

Review Article

Genome Mapping and Molecular Breeding of Tomato

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The cultivated tomato, *Lycopersicon esculentum*, is the second most consumed vegetable worldwide and a well-studied crop species in terms of genetics, genomics, and breeding. It is one of the earliest crop plants for which a genetic linkage map was constructed, and currently there are several molecular maps based on crosses between the cultivated and various wild species of tomato. The high-density molecular map, developed based on an *L. esculentum* × *L. pennellii* cross, includes more than 2200 markers with an average marker distance of less than 1 cM and an average of 750 kbp per cM. Different types of molecular markers such as RFLPs, AFLPs, SSRs, CAPS, RGAs, ESTs, and COSs have been developed and mapped onto the 12 tomato chromosomes. Markers have been used extensively for identification and mapping of genes and QTLs for many biologically and agriculturally important traits and occasionally for germplasm screening, fingerprinting, and marker-assisted breeding. The utility of MAS in tomato breeding has been restricted largely due to limited marker polymorphism within the cultivated species and economical reasons. Also, when used, MAS has been employed mainly for improving simply-inherited traits and not much for improving complex traits. The latter has been due to unavailability of reliable PCR-based markers and problems with linkage drag. Efforts are being made to develop high-throughput markers with greater resolution, including SNPs. The expanding tomato EST database, which currently includes ~214 000 sequences, the new microarray DNA chips, and the ongoing sequencing project are expected to aid development of more practical markers. Several BAC libraries have been developed that facilitate map-based cloning of genes and QTLs. Sequencing of the euchromatic portions of the tomato genome is paving the way for comparative and functional analysis of important genes and QTLs.

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1. INTRODUCTION

1.1. Economic importance

The cultivated tomato, *Lycopersicon esculentum* Mill., a fruit that is often treated as a vegetable, is widely grown around the world and constitutes a major agricultural industry. Worldwide, it is the second most consumed vegetable after potato (FAOSTAT 2005; <http://faostat.fao.org>) and unquestionably the most popular garden crop. In the U.S., it is the third most economically important vegetable (with a total farm value of \$2.062 billion) following potato (\$2.564 billion) and lettuce (\$2.064 billion) (USDA 2005; <http://www.usda.gov/nass/pubs/agr05/agstats2005.pdf>). In addition to tomatoes that are eaten directly as raw vegetable or added to other food items, a variety of processed products such as paste, whole peeled tomatoes, diced products, and various forms of juice, sauces, and soups have gained

significant acceptance. There are more varieties of tomato sold worldwide than any other vegetable. Although a tropical plant, tomato is grown in almost every corner of the world from the tropics to within a few degrees of the Arctic Circle. It is grown in greenhouses where outdoor production is restricted due to cool temperatures. Major tomato producing countries in descending orders include China, USA, India, Turkey, Egypt, and Italy (<http://faostat.fao.org>). Other leading countries include Spain, Brazil, Iran, Mexico, Greece, and Russia. In North America, production occurs in the U.S., Canada, and Mexico, comprising a total of 310 000 ha. In 2004, the total harvested area in the U.S. was estimated to be 170 808 ha (50 560 ha fresh market and 120 248 ha processing tomatoes) with a total farm value of ~\$2.06 billion (\$1.34 billion fresh market and \$0.72 billion processing) (USDA 2005; <http://www.nass.usda.gov:8080/QuickStats/index2.jsp>). California and Florida are by far the leading producers of processing and fresh

market tomatoes, respectively (USDA 2005). Worldwide, tomatoes are an important part of a diverse and balanced diet [1]. The tomato does not rank high in nutritional value; one medium fresh tomato (135 g) provides 47% RDA of vitamin C, 22% RDA vitamin A, and 25 calories. However, by virtue of volume consumed, it contributes significantly to the dietary intake of vitamins A and C as well as essential minerals and other nutrients. In the U.S. diet, for example, tomato ranks first among all fruits and vegetables as a source of vitamins and minerals [2] and phenolic antioxidants [3]. Also, fresh and processed tomatoes are the richest sources of the anti-oxidant lycopene [4], which arguably protects cells from oxidants that have been linked to cancer [5].

1.2. Botanical description

Tomato belongs to the nightshade family Solanaceae, which is in division Magnoliophyta, class Magnoliopsida, subclass Asteridae, order Solanales, and suborder Solanineae. The extremely diverse and large Solanaceae family is believed to consist of 96 genera and over 2800 species in three sub-families, Solanoideae (in which *Lycopersicon* belongs), Cestroideae, and Solanineae [6, 7]. Solanaceae is one of the economically most important families of angiosperms and contains many of the commonly cultivated plants, including potato, tomato, pepper, eggplant, petunia, and tobacco. This family is the most variable of all crop species in terms of agricultural utility, the 3rd most economically important crop family, exceeded only by the grasses and legumes, and the most valuable in terms of vegetable crops [8]. Among all plant families, members of the Solanaceae are extremely diverse in terms of growth habit (from trees to small annual herbs), habitat (from deserts to the wettest tropical rain forest), and morphology [6]. Many Solanaceous species have played important roles as model plants, including tomato, potato, pepper, tobacco, and petunia.

The tomato genus *Lycopersicon* is one of the smallest genera in Solanaceae, though the centerpiece in the family for genetic and molecular research. It is the closest to the genus *Solanum* (nightshade), an association which originally led people to believe tomato was poisonous [9]. The cultivated tomato was originally named *Solanum lycopersicum* by Linnaeus [10]. In 1754, Miller separated tomatoes and designated the genus *Lycopersicon* and the species *esculentum* for the cultivated tomato [11]. This helped with the acceptability of tomato as a food. The genus *Lycopersicon* was initially distinguished from the genus *Solanum* by its distinct characteristics of anthers and leaves. While *Lycopersicon* has anthers that dehisce laterally, and leaves that are mostly pinnate or pinnatifid, *Solanum* has anthers that dehisce from the terminal ends and leaves that tend to be simple. The *Solanum* species most closely related to and with some level of difficulty crossable with *Lycopersicon* are *S. juglandifolium* Dun., *S. ochranthum* Dun., *S. lycopersicoides* Dun., and *S. rickii* Corr. [12–14].

Phylogenetic relationships between *Solanum* and *Lycopersicon* have been the subject of a great debate for a long time, with many Solanaceae researchers recognizing *Lycop-*

ersicon as a distinct genus while others suggesting its merger with *Solanum*. More recently, based on much molecular and morphological information, a new taxonomic classification of tomato and re-adoption of *S. lycopersicum* for the cultivated tomato have been suggested [6, 15–18]. The other species of *Lycopersicon* have also been assigned or reassigned to *Solanum* [16, 19–21]. In this review, however, due to the use and citation of numerous historical references and in order to be consistent with much of the literature, Miller's classification [22] is followed.

1.3. Genetic variation

In addition to the cultivated species *L. esculentum* and its wild form *L. esculentum* var. *cerasiforme* (Dun.) Gray (wild cherry), there are eight related wild species, including *L. pimpinellifolium* (Jusl.) Mill. (currant tomato), *L. cheesmanii* Riley, *L. chmielewskii* Rick, Kes., Fob. and Holle, *L. chilense* Dun., *L. parviflorum* Rick, Kes., Fob. and Holle, *L. peruvianum* (L.) Mill., *L. hirsutum* Humb. and Bonpl., and *L. pennellii* (Corr.) D'Arcy [23, 24]. All species are native to Western South America, mainly Peru. Only the cultivated species and wild cherry are found outside this range and are common throughout many parts of the world, especially in Mesoamerica and the Caribbean [25]. However, the natural habitat of *Lycopersicon* is highly variable, from very dry to very wet and from coastal to mountainous areas of more than 3300 m elevation [14]. This diversity in habitat has undoubtedly contributed to the great variation that can be found in *Lycopersicon*.

All species within *Lycopersicon* produce perfect, hermaphrodite flowers. A complete range of mating systems is found, from autogamous *L. cheesmanii* and *L. parviflorum* to obligately outcrossed self-incompatible biotypes of *L. chilense*, *L. hirsutum*, *L. peruvianum*, and *L. pennellii* [26]. Self fertility with various degrees of facultative outcrossing is found in *L. chmielewskii*, *L. esculentum*, *L. pimpinellifolium*, and the self-compatible biotypes of *L. hirsutum* and *L. pennellii* [27]. All tomato species are diploid ($2n = 2x = 24$) and are similar in chromosome number and structure [28]. The nine species have been grouped into two intracrossable, interincrossable groups (or complexes): the “*esculentum* complex,” including *L. esculentum*, *L. esculentum* var. *cerasiforme*, *L. pimpinellifolium*, *L. cheesmanii* (including *L. cheesmanii* f. *minor*), *L. chmielewskii*, *L. parviflorum*, *L. hirsutum* (including f. *typicum* and f. *glabratum*) and *L. pennellii*, and the “*peruvianum* complex” including *L. peruvianum* and *L. chilense* [12, 29, 30]. All species within the *esculentum* complex can be hybridized with the cultivated tomato and most (except *L. hirsutum* f. *typicum* and some *L. pennellii*) are self compatible [12, 23, 31]. They have yellow flowers and the stamens are joined to produce an anther cone. Fruit color varies depending on the species, from red to orange to yellow to green. Several members of the *esculentum* complex have provided sources of pest resistance and other desirable characteristics in the cultivated tomato, as discussed below. The two species within the *peruvianum* complex are extremely diverse and represent a wealth of characteristics, which are potentially valuable for crop improvement. These species, which

are mostly self incompatible and produce green fruit, have been rather partial in their usefulness to cultivated forms due to various barriers present in sexual hybridization and gene transfer. However, they can be hybridized with members of the *esculentum* complex by the application of techniques such as embryo rescue [23, 24, 32] or by the use of pollen mixture (with tomato pollen) when fertilizing tomato plants [33]. There are documented examples of crosses with *peruvianum* complex which have been utilized in tomato breeding, including transfer of tobacco mosaic virus and nematode resistance [30, 34].

