]Fruit metabolism and yield-associated traits, respectively
[h]Per population

Table 9.8 Summary of abiotic stress tolerance/resistance QTL mapping studies conducted in *Solanum* sect. *Lycopersicon*

Type and source of tolerance/resistance[a]	Developmental stage[b]	No. traits or treatments	No. QTL (Q)	Chromosome	Mapping population	Marker type[c]	No. Markers[d]	References
Cold								
S. habrochaites LA1777	Pollen selection	1	2	6, 12	BC_1	ISO	9	Zamir et al. (1982)
S. habrochaites	VG	1	3	6, 7, 12	BC_1	ISO	11	Vallejos and Tanksley (1983)
S. habrochaites LA1778	VG	7	10	1, 3, 5, 6 (three Q), 7, 9, 11, 12	BC_1	RFLP	89	Truco et al. (2000)
S. pimpinellifolium LA0722	SG	1	3–5	1 (two Q), 4	BC_1S_1	RFLP	151	Foolad et al. (1998b)
Drought								
S. pennellii (ns)[e]	VG	1	3	ns[e]	F_3, BC_1S_1	RFLP	17	Martin et al. (1989)
S. pennellii LA0716	VG	1	6	2, 3, 5, 7, 9, 12	ILs, sub-ILs of IL5-4	STS, CAPS, AFLP, SSR	29	Xu et al. (2008)
S. pimpinellifolium LA0722	SG	1	4	1, 8, 9, 12	BC_1S_1	RFLP	119	Foolad et al. (2003)
Salt								
S. galapagenese (L2) and *S. pimpinellifolium* (L1 and L5)	RS	4	31	1–5,7, 9–12	three F_2	RFLP, ISO	19, 3	Monforte et al. (1997a)
S. galapagenese (L2) and *S. pimpinellifolium* (L1 and L5)	RS	2, 4	43	1–5, 7, 9–12	three F_2	RFLP, ISO	19, 3	Monforte et al. (1997b)
S. galapagense L2	VG, RS	6	8	1, 2, 5, 7, 9, 12	F_2	RFLP, ISO	20, 3	Monforte et al. (1999)
S. galapagense (L2) and *S. pimpinellifolium* (L5)	VG, RS	19	12, 23	1–8, 10–12	two F_7-RILs	RFLP, SSR, CG	153, 124	Villalta et al. (2007)
S. galapagense (L2) and *S. pimpinellifolium* (L5)	VG	10	18, 25	1, 3, 5–8, 11, 12	two F_8-RILs	RFLP, SSR, CG	153, 124	Villalta et al. (2008)
S. galapagense (L2) and *S. pimpinellifolium* (L5)[f]	RS	3	8	3, 9, 11	two F_9-RILs	RFLP, SSR, CG	153, 124	Estañ et al. (2009)
S. pennellii LA0716	VG	3	6	1, 2, 4–6, 12	F_2	ISO	15	Zamir and Tal (1987)
S. pennellii LA0716	SG	2	5	1, 3, 7, 8, 12	F_2 (SGe)[g]	ISO	16	Foolad and Jones (1993)
S. pennellii LA0716	SG	1	8	1–3, 7–9 (two Q), 12	F_2 (SGe)	ISO, RFLP	16, 68	Foolad et al. (1997)
S. pennellii LA0716	SG	1	8	1, 3, 5 (two Q), 6, 8, 9, unknown	F_2 (SGe)	RAPD	53	Foolad and Chen (1998)
S. pennellii LA0716	VG	12	125	All	ILs	PCR	122	Frary et al. (2010)
S. pimpinellifolium L1	RS	3	6	1–4, 10, 12	F_2, F_3	ISO, RAPD, RFLP	2, 2, 10	Bretó et al. (1994), Monforte et al. (1996)
S. pimpinellifolium L1	RS	3	12	1–4, 10, 12	F_2	ISO, RFLP	2, 14	Monforte et al. (1996)
S. pimpinellifolium LA0722	SG	1	7	1 (two Q), 2, 5, 7, 9, 12	BC_1S_1	RFLP	151	Foolad et al. (1998a)
S. pimpinellifolium LA0722	VG	1	5	1 (two Q), 3, 5, 9	BC_1S_1	RFLP	151	Foolad and Chen (1999)
S. pimpinellifolium LA0722	VG	1	5	1, 3, 5, 6, 11	BC_1 (SGe)	RFLP	115	Foolad et al. (2001)

[a]*S. galapagense* L2 = it was *Lycopersicon cheesmanii* f. *minor* in the original study by Monforte et al. (1997a)
[b]*RS* reproductive stage, *SG* seed germination, *VG* vegetative growth
[c]For markers abbreviations see legends to Tables 9.5 and 9.6
[d]Per marker type
[e]*ns* accession number, or other data, not specified
[f]Used as a rootstock
[g]*SGe* Selective genotyping

Subsequently, an F_2 population of 83 individuals derived from the cross *S. lycopersicum* (LA0925) × *S.pennellii* (LA0716) was used to construct the first PCR-based reference genetic map covering the entire tomato genome (Frary et al. 2005). The same population has been used to develop a new molecular linkage map using conserved ortholog set (COS) and conserved ortholog set II (COSII) markers derived from a comparison of the tomato expressed sequence tag (EST) database against the entire *Arabidopsis* genome (Fulton et al. 2002b; Wu et al. 2006). These markers have been selected to be single/low copy and to have a highly significant match with a putative orthologous locus in the model species *Arabidopsis thaliana* (L.) Heynh. This map, referred to as Tomato-EXPEN 2000, contains also a subset of RFLP markers from the Tomato-EXPEN 1992 map, a significant number of SSRs identified in ESTs, and other CAPSs, which, as of July 2010, add up to a total of over 2,500 markers (http://solgenomics.net/). Recently, the Tomato-EXPEN 2000 mapping population was used to generate a new linkage map based on SSRs derived from EST (TES) and from genome sequences (TGS) as well as intronic polymorphism markers (TEI) (Table 9.5; Shirasawa et al. 2010). Altogether, this new high-density linkage map includes a total of 2,116 marker loci (1,433 new and 683 existing) covering 1,503.1 cM. The large number of SSR and SNP markers developed in this study provide new useful tools also for molecular breeding in tomato.

Online versions of some of the aforementioned maps are available at the SOL Genomics Network (SGN; http://solgenomics.net/) (Mueller et al. 2005a), the National Center for Biotechnology Information (NCBI) (Wheeler et al. 2004), and http://www.tomatomap.net (Van Deynze et al. 2006) (Table 9.5). Information on the DNA markers developed by Shirasawa et al. (2010) is available at http://www.kazusa.or.jp/tomato/.

The comparison of genetic maps based on interspecific crosses between *S. lycopersicum* and wild tomato species shows a generally conserved gene order (with a few exceptions), suggesting a strong synteny within this plant group (see Sect. 9.2.5), although the total genetic lengths of these published maps can vary (reviewed by Ji and Scott 2007). As was already reported by Rick (1969), recombination is not a process that occurs randomly over the entire genome. Recombination frequencies may vary dramatically in intensity between chromosomal regions and among populations, although it is not yet clear to what extent they might be affected by the phylogenetic relationship between species. Whatever the cause, these phenomena have been exploited to generate dense molecular linkage maps around specific gene(s), sometimes by using combinations of several inter- and/or intraspecific mapping populations (e.g., Balint-Kurti et al. 1994; Ganal and Tanksley 1996; Bonnema et al. 1997). Skewed segregation is another phenomenon that has been reported in many interspecific crosses of tomato, with the extent of skewness generally being greater in wider crosses compared to crosses between closely related species, and also generally greater in F_2 than in BC populations, as well as in F_7 compared to the original F_2 generation (Chen and Foolad 1999; Paran et al. 1995; Villalta et al. 2005).

Comparative genetic mapping studies have been conducted to understand the genetic relationships between the sects. *Lycopersicoides* and *Juglandifolia* species and cultivated tomato, and therefore to evaluate their potential use in breeding programs, as well as their history of evolution and speciation. One such study, based on a *S. lycopersicoides* and *S. sitiens* F_2 population, revealed a high degree of colinearity, except for chromosome 10, where a paracentric inversion was detected (see also Sect. 9.2.5; Pertuzé et al. 2002). More recently, the genetic relationships of the two nightshades *S. ochranthum* and *S. juglandifolium* to tomato and other *Solanum* species were also investigated using comparative genetic linkage maps obtained from a *S. ochranthum* × *S. juglandifolium* F_2 population (Albrecht and Chetelat 2009). This study shows that, in spite of the strong reproductive barriers that isolate these two taxa from the tomatoes (*Solanum* sect. *Lycopersicon*), most regions of the identified twelve linkage groups were co-linear with the tomato reference maps.

9.6.4 Mapping of Genes and Polygenic Clusters

Interspecific crosses have been widely used for genetic analysis in tomato (Stevens and Rick 1986; Kalloo 1991). The reduced polymorphism at the DNA level between cultivated tomato varieties has stimulated the extensive utilization of domesticated-by-wild crosses

for mapping studies. Due to the wealth of molecular marker loci available for this crop, progenies deriving from interspecific crosses have also played an important role in gene mapping as well as development of QTL analysis strategies, including map-based cloning approaches (Paterson et al. 1988; Martin et al. 1993; Tanksley 1993; Eshed and Zamir 1995; Tanksley and Nelson 1996; Frary et al. 2000; Fridman et al. 2000). Since the earliest QTL mapping reports based on isozymes and morphological markers, it has been clear that this approach allows more efficient uncovering of "cryptic" genetic variation, and that wild relatives would provide a rich source of favorable alleles for the improvement of elite germplasm, as well as for traits in which the unimproved (wild) species show an inferior phenotype (Tanksley et al. 1982; Weller et al. 1988). Following the demonstration by Paterson et al. (1988) that molecular linkage maps covering the entire genome could be used to resolve quantitative traits into Mendelian factors, QTL mapping studies in tomato, based on interspecific crosses, were extended to hundreds of agronomically important traits involved in plant morphology, adaptation, yield, fruit quality, metabolism, and gene expression. The outcome of these studies has been the identification of thousands of QTLs, many of which are of potential value for tomato breeding, and whose molecular basis is still to be deciphered.

The status of gene and/or QTL mapping in tomato has been the subject of several recent reviews (Labate et al. 2007; S. Grandillo personal communication), and most of the studies have been summarized in Tables 9.6–9.8. Here we will describe some of the main mapping results obtained so far using each species.

9.6.4.1 *Solanum arcanum, Solanum corneliomulleri, Solanum huaylasense, Solanum peruvianum*

These four green-fruited wild species have been segregated from *Solanum peruvianum* s.l. (see Sects. 9.2 and 9.3; Peralta et al. 2005, 2008), formerly considered the most widespread and polymorphic species in *Solanum* sect. *Lycopersicon* (Peralta et al. 2005). *S. arcanum* Peralta and *S. huaylasense* Peralta have been described as new species (Peralta et al. 2005) from Peru, while the other two, *S. peruvianum* s.str. and *S. corneliomulleri* had already been named by Linnaeus (1753) and MacBride (1962), respectively. In some of the reviewed studies that used the old nomenclature, the accession number was not available; therefore, in these cases, genotypes have been referred to as *S. peruvianum* s.l. here. These four species cover a wide diversity of habitats that range from approximately sea level to nearly 3,000 m, thus explaining their adaptation to extreme environments. They also represent a rich reservoir of potentially valuable genes for disease resistance as well as other agronomically important traits. However, mainly due to the hybridization barriers that exist between these species and the cultivated tomato, they have not been thoroughly exploited for breeding purposes (Taylor 1986).

Within *S. arcanum*, the SC accession LA2157, originating from 1,650 m above sea level in northern Peru, is known as source of several beneficial traits for cultivated tomatoes such as cold tolerance, resistance to bacterial and fungal diseases, as well as heat-stable resistance to root nematode caused by *Meloidogyne* spp. (Table 9.6). The cross with *S. lycopersicum* is difficult but possible through in vitro embryo rescue (Brüggemann et al. 1996). Molecular linkage maps have allowed the identification of QTLs underlying the resistance of *S. arcanum* LA2157 to bacterial canker caused by *Clavibacter michiganensis* subsp. *michiganensis* (*Cmm*) (Table 9.6). A first RFLP mapping study was conducted on BC populations derived from the intraspecific cross between *S. arcanum* LA2157 and the susceptible *S. arcanum* accession LA2172, and five QTLs were identified (Sandbrink et al. 1995). Subsequently, Van Heusden et al. (1999) used RFLPs in a F_2 derived from the interspecific *S. lycopersicum* cv. "Solentos" × *S. arcanum* LA2157 cross, and detected three QTLs, which showed a substantial influence on resistance to *Cmm* (Van Heusden et al. 1999).

Recently, a strong source of resistance to an Indonesian isolate of *Alternaria solani*, the causal agent of early blight (EB) was identified in *S. arcanum* LA2157 (Chaerani et al. 2007). Early blight is a devastating fungal disease of tomato worldwide, and most commercial cultivars are susceptible. Classical genetic studies revealed at least two loci with additive and dominance effects and epistatic interactions for resistance to EB symptoms (see references in Chaerani et al. 2007). However, classical breeding approaches have not been successful in developing cultivars with

a sufficient level of resistance and adequate commercial quality. Therefore, molecular-based breeding strategies are foreseen as a possible solution to obtain resistant cultivars with early to mid-season maturity and high yield potential. In order to study the genetic basis of this resistance, a QTL analysis was conducted in F_2 and F_3 populations derived from a *S. lycopersicum* cv. "Solentos" × *S. arcanum* LA2157 cross, using AFLP, SSR and SNP markers, which allowed the identification of six QTLs for resistance to EB, some of which also conferred resistance to stem lesions in the field (Chaerani et al. 2007).

The *S. arcanum* accession LA2172 is completely resistant, almost immune, to *Oidium neolycopersici* (previously named *O. lycopersici*) (Kiss et al. 2001), the causal agent of powdery mildew (PM) in tomato (Lindhout et al. 1994a, b). The gene *Ol-4* responsible for this complete resistance was mapped, and subsequently fine-mapped, on tomato chromosome 6 in a pseudo-F_2 population from an interspecific cross between *S. lycopersicum* cv. "Moneymaker" and *S. arcanum* LA2172 (Bai et al. 2004, 2005).

All tomato cultivars with resistance to *Meloidogyne* spp. (*Meloidogyne incognita, M. arenaria* and *M. javanica*) carry the dominant gene *Mi-1* deriving from *S. peruvianum* accession PI 128657, which was mapped on chromosome 6 (Smith 1944; Gilbert and McGuire 1956; Medina-Filho 1980; Klein-Lankhorst et al. 1991; Messeguer et al. 1991). The *Mi-1* gene of tomato was isolated by a positional cloning approach, and it was shown to belong to the NBS-LRR class of *R* genes and to have a dual specificity resistance to the root-knot nematode *M. incognita* and to an unrelated pathogen, the potato aphid *Macrosuphum euphorbiae* (Milligan et al. 1998; Vos et al. 1998). However, this resistance is not active at soil temperatures above 28°C; in contrast, *S. arcanum* LA2157 has been identified as a source for heat-stable resistance, and the gene conferring this resistance, named *Mi-9,* was mapped to the short arm of chromosome 6 in a similar genetic interval as *Mi-1* (Veremis et al. 1999; Veremis and Roberts 2000; Ammiraju et al. 2003). Using virus-induced gene silencing (VIGS) targeted to silence *Mi-1* homologs in *S. arcanum* LA2157, Jablonska et al. (2007) showed that *Mi-9* is likely a homolog of *Mi-1*. Another resistance gene, *Mi-3,* which confers resistance to *Mi-1*-virulent nematode isolates, was mapped to the telomeric region of chromosome 12, using a segregating population of *S. peruvianum* accession PI 126443 clone 1MH (Yaghoobi et al. 1995). Veremis and Roberts (1996a, b) revealed a spectrum of *Meloidogyne* resistance genes in *S. peruvianum* s.str., which are expressed in single dominant gene fashion. They showed the presence of a linked additional gene (*Mi-5*) for heat-stable resistance in the same region of *Mi-3*, and found two weakly linked pairs of genes (*Mi-2* and *Mi-8* in PI 270435 clone 2R2 and *Mi-6* and *Mi-7* in PI 270435 clone 3MH), which seemed to be independent of each other and of the *Mi-1* region on chromosome 6, and also independent from the *Mi-3*/*Mi-5* region on chromosome 12.

Resistances to tobacco mosaic virus (TMV), tomato spotted wilt virus (TSWV), and tomato yellow leaf curl virus (TYLCV) have been studied in *S. peruvianum* s.l. The two allelic genes, *Tm-2* and *Tm2a* (a.k.a.$Tm2^2$), which confer resistance to TMV, were introgressed from *S. peruvianum* PI 128650 into *S. lycopersicum* (Labate et al. 2007 and references there in). The durable $Tm\text{-}2^2$ resistance gene was mapped and fine-mapped to the centromeric region of chromosome 9 (Young et al. 1988; Pillen et al. 1996a). Subsequently, $Tm\text{-}2^2$ was isolated from tomato via transposon tagging, and was shown to be functional in both tomato and tobacco (Lanfermeijer et al. 2003, 2004). The isolation and characterization of the broken *Tm-2* resistance gene showed that the two resistance alleles, $Tm\text{-}2^2$ and *Tm-2,* from tomato differ in four amino acids (Lanfermeijer et al. 2005). CAPS markers have been developed to differentiate the *Tm-2*, $Tm\text{-}2^2$, and *tm-2* (susceptible) alleles (Lanfermeijer et al. 2005).

The single dominant gene (*Sw-5*) originating from *S. peruvianum* s.l. that confers resistance to common strains of TSWV was mapped to the long arm of chromosome 9 (Stevens et al. 1995). The map-based cloning of the *Sw-5* locus showed that it contains a single gene capable of providing resistance to different Tospovirus species and it is a homolog of the root-knot nematode resistance gene *Mi-1* (Brommonschenkel and Tanksley 1997; Brommonschenkel et al. 2000). PCR-based marker systems have been developed that can aid MAS for the *Sw-5* gene (Folkertsma et al. 1999; Garland et al. 2005).

TYLCV is currently considered as one of the most devastating viruses of cultivated tomatoes in tropical and subtropical regions, and resistant cultivars are highly effective in controlling the disease. The breeding line TY172, originating from *Solanum peruvianum* s.l., is highly resistant to TYLCV (Anbinder et al.

2009). QTL analysis showed that TYLCV resistance in TY172 is controlled by a previously unknown major QTL, named *Ty-5*, originating from the resistant line and mapping on chromosome 4, and by four additional minor QTLs, originating either from the resistant or susceptible parents, and mapping on chromosomes 1, 7, 9, and 11 (Anbinder et al. 2009).

Genetic resistance to the soil-borne fungus *Pyrenochaeta lycopersici*, the casual agent of corky root rot, which can cause big losses in tomato production, has been identified in accessions of *S. peruvianum* s.l. and *S. habrochaites* (Hogenboom 1970). Subsequently, a single recessive gene (*pyl*) was shown to control this resistance and was introgressed into *S. lycopersicum* from *S. peruvianum* s.l. (Laterrot 1983). However, breeding programs aimed at transferring this resistance based on phenotypic selection have been hampered by the difficulties associated with greenhouse inoculation and with direct screening of corky root rot resistance. In order to overcome these difficulties, the *pyl* gene was mapped on tomato chromosome 3 using RAPD and RFLP markers, and then codominant CAPS markers were developed to allow a more efficient MAS approach (Doganlar et al. 1998).

S. arcanum has also been used in QTL mapping efforts aimed at exploring the potential value of this wild relative as source of favorable alleles for the improvement of yield, fruit quality, and other horticultural traits (Table 9.7). For this purpose an advanced backcross (AB) population of 200 BC_4 families, derived from the *S. lycopersicum* E6203 × *S. arcanum* LA1708 cross, was analyzed with 205 RFLPs and was evaluated for 35 traits involving yield, processing fruit quality, and plant characteristics. A total of 166 QTLs were identified for 29 of the traits, and, interestingly, for half of the favorable alleles originated from the wild parent (Fulton et al. 1997). The same population was also evaluated for sugars, organic acids, and other biochemical properties possibly contributing to flavor, and 103 QTLs were identified for the 15 analyzed traits (Fulton et al. 2002a). Also in this case, favorable wild QTL alleles were detected for several of the analyzed traits.

9.6.4.2 *Solanum cheesmaniae* and *Solanum galapagense*

The two yellow- to orange-fruited wild species *Solanum cheesmaniae* and *Solanum galapagense* are very closely related to the cultivated tomato and can be reciprocally hybridized with it. Therefore, a number of genes have been transferred from these wild relatives to the cultigen (Rick 1956). *Solanum galapagense* is also particularly valuable as a source for salt tolerance (ST) (Taylor 1986). In contrast, their role as sources of disease and insect resistances has been more limited, probably due to their isolation on the Galápagos islands, which has reduced the exposure of these two taxa to the numerous pests and diseases that instead can be found on the mainland and that attack the other sect. *Lycopersicon* species (Taylor 1986).

One gene that has been introgressed from *S. cheesmaniae* LA0166 into cultivated tomato is the jointless pedicel gene, *jointless-2* (*j-2*); a recessive mutation that completely suppresses the formation of flower and fruit pedicel abscission zone, and which was discovered on the Galápagos Islands of South America by Rick (1956). This gene has been widely used for more than 40 years in the tomato processing industry (Zhang et al. 2000). High resolution genetic and physical mapping have located the *j-2* gene in the centromeric region of tomato chromosome 12 (Zhang et al. 2000; Budiman et al. 2004). Two other genes, the *Beta* (*B*) and the *Beta*-modifier (Mo_B), which control the high concentrations of β-carotene in orange-pigmented tomatoes, were mapped to the long arm of chromosome 6 using segregating populations derived from the two interspecific crosses *S. lycopersicum* × *S. galapagense* LA0317 and *S. lycopersicum* × *S. habrochaites* PI 126445 (Zhang and Stommel 2000). The *B* gene was isolated by map-based cloning approach (Ronen et al. 2000; see also Sect. 9.6.4.9), and codominant SCAR and CAPS markers were developed for use in MAS programs (Zhang and Stommel 2001). Furthermore, interspecific mapping populations derived from crossing between *S. lycopersicum* and *S. galapagense* LA0483 were used to map several genes involved in pigment content and fruit ripening including *high pigment-1* (*hp-1*), *non-ripening* (*nor*), and *ripening-inhibitor* (*rin*) (Giovannoni et al. 1995; Yen et al. 1997; Peters et al. 1998).

Solanum cheesmaniae has been used as source of resistance to blackmold caused by *Alternaria alternata* (Rick 1986a) (Table 9.6). Cassol and St. Clair (1994) showed that resistance in *S. cheesmaniae* LA0422 was quantitatively inherited, and blackmold resistance QTLs were mapped in a progeny derived from a *S. lycopersicum* cv.

"VF145B-7879" × *S. cheesmaniae* LA0422 cross; subsequently, by means of MAS, five resistant QTLs from *S. cheesmaniae* LA0422 were introgressed into cultivated tomato (Robert et al. 2001). The QTL on chromosome 2 had the largest positive effect on black-mold resistance, and was also associated with earliness, a positive horticultural trait.

Solanum galapagense as well as several other wild tomato species including *S. pimpinellifolium*, *S. chilense*, *S. cheesmaniae*, *S. pennellii,* and *S. peruvianum* s.l. represent genetic sources of ST (reviewed by Foolad 2004, 2005). Given the complex nature of ST, most studies have focused on specific developmental stages. In the case of *S. galapagense,* QTL analyses have focused on the vegetative (VG) and/or reproductive (RS) stage of the plant (Table 9.8) (Monforte et al. 1997a, b, 1999; Villalta et al. 2007, 2008). These studies were conducted on F_2 or recombinant inbred line (RIL) populations derived from interspecific crosses between the salt-sensitive *S. lycopersicum* and *S. lycopersicum* "cerasiforme" and the two ST wild species *S. galapagense* and *S. pimpinellifolium* to analyze the effect of salinity on several yield related traits, including fruit weight, fruit number, total fruit weight, as well as Na^+ and K^+ in stems and leaves. Villalta et al. (2007) found that, contrary to the expected, the allele from the wild ST genotype had a favorable effect only at one total fruit yield QTL. These results suggested that alternative approaches need to be pursued in order to improve tomato crop productivity under salinity, and one possibility is by grafting cultivars onto ST wild relatives. Therefore, Estañ et al. (2009) analyzed the rootstock effect on fruit yield of a grafted tomato variety under moderate salinity (75 mM NaCl) using as rootstocks F_9 lines of the two interspecific RIL populations previously used by Villalta et al. (2007, 2008). This study detected at least eight QTLs that contributed to this ST rootstock effect, with the most relevant component being the number of fruits. In addition, Albacete et al. (2009) found that in the *S. galapagense* RIL population rootstock-mediated changes in xylem ionic and hormonal status were correlated with delayed leaf senescence, and increased leaf area and thus crop productivity in salinized tomato.

The *S. galapagense* accession LA0483 has been used in QTL mapping studies aimed at deciphering the genetic basis of fruit quality traits (Table 9.7). Work by Paterson et al. (1991) detailed the identification of 29 putative QTLs for soluble solids content (SSC) measured by brix value, mass per fruit, and pH in a F_2 population derived from a cross between the inbred cultivar "UC204C" and *S. galapagense* LA0483. Subsequently, 97 F_8 RILs were developed from the same cross and were used to identify QTLs for seed weight, fruit weight, SSC, and morphological traits (Goldman et al. 1995; Paran et al. 1997).

9.6.4.3 *Solanum chilense*

Among all wild species of tomato, the green-fruited *Solanum chilense* seems to be one of the most notable as a source of a broad spectrum of disease resistance. In fact, this species shows resistance to several bacterial, fungal, and viral diseases, as well as to root knot nematodes and parasitic plants, such as dodder (*Cuscuta* spp., Convolvulaceae, Rick and Chetelat 1995). Moreover, *S. chilense*, being indigenous to arid and semi-arid environments in South America, has also been considered of interest for its drought tolerance (Rick 1973).

Among viral diseases, cucumber mosaic virus (CMV) is an important disease for tomatoes growing in temperate regions and is the most destructive virus in some areas. Fortunately, several wild tomato species are resistant or tolerant to CMV, including *S. chilense, S. pimpinellifolium*, *S. peruvianum* s.l., *S. habrochaites*, *S. galapagense*, and *S. lycopersicoides* (Stamova and Chetelat 2000 and references therein). In order to explore the genetic basis of CMV resistance, Stamova and Chetelat (2000) used isozyme and RFLP markers in BILs derived from a *S. lycopersicum* × *S. chilense* LA0458 cross and identified a single dominant resistance gene, *Cmr,* which mapped on chromosome 12 (Table 9.6).

Within *S. chilense*, high levels of resistance to begomoviruses, such as monopartite tomato yellow leaf curl virus (TYLCV) and bipartite tomato mottle virus (ToMoV), transmitted by the whitefly, *Bemisia tabaci*, have been identified in several accessions including LA1969, LA1932, LA2779, and LA1938, which have been useful sources of resistance in tomato breeding programs (Ji et al. 2007b and references therein). The accession LA1969 has been used as source for the TYLCV tolerance locus, *Ty-1*, a partially dominant major gene, which was located on chromosome 6 of tomato using RFLP markers, and

subsequently introgressed into cultivated tomato (Table 9.6; Michelson et al. 1994; Zamir et al. 1994). Conventional genetic analysis and QTL mapping conducted in F_2 populations derived from *S. chilense* accessions LA1932, LA1938, and LA2779 revealed three regions on chromosome 6 contributing to resistance to both TYLCV and ToMoV, and RAPD markers linked to each region were identified (Griffiths and Scott 2001; Ji and Scott 2005; Agrama and Scott 2006; Ji et al. 2007a). The first region includes the *Ty-1* locus, while the other two regions flank either side of the *self-pruning* (*sp*) and *potato leaf* (*c*) loci. Two additional TYLCV resistance genes, *Ty-3* and *Ty-4*, were recently discovered in *S. chilense* accessions (LA2779 and LA1932) and mapped to chromosomes 6 and 3, respectively (Ji et al. 2007a, 2009a). The partially dominant gene, *Ty-3,* deriving from *S. chilense* accession LA2779, was mapped on chromosome 6 near the *Ty-1* locus (Ji et al. 2007a). RILs carrying both resistance genes had the highest level of TYLCV resistance (Ji et al. 2009a). PCR-based markers tightly linked to both genes have been developed and used in MAS breeding programs (Jensen et al. 2007; Ji et al. 2007a, b). Finally, TSWV resistance was identified in a breeding line derived from a cross with *S. chilense* LA1938; the same line was previously selected for ToMoV resistance in Florida (Canady et al. 2001).

The *S. chilense* accession LA1969 was identified also as a source of resistance to *Leveillula taurica*, one of the two pathogens responsible for PM in tomato, which has become a serious problem to tomato growers and breeders around the world, but especially in subtropical regions (Chunwongse et al. 1997). A single dominant gene, *Lv*, conferring resistance to this pathogen has been described from *S. chilense* LA1969 and has been introgressed into the cultivated tomato via backcross breeding (Stamova and Yordanov 1990). Subsequently, *Lv* was mapped to a high resolution map position near the centromere of chromosome 12 (Chunwongse et al. 1994, 1997).

Recently, the *S. chilense* accession LA1932 has been used in an AB-QTL mapping study aimed at exploring the potentials of this wild relative as a source of useful QTL alleles for yield-related and fruit quality traits (Termolino et al. 2010; S. D. Tanksley personal communication). Results from this study have demonstrated that, despite its inferior horticultural characteristics, *S. chilense* contains alleles capable of improving several traits of economic importance for processing tomatoes including brix, firmness, and viscosity.

9.6.4.4 *Solanum chmielewskii*

This green-fruited wild species has been studied extensively for its high concentration in soluble solids (SSC or brix; mainly sugars and organic acids), which can reach approximately 10%, almost twice the concentration found in mature fruit of the domestic tomato (Rick 1974). By means of extensive backcrossing and selection, genes for enhanced SSC from *S. chmielewskii* accession LA1028 have been introgressed into *S. lycopersicum* cv. "VF 36" and cv. "VF 145-22-8" resulting in BC_5S_5 lines (including LA1500-1503 and LA1563) with a 40% higher SSC (about 7–8%), but a similar yield, fruit size, and color to the recurrent parent (Rick 1974). Subsequently, the segments introgressed from *S. chmielewskii* were identified using RFLP and isozyme markers and characterized for their effects on SSC, pH, and yield (Table 9.7; Osborn et al. 1987; Tanksley and Hewitt 1988; Azanza et al. 1994). Paterson et al. (1988) conducted a QTL analysis on a *S. lycopersicum* UC82B × *S. chmielewskii* LA1028 BC_1 population using a whole genome RFLP map, and they identified 15 QTLs related to SSC, fruit weight, and pH; some of them were then fine-mapped using a substitution mapping method (Paterson et al. 1990). One of the near isogenic lines (NILs) developed by Paterson et al. (1990), TA1150, contained a 56-cM introgression from *S. chmielewskii* chromosome 1 and had several interesting phenotypic characteristics including fruit with high levels of brix, orange color, thicker pericarp, smaller stem scars, and higher firmness than the control *S. lycopersicum* cv. "E6203" (Frary et al. 2003). The development and field characterization of a set of derived overlapping sub-ILs allowed breaking the undesirable linkage between high brix and orange color (Frary et al. 2003). Moreover, in contrast to *S. lycopersicum*, *S. chmielewskii*, as well as *S. peruvianum* s.l. and *S. habrochaites* fruit, accumulates soluble sugars primarily as sucrose, rather than glucose and fructose (Davies 1966; Yelle et al. 1988). High sucrose accumulation in *S. chmielewskii* and *S. habrochaites* has been suggested to be recessive and monogenic (Yelle et al. 1991), and the gene, denominated *sucr*, was mapped to the pericentromeric region of chromosome

3 using RFLPs (Chetelat et al. 1993). However, after introgressing the *S. chmielewskii* LA1028 *sucr* gene into the genetic background of a hexose-accumulating cultivated tomato, it was observed that associated reduced fertility, due to tightly linked genes or to pleiotropic effects of *sucr*, did not allow a net gain in yield of SSC (Chetelat et al. 1995a, b).