The cultivated tomato has limited variability, largely because of several population bottlenecks in the forms of founder events and natural and artificial selections that occurred during domestication and evolution of modern cultivars [25]. For example, tomatoes that were first introduced to Europe by Spanish explorers furnished the entire genetic base for the modern cultivars and consequently the current European and U.S. cultivars are highly similar to each other. It is estimated that only ~5% of the total genetic variation within *Lycopersicon* can be found within *L. esculentum* [35, 36] and genes for many desirable agricultural characteristics do not exist in this species. The related wild tomato species, however, are a rich source of desirable genes and characteristics for crop improvement, though they remain largely under exploited. The species with the greatest variability are *L. chilense*, *L. hirsutum*, *L. peruvianum*, and *L. pennellii* whereas the least variable species are *L. cheesmanii* and *L. pimpinellifolium* [35, 37].

During the past 70 years wild species of tomato have been utilized in breeding programs to improve the cultivated tomato [24, 27, 32]. For example, much of the disease resistance in most commercial cultivars has been derived from the related wild species. In fact, the cultivated tomato is a prime example of a crop plant that has benefited significantly from exotic germplasm introgressions, probably more so than any other crop species. Furthermore, the great diversity available in tomato wild species promises many more advances in this area. Numerous wild accessions have been identified with desirable horticultural characteristics such as high fruit quality and tolerance to abiotic stresses. Recent advancements in molecular markers and marker-assisted selection (MAS) technology are expected to make tomato improvement via introgression from wild species more feasible. It is estimated that over 62 800 accessions of the cultivated and wild species of tomato (mostly *L. esculentum* accessions) are maintained in genebanks around the world [38], including those in the Asian Vegetable Research and Development Center (AVRDC) at Tainan, Taiwan, China, the United States Department of Agriculture (USDA), Plant Genetic Resources Unit at Geneva (PGRU), Ny, USA, and the CM Rick Tomato Genetics Resource Center (TGRC), University of California, Davis, Calif, USA. The TGRC (<http://tgrc.ucdavis.edu>) is known to maintain the largest collection of tomato wild species while PGRU has a large collection of open-pollinated cultivars. Good collections of tomato germplasm are also maintained in The Netherlands (IVT), Russia (VIR), Japan (NIAS), Peru (DHUNA), and Cuba (INIFAT) [39]. In addition to the wild

and cultivated accessions, there are thousands of tomato monogenic stocks and mutants that have been phenotypically characterized and cataloged (<http://tgrc.ucdavis.edu>; <http://www.zamir.sgn.cornell.edu>).

1.4. Domestication and crop production

Among the nine *Lycopersicon* species, only *L. esculentum* has become a domesticated crop though *L. pimpinellifolium* (with fruit diameter ~1 cm) is also casually planted for consumption [9]. According to [25], domestication of *L. esculentum* was accompanied by a transition from exerted to inserted stigmas, and consequently changing from facultative outcrossing to enforced inbreeding. As a result of this autogamy, most accessions within the cultivated species, including the common fresh market and processing tomatoes, landraces, primitive cultivars, and the wild cherry are essentially pure lines. Fruits of the cultivated species come in a wide range of shapes, sizes, and colors. Some may be globe, round, flattened, oval, heart, or elongated shaped. Their colors may be red, pink, golden, yellow, striped, purple, green, or white [30, 34]. The average weight for the garden tomato used for slicing is 4 to 6 oz., but some varieties such as Giant Heirloom may weigh up to 2 pounds [40]. It is arguably accepted that the wild cherry (*L. esculentum* var. *cerasiforme*, with fruit diameter of ~1.5–3 cm) is the immediate progenitor of the cultivated tomato though *L. pimpinellifolium* is also a likely candidate [25, 41]. The isozyme and molecular phylogenetic and diversity studies have not clarified this issue [35, 36, 42].

The cultivated tomato is thought to have originated in the new world, since all of its related wild species are native to the Andean region now encompassed by parts of Peru, Chile, Colombia, Ecuador, and Bolivia [9, 25, 41]. Some distinct relatives (e.g., *L. pennellii*) are also found among the flora of the Galapagos Islands. Although Peru was earlier widely accepted as the center of domestication, “the bulk of the historical, linguistic, archaeological, and ethno-botanical evidence favors Mexico as the source of the cultivated tomatoes” [25]. Also, despite the wide distribution of the genus in Andean region, Mexico has been considered the most likely center of domestication of tomato. The name “tomato” is derived from the Spanish “tomate” which in turn is derived from the Mexican Nahuatl name “tomatl,” which actually means tomatillo, and applied both to the tomato as we know it and the husk tomato, genus *Physalis* [9]. It is not known exactly when domestication of tomatoes occurred, however, by the time the Spanish conquered Mexico in 1523, they were already domesticated [9]. A comparison of hereditary enzyme variants reveals much greater similarity between the older European cultivars and the primitive cultivars and cherry tomatoes of Mexico and Central America than between the European cultivars and the primitive plants of the Andean region [25, 43]. The first record of tomatoes in Europe is credited to descriptions published in 1554 by Italian herbalist Pier Andrea Mattioli. The plant was first known as *pomi d'oro*, *mala aurea* (golden apple), *poma amoris* (love apple), and garden apple [9]. These and equivalent names persisted well into the 19th century. Tomato first appeared in a cookbook in 1692, nearly two hundred years after Columbus headed for the new

world. However, even then, because of the persistent superstitions regarding the poisonous nature of the tomato, it was remarkably slow to gain acceptance except as an ornamental, a medicinal, or a curiosity [9]. Such unfounded superstitions persisted into the 19th century in many parts of the world, including North America, to which the plant had been taken by immigrants in the 1600s and early 1700s [9]. Commercial production of tomato in a small scale in the U.S. began in 1847 at Lafayette College at Easton, Pa, which grew to become a major vegetable crop in the mid 20th century.

1.5. A model organism

Tomato has been an excellent model system for both basic and applied plant research. This has been due to many reasons [44], including ease of culture under a wide range of environments, short life cycle, photoperiod insensitivity, high self fertility and homozygosity, great reproductive potential, ease of controlled pollination and hybridization, diploid species with a rather small genome (~0.95 pg/1C, 950 Mbp) [45, 46], lack of gene duplication, amenability to asexual propagation and whole plant regeneration [47, 48], the ability to develop haploids [49], and availability of a wide array of mutants [50] and genetic stocks (including wild species; <http://tgrc.ucdavis.edu>; <http://www.sgn.cornell.edu>). Tomato's regenerative plasticity also allows easy grafting, an attribute that facilitates certain developmental and practical studies. Recent availability of high molecular weight insert genomic libraries, including both YAC [51] and BAC [52, 53] libraries, has facilitated map-based or positional cloning. Furthermore, members of *Lycopersicon* are easily transformed, and transgenic tomatoes are routinely produced using cocultivation with *Agrobacterium tumefaciens* [47, 54]. Tomato was the first food crop in the U.S. for which a genetically engineered variety was marketed [55] and also for which a disease resistance gene was positionally cloned [56, 57]. Currently, the euchromatic portions of the 12 tomato chromosomes are being sequenced, which will make tomato even more of ideal crop plant system for genomic studies.

1.6. Breeding objectives and previous achievements

Breeding new cultivars of tomato with improved characteristics started more than 200 years ago in Europe (mainly in Italy). In the U.S., however, tomato breeding started only a little over a century ago and AW Livingston is recognized as the first tomato breeder in 1870s [30, 34]. Until 1950s, tomato breeding included development of multipurpose cultivars to meet several needs, including fresh market and processing industries. Subsequently, breeding objectives have depended upon method of culture, that is, field or greenhouse grown, and whether the product has to be used fresh or processed [30, 34]. Today, fresh market and processing cultivars are quite distinct, largely as a result of the different quality requirements for intended use. However, the universal goal of tomato breeding for both fresh market and processing purposes has been to increase fruit yield per unit

area. Other essential characteristics common to both industries include disease resistance, broad adaptability, earliness in maturity, ability to set fruit at adverse temperatures, resistance to rain-induced cracking, tolerance to major ripe-fruit rots, adequate vine cover, fruit firmness, and several other fruit quality characteristics. Specific traits needed in processing cultivars include compact, determinate plant habit and concentrated flowering and fruit set suitable for once-over machine harvest, ease of fruit separation from the vine (*jointless* characteristic), and specific fruit quality characteristics such as color, pH, total acidity, soluble solids, total solids, and viscosity (consistency). Specific traits of interest in fresh market cultivars include large, round fruit with adequate firmness and shelf-life, uniform fruit size, shape and color, appearance, freedom from external blemishes or abnormalities, texture, taste and flavor [30, 34]. Currently, in the U.S. much of the tomato breeding work is conducted in private sector (seed companies). However, a few major public tomato breeding programs include those in the University of Florida (JW Scott, fresh market), North Carolina State University (RG Gardner, fresh market), Ohio State University (DM Francis, processing), Pennsylvania State University (Foolad, fresh market and processing) and Cornell University (MA Mutschler). In what follows, some of the major breeding achievements in different areas are briefly discussed.