More recently, fruit quality traits and physiological parameters were evaluated on 20 ILs derived from the introgression of *S. chmielewskii* LA1840 into *S. lycopersicum* cv. "Moneyberg" under high (unpruned trusses) and low (trusses pruned to one fruit) fruit load conditions (Table 9.7; Prudent et al. 2009). The results obtained in this study suggested that the relationships between fruit weight and its composition could be mainly related to sink strength through cell division whose intensity was modulated by fruit load (Prudent et al. 2009). Phenotypic analysis of the same *S. chmielewskii* LA1840 IL population revealed three overlapping ILs on chromosome 1 conferring a pink fruit color (Ballester et al. 2010). Genetic mapping, segregation analysis, and VIGS results suggested strongly that the *MYB12* gene is a likely candidate of the locus leading to pink fruit, probably the *Y* locus (Ballester et al. 2010).

Finally, an F_2 population derived from *S. lycopersicum* and its late-flowering wild relative *S. chmielewskii* (line CH6047) was used to study the genetic mechanisms underlying flowering time in tomato (Table 9.7; Jiménez-Gómez et al. 2007). This work allowed the identification of two QTLs affecting days to flowering and six QTLs for leaf number (the number of leaves under the first inflorescence). Interestingly, some of the early flowering QTL alleles were contributed by the *S. chmielewskii* parent, highlighting the usefulness of this wild species for the improvement of flowering time, and in general the importance of exploiting the genetic variation existing among all wild relatives of tomato.

9.6.4.5 *Solanum habrochaites*

This green-fruited wild species is typically found at high elevations, often above 3,000 m, and therefore is expected to be a source of tolerance to low temperatures (Patterson 1988). Moreover, *S. habrochaites* has been typically associated with resistance to a wide range of insect predators and is also a good source of genes for resistance to other pathogens (Rick 1973; Taylor 1986; Farrar and Kennedy 1991; Lukyanenko 1991; Labate et al. 2007). QTL mapping studies conducted with *S. habrochaites* have shown that this wild species is also a valuable source of favorable QTL alleles for numerous other traits including yield and fruit quality, for which the wild phenotype is inferior compared to elite tomato germplasm (Bernacchi et al. 1998a, b; Monforte et al. 2001; S. Grandillo personal communication).

With respect to viral diseases, sources of resistance have been found in *S. habrochaites* accessions. For example, resistances to alfalfa mosaic virus (AMV) have been identified in three accessions of *S. habrochaites* (PI 134417, LA1777, and "Bruinsma") (Parrella et al. 2004). The single dominant gene, *Am*, from *S. habrochaites* PI 134417, which confers resistance to most strains of AMV, was mapped to the short arm of tomato chromosome 6 in the resistance hotspot, which includes the *R*-genes *Mi-1* and *Cf-2*/*Cf-5* and the quantitative resistance factors *Ty-1*, *Ol-1*, and *Bw-5* (Table 9.6; Parrella et al. 2004). A complete resistance to potyviruses (PVY – potato *virus Y*- and TEV – tobacco etch virus) was identified in *S. habrochaites* accession PI 247087, and the recessive gene *pot-1* was mapped to the short arm of tomato chromosome 3 in the vicinity of the recessive *py-1* locus for resistance to corky root rot (Parrella et al. 2002). A comparative genomic approach was used for the molecular characterization of the *pot-1* gene, which was shown to be the tomato ortholog of the pepper *pvr2–elF4E* gene (Ruffel et al. 2005).

The resistance gene, *Tm-1,* to tomato mosaic virus (ToMV), one of the most serious diseases in tomato, originated from *S. habrochaites* by interspecific crossing (Holmes 1957). This gene has been used, either alone or together with one of the other ToMV-resistance genes, *Tm-2* or *Tm-2a* (*a.k.a Tm2*^{2}), to develop resistant varieties. The *Tm-1* gene was mapped near the centromere of chromosome 2, and a number of DNA markers linked to the locus have so far been identified, including RFLPs, RAPDs, SCARs (Table 9.6; Levesque et al. 1990; Tanksley et al. 1992; Ohmori et al. 1996). Due to the reduced frequency of recombination, previous attempts to isolate the *Tm-1* gene using map-based cloning proved unsuccessful; therefore the gene was identified by purifying its inhibitory activity toward ToMV RNA replication in vitro (Ishibashi et al. 2007). *S. habrochaites* is also

a source for high resistance to TYLCV, and resistant tomato lines carrying resistance derived from *S. habrochaites* accession B6013 were developed by Kalloo and Banerjee (1990). Later the TYLCV resistance locus, originating from B6013, was mapped to the long arm of chromosome 11, using RFLP markers (Hanson et al. 2000), formally designated *Ty-2*, and further fine-mapped (Hanson et al. 2006; Ji et al. 2007b). PCR markers have been developed, which allow precise monitoring of the introgression of the *Ty-2* gene into elite breeding lines (Ji et al. 2009b).

With respect to bacterial diseases, a source of resistance to *Cmm*, the casual agent of bacterial canker, was identified in *S. habrochaites* accession LA0407, and two major QTLs for resistance to *Cmm* were mapped using a BIL population derived from a *S. lycopersicum* × LA0407 cross (Kabelka et al. 2002). These QTLs were subsequently fine-mapped and an additive-by-additive epistasis between them was confirmed (Coaker and Francis 2004).

Resistances to several fungal diseases have also been identified in *S. habrochaites*. For example, the *S. habrochaites* accession PI 126445 was identified as a source of resistance to EB (*Alternaria solani*) (Nash and Gardner 1988) and was crossed to a susceptible tomato breeding line to generate BC populations suitable for QTL mapping (Foolad et al. 2002; Zhang et al. 2002, 2003b). In total 14 QTLs affecting EB response were detected using different populations and mapping strategies, and four of them, detected as major QTLs in both studies, were considered of potential value for MAS breeding programs (Foolad et al. 2002; Zhang et al. 2002, 2003b). Tomato gray mold (GM) (*Botrytis cinerea*) is a common fungal disease worldwide, which often causes serious production loss by infecting leaves, stems, flowers, and fruits. No modern hybrid tomato cultivars completely resistant to GM are available, although a few cultivars show a certain level of quantitative resistance (ten Have et al. 2007). In contrast, accessions of *S. chilense*, *S. habrochaites,* and *S. neorickii* show marked quantitative resistance to GM, in both leaf and stem segment assays (Egashira et al. 2000; ten Have et al. 2007). Among others, the *S. habrochaites* accession G1.1560 (LYC4) was selected for high level of resistance (ten Have et al. 2007). Finkers et al. (2007a, b) identified three and 10 QTLs for resistance to *B. cinerea*, in an F_2 and an IL population, respectively, both derived from a *S. lycopersicum* cv. "Moneymaker" × *S. habrochaites* LYC4 cross. In similar studies resistance to late blight (LB) (*Phytophthora infestans*) was described for several accessions of *S. habrochaites* (Lobo and Navarro 1987). The multigenic resistance to LB of the highly resistant *S. habrochaites* accession LA1033 was studied using AFLP markers in BC populations derived from an interspecific cross with the cultivated tomato (Lough 2003). QTLs affecting LB response were detected on four to nine linkage groups depending upon the method of analysis used. At least 15 QTLs for quantitative resistance to *P. infestans* have also been identified in reciprocal BC populations derived from a *S. lycopersicum* × *S. habrochaites* LA2099 cross (Brouwer et al. 2004). Three of these QTLs, *lb4, lb5b*, and *lb11b*, were fine-mapped using NILs and sub-NILs (Brouwer and St. Clair 2004).

S. habrochaites has been the source of the gene *Cf-4,* which confers resistance to *Cladosporium fulvum*, the casual agent of tomato leaf mold (Kerr and Bailey 1964; Stevens and Rick 1986). The *Cf-4* gene from *S. habrochaites*, and the gene *Cf-9* derived from *S. pimpinellifolium*, were introgressed into cultivated tomato (Stevens and Rick 1986). A combination of classical and RFLP mapping showed that they are both located on the short arm of tomato chromosome 1 (Jones et al. 1993; Balint-Kurti et al. 1994); subsequently, *Cf-4* was cloned and characterized by Thomas et al. (1997).

Several accessions of *S. habrochaites* (G1.1257, G1.1290, G1.1560, G1.1606 = CPRO742208, LA1775, PI 247087) have been found to be resistant to PM, caused by *Oidium neolicopersici* (Huang et al. 2000b and references therein). The resistance found in the *S. habrochaites* accession Gl.1560 resulted to be largely controlled by an incompletely dominant gene, *Ol-1*, that was mapped by means of RAPD and RFLP markers on the long arm of chromosome 6, near the *Aps-1* locus in the vicinity of the resistance genes *M-1* and *Cf-2*/*Cf-5* to *Meloidogyne* spp. and *C. fulvum*, respectively (Van der Beek et al. 1994; Huang et al. 2000a). Subsequently, the *Ol-1* gene was fine-mapped, and the use of another resistant *S. habrochaites* accession, G1.1290, allowed the identification of a new incompletely dominant gene, designated *Ol-3*, which was also mapped to chromosome 6, in the same chromosome region as *Ol-1* (Huang et al. 2000b; Bai et al. 2005). Another source of resistance to *O. neolycopersici* was identified in the *S. habrochaites* accession PI 247087 and it was shown to be polygenic but with

a major gene, *Ol-5,* mapping on the long arm of chromosome 6, about 1 cM proximal of the *Ol-1* locus (Bai et al. 2005).

S. habrochaites is a remarkable source of resistance to many arthropod pests that attack cultivated tomato (Rick 1982; Taylor 1986; Farrar and Kennedy 1991). This resistance is mediated by several factors, including glandular trichome type and density, and presence of particular compounds in trichome glands that possess toxic properties against Lepidoptera or aphids. Great morphological variation and chemical differentiation of trichome secretions can be observed among *S. habrochaites* accessions; in some cases, trichome secretions are predominated by methylketones, often 2-tridecanone (2-TD) and/or 2-undecanone, while in other cases by sesquiterpenoids, often sesquiterpene hydrocarbons (Van der Hoeven et al. 2000; Zhang et al. 2008; Sallaud et al. 2009 and references therein). Moreover, *S. habrochaites* can be immune to insects, suggesting that repellence may be a mechanism of protection (Rick 1982). In this respect, Guo et al. (1993) and Snyder et al. (1993) found that spider mite repellence in trichome secretions on the *S. habrochaites* accessions LA1927 and LA1363 was mainly due to the presence of 2,3-dihydrofarnesoic acid, a sesquiterpene acid. The inheritance of this compound was studied in segregating generations deriving from interspecific crosses between *S. lycopersicum* and *S. habrochaites* LA1363 but no conclusive results were reported (Zhang et al. 2008).

The inheritance of allelochemicals, as well as of other characters related to insect resistance, appears to be complex, and molecular markers have been used to identify QTLs underlying some of these traits. For example, Zamir et al. (1984) reported association of the level of 2-tridecanone in *S. habrochaites* with five isozyme markers mapping on at least four different chromosomes. Nienhuis et al. (1987) found association of 2-TD levels with RFLPs on three linkage groups and of type VI trichome density with one of these marker loci.

Subsequently, RFLP markers were used in an F_2 population derived from an interspecific cross between *S. lycopersicum* cv. "Moneymaker" and *S. habrochaites* to identify QTL for greenhouse whitefly (*Trialeurodes vaporariorum*) resistance (Maliepaard et al. 1995). Two QTLs affecting oviposition rate were mapped to chromosome 1; while two QTLs affecting trichome type IV density and one affecting type VI trichome density were mapped to chromosomes 5, 9, and 1, respectively (Maliepaard et al. 1995). The genetic control of the concentration of 2-TD and 2-undecanone was studied in F_1 and F_2 populations derived from the interspecific cross between *S. lycopersicum* cv. "IPA-6" × *S. habrochaites* PI 134418 (Pereira et al. 2000). Using the ILs resulting from a cross between *S. lycopersicum* and *S. habrochaites* LA1777, Van der Hoeven et al. (2000) showed that the biosynthesis of class I and II sesquiterpene olefins is controlled by two independent loci, *Sst1* and *Sst2*, respectively, mapping on chromosome 6, *Sst1*, and 8 (*Sst2*). By searching into a *S. habrochaites* trichome EST database, Sallaud et al. (2009) identified two candidate genes that are highly and specifically expressed in trichome cells and that mapped to the *Sst2* locus on chromosome 8. These two genes are responsible for the biosynthesis of all chromosome 8-associated class II sesquiterpenes.

A few studies have investigated the genetic basis of chilling tolerance in tomato using interspecific crosses between the cultigen and *S. habrochaites* accessions (Table 9.8). Vallejos and Tanksley (1983) analyzed a BC_1 between *S. lycopersicum* and a *S. habrochaites* cold-tolerant accession with 17 isozyme markers and identified a minimum of three QTLs for growth at low temperatures, two of which had positive effects, and the other negative. In crosses between the same two species, Zamir et al. (1982) conducted pollinations at low temperatures and, using nine isozyme markers, detected two regions of the *S. habrochaites* LA1777 genome on chromosomes 6 and 12, which were highly favored in crosses at low temperature. More recently, Truco et al. (2000) conducted a QTL analysis using RFLPs on a BC_1 between *S. lycopersicum* and *S. habrochaites* LA1778, which allowed the identification of multiple QTLs related with shoot wilting and root ammonium uptake under chilling temperatures. For example, three QTLs were detected for wilting at 2 h, on chromosomes 5, 6, and 9, and the presence of the *S. habrochaites* allele had a favorable effect in decreasing wilting at the two QTLs on chromosomes 5 and 9.

S. habrochaites has also been useful for studying the genetic basis of numerous yield and fruit quality-related traits (Table 9.7). With respect to single genes, for example, Levin et al. (2000) described a locus, *Fgr*, that controls the fructose–glucose ratio in mature fruit, with a *S. habrochaites* LA1777 allele yielding a

higher ratio. Later, it was shown that alleles of *S. habrochaites* at two loci interacted to increase this ratio (Levin et al. 2004). The action of the *Beta* (*B*) gene (which increases fruit β-carotene content at the expense of lycopene, resulting in orange-pigmented fruit) was first described in segregants descended from a cross between cultivated tomato and *S. habrochaites* PI 126445 (Lincoln and Porter 1950). Subsequently, studies by Tomes et al. (1954) determined that *B* was dominant but subject to influence by a modifier gene, Mo_B, which segregated independently of *B*. Both genes were mapped to the long arm of chromosome 6 (Zhang and Stommel 2000, 2001), and *B* was cloned (Ronen et al. 2000) (see also Sects. 9.6.4.2 and 9.6.4.9).

Progenies deriving from a *S. lycopersicum* cv. "E6203" × *S. habrochaites* LA1777 cross have also been used in numerous QTL mapping studies (Table 9.7). An AB population (BC_2/BC_3) was analyzed for 19 quantitative traits of agronomic importance in replicated field trials conducted in several locations around the world (Bernacchi et al. 1998a). A total of 121 QTLs were identified for all traits evaluated, and interestingly, for 25 of the QTLs (20%) corresponding to 12 traits (60%), the wild parent allele had a favorable effect on the trait from a horticultural perspective. Favorable wild QTL alleles were identified also for traits for which the wild parent had an inferior phenotype compared to the cultivated parent. For example, wild alleles were associated with increased yield or with improved red color of the fruit, despite the fact that *S. habrochaites* has low yield and produces green fruit that lacks lycopene. The same AB population has been evaluated for traits possibly contributing to flavor, including sugars, organic acids, and other biochemical properties, and 34 QTLs were identified for the 15 analyzed traits (Fulton et al. 2002a). Also in this case, favorable wild QTL alleles were identified for several traits. Starting from the same population, a few cycles of MAS selection allowed the development of improved-processing tomato NILs carrying *S. habrochaites* LA1777 specific QTL alleles (Bernacchi et al. 1998b). The NILs were evaluated for their agronomic performance in five locations worldwide, and for most of them quantitative factors showed the phenotypic improvement predicted by QTL analysis of the BC_3 populations. The same interspecific cross was used to develop a population of 99 NILs, or ILs, and backcross recombinant inbred lines (BCRILs), which were genotyped with 95 RFLP markers (Monforte and Tanksley 2000a). Most of these lines have been evaluated for yield related and fruit quality traits, and several of them showed to carry beneficial wild QTL alleles (Grandillo et al. 2000; S. Grandillo et al. unpublished results). For a few of these lines (e.g., bottom of chromosomes 1 and 4), sub-ILs have been developed and evaluated in order to fine-map the QTLs and find more tightly linked markers, as well as to break undesirable linkages (Monforte and Tanksley 2000b; Monforte et al. 2001; Yates et al. 2004). More recently, the *S. habrochaites* LA1777 NIL/BCRIL population has been used to identify QTLs associated with the emission of fruit volatile compounds associated with flavor and a total of at least 30 QTLs affecting the emission of one or more of 24 volatiles were identified (Mathieu et al. 2009). In a framework of a collaborative project (EU-SOL, funded by the European Commission under FP6, PL 016214–2 EU-SOL) a new set of *S. habrochaites* LA1777 ILs has been produced, anchored to the high density tomato molecular map by means of PCR-based markers (mostly COSIIs), and which will allow a better coverage of the wild parent species genome (Tripodi et al. 2006, 2009; S. Grandillo personal communication).

Another *S. habrochaites* accession, PI 247087, was used to identify QTLs associated with ascorbic acid content (Stevens et al. 2007). A comparison of the results obtained using three different mapping populations (the *S. habrochaites* PI 247087 advanced BC, the *S. pennellii* LA0716 ILs, and the cherry-RILs) allowed the identification of common regions controlling ascorbic acid content on chromosomes 2, 8, 9, 10, and 12; in general, the wild alleles increased ascorbic acid content (Stevens et al. 2007). The same *S. lycopersicum* × *S. habrochaites* LA0407 BIL population, used by Kabelka et al. (2002) to map QTL for resistance to *Cmm*, was also evaluated for fruit color traits. Although no significant fruit color QTL was identified with the favorable allele contributed by the wild parent, the performance of a few lines did suggest some potential of the LA0407 BIL population for the improvement of color (Kabelka et al. 2004).

Gorguet et al. (2008) studied the genetics of parthenocarpy in two different lines, IL5-1 and IVT-line 1, carrying chromosome segments from *S. habrochaites* LYC4 and from an unknown accession, respectively. Four novel parthenocarpy QTLs (on chromosomes 4,

5, and 9) responsible for the seedless fruit development in IL5-1 and IVT-line 1 were identified; moreover, one stigma exsertion locus (*se5.1*) was detected in the line IL5-1.

Progenies deriving from interspecific crosses between the SC tomato *S. lycopersicum* and SI accessions of *S. habrochaites* have been used to explore the genetic basis of the evolution of mating system and of hybrid incompatibility. Bernacchi and Tanksley (1997) used a BC_1 population between *S. lycopersicum* (SC) and *S. habrochaites* LA1777 (SI) for a QTL study of sexual compatibility factors and floral traits. The only QTL for SI identified in this population mapped at the SI locus, *S*, on chromosome 1 (Tanksley and Loaiza-Figueroa 1985; Bernatzky 1993), indicating that the transition from SI to SC that ultimately led to cultivated tomato was mainly the result of mutations that occurred at the *S* locus (Bernacchi and Tanksley 1997). The major QTL controlling unilateral incongruity (UI) also mapped to the *S* locus, which supports the hypothesis that SI and UI are related mechanisms. In addition, the fact that most major QTLs for several floral traits important to pollination biology (e.g., number and size of flowers) were also located at the *S* locus region of chromosome 1, suggested the presence of a gene complex controlling both genetic and morphological mechanisms of reproduction control (deVicente and Tanksley 1993; Bernacchi and Tanksley 1997). In order to guarantee self-fertilization, besides SI, changes in floral morphology are also required. In this respect, one key morphological trait is stigma exsertion, since an exserted stigma promotes outcrossing, while a recessed stigma, below the anthers, promotes self-fertilization (Rick 1979). In the *S. lycopersicum* × *S. habrochaites* LA1777 BC_1 population, Bernacchi and Tanksley (1997) mapped a single major QTL on chromosome 2, called *stigma exsertion 2.1* (*se2.1*) which explained most of the morphological changes that occurred in the evolutionary transition from allogamous to autogamous flowers. The same major QTL was also detected in a *S. lycopersicum* (SC) × *S. arcanum* LA1708 (SI) cross (Fulton et al. 1997). Fine-mapping studies showed that *se2.1* is a complex locus composed of at least five closely linked genes: three controlling stamen length, one controlling style length, and one conditioning anther dehiscence (Chen and Tanksley 2004). The locus controlling style length, named *Style 2.1*, which explained the largest change in stigma exsertion was cloned using map-based cloning method, and the gene resulted to encode a putative transcription factor that regulates cell elongation in developing styles (Chen et al. 2007).

The *S. habrochaites* LA1777 NIL/BCRIL population has also been used to examine the genetic basis of hybrid incompatibility, in terms of traits that potentially contribute to pre-zygotic isolation that can influence pollinator preferences and/or selfing rates (e.g., flower size, flower shape, stigma exsertion, and inflorescence length) and post-zygotic isolation (pollen and seed sterility) between *S. lycopersicum* and *S. habrochaites* (Moyle and Graham 2005; Moyle 2007). The results obtained with the post-zygotic traits showed that hybrid pollen and seed infertility are each based on a relatively small and comparable number of QTLs (Moyle and Graham 2005). Interestingly, similar results were obtained using the *S. pennellii* LA0716 IL population (Moyle and Nakazato 2008). The fact that QTLs for pollen and seed sterility from the two *Solanum* studies colocalized suggested a shared evolutionary history for these QTLs, and also that loci causing sterility are not randomly distributed in the genome.

9.6.4.6 *Solanum lycopersicoides*

This nightshade species possess unique traits, including extreme abiotic stress tolerance and resistance to several insect pests and pathogens that have an impact on the production of tomatoes (Rick 1988; Chetelat et al. 1997). The *S. lycopersicoides* accession LA2951, which was used to develop a population of ILs within the background of *S. lycopersicum* cv. "VF36" (Canady et al. 2005), exhibits high foliar resistance to GM (*Botrytis cinerea*) (Rick 1987; Rick and Chetelat 1995; Chetelat et al. 1997). In order to identify QTLs for resistance to *B. cinerea*, 58 *S. lycopersicoides* LA2951 ILs, which collectively represent more than 96% of the map units in the *S. lycopersicoides* genome, were screened for foliar resistance and susceptibility to *B. cinerea* over a period of more than 2 years (Davis et al. 2009). A total of five putative resistance QTLs were identified, and two for susceptibility, with the major resistance and susceptibility QTL mapping on the long arm of chromosome 1 and on chromosome 11, respectively.

9.6.4.7 *Solanum lycopersicum* "cerasiforme"

The red-fruited cherry tomato, *S. lycopersicum* "cerasiforme," has been postulated as the expected ancestor of the domesticated form, while others more recently have suggested that it is merely a small-fruited form and not necessarily involved in the direct origins of the cultivar (Peralta et al. 2008). In the Andean region, putatively wild and feral forms can be found and *S. lycopersicum* "cerasiforme" is also described as highly invasive (Rick 1976). Recently, a molecular study was conducted to clarify the position of *S. lycopersicum* "cerasiforme" in the evolution of the cultivated tomato (Ranc et al. 2008). The study focused on the red-fruited tomato clade (*S. lycopersicum*, *S. pimpinellifolium*, *S. galapagense,* and *S. cheesmaniae*), and a total of 360 wild, feral, and cultivated accessions (144 of which were cherry tomatoes) were genotyped with 20 SSR markers. The results confirmed the admixture status of *S. lycopersicum* "cerasiforme"; in fact, part of this taxon is genetically close to the cultivated *S. lycopersicum* group and the other part is an admixture of the *S. lycopersicum* and *S. pimpinellifolium* genomes. The molecular data also showed that domesticated and wild tomatoes have evolved as a species complex with intensive level of hybridization; *S. lycopersicum* and *S. pimpinellifolium* have occasionally been classified as conspecific (see Peralta et al. 2008).

Sources of resistance to some diseases have been found in *S. lycopersicum* "cerasiforme." Danesh et al. (1994) used DNA markers to identify regions associated with partial resistance to bacterial wilt (caused by *Pseudomonas solanacearum* a.k.a *Ralstonia solanacearum*) in a F_2 population derived from a cross between a highly resistant line (L285) of cherry tomatoes and a highly susceptible cultivar (Table 9.6). In plants inoculated through roots, genomic regions on chromosomes 6 and 10 were correlated with resistance, while in plants inoculated through shoots significant regions correlated with resistance were identified on chromosomes 6, 7, and 10.

Several different *Cf* genes confer resistance to specific races of *C. fulvum* and have been bred into cultivated tomato to generate NILs (Stevens and Rick 1986; Rivas and Thomas 2005; see also Table 9.6). The gene *Cf-5* was identified in *S. lycopersicum* "cerasiforme" PI 187002 and was mapped to a complex locus on chromosome 6, very closely linked to *Cf-2* (Dickinson et al. 1993; Jones et al. 1993). Dixon et al. (1998) reported the isolation of the *Cf-5* gene and the characterization of the complex locus from three genotypes. Resistance to PM caused by *O. neolicopersici* was identified in the line (LC-95), selected within the LA1230 accession of *S. lycopersicum* "cerasiforme" collected in Ecuador, and an F_2 population obtained by crossing LC-95 and the susceptible cultivar "Super Marmande" was used to study the genetic basis of this resistance. A single recessive gene, named *ol-2*, responsible for a broad-spectrum resistance was mapped around the centromere of chromosome 4 (De Giovanni et al. 2004). Using a candidate gene approach based on comparative genetics, Bai et al. (2008) showed that loss of function of a tomato *Mlo* gene (*SlMlo1*) is responsible for PM resistance conferred by the *ol-2* gene.

S. lycopersicum "cerasiforme" has also been used as a source of favorable alleles for fruit quality traits. In this respect, a population of 144 RILs was developed from a cross between a common *S. lycopersicum* line with large fruit and a common taste, and a cherry tomato line with fruit having very good taste and high aroma intensity (Saliba-Colombani et al. 2000). The cherry-RIL population was used to study the genetic control of several traits involved in the organoleptic quality of tomato including physical and chemical components, and sensory attributes (Table 9.7; Causse et al. 2001; Saliba-Colombani et al. 2001). Eight clusters of QTLs were detected that controlled most of the variation of the organoleptic quality traits, and most of the favorable alleles were conferred by the cherry tomato parent for all of the quality traits (Causse et al. 2002). This allowed the selection of five chromosome regions that showed promise for improving fruit quality. These regions were introgressed into three cultivated tomato lines by means of a marker-assisted BC scheme, and the analysis revealed interactions between QTLs and genetic backgrounds (Lecomte et al. 2004a). Further studies showed that both additivity and epistasis control the genetic variation for fruit quality traits in tomato (Causse et al. 2007). The same cherry-RIL population was used to identify QTLs associated with ascorbic acid content of the fruit (Stevens et al. 2007). Six QTLs were identified, and the cherry allele had a positive effect for the four QTLs expressed in percentage fresh weight.

9.6.4.8 *Solanum neorickii*

Solanum neorickii is a green-fruited wild species, with small fruits and flowers; it can be reciprocally hybridized with the cultivated tomato without having to overcome any major interspecific barriers. However, in spite of the relatively easy of crossability with the cultigen, *S. neorickii* has not been extensively used by plant breeders, partly due to its comparatively recent discovery (Taylor 1986). This can be explained in part by the rather restricted geographic range of *S. neorickii* and the similar *S. chmielewskii* (Taylor 1986; although see Peralta et al. 2008; see Sect. 9.2.2).

The first extensive genetic study conducted on an interspecific tomato cross involving the wild species *S. neorickii* used an AB-QTL mapping strategy to explore the *S. neorickii* LA2133 genome as a potential source of useful QTL alleles for traits of agronomic importance including yield and fruit quality-related characteristics (Fulton et al. 2000) (Tables 9.5 and 9.7). One hundred and seventy BC_2 plants were scored for 131 RFLPs and ~170 BC_3 families were evaluated for 30 horticultural traits, in replicated field trials conducted in three different locations. A total of 199 QTLs were detected for the 30 analyzed traits, and for 19 traits at least one QTL was identified for which the wild allele had a favorable effect, despite the overall inferior phenotype of *S. neorickii*. This AB population was also evaluated for sugars, organic acids, and other biochemical properties possibly contributing to flavor, and 52 QTLs were identified for the 15 analyzed traits (Fulton et al. 2002a). Starting from the same *S. lycopersicum* cv. E6203 × *S. neorickii* LA2133 AB population, a set of 142 BILs (BC_2F_7) has been developed by D. Zamir and collaborators. Within the framework of the EU-SOL project (see above and http://www.eusol.net/), the 142 BILs have been anchored to a common set of COSII markers, and have been evaluated for agronomic traits, including yield, brix, and fruit weight (Tripodi et al. 2010; D. Zamir and S. Grandillo personal communication). Several favorable *S. neorickii* alleles were identified that could be targeted for further marker-assisted introgression into cultivated tomato.

The *S. neorickii* accession G1.1601 has been identified as a source of resistance to PM (caused by *Oidium lycopersici*), and an F_2 mapping population derived from the *S. lycopersicum* cv. "Moneymaker" × *S. neorickii* G1.1601 cross was used for QTL analysis (Bai et al. 2003; Table 9.6). The resistance was found to be controlled by three QTLs: *Ol-qtl1* mapping on chromosome 6, in the same region as the *Ol-1* locus (found in *S. habrochaites*), which is involved in a hypersensitive resistance response to the pathogen, and other two linked QTLs (*Ol-qtl2* and *Ol-qtl3*) that are located on chromosome 12, near the *Lv* locus conferring resistance to the other PM species, *L. taurica* (Bai et al. 2003). Since the *S. neorickii* accession G1.1601 showed also a certain level of resistance to GM (*Botrytis cinerea*) (ten Have et al. 2007), F_3 lines derived from the above-mentioned F_2 population were used to identify QTLs underlying the resistance response to *B. cinerea* using a stem bioassay (Finkers et al. 2008). Three putative QTLs were identified, and for each of them a putative homologous locus had been previously identified in *S. habrochaites* LYC4 (Finkers et al. 2007a, b).

9.6.4.9 *Solanum pennellii*

Solanum pennellii is a green-fruited species that grows at a wide range of elevations along the western slopes of the Andes, and is found on arid slopes and dry washes (see Sect. 9.2.2; Rick 1973). The extreme drought tolerance of this species has motivated numerous studies aimed at transferring its tolerance to the cultivated tomato. Another important characteristic of many *S. pennellii* accessions is their high level of resistance to numerous insects, which has been correlated with high density of type IV glandular trichomes and the presence of high levels of toxic acylsugars in their exudates (Farrar and Kennedy 1991; Labate et al. 2007 and references therein). *S. pennelli* has also been used as a source of disease resistances and, more recently, with the availability of the *S. pennellii* LA0716 IL population, the use of this wild species has greatly increased, and extended to hundreds of different traits of agronomical and biological relevance (Tables 9.6–9.8; see also reviews by Lippman et al. 2007; Grandillo et al. 2008).