Yield

Unless a new cultivar has a yield potential equal to or exceeding that of current cultivars, it generally cannot be successful even if it may contain other improved characteristics. Because selection for yield *per se* is seldom very effective, breeders often define individual components that contribute to yield and emphasize selection for those attributes. Breeding for improved fruit yield in tomato has been very successful. For example, between 1920s and 1990s fruit yield of processing tomato cultivars in the U.S. increased from 10.1 tons/ha to 72.4 tons/ha, a 7.2-fold increase [58]. A recent statistic by the USDA indicated processing tomato yield of ~102 tons/ha in the U.S. in 2004 (<http://www.nass.usda.gov:8080/QuickStats/index2.jsp>). It is estimated that on an average about half of the increase in crop productivity has been due to cultivar improvement through plant breeding [59]. Greater farming inputs and advancements in cultural practices are considered other major causes of increases in productivity. Even today, increased yield and quality of tomato is the universal goal of most tomato breeding programs, though this increase may be achieved by selecting for other desirable characteristics such as disease resistance, tolerance to abiotic stresses, earliness, and improved fruit sugar contents. In the fresh market tomato breeding program at the University of Florida, for example, increased yield has been achieved by breeding for heat tolerance for production under hot and humid conditions [60, 61]. Because of the difficulties associated with phenotypic selection for improved yield, more recently molecular

markers have been identified for traits that are directly or indirectly related to yield in tomato.

Disease resistance

Diseases are first concern to processing and fresh market tomato industries throughout the world and economic losses due to crop damage or disease control measures are significant (<http://faostat.fao.org>). Tomato is susceptible to over 200 diseases caused by pathogenic fungi, bacteria, viruses, or nematodes [62]. Without question, the greatest contribution of modern plant breeding to tomato improvement has been through development of cultivars with improved disease resistance. Resistance has been identified, and in many cases characterized, for more than 30 of the major tomato diseases. Most commercial cultivars possess up to 6 (in true breeding lines) or 10 (in hybrids) disease-resistance attributes. These mainly include diseases for which major resistance genes have been identified, including fusarium wilt, verticillium wilt, root-knot nematode, alternaria stem canker, gray leaf spot, and some bacterial and viral diseases. However, horizontal (a.k.a. field or polygenic) resistance has also been reported for several tomato diseases, where major genes for resistance to a particular pathogen or race are not found, such as early blight, powdery mildew, bacterial canker, and bacterial wilt. Except in a few cases (e.g., [63–69]), tomato wild species have been utilized as the source of resistance for all tomato diseases. Resistance resources have been identified in most related wild species of tomato, in particular *L. pimpinellifolium*, *L. peruvianum*, and *L. hirsutum*. For some tomato diseases, such as late blight (caused by oomycete *Phytophthora infestans*) and powdery mildew (caused by fungus *Oidium lycopersicum*), both vertical and horizontal resistances have been identified. All original characterization, disease evaluation, and incorporation of resistance genes were through phenotypic selection and traditional breeding protocols, and still today much of the disease resistance breeding in tomato is through the use of similar protocols. However, the difficulties encountered when transferring resistance from wild species to the cultivated tomato via traditional protocols have restricted transfer of resistance to many tomato elite lines. This is in addition to the lack of suitable screening facility or expertise in many tomato breeding programs to develop cultivars with multiple disease resistances. Thus, breeders have consistently sought more effective approaches for resistance breeding. During the past two decades, the use of molecular markers and MAS techniques have facilitated identification, mapping, and transferring of many disease resistance genes and quantitative trait loci (QTLs) in tomato. The use of marker technology in disease resistance breeding in tomato is becoming a routine procedure. Furthermore, breeding for disease resistance remains a major goal of most public and private tomato breeding programs as new diseases achieve significance or new races of existing pathogens become established. The ultimate goal is to eliminate or significantly reduce the use of pesticides in tomato production by the use of host resistance.

Insect resistance

The cultivated tomato is subject to attack by numerous insects, including various species of mites, whiteflies, aphids, Lepidoptera (e.g., tomato fruitworm, beet armyworm, cotton bollworm, southern armyworm, soybean podworm, and Egyptian cottonworm), Coleoptera (e.g., Colorado potato beetle and tobacco flea beetle), Diptera (e.g., leafminers and fruit fly), thrips, sinkbugs, and cutworms, many of them capable of causing devastating losses. Insect resistance in tomato has received considerably less attention than disease resistance, and few commercial cultivars have been developed with specific insect resistance. However, resistance to major insect pests of tomato has been identified within the related wild species, in particular *L. hirsutum* and *L. pennellii* [34, 70–75]. *L. hirsutum*, the most notable source of arthropod resistance, occurs in two distinct forms, *L. hirsutum* f. *typicum* and *L. hirsutum* f. *glabratum* CM Mull [75], each showing resistance to at least 16 pest species [76]. Resistance to at least nine insect species has been reported in *L. pennellii*, including greenhouse whitefly, carmine and two-spotted spider mites, and the potato aphid [72]. Some insect resistance has also been reported in *L. esculentum* var. *cerasi-forme*, *L. pimpinellifolium*, *L. cheesmanii* and *L. chmielewskii*, *L. peruvianum* and *L. chilense* [76]. Unfortunately, most of these resources have not been characterized or utilized for insect resistance breeding, though a few inheritance studies have been undertaken [70, 77, 78]. Breeding for insect resistance in tomato has generally encountered more difficulties than breeding for disease resistance, linkage drag being a major impediment [34, 72, 79, 80]. It is expected that identification of markers associated with insect resistance and use of MAS will help alleviate some of the difficulties in developing insect resistant cultivars.

Abiotic stress tolerance

Although the cultivated tomato is widely adapted to different climates, its growth and development is rather sensitive to different environmental stresses, including salinity, drought, excessive moisture, extreme temperatures, mineral toxicity and deficiency, and environmental pollution. There is limited genetic variation for abiotic stress tolerance within the cultivated species and most commercial cultivars are considered moderately to highly sensitive to different stresses. Fortunately, sources of genetic tolerance (or resistance) to different abiotic stresses are found within the related wild species, including *L. chilense*, *L. peruvianum*, *L. pennellii*, *L. pimpinellifolium*, *L. hirsutum*, *L. cheesmanii*, *L. chmielewskii*, and *L. parviflorum* [81]. In addition, there are a few species within *Solanum* that exhibit tolerance to environmental stresses and which may be utilized in tomato breeding for stress tolerance. These include *S. lycopersicoides* Dun. and *S. rickii* Corr., which are more closely related to tomato and *S. juglandifolium* Dun. and *S. ochranthum* Dun., which are more distantly related [12, 13, 31, 82, 83].

Several tomato wild species have been utilized for genetic and physiological characterization of abiotic stress tolerance and for breeding purposes [60, 84–91]. However, there is

only few report of stress-tolerant tomatoes developed via traditional breeding protocols. This is in part due to the complexity of abiotic stress tolerance traits. A plant's response to environmental stress is modulated by many physiological and agronomical characteristics, which may be controlled by the actions of several to many genes whose expressions are influenced by various environmental factors. In addition, stress tolerance is a developmentally regulated, stage-specific phenomenon; tolerance at one stage of plant development is often not correlated with tolerance at other developmental stages [92–97]. For successful tomato production under environmental stress, tolerance may be needed at all major stages of plant development, including seed germination, the vegetative stage, and flowering and fruit production. Each developmental stage (which may be considered as a separate trait) may require a different screening procedure and simultaneous or sequential screening may be impractical or impossible. However, quantification of tolerance often poses serious difficulties. Phenotypic selection under field conditions is difficult because uncontrollable environmental factors adversely affect the precision and repeatability of such trials. There is often no reliable screening technique that could be used year after year or generation after generation. Furthermore, selection for stress tolerance using phenotypic measurements requires specialized personnel and extensive investments in field nurseries or greenhouse facilities. Thus, the challenge has been to improve the efficiency of selection and breeding for stress tolerance. For the past two decades, the identification and use of genetic markers that are associated with traits related to stress tolerance has been considered and suggested as a promising approach. Thus, rather extensive research has been conducted in tomato to identify QTLs for tolerance to different environmental stresses, as described below.

Fruit quality

Fruit quality has been a major focus of most tomato breeding programs during the past century. Major fruit quality characteristics of interest to both fresh market and processing tomato industries include fruit size, shape, total solids, color, firmness, ripening, nutritional quality and flavor. Fruit total solids content is particularly important to the processing industry and probably has received more attention than any other fruit trait. The total solids of the cultivated tomato comprise 4–7.5% of its fresh weight, though this percentage can be much higher in some wild species [98, 99]. The total solids are composed of all fruit components except water and volatiles. In the cultivated tomato, the soluble (SS) and insoluble solids (ISS) account for about 75% and 25%, respectively, of the total solids [100]. Reducing sugars glucose and fructose are the major components of the SS [101]. Sucrose is also present but in very small quantities [102], although some wild species of tomato, including *L. chmielewskii* [103] and *L. hirsutum* [102], have higher concentration of sucrose. The remaining soluble solids are composed of organic acids, lipids, minerals, and pigments. The ISS include proteins, cellulose, hemicellulose, pectins, and polysaccharides, which determine fruit viscosity [34, 104, 105]. Quality of tomato

juice, catsup, sauce, soup, and paste are influenced by viscosity of the product. Both SS and ISS are related to yield of concentrated tomato products, and yield and quality of certain processed products are determined by sugar contents of the fruit [105]. For tomato products that are sold on the basis of solids content, the higher the solids of the raw products the greater the value of crop yields. For example, an increase in solids of just 1% represents ~20% increase in yield of certain processed products [106, 107]. High sugar content also increases the overall taste and flavor of the fresh fruit [108, 109]. For these reasons, increasing fruit solids content has been the focus of numerous tomato breeding programs. Estimates of the SS contents of the commercial cultivars of tomato range between 4.6% (mostly in fresh market) and 6.3% (mostly in processing) of the fresh weight [106]. However, accessions have been identified within related wild species of tomato, including *L. pimpinellifolium*, *L. chmielewskii* and *L. cheesmanii*, with much higher concentrations (~9–15%) of SS [105, 110]. Despite the presence of this genetic variability, breeders have had limited success in increasing fruit SS or combining high SS with high yield. This has been due to various reasons, including the complex, quantitative nature of the trait [111] and the negative relationship between yield and percentage of SS [112, 113].