With respect to disease resistance, *S. pennellii* LA0716 was found to display an incompatible reaction with race 3 (T3) strains of *Xanthomonas campestris* pv. *vesicatoria,* the casual agent of bacterial spot, indicating the existence of hypersensitive response (HR)-related resistance in this wild species. Using the *S. pennellii* LA0716 IL population a dominant

resistance gene, called *Xv4,* was mapped on chromosome 3, and the avirulence gene, *avrXv4,* was isolated (Astua-Monge et al. 2000; Table 9.6).

S. pennellii has been used as a source of resistance to fungal diseases. *Alternaria* stem canker disease in tomato is caused by the necrotrophic fungus *A. alternata* f. sp. *lycopersici*. Genetic analyses showed that high insensitivity to AAL toxins from *S. pennellii* LA0716 is inherited in tomato as a single complete dominant locus, *Asc*, which has been genetically mapped on chromosome 3 of tomato using RFLPs (Van der Biezen et al. 1995). Subsequently, Mesbah et al. (1999) reported the physical analysis of a yeast artificial chromosome (YAC) contig spanning the *Asc* locus. Positional cloning of *Asc* showed that sensitivity is associated with a mutation in the gene that leads to a predicted aberrant ASC protein, a new plant member of the longevity assurance protein family (Brandwagt et al. 2000).

S. pennellii accessions have also been found to be sources of resistance to the soil-borne fungus *Fusarium oxysporum* f.sp. *lycopersici,* the causal agent of *Fusarium* wilt disease. The resistance conferred by genes *I* and *I-2* (both derived from accessions of *S. pimpinellifolium*) was overcome by a new race 3 of the fungus, and therefore a new dominant resistance gene, *I-3*, was identified in two *S. pennellii* accessions, PI 414773 (McGrath et al. 1987) and LA0716 (Scott and Jones 1989), and introgressed into *S. lycopersicum*. The *I-3* gene from LA0716 was mapped to chromosome 7 near the isozyme marker *Got-2* (Bournival et al. 1989, 1990; Sarfatti et al. 1991). The isolation of this resistance gene is being pursued via map-based cloning, and a high resolution genetic and physical map of the *I-3* region has been reported (Hemming et al. 2004; Lim et al. 2008). In addition, a new locus conferring resistance against *F. oxysporum* f. sp. *lycopersici* race 1 was mapped using RFLPs in a BC_1 population derived from a *S. lycopersicum* cv. "Vendor" (susceptible to race 1) × *S. pennellii* LA0716 (resistant) cross (Sarfatti et al. 1991). The locus, called *I-1*, was located on chromosome 7 and was not allelic to *I*, the traditional gene for resistance against the same fungal pathogen that was derived from *S. pimpinellifolium* (Sarfatti et al. 1991). These genes have been introgressed into commercial tomato and their map position further defined (Scott et al. 2004). A genome-wide dissection of *Fusarium* resistance was conducted using the *S. pennellii* LA0716 IL population (Sela-Buurlage et al. 2001). The study allowed the identification of six independent loci; the *I* and *I2* loci, previously introgressed from *S. pimpinellifolium,* were shown to reside on different arms of chromosome 11; three novel loci were identified on chromosomes 2 (loci *I-4* and *I-5*) and 10 (locus *I-6*). The loci *I-5* and *I-6* represented new *S. pennellii* resistance loci with varying degrees of potency; in contrast, the origin of the *I-4* locus was not defined. This study emphasized the complexity of wilt disease resistance revealed at both inter- and intralocus levels.

With respect to insect resistance, the genetic control of acylsugar accumulation in exudates of type IV glandular trichomes has been studied in an interspecific F_2 population derived from the cross *S. lycopersicum* × *S. pennellii* LA0716 (Mutschler et al. 1996). A total of five QTLs were identified, which were subsequently transferred by MAS pyramiding into the cultivated tomato genetic background (Lawson et al. 1997). Although, the obtained multiline accumulated acylsugars, the levels were lower than those of the interspecific F_1 control, suggesting that in order to reach higher level of acylsugar accumulation additional QTLs, still unidentified, might be necessary. Furthermore, the inheritance of acylsugar fatty acid composition was analyzed in an intraspecific F_2 population derived from a cross between *S. pennellii* LA0716 and *S. pennellii* LA1912, and six QTLs were detected for the nine segregating fatty acid constituents (Blauth et al. 1999).

The drought tolerance of *S. pennellii* was found to be related to greater WUE and less negative carbon isotope composition (δ^{13} C) (Martin et al. 1999), compared to the cultivated tomato, due to the ability of its leaves to take up dew (Rick 1973), and also to a rapid closure of stomata upon water deficit stress (Kebede and Martin 1994). Carbon isotope composition (δ^{13} C) is considered an attractive substitute for WUE in research and breeding programs, since in C_3 plants it varies in concert with leaf WUE, and δ^{13} C can be measured with minimal tissue destruction. Therefore, identification and MAS of QTL for WUE by means of δ^{13} C is considered a particularly promising way to break negative pleiotropy between WUE and yield in C_3 species. An RFLP mapping study conducted in F_3 and BC_1S_1 tomato populations derived from an *S. lycopersicum* × *S. pennellii* cross allowed the identification of three genomic regions explaining a large proportion of the genetic variance for δ^{13} C (Martin

et al. 1989). More recently, the use of the *S. pennellii* LA0716 IL library allowed the detection of a dominant QTL for δ^{13} C, *QWUE5.1*, in *S. pennellii* IL5-4; at this QTL the wild allele had a favorable effect, since it determined high δ^{13} C (small negative value) (Xu et al. 2008).

S. pennellii LA0716 has also been used to identify QTLs conferring ST during seed germination (SG) (Foolad and Jones 1993; Foolad et al. 1997; Foolad and Chen 1998) or during the vegetative stage (VG) (Zamir and Tal 1987; Frary et al. 2010) (Table 9.8). The studies conducted during SG have shown that ST at this stage in tomato was controlled by a few major QTLs, which act together with a number of smaller effect QTLs. Moreover, some of these QTLs were conserved across species, while other were species specific (Foolad et al. 1997, 1998a; Foolad and Chen 1998). Zamir and Tal (1987) used a *S. lycopersicum* × *S. pennellii* LA0716 F_2 population and 15 isozyme markers to identify QTL that affect Na^+, Cl^-, and K^+ ion contents. The authors detected a minimum of four major loci that affected the contents of both Na^+, Cl^- in leaves, and two other loci influencing K^+ uptake. Recently, the *S. pennellii* LA0716 IL population, along with its parental lines, has been evaluated for growth parameters and for antioxidant parameters of the leaves, under both control and salt stress (150 mM NaCl) conditions (Frary et al. 2010). The data allowed the identification of 125 QTLs for seven traits related to antioxidant content and to the response of tomato antioxidants to salt stress. It was generally observed that salt stress resulted in higher levels of antioxidant compounds and enzymes in the wild species. However, a direct correlation between antioxidant levels and salinity tolerance could not be definitely shown, and further studies are necessary in order to verify whether higher antioxidant tomato cultivars will show improved ST in the field.

Interspecific mapping populations deriving from crosses between *S. lycopersicum* and *S. pennellii* LA0716 have been used to map several genes involved in pigment content and fruit ripening including *high pigment-2* (*hp-2*) and *jointless* (*j*) loci (Kinzer et al. 1990; Wing et al. 1994; Zhang et al. 1994; van Tuinen et al. 1997; Mustilli et al. 1999; Liu et al. 2003; Rousseaux et al. 2005). In addition, *S. pennellii* LA0716, as well as other green-fruited wild species of tomato, has been the source of the mutation *Delta* (*Del*) that changes fruit color from red to orange as a result of accumulation of δ-carotene at the expense of lycopene. The *Del* gene was located on the RFLP map of tomato chromosome 12, and evidence strongly suggested that the locus *Del* in the fruit-color mutation *Delta* encoded the gene for lycopene ε-cyclase (Ronen et al. 1999). Furthermore, the two *S. pennellii* LA0716 ILs, IL-3-2 and IL3-3, have been used for the positional cloning of the *Beta* (*B*) gene, which encodes a novel type of lycopene β-cyclase, an enzyme that converts lycopene to β-carotene (Ronen et al. 2000).

Progenies derived from the *S. lycopersicum* × *S. pennellii* LA0716 cross have been extensively used to explore the genetic basis of numerous quantitative traits related to yield and fruit quality, and to identify molecular markers linked to favorable wild alleles to be used in MAS breeding programs. The first study, conducted in a *S. lycopersicum* × *S. pennellii* LA0716 BC_1 population, used isozymes to analyze the genetic basis of the four metric traits: leaf ratio, stigma exsertion, fruit weight, and seed weight (Tanksley et al. 1982; Table 9.7). Interestingly, already in this study, it was reported the identification of specific QTL alleles with effects opposite to those expected from the parental phenotypes. A more comprehensive investigation of the genetic basis of wide-cross transgressive segregation was conducted by deVicente and Tanksley (1993) on a large F_2 population derived from the *S. lycopersicum* cv. "Vendor TM2a" × *S. pennellii* LA0716 cross using RFLP markers. A total of 74 significant QTLs were identified for the 11 biological traits evaluated, and 36% of these QTLs had alleles with effects opposite to those predicted by the parental phenotypes, which could be directly related to the appearance of transgressive individuals in the F_2. Another *S. lycopersicum* × *S. pennellii* LA0716 F_2 population was used to study the genetic basis of leaf and flower morphology (Frary et al. 2004b).

In 1994, Eshed and Zamir reported the development of the first generation of the *S. pennellii* LA0716 IL library in the genetic background of *S. lycopersicum* cv. "M82," consisting of 50 ILs, each containing a single RFLP-defined introgression from *S. pennellii* in an otherwise cultivated genomic background. Collectively these lines provide coverage of the entire wild species genome. This new kind of genetic resource, also referred to as "exotic library" (Zamir 2001) was developed with the purpose of improving the efficiency with which wild germplasm could be used in tomato breeding and genetic studies.

The numerous advantages and potentialities of IL populations for the analysis of complex traits have been obvious since the first studies conducted to map and fine-map QTLs underlying horticultural yield and fruit quality traits using this type of genetic resource (Eshed and Zamir 1995, 1996; Eshed et al. 1996; as reviewed by Zamir and Eshed 1998a, b). Since then, the *S. pennellii* IL library, as well as its second generation consisting of 76 ILs and sub-ILs (Liu and Zamir 1999; Pan et al. 2000), has been used to analyze hundreds of traits of agronomical and biological interest including fruit weight, fruit shape, brix, pH, yield, traits related to reproductive fitness (Eshed and Zamir 1995, 1996; Eshed et al. 1996; Monforte et al. 2001; Causse et al. 2004; Baxter et al. 2005; Semel et al. 2006), disease resistance (Astua-Monge et al. 2000; Sela-Buurlage et al. 2001), leaf and flower morphology (Holtan and Hake 2003), locule number (Barrero and Tanksley 2004), carotenoid content in relation to fruit color (Liu et al. 2003), fruit nutritional and antioxidant content (Rousseaux et al. 2005; Stevens et al. 2007, 2008), fruit primary metabolites (Causse et al. 2004; Schauer et al. 2006, 2008), aroma compounds (Tadmor et al. 2002; Tieman et al. 2006), hybrid incompatibility (Moyle and Nakazato 2008), and antioxidant content of the leaves related to salt stress conditions (Frary et al. 2010). All these mapping efforts have allowed the identification of more than 2,800 QTLs (Tables 9.6–9.8; for reviews, see Lippman et al. 2007; Grandillo et al. 2008). Recently, in order to detect the genetic basis of metabolic regulation in tomato fruit, Kamenetzky et al. (2010) constructed a detailed physical map of five genomic regions associated with 104 previously described metabolic QTLs of the *S. pennellii* LA0716 IL population. For this purpose, the genetic and physical maps of *S. pennellii* and *S. lycopersicum* were integrated, providing a large dataset that will constitute a useful tool for QTL fine-mapping and relatively easy screening of target clones in map-based cloning approaches.

Another *S. pennellii* accession, LA1657, has been used in an AB-QTL mapping study aimed at identifying loci for yield, processing, and fruit quality traits (Frary et al. 2004a). A total of 175 BC_2F_1 families derived from the interspecific cross *S. lycopersicum* E6203 × *S. pennellii* LA1657 were grown and phenotyped for 25 traits in three locations, and 84 QTLs were identified. Also in this case a high proportion (26%) of the identified QTLs had *S. pennellii* alleles that enhanced the performance of the elite parent, also for traits for which the wild parent had an inferior phenotype (Frary et al. 2004a).

All these studies have allowed the identification of numerous *S. pennellii* QTL alleles that are of potential interest for breeding. Furthermore, the *S. pennellii* IL library facilitated exploration of the genetic basis of heterosis for "real-world" applications, as shown by the development of a new leading hybrid of processing tomato (Lippman and Zamir 2007; Lippman et al. 2007) (see Sect. 9.7.2.5).

9.6.4.10 *Solanum pimpinellifolium*

This red-fruited wild relative of tomato can be reciprocally hybridized with *S. lycopersicum*, and due to its close relationship with the cultigen and ease of backcrossing it has been extensively used as an attractive source of germplasm for various agriculturally important traits such as disease and insect resistance/tolerance as well as fruit quality traits (Taylor 1986; Peralta and Spooner 2001; Kole et al. 2006; Ashrafi et al. 2009). Additionally, some *S. pimpinellifolium* accessions have been identified as potential sources for abiotic stress tolerance (Foolad 2004, 2005).

With respect to viral diseases, tolerance to TYLCV infection has been reported in *S. pimpinellifolium* accessions, including LA0121, LA0373, and LA0690 (reviewed by Stevens and Rick 1986). Bulk RAPD analyses were performed on F_4 lines segregating for resistance to TYLC derived from *S. pimpinellifolium* "hirsute INRA" (Montfavet, INRA, France), and a major QTL responsible for up to 27.7% of the resistance was identified on chromosome 6 (Table 9.6; Chaguè et al. 1997).

In tomato, resistance to *Pseudomonas syringae* pv. "tomato" strains expressing the avirulence gene *avrPto* requires the presence of at least two host genes, designated *Pto* and *Prf* . The *Pto* gene has been introgressed into a *S. lycopersicum* cultivar from *S. pimpinellifolium* (Pitblado et al. 1984). *Pto* was isolated by a map-based cloning approach and it was shown to be a member of a clustered multigene family, located on the short arm of chromosome 5, with similarity to various proteinserine/threonine kinases (Martin et al. 1991, 1993). Subsequently, the gene *Prf* was identified through a mutational approach and was shown to be tightly linked to *Pto* (Salmeron

et al. 1996). Another member of the *Pto* gene cluster termed *Fen* was found to confer sensitivity to fenthion (Loh and Martin 1995).

As discussed in Sect. 9.6.4.9, several studies have been conducted to identify resistances to the soil-borne fungus *F. oxysporum* f. sp. *lycopersici* which causes *Fusarium* wilt of tomato. The first gene (*I*), coferring vertical resistance to race 1 of the pathogen, was found in *S. pimpinellifolium* accession PI 79532 (Bohn and Tucker 1939) and was assigned to chromosome 11 (Paddock 1950). A second dominant gene, *I-2*, for resistance to race 2 was discovered in *S. pimpinellifolium* accession PI 12915 (Stall and Walter 1965; Cirulli and Alexander 1966), and was mapped to chromosome 11 using morphological markers (Laterrot 1976) and later by RFLPs (Sarfatti et al. 1991; Segal et al. 1992). The functional *I-2* resistance gene was isolated by a positional cloning approach and it was shown to be a complex locus (Ori et al. 1997; Simons et al. 1998). More recently, Scott et al. (2004) showed that the race 1 resistance, also present in PI 12915, was controlled by the *I* gene. Both genes have been incorporated into a wide number of commercial tomato cultivars (Bournival et al. 1989).

Resistances to other fungal diseases have also been identified in *S. pimpinellifolium* accessions. For example, the resistance of tomato to gray leaf spot disease caused by four *Stemphylium* species is conferred by a single incompletely dominant gene, *Sm*, which was introgressed into cultivars from *S. pimpinellifolium* accession PI 79532 and was found to be linked to a *Fusarium* race 1 resistance gene, *I*, on chromosome 11 (Dennett 1950). The *Sm* gene was then placed on the RFLP map of tomato using an F_2 population segregating for the resistance (Behare et al. 1991). Numerous cultivars with stable resistance to gray leaf spot have been released (Stevens and Rick 1986). Sources of resistance to GM (*Botrytis cinerea*) have also been identified in *S. pimpinellifolium*. In a study conducted to find new breeding material for resistance to GM, *S. pimpinellifolium* accession LA1246 showed high resistance both in the leaflet and in the stem (Ignatova et al. 2000).

LB caused by the fungal pathogen *P. infestans* is one of the most important diseases of the cultivated tomato and potato (Robertson 1991). Breeding for resistance to LB in tomato has followed two directions: one has been the search for "*R*" genes that confer race-specific or isolate-specific resistance that often exhibit qualitative inheritance, and the other has been the search for quantitative resistance, also referred to as partial resistance, which tends to be multigenic and quantitatively inherited (Wastie 1991; Umaerus and Umaerus 1994). In tomato, three isolate-specific *R* genes have been reported, *Ph-1* (a completely dominant gene), *Ph-2*, and *Ph-3* (both incompletely dominant genes), and *S. pimpinellifolium* was the original source for all of them (Table 9.6; Peirce 1971; Chunwongse et al. 1998; Moreau et al. 1998). The gene *Ph-1* was located on chromosome 7 (Peirce 1971) and *Ph-2* gene, originating from *S. pimpinellifolium* WVa700 was located on the long arm of chromosome 10 by RFLP analysis (Moreau et al. 1998). The *Ph-3* gene was found in an interspecific cross of *S. lycopersicum* and *S. pimpinellifolium* L3708, and mapped to chromosome 9 (Chunwongse et al. 2002). The same interspecific cross was used to study the genetic basis of quantitative resistance to LB in field trials, and two QTLs were identified (Frary et al. 1998). More recently, Kole et al. (2006) mapped another *R*-gene (*Ph-4*) conferred by *S. pimpinellifolium* from a similar cross. Their QTL analysis resulting in significantly high contribution to phenotypic variance also confirmed qualitative nature of inheritance.

Kerr and Bailey (1964) investigated *S. pimpinellifolium* resistance to tomato leaf mold (*C. fulvum*), and identified two genes, *Cf-2* and *Cf-9,* which were later introgressed into commercial tomato (Stevens and Rick 1986). Classical and RFLP mapping allowed more precise positioning of these genes, and revealed the existence of two complex resistance loci in tomato, one on chromosome 6, of which *Cf-2* and *Cf-5* are members, and another on chromosome 1, the *Milky Way* (*MW*) complex locus, of which *Cf-4* and *Cf-9* are members (van der Beek et al. 1992; Dickinson et al. 1993; Jones et al. 1993; Balint-Kurti et al. 1994; reviewed by Rivas and Thomas 2005). *Cf-2* was isolated by positional cloning (Dixon et al. 1996), while the *Cf-9* gene was isolated by transposon tagging (Jones et al. 1994). Functional analysis of a limited number of *S. pimpinellifolium* accessions allowed the identification of novel *Cf* genes (*Cf-ECP1*, *Cf-ECP2*, *Cf-ECP3*, *Cf-ECP4,* and *Cf-ECP5*) that trigger an HR in response to the *C. fulvum* extracellular proteins ECP1, ECP2, ECP3, ECP4, and ECP5 (Laugé et al. 1998a, b, 2000). Genetic mapping showed that *Cf-ECP2* and *Cf-ECP3* defined a new

complex locus for *C. fulvum* resistance at *Orion* (*OR*) on the short arm of chromosome 1 (Haanstra et al. 1999a; Yuan et al. 2002) and the mapping of *Cf-ECP5* also defined a new complex locus, located 3 cM proximal to *MW*, which was designated *Aurora* (*AU*) (Haanstra et al. 2000) (see also review by Rivas and Thomas 2005). Soumpourou et al. (2007) showed that both genes, *Cf-ECP1* and *Cf-ECP4,* are located at *MW* complex locus together with *Cf-9* and *Cf-4*.

The *Hero* gene of tomato, a broad spectrum resistance gene that confers a high level of resistance to all pathotypes of the potato cyst nematodes *Globodera rostochiensis* and partial resistance to *G. pallida*, was introgressed into tomato cultivar LA1792 from the wild species *S. pimpinellifolium* LA0121 (Ellis and Maxon-Smith 1971). The gene was mapped to chromosome 4 (Ganal et al. 1995) and subsequently isolated by a map-based cloning approach (Ernst et al. 2002).

With respect to tolerance to abiotic stresses, the *S. pimpinellifolium* accession LA0722 was identified as a source of ST during both SG and VG (Foolad et al. 1998a; Foolad and Chen 1999; Zhang et al. 2003a); in addition it exhibited rapid SG in cold conditions (Foolad et al. 1998b) and under drought stress (Foolad et al. 2003; Table 9.8). QTL analysis of BC_1S_1 families derived from a cross between *S. pimpinellifolium* LA0722 and a moderately salt-sensitive *S. lycopersicum* line (NC84173) allowed the identification of seven QTLs for ST during SG (Foolad et al. 1998a), and of five QTLs for ST during VG in saline solution cultures (Foolad and Chen 1999). The *S. pimpinellifolium* accession had favorable QTLs at six of the seven QTLs identified during SG, and at all five ST QTLs identified during VG. Three of these QTLs for ST during VG were subsequently validated using the selective genotyping approach (Foolad et al. 2001). The same BC_1S_1 families were evaluated for germination at low temperature (11 ± 0.5°C), and two chromosomal locations (3–5 putative QTLs) with significant effects on low temperature germination were identified; the wild species had favorable QTL alleles on chromosomes 1 (Foolad et al. 1998b). Finally, the same population was evaluated for drought tolerance during SG and four QTLs were identified for rate of germination under drought stress. For the two QTLs with larger effect, located on chromosomes 1 and 9, the favorable allele was contributed by *S. pimpinellifolium* donor parent (Foolad et al. 2003).

As described for *S. galapagenense* in Sect. 9.6.4.2, two other *S. pimpinellifolium* accessions (L1 and L5) have been used to identify QTLs for ST during the vegetative and/or reproductive stages (Bretó et al. 1993; Monforte et al. 1996, 1997a, b; Villalta et al. 2007, 2008; Estañ et al. 2009). Also in this case, the *S. lycopersicum* "cerasiforme" × *S. pimpinellifolium* interspecific RILs were used as rootstocks for a commercial hybrid, and were tested under saline conditions (Estañ et al. 2009). The results showed that up to 65% of the rootstock lines raised the fruit yield of the commercial hybrid under saline conditions, and QTLs underlying the ST rootstock effect were identified. Correlation and QTL analyses suggested that rootstock-mediated improvement of fruit yield in the *S. pimpinellifolium* population under salinity was mainly explained by the rootstock's ability to minimize perturbations in scion water status (Asins et al. 2010).

S. pimpinellifolium has been used as a source for a number of plant and fruit desirable traits like earliness, yield, and fruit quality also by means of classical genetic approaches (Kalloo 1991). The first QTL mapping study was conducted by Weller et al. (1988) on a large F_2 population derived from a *S. lycopersicum* × *S. pimpinellifolium* CIAS27 cross using six morphological markers and four isozymes. A total of 85 significant marker by trait combinations were identified for 18 quantitative analyzed traits including brix, fruit weight, fruit shape, and sugar content (Weller et al. 1988). For 14 traits at least one highly significant effect of opposite sign to the one expected based on the parental values was identified.

During the past 15 years, crosses between *S. lycopersicum* and the *S. pimpinellifolium* accession LA1589 have been used for numerous mapping studies. Grandillo and Tanksley (1996a) analyzed a BC_1, population deriving from the above-mentioned cross, for 19 quantitative traits related to fruit quality, flower morphology, flowering and ripening time, and identified 54 QTLs. From the same interspecific cross, an AB population was generated, and approximately 170 BC_2 plants were analyzed with segregating molecular markers covering the entire tomato genome. BC_2F_1 and BC_3 families were evaluated for 21 horticultural traits including yield and fruit quality (Tanksley et al. 1996). A total of 87 QTLs were identified for 18 of the analyzed traits, and, interestingly, trait-enhancing QTL alleles derived from *S. pimpinellifolium* were

identified for most traits important in processing tomato production, including traits for which the wild parent had an inferior phenotype. This AB population, along with the ones obtained with *S. arcanum* LA1708, *S. habrochaites* LA1777 and *S. neorickii* LA2133, has been evaluated for sugars, organic acids, and other biochemical properties possibly contributing to flavor, and 33 QTLs were identified for the 15 analyzed traits (Fulton et al. 2002a). Starting from the same interspecific cross, Doganlar et al. (2002b) developed a population of 196 BILs (BC_2F_6), which were genotyped for 127 marker loci covering the entire tomato genome, and were evaluated for 22 quantitative traits, including several fruit quality related traits. In all, 71 significant QTLs were identified and for 48% of them the wild allele was associated with improved agronomic performance.

Other studies have used mapping populations derived from cultivated *S. lycopersicum* × *S. pimpinellifolium* LA1589 crosses to study the genetic basis of extreme fruit size (Lippman and Tanksley 2001), or to map QTL influencing fruit shape (Grandillo et al. 1996; Ku et al. 1999, 2000; Van der Knaap and Tanksley 2001, 2003; Van der Knaap et al. 2002; Brewer et al. 2007; Gonzalo and Van der Knaap 2008). Chen et al. (1999) used the same BC_1S_2 population derived from the cross *S. lycopersicum* fresh-marker breeding line NC84173 × *S. pimpinellifolium* LA0722, used to detect abiotic stress tolerance QTL, to map 59 QTLs related to brix, fruit shape, lycopene content, and pH.

S. pimpinellifolium is a SC species with variation in outcrossing rate correlated with floral morphology, and therefore is an ideal taxon with which to study mating system evolution (Rick et al. 1977). Traits that affect mating behavior (petal, anther, and style lengths) differ greatly between inbreeding and outcrossing populations, whereas other flower parts (sepals, ovaries) show minimal differences. In order to analyze the genetic basis of traits distinguishing outcrossing and self-pollinating forms of *S. pimpinellifolium*, Georgiady et al. (2002) conducted a QTL mapping study on a F_2 population derived from a cross between two accessions with contrasting mating systems; LA1237 the "selfer" and LA1581 the "outcrosser". A total of five QTLs were found to underlie the variation for four of the six morphological traits analyzed. Interestingly, each of these four traits had a QTL of major (>25%) effect on phenotypic variance, which suggests that the genetic basis for these traits follows the pattern of a macromutation with modifiers, as described by Grant (1975).

9.7 Role in Crop Improvement Through Traditional and Advanced Tools

9.7.1 Tomato Domestication and Early Breeding

Wild tomatoes (*Solanum* sect. *Lycopersicon*) are native to western South America, and their natural distribution goes from central Ecuador, through Peru to northern Chile, with two endemic species in the Galápagos Islands (Darwin et al. 2003; Peralta and Spooner 2005). *S. lycopersicum* was domesticated by native Americans, but the original site of this process is still considered an unsolved question (Peralta and Spooner 2007), and two competing hypotheses have been proposed for the original place of domestication, one Peruvian (DeCandolle 1886), and the other Mexican (Jenkins 1948). Very likely, early humans selected for plants with mutations associated with a preferred genotype (e.g., larger fruit), and gradually, enough favorable (e.g.,"large-fruited") mutations accumulated resulting in the domesticated tomato. *S. lycopersicum* "cerasiforme", the cherry tomato, which has fruit weighing only a few grams, was thought to be the putative wild ancestor of the domesticated tomato (Cox 2000); however, recent studies have shown that the plants known as "cerasiforme" are a mixture of wild and cultivated forms rather than being "ancestral" to the cultivated tomatoes (Nesbitt and Tanksley 2002; Ranc et al. 2008).

Severe genetic bottlenecks were associated with tomato domestication as the crop was carried from the Andes to Central America and subsequently to Europe. By the time Europeans arrived to America in the fifteenth century, large fruited types already existed, indicating that tomato domestication was already at a fairly advanced stage (Jenkins 1948; Rick 1995). Further domestication occurred throughout Europe in the 18th and 19th centuries (Sims 1980). In addition, it is possible that the return of tomato from Europe to the New World might have caused further reduction of genetic variation (Rick 1988). During the nineteenth century, tomato cultivars were selected for

different purposes, including adaptation to local climate conditions. As a result, by the end of the century, numerous cultivars of tomato were available, which could be considered as landraces and the result of domestication and some early breeding, and most of them required open pollination (Bai and Lindhout 2007).

Similarly to other crops, tomato domestication has resulted in drastic phenotypic changes that can be observed in the wide range of morphological and physiological traits that distinguish domesticated tomato from its wild ancestors. Particularly extreme changes have occurred in the tissues and organs important to humans (for example, seeds, roots, and tubers). Collectively, these changes are referred to as the domestication syndrome, and the exact trait composition varies for each crop (Frary and Doganlar 2003). In tomato, one of the most obvious outcomes of domestication is the enormous increase in fruit size, which has been accompanied by a tremendous variation in fruit shapes; wild and semi-wild forms of tomato bear small, almost invariably round fruit, while fruit of cultivated tomatoes comes in a wide variety of sizes (as much as 1,000 times larger than those of wild progenitors) and shapes including round, oblate, pear-shaped, torpedo-shaped, and bell pepper-shaped (Tanksley 2004). Additionally, domesticated tomatoes produce seeds up to several times larger than their wild relatives (Doganlar et al. 2000; Orsi and Tanksley 2009). However, it is not clear why seed size increased during domestication in crops such as tomato, which are not consumed for their seeds. One explanation might be that, in these species, seed size increased as a result of indirect selection for greater seedling vigor and germination uniformity under field production (Harlan et al. 1973) or as an overall allometric effect.

In tomato, the genetic basis of these domestication syndrome traits has been explored for fruit characters (size, shape, color, morphology, and set) and growth habit (self-pruning, plant height, and earliness) (Pnueli et al. 1998; Grandillo et al. 1999a; Doganlar et al. 2000; Lippman and Tanksley 2001; Frary and Doganlar 2003; Tanksley 2004; Gonzalo and Van der Knaap 2008; see also Sect. 9.6.4). The studies have shown that tomato fruit size and shape are controlled by major and minor QTL loci, and that a relatively small number of genes were involved in the dramatic transition from small-sized fruit of wild progenitors to the extremely large size of some modern cultivars, and these genes control two processes: cell cycle and organ number determination (Lippman and Tanksley 2001; Tanksley 2004). The molecular basis of some of these major QTLs has been deciphered; *FW2.2* and *FAS* control fruit mass by increasing the placenta area and locule number, respectively, and thus affect patterning along the medio-lateral axis (Frary et al. 2000; Cong et al. 2008); the two fruit shape QTLs, *SUN* and *OVATE,* control fruit elongation and therefore affect patterning along the apical–basal axis (Liu et al. 2002; Xiao et al. 2008). Additionally, comparative studies have shown a co-localization of many loci associated with similar characteristics in tomato, pepper, and eggplant, all also members of the family Solanaceae (Doganlar et al. 2002a; Frary and Doganlar 2003).