Fruit color is another quality characteristic in tomato that has received intensive attention. The two major groups of pigments found in tomato fruit are carotenoids and chlorophylls. However, the final color in tomato fruit is conditioned by the total amount and proportion of different carotenoids. Lycopene is the red pigment and major carotenoid in tomato. The red color is the most visible and important quality attribute of the mature tomato fruit for both fresh consumption and processing. In processing tomato, fruit color influences the grades and standards of the processed commodity. In fresh market tomato, fruit color has significant effect on its marketability. The attention to fruit color has recently been on the rise due to the increasing knowledge of the health benefits of different carotenoids. For example, fresh tomatoes and tomato products are presently major sources of lycopene, a potent natural antioxidant that is increasing in demand. Numerous epidemiological and intervention studies have demonstrated that dietary intake of lycopene-rich foods results in decreased incidence of certain cancers, including the prostate, lung, mouth, and colon cancers, and the coronary heart diseases, cataracts and may be macular degeneration [1, 5, 114–117]. This attention to lycopene is well deserved, as its antioxidant capacity is roughly twice that of β -carotene [118]. Unlike β -carotene, however, lycopene does not have any provitamin A activity. As the scientific community has become more aware of the impact of carotenoids on human health, attention has shifted to increasing tomato fruit lycopene content. Thus, an important goal of many tomato breeding programs is to develop cultivars with enhanced fruit lycopene content. In addition to lycopene, ripe tomato fruit contains β -carotene and small amounts of phytoene, phytofluene, ζ -carotene, γ -carotene, neosporine, and lutein [119].

Lycopene levels of “normal” tomatoes vary with variety, and tomatoes with better red color tend to be higher in lycopene. Spontaneous mutations contributing to high fruit lycopene content have been identified within *L. esculentum*. In particular, two recessive mutant genes, *hp1* (*high pigment 1*; [120]) and *hp2* [121], were identified a few decades ago and introgressed into several tomato cultivars [122–125]. The *hp* genes increase total fruit carotenoids, including β -carotene [126]. However, the adverse pleiotropic effects of these genes, such as slow germination and seedling growth, seedling mortality, inferior leaf coverage, brittle stems, low yield, reduced total acidity and SS contents, high sensitivity to various pathogens and premature defoliation, have prohibited widespread commercial use of these genes [127–129]. Efforts to reduce these negative effects have largely failed and thus, currently only a handful of “lycopene rich” tomato cultivars carrying *hp1* or *hp2* are used in production. In contrast, the crimson gene (*og^c*, *cr*), which increases fruit lycopene content at the expense of β -carotene [130–133], has been incorporated in many recent tomato genotypes, including breeding lines and cultivars developed at the University of Florida (<http://tombreeding.ifas.ufl.edu>) and North Carolina State University (<http://www.ces.ncsu.edu/fletcher/staff/rgardner>). Cultivars containing *og^c* on average contain 25% more lycopene than normal cultivars. However, recently other sources of high fruit lycopene content have been identified at the Pennsylvania State University, and some processing and fresh market lines with high lycopene content have been developed by Foolad et al. (unpubl.).

Other important fruit quality characteristics of tomato include pH, titratable acidity, fruit firmness, and vitamin contents. Acidity influences the storability of processed tomato. Lower pH reduces the risk of pathogen growth in tomato products by contributing to heat inactivation of thermophilic organisms [134]. Growth of *Bacillus coagulans*, the organism that causes flat sours in tomato products, was found to be completely inhibited by a pH below 4.1 [135]. Titratable acidity has no significant effect unless pH is low. For this reason, a pH below 4.5 and citric acid of above 0.35 g/100 g of fruit fresh weight are desirable. Toward this goal, efforts have been made in different processing tomato breeding programs and some progress has been made. Although tomatoes have intermediate levels of vitamins A and C, compared with other vegetables, they rank near the top for U.S. dietary intake of vitamin A and make an important contribution to intake of vitamin C [9]. This is because tomatoes are consumed in large quantities. Plant carotenoids, in particular β -carotene, a major carotenoid in orange-yellow tomatoes, are the primary sources of vitamin A in tomato. The identification of genes and utilization in breeding programs for improved tomato fruit vitamin content can have significant economic as well as nutritional impacts.

Another important consideration in fruit quality improvement in tomato is in regard to flavor. Flavor is a very complex trait that is affected by numerous genetic components and nongenetic factors, not all of which are known or well understood [136–138]. Taste and smell, texture, appearance, fruit temperature, and mouth feel are among many

factors that influence perception of flavor. However, a primary determinant of tomato flavor is the ratio of sugars to acids [112, 139]. High levels of SS are directly correlated with tomato-like flavor, and studies have suggested that tomato flavor can be improved by breeding for high SS and high acidity [108, 109]. Fructose and citric acid are more important to sweetness and sourness than glucose and malic acid, respectively, and pH is a better objective measure of tart taste than titratable acidity [140]. A single incomplete-dominant gene (*Fgr*) has been identified in *L. hirsutum* that increases the proportion of fructose over glucose, thus contributing to fruit sweetness [141]. Numerous aromatic volatile compounds play a major role in tomato fruit flavor, many of which are not known definitely [136–138, 142, 143]. However, from among over 400 aromatic volatiles in tomato fruit only 16 are of primary importance to flavor [144]. In addition, expression of flavor is subject to environmental variation, which hampers breeding progress [145]. Same tomato cultivars may exhibit different fruit quality characteristics under different conditions. Stage of ripeness at harvest also has significant effects on flavor [146]. Tomatoes harvested at later stages of ripeness usually are sweeter and have more “tomato-like” flavor than those harvested at “mature green” or “breaker” stage. Furthermore, environmental stresses during plant growth and fruit ripening may have positive or negative effects on fruit quality and flavor. High salinity in the growing media at certain stage of plant growth may improve tomato flavor though it may cause a reduction in fruit size [147, 148]. Flavor of fresh tomato can also be highly affected by post-harvest handling procedure and premarketing storage of the fruit [146, 149].

In summary, unlike the perception by many consumers who complain about deficiencies in the quality of modern tomatoes, fruit quality has been a major consideration in most tomato breeding programs during the past century [150]. The expectation that fresh tomatoes be harvested (usually “mature green”) and shipped thousands of kilometers during off seasons and still have a taste equivalent to a fully-mature fruit picked from the home garden may be more than the modern technology can provide [34]. In addition to varietal differences, the harvest and post-harvest procedures such as shipping and storage have significant effects on tomato quality as a whole and flavor more specifically. However, recently many tomato research programs have focused on the possibility of developing cultivars that can be harvested at later stages of maturity and yet can stand the handling necessary to transport them from the field to the market. Because stage of ripeness has so dramatic effects on fruit quality as a whole, for the past two decades significant amount of research has been devoted to better understanding of the ripening process in order to facilitate manipulation and development of cultivars with desirable fruit quality.

Fruit ripening

In most field production systems around the world, fresh market tomatoes are harvested at the “mature green” or “breaker” stage. This is mainly done to prevent post-harvest damage to fruit caused by various physical and biotic or

abiotic factors. Tomatoes are then allowed to ripen in storage before marketing. Such tomatoes naturally do not have the expected quality that consumers demand, certainly not the quality of home-grown vine-ripe tomatoes. In addition to the stage of ripeness, other factors that may positively or negatively affect quality attributes of fresh tomatoes include fruit firmness and shelf life. An approach to improve tomato fruit quality is to develop cultivars with extended shelf life so that tomato can be harvested at a later maturity stage [146]. However, to facilitate development of tomatoes with extended shelf life, a good understanding of the ripening process and the contributing genetic and physiological factors is necessary. During the past two decades, numerous studies have identified critical components involved in fruit ripening and softening in tomato [151–153]. The role of ethylene in initiation of ripening [154, 155] and the enzyme polygalacturonase (PG) in fruit softening [156, 157] have been well studied and characterized [152, 158]. Physiological and genetic studies have resulted in the identification and characterization of several ripening mutants such as *never ripe* (*Nr*), *nonripening* (*nor*), and *ripening inhibitor* (*rin*), genes of which are located on chromosomes 9, 10, and 5, respectively. While fruits of *Nr* mutant ripen slowly, fruits of *nor* and *rin* fail to ripen and do not exhibit any climacteric rise [158]. All three mutants show little or no activity of PG during ripening. Another ripening mutant of tomato originally found in a landrace of tomato (known as alcobaca) is *alc*, fruits of which exhibit prolonged keeping quality [159]. This mutant is controlled by a single gene (*alc*) located on the short arm of chromosome 10, about 20 cM apart from *u*, a gene conferring *uniform ripening* in tomato [160]. Traditional breeding has allowed utilization of *Nr*, *nor*, and *rin* genes and development of lines and cultivars with delayed ripening [161]. It has been determined that in most cases the use of these genes in homozygous conditions is worthless as the fruit does not ripen at all. Hybrids with ripening genes in heterozygous conditions, however, have been successful in providing for delayed ripening, longer shelf life, and increased firmness. To date, many commercial cultivars of tomato are available with these genes. Recent molecular techniques, however, have provided tools for better understanding of fruit ripening and softening in tomato and more precise mapping and cloning of related genes. Such techniques have also facilitated development of tomatoes with delayed fruit ripening, as discussed below.