9.7.2 Role of Wild Species for Tomato Breeding

At the beginning of the twentieth century tomato breeding programs began in public institutes, mainly in the USA, and breeders started introducing disease resistant cultivars, which dominated the US market in the 1920s and 1930s (Bai and Lindhout 2007). Subsequently, the formation of private companies favored the shift from open pollinated cultivars to hybrids, and the first hybrid tomato cultivar "Single Cross" was released in 1946 (Dorst 1946). Eventually, hybrids cultivars ended up dominating the fresh market, as well as an increasing quote of cultivars used for processing market.

Tomato breeding priorities have changed over the years. Until 1950s, cultivars have been developed that assembled several traits useful for both the processing industries and the fresh market. Afterwards, fresh market and processing cultivars started to be reasonably different. In the 1970s the main breeding goal was to increase yield, while in the 1980s the improvement of fruit shelf-life became a priority. Currently, sensorial and nutritional quality has become an important consumer demand (Bai and Lindhout 2007).

Closely related wild species within *Solanum* sect. *Lycopersicon* started to be used in tomato breeding programs in the early 1940s, when they began to be screened for additional disease resistances (Alexander et al 1942). Before that time, breeders had relied entirely on genetic variation in the European sources and their derivatives. This explains the difficulties

breeders experienced in achieving most of their breeding objectives, in terms of improved yield, disease resistance, and other important traits (Rick 1988). As a result tomato improvement has been very slow, with very retarded gain in fruit yields until about 1940, when Bohn and Tucker discovered a strong resistance to Fusarium wilt in *S. pimpinellifolium*. Eventually, wild species began to play a significant role in tomato research and breeding. Despite the various difficulties often associated with the use of unadapted germplasm, numerous attributes were transferred from wild species to commercial cultivars, in particular resistance to pathogens, but also tolerance to abiotic stresses, and fruit quality-related traits (Stevens and Rick 1986; Kalloo 1991; Rick and Chetelat 1995; Tanksley and McCouch 1997; Zamir 2001; Bai and Lindhout 2007; Labate et al. 2007; Osborn et al. 2007). However, the potential of wild species in terms of source of valuable alleles for the improvement of cultivated germplasm is far from being fully exploited. During the past two decades, the advent of molecular markers technology has opened new opportunities for a more efficient use of wild germplasm. Molecular mapping studies have demonstrated that favorable alleles in wild relatives can remain cryptic until expressed in an improved background. These results have favored the development of new concepts and approaches aimed at a more efficient use of the genetic variation stored in wild germplasm (Tanksley and Nelson 1996; Tanksley et al. 1996; Tanksley and McCouch 2007; Zamir 2001; McCouch 2004; Lippman et al. 1997; Grandillo et al. 2008).

In this section, we will give an overview of the status of wild tomato species as a source of useful traits for the improvement of cultivated tomato and the main achievements reached in tomato breeding using genes derived from wild species. Moreover, strategies and tools that can facilitate studies on the genetic control of novel traits derived from wild species, the understanding of mechanisms underlying these traits, and their use for tomato improvement will also be discussed.

9.7.2.1 Disease Resistance

Tomato is susceptible to over 200 diseases caused by all types of pathogens, including viruses, bacteria, fungi, and nematodes (Lukyanenko 1991). Since the chemical control of these diseases is often too expensive for growers and in some cases ineffective, the development of resistant cultivars has always been a major breeding objective. Except for a few cases (Table 9.6; e.g., Lukyanenko 1991; Foolad and Sharma 2005; Ji and Scott 2007; Labate et al. 2007; Robertson and Labate 2007), all resistance genes have been derived from tomato wild relatives, with *S. chilense*, *S. peruvianum* s.l., *S. habrochaites,* and *S. pimpinellifolium* being the richest sources. Overall, resistances to over 42 major diseases have been discovered in tomato wild relatives, and at least 20 of them have been bred into tomato cultivars (Rick and Chetelat 1995; Ji and Scott 2007; Robertson and Labate 2007). For example, most commercial tomato hybrids carry different combinations of 15 independently introgressed disease-resistance genes originating from various wild accessions (Laterrot 2000; Zamir 2001; Foolad and Sharma 2005). Generally, they are major resistance genes for diseases such as root-knot nematode, fusarium wilt, verticillium wilt, alternaria stem canker, gray leaf spot, and some bacterial and viral disease (Laterrot 2000; Foolad and Sharma 2005; Ji and Scott 2007; Scott and Gardner 2007). However, in some cases (e.g., for diseases such as early blight, powdery mildew, bacterial canker, and bacterial wilt) horizontal resistance has been transferred since major genes for resistance were not available (Foolad and Sharma 2005). There is no doubt that, so far, the achievements in this area represent the greatest economic contribution of the wild species for the improvement of cultivated tomato germplasm.

Many of these resistance genes have been transferred into tomato cultivars or breeding lines through conventional breeding (see Table 3.2 in Ji and Scott 2007). One of the first examples was the exploitation of *C. fulvum* resistance from *S. pimpinellifolium* in 1934 (Walter 1967). During the last two decades, the use of molecular markers and MAS approaches have facilitated identification, mapping, and transfer of many disease resistance genes and QTLs in tomato (see Sect. 9.6.4) (Foolad and Sharma 2005; Labate et al. 2007). Currently, molecular markers are routinely employed in breeding programs by many seed companies in order to reduce cost and screening time mostly for transferring genes controlling vertical (race-specific) resistance to tomato diseases including bacterial speck, corky toot, fusarium wilt, LB, nematodes, powdery mildew, tobacco/tomato mosaic virus,

tomato spotted wilt virus, tomato yellow leaf curl virus, and verticillium wilt (Foolad and Sharma 2005; Labate et al. 2007). Although in most tomato seed companies MAS is not yet employed as a routine approach for manipulating QTLs it has, however, been used to improve quantitative resistance to bacterial canker, bacterial wilt, and TYLCV (Foolad and Sharma 2005). More limited is the application of MAS in public tomato breeding programs; a few examples are given by its use to improve horizontal resistances to blackmold (Robert et al. 2001) and LB (Brouwer and St. Clair 2004) (reviewed by Foolad and Sharma 2005; see also Sect. 9.6).

MAS may not only accelerate the procedure of gene transfer, but, through it, the pyramiding of desirable genes and QTLs for different traits can be also simpler and more effective (Barone and Frusciante 2007). However, many disease resistance genes are clustered in the genome. Therefore, the transfer of multiple resistance genes into single varieties might have to overcome difficulties associated with unfavorable repulsion linkages between clustered resistance loci and unforeseen actions of the resistance genes themselves. In this respect, the use of molecular markers will be a valuable tool for identifying rare recombinants that can be evaluated for improved performance. A solution could be to combine favorable alleles of the target loci in coupling phase linkage; an approach that was applied for the *Mi-1* and *Ty-1* resistance genes located near the centromere of tomato chromosome 6, a region where several other important resistance genes cluster (Hoogstraten and Braun 2005).

Further progress is to be expected in this field in light of the numerous new genetic, genomic, and bioinformatic tools that are becoming available for tomato and other species (Mueller et al. 2009; Sanseverino et al. 2010; see also Sect. 9.8).

9.7.2.2 Insect Resistance

The cultivated tomato is susceptible to a wide array of arthropod pests, some of which can cause severe losses (Farrar and Kennedy 1991; Kennedy 2003). Wild tomato species represent a rich reservoir of resistances to most important insects in tomatoes (Farrar and Kennedy 1991; Kennedy 2007). In particular, *S. habrochaites* is the most significant source of arthropod resistances, carrying resistance to at least 18 pest species (Ji and Scott 2007), followed by *S. pennellii* which shows resistance to at least nine insect species, with one accession, LA0716, being resistant to eight of these pests (Muigai et al. 2003). In addition, some insect resistance has also been found in *S. lycopersicum* "cerasiforme," *S. pimpinellifolium*, *S. cheesmaniae*, *S. chmielewskii*, *S. peruvianum., S. corneliomulleri*, *S. arcanum*, and *S. chilense* (Farrar and Kennedy 1991).

As described in Sects. 9.6.4.5 and 9.6.4.9, several mechanisms can be responsible for tomato resistance to arthropods, including physical and chemical properties of glandular trichomes, and chemical defenses associated with the leaf lamella (Farrar and Kennedy 1991). More specifically, methyl-chetones, such as 2-TD, and sesquiterpenes have been found to be associated with pest resistance in *S. habrochaites,* whereas in many *S. pennellii* accessions high level of resistance to numerous insects, including aphids, whiteflies, tomato fruitworm, beet armyworm, and the agromyzid leafminer is correlated with high density of type IV glandular trichomes and with the presence of high levels of toxic acylsugars in their exudates (references in Labate et al. 2007). QTLs underlying some of these traits have been identified (see Sects. 9.6.4.5 and 9.6.4.9).

Despite the rich source of natural resistance available, partly due to the mobile nature of the organisms involved, breeding for insect-resistance has been more complicated than breeding for disease resistance. As a result, only a few insect-resistant cultivars have been developed so far, and hence advanced molecular-based approaches are foreseen as the tools that might change this trend, although it might be advisable to apply them after having used a combination of breeding and biochemical methods (Mutschler 2006).

9.7.2.3 Abiotic Stress Tolerance

Several environmental stresses, including salinity, drought, excessive moisture, extreme temperature, mineral toxicity, and deficiency as well as pollution can challenge tomato crop, reducing its growth and production. The development of cultivars tolerant to various abiotic stresses is a goal of great economic importance and has been a major practice in tomato

breeding (Kalloo 1991; Foolad 2005). Tomato wild relatives represent a rich source of genetic diversity that can be used to improve abiotic stress tolerance of cultivated tomato germplasm. Predicting tolerance to abiotic stresses from observations of habitats of wild species, as proposed by Rick (1973), allowed to identify some useful sources for these traits. For instance, the arid habitats of *S. pennellii* and *S. sitiens* have led the detection of drought tolerance, while the high altitude accessions of *S. habrochaites* have been shown to possess resistance to cold temperatures. Resistance or tolerance to numerous adverse environmental conditions have been transferred in cultivated tomato including cold, heat, drought, excessive moisture conditions, as well as soil salinity and alkalinity (Kalloo 1991). A number of stress tolerant wild species stocks are maintained at TGRC that have been used in breeding programs (Robertson and Labate 2007; http//tgrc.ucdavis.edu/). However, traditional breeding for abiotic stress tolerance has been generally unsatisfactory mainly due to the very complex nature of such traits, except for heat tolerance (Scott et al. 1995).

As described in Sect. 9.6.4, extensive research has been conducted for identifying wild QTL alleles potentially involved in tolerances to different abiotic stresses, and considerable efforts have been invested in mapping research for tomato ST also at the reproductive stage. Several QTLs for drought related traits during important growth stages have been identified from *S. pimpinellifolium* and *S. pennellii*, while *S. habrochaites* has been the source for cold tolerance alleles (Foolad 2005). Moreover, recent QTL mapping studies have provided evidence that in order to be able to fully exploit the genetic potential of wild germplasm for the improvement of tomato crop productivity under salinity alternative approaches might be necessary. For instance, a more effcient utilization of wild germplasm could be via the improvement of rootstocks that confer ST, instead of introgression of beneficial QTL alleles into the genome of the cultivated tomato (Estañ et al. 2009).

In order to improve the effectiveness of these molecular tools, reliable QTLs at all stages of plant development should be identified, which can then be used to enable powerful MAS. In addition, new methodologies that integrate molecular, physiological, and phenotypic data should be explored in order to facilitate the pyramiding of QTLs.

9.7.2.4 Fruit Quality

Breeding objectives for fruit quality vary depending on whether the product is used fresh or processed, and whether we consider the producers', distributors', or consumers' needs. Quality traits important for processing tomato include the content of total soluble solids (SSC or brix; mainly sugars and acids), pH, and paste viscosity; shelf-life and firmness are priorities for distributors and retailers; while nutritional (e.g., antioxidants and vitamins) and sensorial quality play a major role in driving consumers' choices (Causse et al. 2001; Sinesio et al. 2010). Tomato sensorial quality for fresh consumption is a complex character as it relates to visual appearance (size, shape, and color), texture (firmness, mealiness, juiciness), and flavor attributes. The typical flavor of tomato fruit depends on a complex mixture of sugars, acids, amino acids, minerals, and volatile compounds (Baldwin et al. 1991).

Within wild species of tomato, there is a wealth of genetic variability also for fruit quality characters (Sect. 9.6.4; e.g., Stevens and Rick 1986; Rick and Chetelat 1995; Labate et al. 2007; Grandillo et al. 2008). For some of these traits, the value of the wild accession as a source of useful alleles can be assessed on a mere phenotypic basis (e.g., brix, nutritional quality, and in a few cases fruit color), whereas for other traits, such as fruit size, shape, and color, the breeding value depends on cryptic genetic variation that can become manifest once introgressed into cultivated genetic backgrounds, and that can be localized by means of molecular mapping approaches (Tanksley and McCouch 1997; Grandillo et al. 1999a; Zamir 2001; Lippman et al. 2007; Grandillo et al. 2008).

Among others, SSC of tomato fruit is a major concern in both fresh and processed market tomato production (Stevens 1986). This explains why much effort has been invested in trying to improve this quality trait. The SSC of commercial hybrid cultivars generally ranges from 4.5 to 6.0% of the fruit fresh weight, whilst the percentage of some tomato wild species can be much higher (Stevens 1972; Rick 1974; Hewitt and Garvey 1987). For example, *S. pimpinellifolium* and *S. chmielewskii* showed high concentrations (9–15%) of total soluble solids (Rick 1974; Hewitt and Garvey 1987). Generally, the efforts to breed for higher fruit solids have not been very successful because of the negative correlation between

yield and SSC. However, Rick (1974) by introgressing *S. chmielewskii* genes into a cultivated tomato variety, developed lines with approximately 40% greater total soluble solids, without any major penalty on yield.

The wild relatives of tomato are also sources of alleles that affect other components of flavor, such as the concentration of specific sugars and organic acids (Fulton et al. 2002a) as well as the accumulation of nutritional compounds, such as lycopene, β-carotene, and ascorbic acid (see Sect. 9.6.4). For example, while fruit of *S. lycopersicum* accumulates primarily reducing sugars (glucose and fructose) and very little sucrose, fruit of *S. chmielewskii*, *S. habrochaites,* and of other green-fruited wild species accumulate high amounts of sucrose, due to the action of the recessive sucrose accumulator gene (*sucr*) (Davies 1966; Yelle et al. 1988; Chetelat et al. 1995a, b). The fructose-to-glucose ratio in the mature tomato fruit was found to be modulated by a major gene (*Fgr*) on chromosome 4, which does not affect total sugar levels (Levin et al. 2000); the incompletely dominant *S. habrochaites* (LA1777) allele at this locus increases the fructose-to-glucose ratio. Firmness of most cultivars has been improved using a *S. pimpinellifolium* background introgressed in the 1940s (Scott 1984).

The red color and the antioxidant activity of tomato fruit is principally determined by their carotenoid pigments content. An important gene that was introduced from several wild tomato species is *Beta* (*B*); the wild allele increases the level of provitamin A (β-carotene) in the fruit by more than 15-fold (as reviewed by Labate et al. 2007). Breakage of the linkage between *B* and *sp* + (the gene for indeterminate growth habit), both located on chromosome 6, allowed the use of *B* for commercial production (Stommel et al. 2005a, b). Another important nutrient of tomato fruit is vitamin C. There is wide range of variation in vitamin C level among tomato and wild tomato species; the concentration may range from 8 to 119 mg per 100 g. Wild tomato accessions are rich in ascorbic acid, a quality that has been lost in many commercial varieties, which contain up to five times less ascorbic acid, although small-fruited varieties are richer in this vitamin than are standard varieties (Stevens 1986). Cultivars with high level of vitamin C have been developed from a cross with *S. peruvianum* s.l., but with little commercial success at that time (Stevens and Rick 1986).