Growth habit and machine harvestability

Tomato plants may have different growth habits, including determinate, semi-indeterminate, and indeterminate [30, 34]. The necessity for once-over harvest resulted in the development of machinery for mechanization of processing tomatoes in the late 1960s. The first machine-harvestable cultivar was developed by GC Hanna at the University of California, Davis; [30, 162, 163]. Since then, processing tomato cultivars with determinate growth habit, small vine size, concentrated flowering and fruit set, slow fruit maturing and softening, and high harvest index have been developed and released for commercial use. Currently, almost 100% of the processing

tomato production in the U.S. is mechanized, and almost all commercial cultivars are compact and highly determinate suitable for once-over machine harvest. Similarly, most of the fresh market tomato cultivars for field production are determinate, although with larger vine than processing types. The determinate growth habit in tomato was first reported by [164] and the gene *self-pruning* controlling it (*sp* = determinate) was first characterized by [165]. The *sp* gene was originally mapped onto the short arm of tomato chromosome 6 using a classical linkage map of tomato [28, 30] and later it was mapped to the same location on the tomato molecular linkage map [166, 167]. The introduction of the *sp* allele into processing tomato cultivars transformed the industry by creating a major modification in plant architecture. However, fruits of determinate type plants in all cultivar backgrounds tend to have less sugar than congenic indeterminate types [112]. Also, fruit yield and quality of determinate plants are often inferior to those of indeterminate plants [168]. Recently the *sp* gene was fine mapped, cloned, and physically characterized [169, 170].

Hybrid production

For a long time tomato breeding was mainly based on developing open-pollinated inbred cultivars and their use for commercial production. Since 1970s, however, major emphasis has been placed on production of F₁ hybrids. Currently in many tomato producing countries, including the U.S., Japan, and Europe, tomato production is mainly based on using hybrid cultivars. The use of hybrids in tomato is not so much due to the benefits of heterosis *per se*, but to factors such as protection of breeders' research investment, combining a complex of valuable attributes such as multiple disease resistance, and production of cultivars with ripening attenuating genes in heterozygous conditions [171, 172]. However, the presence of heterosis for many important traits in tomato has been reported (see [172] for a review). Currently, in the U.S. almost all commercial cultivars of fresh market (JW Scott, University of Florida, pers. commun.) and processing tomatoes (CJ Rivara, California Tomato Research Institute, Inc., pers. commun.; <http://www.ptab.org>) are hybrids.

1.7. Limitations of classical breeding and the need for new protocols

With the rapid increase in the size of human population, the world faces a greater demand for agricultural products than at any time in our history. Currently, the world human population is ~6.6 B and is expected to reach ~9.2 B by 2050 (<http://www.census.gov/ipc/www/popclockworld.html>). To prevent a major food security crisis in the world, it is estimated that food production in the developing countries will have to be doubled or tripled in the next 50 years (<http://www.who.int/en>). In order to achieve such levels of increase in food production, the contribution of plant breeding will have to be greater than in the past. This is due to limitations in nongenetic approaches to increase crop production, including shrinkage of natural resources

(e.g., fresh water and petroleum), lack of additional arable lands, and increased restrictions in the use of chemical fertilizers and pesticides. Thus, more efficient breeding strategies are needed to assure achieving the expected increase in food production.

Traditional protocols of plant genetics and breeding, which are based on phenotypic selection (PS) and progeny testing, have been very effective in improving crop productivity and quality during the past several decades [58, 59, 173]. These methods, however, are often times consuming and not without inherent difficulties. The average length of a breeding project for a seed or vegetable crop, from hybridization and selecting the new genetic combinations to testing them in the field and introducing them in the market, is ~10–15 years. This lengthy process may not allow the time-sensitive need to increase crop productivity in the future. Furthermore, for many desirable agronomic and horticultural characteristics, such as disease and pest resistance, abiotic stress tolerance and improved seed/fruit quality, controlling genes may be found only within exotic genetic backgrounds such as wild species. Utilization of genetic variability within wild species often encounters various difficulties. After interspecific hybridization, a major task becomes eliminating the great bulk of undesirable genes introduced from the wild donor. A series of backcrosses to the cultivated recurrent parent alternated with concurrent inbreeding are required before the desired combinations of parental characteristics can be selected. During this process, however, some of the genes of interest from the wild donor may be lost or eliminated, limiting the level of trait expression in the progeny. In addition, wide phenotypic differences between the cultivated and wild type parents present confounding factors during evaluation and selection procedures, reducing the effectiveness of phenotypic selection. These and other problems associated with the use of traditional breeding methods warrant for the employment of techniques that have higher resolution.

An alternative approach to improving selection efficiency is to discover genetic markers that are associated, through linkage or pleiotropy, with genes or QTLs that control the trait(s) of interest. The use of markers and maps can facilitate determination of the number, chromosomal location, and individual and interactive effects of genes or QTLs affecting desirable traits [174]. Following their identification, useful genes or QTLs can be introgressed into desirable genetic backgrounds via MAS [175] or isolated via chromosome walking and map-based cloning [176]. MAS may not only speed up the process of gene transfer, but it also may allow pyramiding of desirable genes and QTLs from different genetic backgrounds. This may be an effective complementary approach to substantial crop improvement, more than what potentially is feasible through PS alone. Furthermore, in tomato, where most genetic variability can be found within the wild species, identification of genes or QTLs and their transfer into the cultivated species can be significantly facilitated by MAS [177]. In the following sections, the current status of markers and maps development, gene and QTL mapping, and MAS breeding in tomato is reviewed and discussed.

2. GENETIC MARKERS AND MAPS

2.1. Classical genetic markers

By definition, any trait that is expressed in multiple forms and inherited in a simple Mendelian fashion can be considered and used as a genetic marker. The value of genetic markers as indirect selection criteria has been known to breeders since early 1900s. Sax [178] identified an association between seed size and seed coat pigmentation in *Phaseolus vulgaris*, and breeders have used morphological markers to select for superior phenotypes for many decades. The use of morphological markers in genetics and breeding research, however, is often associated with difficulties such as expression of dominance or epistatic interactions, pleiotropic effects, and incomplete penetrance and expressivity. In tomato, there are over 1300 morphological, physiological (e.g., male sterility, fruit ripening, fruit abscission), and disease resistance genes [39], of which only less than 400 have been mapped [179–181]. The second generation of genetic markers, isozymes, became popular during 1970s and early 1980s. In tomato, 41 isozymic genes corresponding to 15 unique enzymatic reactions have been characterized, of which 36 have been mapped onto the 12 tomato chromosomes [180, 182]. Despite their great advantages, isozyme markers are very limited in number and often are not polymorphic among closely-related genotypes [183, 184].

2.2. Classical genetic maps

The first “classical” linkage map of tomato, showing markers on all 12 linkage groups, was reported in 1968 and included a total of 153 morphological and physiological markers [185]. For the next several years, the map was expanded and by 1975 more than 258 morphological and physiological markers were assigned to tomato chromosomes [186]. At that time, tomato had one of the best linkage maps of any plant species. The classical map information in 1970s greatly facilitated the mapping of isozyme loci, which were accomplished by the use of standard methods of segregating filial and backcross progeny as well as the trisomic technique. The first complete isozyme linkage map of tomato was published in 1980, which included 19 mapped isozyme markers, 2 approximated to two chromosomes, and 5 remaining unmapped [187]. Currently, there are 36 known isozyme markers in tomato that have been mapped to different chromosomes [180, 182]. The latest published classical linkage map of tomato consists of ~400 morphological, physiological, isozyme, and disease resistance genes mapped onto the 12 tomato chromosomes [30, 180, 181].

2.3. Contemporary molecular markers

With the advent of DNA marker technology in 1980s [188] and early 1990s, many limitations associated with morphological and isozyme markers were overcome and genetic mapping entered a new exciting and progressive era with the promise to significantly enhance efficiency of plant genetics and breeding research. A DNA marker is typically derived from a small region of DNA that shows sequence

polymorphism between individuals within or between species. DNA markers, which are phenotypically neutral and literally unlimited in number, have allowed scanning of the whole genome and assigning landmarks in high density on every chromosome in many plant species, including tomato. During the past two decades, different types of molecular markers have been developed and evolved, including, but not limited to, restriction fragment length polymorphisms (RFLPs) [188], randomly amplified polymorphic DNAs (RAPDs) [189], amplified fragment length polymorphisms (AFLPs) [190], variable number of tandem repeats (VNTRs or minisatellites) [191], simple sequence repeats (SSRs or microsatellites) [192, 193], cleaved amplified polymorphic sequences (CAPS) [194], sequence characterized amplified regions (SCARs) [195], single-strand conformation polymorphisms (SSCPs) [196], expressed sequence tags (ESTs) [197], conserved ortholog sets (COS) [198], single-nucleotide polymorphisms (SNPs), and insertion deletions (InDels) [199].

Among crop species, tomato is very rich in the number of available molecular markers. Currently there are >1000 RFLP markers, most of which have been mapped onto the 12 tomato chromosomes, and ~214 000 ESTs (<http://compbio.dfci.harvard.edu/tgi/cgi-bin/tgi/gimain.pl?gudb=tomato>), of which only a small portion has been mapped onto tomato chromosomes (http://www.sgn.cornell.edu/cgi-bin/search/markers/cos_list.pl). The ESTs have been derived from over 23 cDNA libraries [8, 153] and their sequences are available on Solanaceae genome network (SGN; <http://www.sgn.cornell.edu>). The development and use of ESTs for various purposes in tomato are described elsewhere [8, 200, 201]; (<http://ted.bti.cornell.edu>). In addition to RFLPs and ESTs, several other molecular marker types, including SSRs [202–212], CAPS [207, 213, 214], RAPDs [166, 183, 215], SCARs [211], RGAs [216, 217], and AFLPs [210, 218] have been developed and mapped in tomato. At least 148 SSR markers and 77 CAPS have been mapped onto the high-density tomato genetic map [207]; (http://www.sgn.cornell.edu/cgi-bin/mapviewer/mapTop.pl?map_id=9).

Recently, the development and use of PCR-based markers have increased in tomato as these markers are generally more user friendly, cheaper, faster, and less labor intensive to develop compared with conventional DNA markers such as RFLPs and AFLPs [207, 213, 214, 219, 220]. However, a major issue in marker development in tomato is that most of the available DNA markers, including RFLPs and PCR-based markers, do not detect polymorphism within the cultivated species or between the cultivated species and closely related species such as *L. pimpinellifolium* [35, 183, 215, 221, 222]. This limited resolution restricts the use of markers in many tomato genetics and breeding programs that attempt to exploit intraspecific genetic variation or the variation within *L. pimpinellifolium*. Thus, most recently significant efforts have been devoted to the discovery of high-resolution genetic markers such as SNPs and InDels [201, 210, 223]. Such markers would allow detection of polymorphism among closely related individuals within species (e.g., between elite cultivars) or between *L. esculentum* and closely related species.

For example, [223] identified one SNP per 8,500 bases when they compared two elite tomato breeding lines for 44 genes. More efforts are currently being devoted to identifying SNP markers in tomato [224–226]; (<http://www.tomatomap.net>). In summary, like in other plant species, the number, variety, and availability of molecular markers in tomato are continuously changing, the latest record can be found at the SGN website (<http://solddb.cit.cornell.edu>).

2.4. Contemporary molecular maps

The first molecular linkage map of tomato was published in 1986, containing 18 isozyme and 94 DNA markers (mostly cDNA clones) [227]. However, the first high density molecular linkage map of tomato, comprising of 1030 markers, was published in 1992 [228]. This map, which was constructed based on 67 F₂ plants of an *L. esculentum* cv. VF36-*Tm2^a* × *L. pennellii* LA716 cross, also displayed the chromosomal locations of 100 genes of known function or phenotype, including morphological, isozyme, and DNA markers. The marker density in this map was approximately one per 1.2 cM. A more saturated version of this map was published in 1996, reducing the intermarker space to ≤1 cM [229]. The density of markers in this map has increased over the past decade. As of March 2007, the high-density molecular linkage map of tomato consists of 2,222 mapped molecular markers, including different types of markers with an average marker distance of <1 cM (http://www.sgn.cornell.edu/cview/map.pl?map_id=9). The average estimate for the total length of the tomato linkage map is ~1300 cM [217].

The haploid DNA content of the tomato genome is estimated to be approximately 950 Mbp (~0.95 pg/1C) [45]. This means that on average 1 cM genetic map distance in tomato equals approximately 750 kb. With the high-density molecular linkage map of tomato, it is likely that any gene of interest, if segregating in this (*L. esculentum* × *L. pennellii*) population, would be within one to a few map units of at least one molecular marker. However, many agriculturally important characteristics are not segregating in this population and many of the markers in this map are not polymorphic in other mapping populations of tomato. These limitations necessitated development of genetic maps based on other inter and intraspecific populations of tomato. Thus, during the past two decades several other molecular linkage maps of tomato have been constructed, mostly based on interspecific crosses between the cultivated and different wild species of tomato (see Table 1). Most of these maps have been developed based on RFLP markers from the 1992 high-density map, although some also used other markers such as RAPDs, ESTs, AFLPs, RAPDs, and resistance gene analogs (RGAs). Most of these maps are of low-to-moderate density, having an average intermarker spacing of around 5 cM and each includes between 70 and 400 markers (see Table 1). A typical molecular linkage map of tomato is displayed in Figure 1.

For some interspecific crosses, particularly those between the cultivated tomato and the closely related wild species *L. pimpinellifolium* and *L. cheesmannii*, identification of sufficient number of polymorphic markers has been

a serious limitation. For example, only about 30% of the RFLP markers in the high-density *L. esculentum* × *L. pennellii* map of tomato detected polymorphism in two different *L. esculentum* × *L. pimpinellifolium* crosses [166, 230]. Despite these limitations, to date molecular linkage maps have been developed based on interspecific crosses between *L. esculentum* and all related wild species of tomato, maybe except *L. chilense*. The latter species is only distantly related to the cultivated tomato and although it can be crossed with the cultivated species, difficult procedures such as embryo rescue or pollen mixture are needed. In addition, low fertility in the interspecific progeny may hinder development of populations suitable for genetic linkage mapping. This may demonstrate the difficulty of using this species in genetics and breeding studies, and lack of a complete linkage map based on an *L. esculentum* × *L. chilense* cross. The interspecific crosses based on which most linkage maps of tomato have been developed are those between the cultivated species and *L. pennellii* and *L. pimpinellifolium* (see Table 1).

To facilitate the use of molecular markers in tomato genetics and breeding research, some efforts have been made to develop linkage maps based on mainly PCR-based markers. One such effort resulted in the development of a map based on an F_2 population of a cross between *L. esculentum* LA925 (E6203) and *L. pennellii* LA716 using a set of 76 SSRs and 76 CAPS [207] (see Table 1). The 152 PCR-based anchor markers covers the tomato genome at intervals of ~20 cM and, according to the authors, can be readily used on standard agarose gel. Accordingly, an advantage of this map is that the majority of its markers also detect polymorphism between *L. esculentum* and wild species such as *L. pimpinellifolium*, so that PCR-based markers can be used for quick genetic mapping and MAS in other interspecific populations. Furthermore, the identified markers in this map may also be useful for germplasm fingerprinting and identification, taxonomy, and studies of species relationships [207]. Recently, the number of CAPS and SSR markers in this map has been significantly increased (http://www.sgn.cornell.edu/cview/map.pl?map_id=9). Another significant effort has been conversion of RFLP markers to more friendly PCR-based markers such as CAPS [207, 213, 214].

As alluded to previously, there is limited molecular marker polymorphism within the cultivated species of tomato [35, 183, 222]. This is consistent with an earlier report of the dearth of molecular genetic diversity within the cultivated species [244]. Due to this major limitation, most of the molecular linkage maps of tomato have been constructed based on interspecific crosses, in which polymorphism is rather abundant at the level of common molecular markers such as RFLPs. Such maps, however, may have limited utility in genetic studies or breeding programs that exploit genetic variation within the cultivated species. As such, the paucity of polymorphic genetic markers has prevented detailed study of many economically important traits in the cultivated species of tomato, in particular complex traits. To overcome this problem, some efforts have been made to identify other types of molecular markers (e.g., RAPDs, SSRs, AFLPs, and SNPs) with higher resolution to develop maps

based on intraspecific populations [183, 210, 215, 245]. In particular, a great deal of effort has been made to identify SNP markers, which detect a greater number of polymorphisms between elite cultivars [68, 201, 210, 223]. The growing tomato databases of DNA sequences, in particular the tomato ESTs, is providing useful information for developing more resolving genetic markers for genome mapping, fingerprinting, trait discovery, and marker-assisted breeding within the cultivated species of tomato. It is expected that the availability of such markers will be on the rise over the next several years.

2.5. Comparative markers, maps, and genomes

Much of the initial comparative mapping studies in plants were done with *Solanaceae* species, including comparisons across tomato, potato ($2n = 4x = 48$), pepper ($2n = 2x = 24$), eggplant ($2n = 2x = 24$), tobacco ($2n = 4x = 48$), and petunia ($2n = 2x = 14$). To date, detailed genetic maps are available for tomato, potato [246, 247]; (<http://potatodbase.dpw.wau.nl/uhddata.html>), pepper [248], and eggplant [249–251]. Molecular maps also have been developed for petunia [252, 253] and tobacco [254]. Although the *Solanaceae* species are phenotypically diverse, their genomes are highly conserved. Comparisons across species have indicated that *Solanaceae* genomes have undergone relatively few genome rearrangements and duplications, and have very similar gene content and order.