Today, new efforts to explore wild species to obtain new cultivars with high sensorial quality and nutritional value are underway. For example, recent studies have shown that IL libraries, derived from interspecific crosses, provide a very efficient tool to access wide genetic variation also in compositional changes in the fruit, including aroma volatiles (Rousseaux et al. 2005; Tieman et al. 2006; Schauer et al. 2006, 2008; Stevens et al. 2007, 2008; Mathieu et al. 2009; see also Sect. 9.6). To accomplish improvement for these traits, breeding will require clear parameters and efficient methods of analysis. In the future, higher attempts in developing multidisciplinary programs in this research fields are expected.

9.7.2.5 Yield

Improved yield and yield stability has long been recognized as an important objective in plant breeding. The continuous growth of world population, combined with improvements in quality of life and with the on-going reduction of land available for farming, has created an urgent need for greater production of vegetables. There is no doubt that the replacement of inbred varieties with hybrid varieties have significantly contributed to the total genetic gains achieved in yield during the past decades. However, it is difficult to determine which traits, besides yield per se, are responsible for increased crop yields, since adaptive and defensive characters may play a major role in determining the higher yields of modern varieties (Tanksley et al. 1997a, b; Grandillo et al. 1999b).

Recent studies conducted in tomato have highlighted the potential of wild germplasm to affect yield stability in diverse environments, and to be able to lift yield barriers (Gur and Zamir 2004). The authors demonstrated that an exotic library derived from a wild tomato species, with no yield potential, can segregate for a wide array of previously unexplored genetic variation, which is rapidly available to plant breeders for the improvement of crop productivity. More specifically, progress in breeding for increased tomato yield was evaluated using *S. lycopersicum* genotypes carrying a pyramid of three independent yield-promoting genomic regions introgressed from the drought-tolerant green-fruited wild species *S. pennellii* (LA0716). Yield of hybrids obtained by crossing the pyramided genotypes was more than 50% higher than that of a control market leader variety under both wet and dry field conditions that received 10% of the irrigation water. Moreover,

the wild introgressions were effective in different cultivated genetic backgrounds, indicating that the cultivated tomato gene pool was missing alleles similar to those of the wild species (Gur and Zamir 2004). The approach of MAS pyramiding beneficial wild species chromosome segments into elite genetic backgrounds provides a new paradigm to revitalize plant breeding (Tanksley and McCouch 1997; Zamir 2001; Morgante and Salamini 2003; Koornneef et al. 2004; Lippman et al. 2007).

The results obtained by Gur and Zamir (2004) using the *S. pennellii* ILs established also a genetic infrastructure to explore the genetic and molecular basis underlying yield heterosis (Semel et al. 2006). This phenomenon has been studied for almost 100 years, and the cumulated research suggests that the genetic basis of hybrid vigor is determined by non-mutually exclusive mechanisms that include dominance complementation, overdominance, and epistasis (Lippman and Zamir 2007; Springer and Stupar 2007). However, the principles that govern heterosis and their molecular basis are still poorly understood. The use of the *S. pennellii* ILs allowed to partition heterosis into defined genomic regions, and, by eliminating a major part of the genome-wide epistasis, it was possible to estimate the importance of loci with overdominant (ODO) effects (Semel et al. 2006). It was shown that classical tomato heterosis is driven predominantly by overdominant QTLs associated with reproductive traits. Recently, Krieger et al. (2010) provided the first example of a single ODO gene for yield. The authors demonstrated that heterozygosity for tomato loss-of-function alleles of *SINGLE FLOWER TRUSS* (*SFT*), which is the genetic originator of the flowering hormone florigen, increases yield by up to 60%. Notably, the effect matched an ODO QTL from the *S. pennellii* LA0716 IL population (Semel et al. 2006). With the coming sequence of the tomato genome it will be easier to isolate those factors that are responsible for the strong ODO effects, and the derived knowledge will surely support further progress in crop breeding.

9.8 Genetic and Genomics Resources

Tomato has long served as a model system for genetic studies in plants, partly due to its importance as a food crop, but also because it has a series of advantageous characteristics including diploid inheritance, self-pollinating nature, ease of seed and clonal propagation, efficient sexual hybridization, easy crossability with most of the wild species, and a relatively short generation time. Tomato is also an excellent species for cytogenetic research, as its 12 chromosomes can be readily identified through analysis of pachytene karyotype, synaptonemal complexes, and chromosome or chromosome arm-specific DNA sequences. Finally, from the perspective of genetic and molecular investigations tomato has the additional advantages of a relatively small genome size among crop species (ca. 950 Mb) (Arumuganathan and Earle 1991). Extensive genetic and genomic tools have been developed in the domesticated tomato (see also reviews by Barone et al. 2008; Moyle 2008). Many of these tools should easily be exportable to tomato wild relatives due to the close relationship between the tomato and the related wild taxa as well as to the ample use of interspecific crosses with the cultigen.

Genetic and genomic resources currently available in tomato include thousands of molecular markers appropriate for use in domesticated and wild species, various molecular linkage maps (see Table 9.5), numerous DNA libraries, including BAC libraries and an advanced physical map, multiple permanent mapping populations, tomato wild species (see also Table 9.4), mutant collections, and Targeting Induced Local Lesions IN Genomes (TILLING) populations. Moreover, well-established genetic transformation protocols, gene-silenced tomato lines, and VIGS libraries (for transient silencing) have been developed, while EST collections are being actively produced worldwide permitting the design of different microarray platforms of which public results are also available. An ongoing genome sequencing initiative is providing insights into the genome structure of tomato with the purpose of generating a reference genome for the family Solanaceae and the Euasterid clade (APG 2009) more broadly. Websites distributed worldwide are providing information about resources for tomato and many of the other members of this plant family, as well as methodologies and bioinformatics tools (Mueller et al. 2005b; Labate et al. 2007). The SOL Genomics Network (SGN) organizes a comprehensive web-based genomics information resource designed to disseminate information for the Solanaceae family and

the related families in the Asterid clade (Mueller et al. 2005a, b; http://solgenomics.net/). Besides providing reference information strictly concerning the genome sequencing, such as BAC registry, project statistics, sequence repository, and viewers for the annotated sequence, SGN catalogs and maintains genetic maps and markers of the Solanaceae species (Mueller et al. 2005b). Additionally, it provides links to related sites of interest representing therefore the reference site for the tomato community.

Other web-based resources available for tomato include the TGRC, founded by Charles M. Rick, the central gene bank for wild relatives, and tomato mutant stocks (http://tgrc.ucdavis.edu); the Germplasm Resources Information Network (GRIN), providing germplasm information (http://www.ars-grin.gov/); the tomato core collection from the EU-SOL initiative https://www.eu-sol.wur.nl/, composed of ~7,000 domesticated (*S. lycopersicum*) lines, along with representative wild species, provided by different international sources and from private collections. Tools such as the Tomato Analyzer, a stand-alone piece of software, which performs semi-automated phenotyping of fruit shape (http://www.oardc.ohio-state.edu/vanderknaap/tomato_analyzer.htm), are also available and are flourishing worldwide. Links to these efforts are and will continue to be provided at SGN.

An international consortium of ten countries is sequencing the tomato genome as the cornerstone of the "International Solanaceae Genome Project (SOL): Systems Approach to Diversity and Adaptation" initiative (http://solgenomics.net/solanaceae-project/). The preliminary effort is to produce a high-quality tomato genome sequence starting from the approximately 220 Mb of estimated gene-dense euchromatin (corresponding to less than 25% of the total DNA) (Peterson et al. 1996). Towards this objective, a BAC-by-BAC strategy has been pursued (Mueller et al. 2009), though a whole-genome shotgun approachhas also been undertaken to support the coverage of the entire genome. Currently (July 2010), more than 1,000 BACs are available. Moreover, the first draft of the whole genome sequencing of *S. lycopersicum* cv. "Heinz" is today available at http://solgenomics.net/genomes/Solanum_lycopersicum/. The research groups of D. Ware, W. R. McCombie, and Z. B. Lippman at Cold Spring Harbor Laboratory have released a draft genome sequence of *S. pimpinellifolium* LA1589 (http://solgenomics.net/genomes/Solanum_pimpinellifolium/). This draft sequence provides a relevant added resource of genomic data useful for biological discovery of the processes of plant domestication and evolution, as well as for a better exploitation of the breeding potential of this wild species.

Genome sequences are being released to the GenBank repository (http://www.ncbi.nlm.nih.gov) and are made available at the SGN website (http://solgenomics.net/) as well. The international Tomato Annotation Group (iTAG), a collaborative effort involving several groups from Europe, USA, and Asia, is taking care of the sequence annotation, to provide a high quality, information-enriched, tomato genome.

While waiting for the publication of the annotated tomato genome, preliminary data concerning the available contigs of BACs are made available on the SGN website (http://solgenomics.net/) as well as on cross-linked resources such as ISOLA (http://biosrv.cab.unina.it/isola; Chiusano et al. 2008). Additionally, a number of chromosome specific curated information resources, as well as web-based tools, have been developed in order to allow researchers to access and exploit the emerging genome sequence as it is released by the different participants in the sequencing project (Mueller et al. 2009).

The organization of tomato and other Solanaceae transcript sequence collections is a prerequisite to provide a reliable annotation of the tomato genome consistently supported by experimental evidence. Moreover, this information is relevant for investigation on expression profiles and provides a reference for microarray chip design. Therefore, the genome sequencing initiative has further encouraged the production of EST collections worldwide.

As reference examples, SGN organizes and distributes ESTs sequenced from cDNA libraries from *S. lycopersicum*, *S. pennellii*, *S. habrochaites*, as well as the corresponding assembled consensus sequences; the Tomato Stress EST Database (TSED) contains ESTs from more than ten stress-treated subtractive cDNA libraries from *S. lycopersicum*; the Micro-Tom Database (MiBASE) (Yano et al. 2006) distributes unigenes obtained by assembling ESTs from full-length cDNA libraries of *S. lycopersicum* cv.

"Micro-Tom" and ESTs from other tomato lines; and TomatEST included in SolEST (D'Agostino et al. 2007, 2009) which is a secondary database of EST/cDNA sequences, currently containing 112 libraries from all the tomato species available at dbEST, the NCBI repository of public collections. Other EST databases available for tomato and related species include DFC http://compbio.dfci.harvard.edu/tgi/plant.html and PLANT GDB http://www.plantgdb.org/.

Moreover, several microarray platforms based on the extensive EST collections available in tomato are now available for transcriptional profiling (Barone et al. 2009): Tom1, a cDNA-based microarray containing probes for approximately 8,000 independent genes; Tom2, a long oligonucleotide-based microarray containing probes for approximately 11,000 independent genes (http://ted.bti.cornell.edu/; SOL project, http://www.eu-sol.net); and an Affymetrix Genechip, which contains probe sets for approximately 9,000 independent genes (http://www.affymetrix.com/products/arrays/specific/tomato.affxspecific/tomato.affx).

Results from the different platforms are available from a variety of specific websites such as the Tomato Expression Database (TED) which is a primary database for tomato microarray data (Fei et al. 2006; http://ted.bti.cornell.edu).

Well-established molecular genetic tools are also available for tomato functional analyses. To date, 1,000 monogenic mutant stocks in a variety of genetic backgrounds are publicly available at the TGRC (http://tgrc.ucdavis.edu); seeds from an isogenic tomato "mutation library" consisting of 6,000 EMS-induced and 7,000 fast neutron-induced mutant lines are publicly available for gene function research (Menda et al. 2004; http://zamir.sgn.cornell.edu/mutants/). Insertional mutagenesis systems exploiting exogenous transposon systems have also been described in tomato (reviewed by Barone et al. 2008). Platforms based on TILLING (McCallum et al. 2000) are also under development for tomato in several countries, including the USA, France, Italy, and India, and the EU-SOL project (http://www.eu-sol.net) is coordinating the Franco-Italian effort. Gene silencing approaches have also been widely used as a tool for functional genomics research in tomato. These include early systems of sense and antisense silencing, as well as the more recent technologies of RNA interference (RNAi) and VIGS.

9.9 Conclusions and Future Actions

In this review, we have looked into the plant group *Solanum* sect. *Lycopersicon* (the clade containing the domesticated tomato and its 12 wild relatives) and the four allied species in the immediate outgroups *Solanum* sect. *Lycopersicoides* (*S. lycopersicoides* and *S. sitiens*) and sect. *Juglandifolia* (*S. ochranthum* and *S. juglandifolium*), belonging to the large and diverse family Solanaceae. We have summarized the geographic distribution and morphological characters of these plant groups, describing their evolutionary relationships in the context of a new taxonomic revision at the species level (Peralta et al. 2008). We have shown that cultivated tomato, like many other crops, has a very narrow genetic basis that has limited the breeding potential of this crop for many years. In contrast, wild species are characterized by a wide range of genetic variation, which represents a rich reservoir of valuable alleles that could be used to address present and future breeding challenges. Over the past 60 years, tomato breeders have been at the forefront of establishing new principles for crop breeding based on the use of wild species to improve modern cultivars (Powers 1941; Rick 1974). Although, the most remarkable achievements have been reached in the area of disease resistances, yet exotic germplasm has also been used as a source of useful genes to improve other important traits. The numerous molecular mapping studies conducted using interspecific crosses have clearly demonstrated that the breeding value of exotic germplasm goes much beyond its phenotype. However, in spite of these successful results, it has to be acknowledged that we are still far from having been able to fully exploit the breeding potential of the thousands of accessions stored in seed banks around the world, and that can still be found in natural habitats (Tanksley and McCouch 1997). We need to capitalize on the acquired knowledge and on the evergrowing genetic and "-omics" resources that are becoming available for tomato, to keep developing new concepts and breeding strategies suitable for a more efficient use of the wealth of genetic variation stored in the wild relatives. In this respect, among all model systems, the wild and domesticated species of the tomato clade have pioneered novel population development, such as "exotic libraries" (Zamir

2001; Lippman et al. 2007). The last 15 years of research conducted on the *S. pennellii* LA0716 ILs (the founding population) using cutting edge phenotyping platforms has demonstrated the value of such a resource in fundamental biology, and for exploring and utilizing the hidden breeding potential of wild species for practical use in agriculture.

These results have encouraged the tomato research community to invest in the development of IL populations, or related pre-breds, such as BILs, for a number of other tomato wild species including *S. habrochaites*, *S. arcanum*, *S. pimpinellifolium*, *S. lycopersicoides*, *S. neorickii*, *S. chmielewskii,* and *S. chilense* (see Sect. 9.6.4). Recently, in order to enhance the rate of introgression breeding in tomato, in the framework of a currently running EU project (EU-SOL), "exotic libraries" of tomato from a diverse selection of accessions are being further refined and anchored to a common set of COSII markers (Tripodi et al. 2009; https://www.eu-sol.wur.nl/).

These genetic resources, combined with advances in other fields such as cytogenetics and tissue culture, along with the increasing knowledge deriving from bioinformatics and the many "omics" tools, including the tomato genome sequence (http://sgn.cornell.edu/solanaceae-project), are expected to further improve the efficiency with which wild tomato relatives will contribute to the improvement of this important crop. At the end, breeders will be able to select the best combinations of alleles and to design programs to combine traits in new, superior genotypes following the "breeding by design" concept (Peleman and Van der Voort 2003).

Given the unquestionable value of wild tomato germplasm there is the need to preserve this precious resource for future generations. Therefore, conservation initiatives have to be taken not only for the excellent ex situ collections available worldwide, but also to preserve populations in situ. The appropriate authorities in national governments of the countries of origin – mainly Ecuador, Peru, and Chile – should be helped to take steps to protect their native tomatoes and their habitats from further catastrophic loss. International organizations, such as the CGIAR, are urged to get involved to initiate and/or support such conservation efforts. Without action, the wealth of wild germplasm in the tomato relatives may not be available to future generations.

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