Comparative genomics in *Solanaceae* was initiated by two studies comparing the genetic maps of tomato and potato [255] and tomato and pepper [256]. These and further studies indicated that the genomes of tomato and potato differed by only five chromosomal rearrangements, each of which involved a single break at or near a centromere resulting in paracentric inversions of the short arms of chromosomes 5, 9, 11, and 12 and of the long arm of chromosome 10 [228, 255, 257]. Such findings reinforced the high propensity (or tolerance) of plants for intrachromosomal rearrangements. The genomes of tomato and pepper, in contrast, are more extensively rearranged. There are ~30 chromosome breaks, including translocations, inversions (both paracentric and pericentric), disassociations or associations of genomic regions, since their divergence from a common ancestor [258, 259]. Hybridization of all examined tomato probes to positions throughout the pepper map led [258] to suggest that no major losses occurred during the divergence of the two species. The authors further reported overwhelming conservation of marker order and large orthologous linkage blocks between tomato and pepper. However, a more recent study has indicated a greater complexity in the correspondence between tomato and pepper genomes and has shown the presence of additional smaller random interruptions in synteny between the tomato and pepper [248]. The overall lengths of the tomato and pepper genetic maps are very similar [248, 258], though the DNA content of pepper is at least 2-fold greater than that of tomato [45].

A comparison of the eggplant and tomato maps revealed conservation of large tracts of collinear markers [249], similar to that observed in potato and pepper. Accordingly,

TABLE 1: Genetic linkage maps of tomato (*Lycopersicon* spp.) developed based on different intra- and interspecific crosses.

Linkage map	Population type ^(a)	Population size	Number of markers	Type of markers ^(b)	Reference
<i>L. esculentum</i> × <i>L. esculentum</i> var. <i>cerasif.</i>					
1. Cervil × Levovil	F ₇ -RIL	153	377	RFLP, RAPD, AFLP	[215]
<i>L. esculentum</i> × <i>L. pimpinellifolium</i>					
1. M82-1-7 × LA1589	BC ₁	257	120	RFLP, RAPD, morphological	[166]
2. NC84173 × LA722	BC ₁	119	151	RFLP	[230]
3. Giant Heirloom × LA1589	F ₂	200	90	RFLP, CAPS	[40]
4. E6203 × LA1589	BC ₂ F ₆ -BIL	196	127	RFLP	[231]
5. NC84173 × LA722	F ₁₀ RIL	119	191	RFLP, RGA	Foolad et al. (unpubl.)
6. NCEBR1 × PSLP125	F ₂	172	256	RFLP, EST, RGA	Foolad et al. (unpubl.)
7. NCEBR1 × PSLP125	F ₈ -RIL	172	255	RFLP, EST	Foolad et al. (unpubl.)
<i>L. esculentum</i> × <i>L. cheesmanii</i>					
1. UC204B × LA483	F ₂	350	71	RFLP	[232]
2. UC204B × LA483	F ₇ -RIL	97	132	RFLP	[233]
<i>L. esculentum</i> × <i>L. parviflorum</i>					
1. E6203 × LA2133	BC ₂	170	133	RFLP, SCAR, morphological	[234]
<i>L. esculentum</i> × <i>L. chmielewskii</i>					
1. UC82B × LA1028	BC ₁	237	70	RFLP, Isozyme	[167]
<i>L. esculentum</i> × <i>L. hirsutum</i>					
1. E6203 × LA1777	BC ₁	149	135	RFLP	[235]
2. E6203 × LA1777	NIL, BIL	111	95	RFLP	[236]
3. NC84173 × PI126445	BC ₁	145	171	RFLP, RGA	[217]
<i>L. esculentum</i> × <i>L. pennellii</i>					
1. VF36 <i>Tm2</i> ^(a) × LA716 (high-density map of tomato)	F ₂	67	1050	Isozyme, RFLP, morphological	[228, 229]
2. Vendor <i>Tm2</i> ^(a) × LA716	F ₂	432	98		[237]
3. M82 × LA716	IL	50	375	RFLP	[238]
4. VF36 <i>Tm2</i> ^(a) × LA716	F ₂	67	1242	AFLP, RFLP	[218]
5. E6203 (LA925) × LA716	F ₂	83	1500	COS	[198]
6. E6203 × LA1657	BC ₂	175	110	RFLP	[239]
7. E6203 × LA716	F ₂	83	152	SSRs, CAPs	[207]
<i>L. esculentum</i> × <i>L. peruvianum</i>					
1. E6203 × LA1706	BC ₃	241	177	RFLP, SCAR	[240]
<i>L. esculentum</i> var. <i>cerasif.</i> × <i>L. pimpinellifolium</i>					
1. E9 × L5	F ₆ -RIL	142	132	SSR, SCAR	[211]
<i>L. esculentum</i> var. <i>cerasif.</i> × <i>L. cheesmanii</i>					
1. E9 × L3	F ₆ -RIL	115	114	SSR, SCAR	[211]
<i>L. peruvianum</i> × <i>L. peruvianum</i>					
1. LA2157 × LA2172	BC ₁	152	73	RFLP	[241]

^(a) RIL: recombinant inbred line; NIL: near isogenic line; BIL: backcross inbred line.

^(b) RFLP: restriction fragment length polymorphism; RAPD: randomly amplified polymorphic DNA; AFLP: amplified fragment length polymorphism; CAPS: cleaved amplified polymorphic sequence; RGA: resistance gene analog; EST: expressed sequence tag; SCAR: sequence characterized amplified region; SSR: simple sequence repeat.

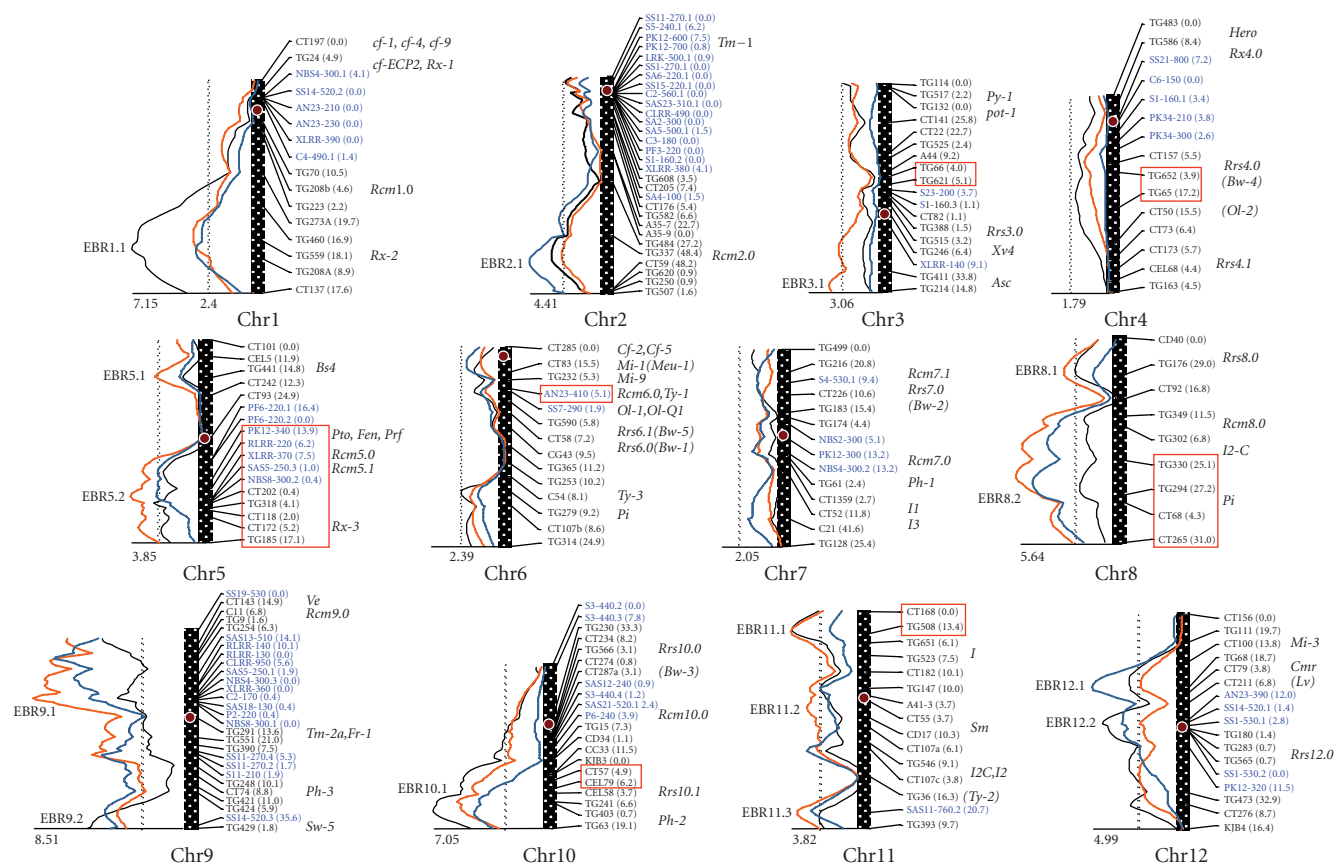


FIGURE 1: A linkage map of the 12 tomato chromosomes constructed based on a BC₁ population of a cross between *L. esculentum* breeding line NC84173 and *L. hirsutum* accession PI126445; the framework map was adapted from [217], however, recently more markers were added to the map. The names of the markers and map distances between them are shown at the right of the chromosomes. The map includes 141 RFLP markers (black color) and 73 resistance gene analogs (RGAs; blue color). The LOD plots at the left of the chromosomes indicate the most likely positions of QTLs for early blight resistance as identified in the BC₁ (black curves), BC₁S₁-1999 (red curves) and BC₁S₁-2000 (blue curves) populations, as adapted from [242]. The dotted black vertical lines indicates a LOD value of 2.4, a threshold value that the LOD score must cross to allow the presence of a QTL to be inferred. The highest LOD score obtained for each chromosome is shown on the Y-axis. Markers denoted in boxes indicate the approximate locations of QTLs detected for early blight resistance in a selective genotyping study [243]. The approximate locations of disease-resistance genes (R genes) and QTLs (Q), as inferred from published research, are shown at the right of the chromosomes. Descriptions of the R genes and QTLs are as displayed in Table 2.

eggplant and tomato were differentiated by 28 rearrangements, including 23 paracentric inversions and five translocations, during their evolution from the species' last common ancestor. The eggplant nuclear genome is slightly larger than that of tomato and contains 1100 Mb of DNA (1.2 pg/1C) [45]. As judged based on genome comparisons across tomato, potato, pepper, and eggplant, it seems that the primary mechanism for chromosome evolution in *Solanaceae* has been paracentric inversion [249]. Furthermore, a recent comparative genome (sequence) analysis of seven *Solanaceae* species, including tomato, potato, pepper, eggplant, petunia, tobacco, and *Nicotiana benthamiana*, confirmed a high degree of sequence conservation [260]. The same study, however, also identified some species-specific sequences suggesting divergence within *Solanaceae* genomes.

A few studies have compared tomato genome with other plant species, including *Arabidopsis* [8, 198, 261, 262] and coffee [263]. Seemingly, there is conservation of gene con-

tent and order between tomato and *Arabidopsis* since their divergence from a common ancestor ~112 million years ago. A comparison of over 27 000 unigenes (unique consensus sequences) revealed that 70% of the unigenes have identifiable homologs in the *Arabidopsis* genome [8]. Furthermore, of the 10 largest conserved multigene families, a majority shares similar copy number in tomato and *Arabidopsis* suggesting that multiplicity of these families may have occurred before their divergence. An exception was observed for the E8-likr protein family, which is associated with fruit ripening and has higher copy number in tomato than *Arabidopsis*. Moreover, genes related to metabolism have remained most conserved whereas those encoding transcription factors are among the fastest evolving. When comparing gene repertoires of tomato and coffee, it appeared that tomato had a perfect gene-for-gene match with coffee [263]. This was not surprising as the two species have similar genome size and chromosome karyotype (coffee $n = 11$) and architecture.

Although from different families (coffee family *Rubiaceae*), both coffee and tomato belong to the Asterid I clade of dicot families. Further information on comparative genomics of tomato can be found elsewhere [6, 264–267].

3. MAPPING GENES AND QTLs

Tagging and mapping of single-gene traits in tomato, including many morphological, physiological, and disease resistance traits, started in 1930s [268], much earlier than in many other crop species. Tagging of single-gene traits with molecular/biochemical markers started in 1970s. [110] reported an association of root-knot nematode (*Meloidogyne incognita*) resistance with a rare form of isozyme acid phosphatase locus, *Aps-1^l*. Later on this association was determined to be due to a tight linkage between the gene controlling nematode resistance in tomato, *Mi* [269], and the *Aps* locus on chromosome 6 [270]. Subsequently, linkages were reported between isozyme markers and genes controlling a few other important traits in tomato, including male-sterility [271] and self incompatibility [272]. Since then, tagging of many other simply inherited traits with molecular markers has been reported and currently linked markers are available for many agriculturally and biologically important traits in tomato.

The use of genetic markers to identify QTLs controlling complex traits in tomato started in the 1980s. Earlier studies mainly used morphological and isozyme markers and filial (e.g., F_2) or backcross (e.g., BC_1) populations to identify QTLs for different quantitative traits, including leaf ratio, stigma exertion, fruit weight, seed weight, internode length, number of nodes, number of flowers, stem width, plant size, plant height, and cold tolerance [273–276]. However, the first comprehensive and systematic analysis of the use of molecular markers to dissect genetic controls of complex traits and to identify underlying QTLs was that of [167]. In this study, a rather complete RFLP linkage map of tomato was used to identify and map QTLs for fruit quality characteristics, including fruit size, pH, and soluble solids content. This study demonstrated for the first time that quantitative traits could be resolved into discrete Mendelian factors. Subsequently, QTL mapping became very popular in tomato genetics and breeding research, where QTLs have been identified for numerous agriculturally and biologically important complex traits. Practically, it is difficult to provide a complete account of all genes and QTLs that have been identified and/or mapped in tomato chromosomes. Rather in this article a tabulated summary of most genes and QTLs which have been identified and mapped in tomato chromosomes during the past two decades is presented (see Tables 2, 3, 4, and 5). Furthermore, a summary discussion of the populations used for mapping as well as mapped genes and QTLs for certain important traits in tomato is provided below.

3.1. Populations used for mapping

As alluded to earlier, because of limited DNA polymorphism within the cultivated species of tomato, most mapping populations have been based on interspecific crosses between the

cultivated tomato and related wild species. In fact, almost all wild species of tomato have been used for gene and/or QTL mapping, although with different frequencies. For example, while *L. pennellii*, *L. pimpinellifolium*, and *L. hirsutum* have been used extensively, wild species *L. chilense* and *L. peruvianum* have been used infrequently and mainly for mapping of a few major disease resistance genes (see Tables 2, 3, 4, and 5). Reasons for this discrepancy include difficulties normally encountered when using *L. chilense* or *L. peruvianum* to develop mapping populations. For example, in addition to problems in making original crosses and developing F_1 hybrids, low fertility and presence of excessive undesirable variation in early filial or backcross populations exacerbate the difficulties. Although *L. pennellii* is also distantly related to the cultivated tomato, the presence of a self-compatible accession (LA716), which was originally used to develop the first molecular linkage map and the high-density molecular map of tomato (see Table 1), facilitated frequent use of *L. esculentum* \times *L. pennellii*-derived populations for gene mapping and QTL identification. On the other hand, crosses with *L. pimpinellifolium* have been used frequently for mapping experiments mainly because of its close phylogenetic relationship with the cultivated tomato, the ease of crosses and handling of segregating populations and its red-fruited characteristic [230].

As to the types of populations, early filial (e.g., F_2 and F_3) and backcross populations (e.g., BC_1 and BC_2) have been used more often than advanced populations for genetic mapping (see Tables 2, 3, 4, and 5). While early segregating populations have the advantages of easiness of development and presence of high linkage disequilibrium, they often have several disadvantages including: (1) limitations in trait evaluation (e.g., in F_2 and BC_1 evaluation is based on individual plant performance that may not be repeatable), (2) detection of loose marker-QTL association due to high levels of linkage disequilibrium, (3) presence of excessive genetic variation when using wide crosses (which may negatively affect the accuracy of detecting and mapping of genes and QTLs), (4) instability due to changes in their genetic constitutions from generation to generation, and (5) not immediately applicable for breeding purposes (see below). To avoid such problems, some more stable segregating populations such as recombinant inbred lines (RILs), advanced backcross populations (AB; e.g., BC_2 and BC_3), backcross inbred lines (BILs, a.k.a. inbred backcross lines or IBC, e.g., BC_2S_3 , BC_3S_2), and introgression lines (ILs) have been developed and used for gene and QTL mapping in tomato, as described below.

The use of RILs in genetic mapping has several advantages, including the possibility of having multiple replications for trait evaluation, repetition of experiments in different years and locations and by different researchers, evaluation of the population for multiple traits in different environments, and detection of mainly tightly linked QTLs (due to low linkage disequilibrium). In tomato, currently there are a few RI populations available, including one based on an *L. esculentum* \times *L. cheesmanii* cross [233] and three based on different *L. esculentum* \times *L. pimpinellifolium* crosses [277, 278]; Foolad et al. (unpubl.). Although RI populations are valuable resources for genetics and mapping studies, there are

several disadvantages in using them, including the long time it takes to develop them, potential difficulties in developing RILs when using interspecific crosses (e.g., sterility or self-incompatibility problems), large genetic diversity among RI lines and presence of large genomic contributions from the wild species (on average 50%), which may cause difficulties with evaluation of certain traits. In tomato, RI populations have been used for mapping QTLs for various characteristics, including fruit weight and SS [279], several morphological traits [280], abiotic stress tolerance [281], seed weight [279] and disease resistance and fruit quality [282]; Foolad et al. (unpubl.).

In comparison to RILs, AB populations and BILs may be more desirable for QTL mapping in self-pollinated crops, in particular when using interspecific crosses [283–285]. Such populations have much smaller genome contributions from the wild donor parent compared to RILs, providing more uniform genetic backgrounds for trait evaluation. These populations are particularly useful for studying the effect of exotic alleles on the agronomic performance of elite cultivated lines [285]. Furthermore, high levels of homozygosity in these populations would allow family/line evaluations over locations and years, an advantage similar to that for RI populations. If properly developed (i.e., having a good coverage of the donor parent in the background of the cultivated recurrent parent), BILs can provide accurate identification and characterization of genes or QTLs. Moreover, such populations can simultaneously be used as breeding materials for crop improvement, a great advantage over other types of mapping populations [283]. During the past several years, BILs have been used frequently for mapping QTLs for many traits in tomato (see Tables 2, 3, 4, and 5), including fruit quality [68, 231, 240, 283, 286] and disease resistance [242, 287–289]. In general, higher levels of homozygosity in RI and BI populations, as compared to early segregating populations, allow more precise estimation of the locations and effects of QTLs.

Another population type that has been developed and extensively used for gene and QTL mapping in tomato is introgression lines (ILs). In comparison, whereas each BIL may contain several chromosomal segments from the wild donor parent in an otherwise *L. esculentum* genetic background, each IL technically contains only a single introgression from a wild species. In other words, ILs are near isogenics to the original *L. esculentum* recurrent parent. Such permanent mapping populations, which are considered as genetic libraries, are a powerful tool for various studies, including placing new markers on tomato chromosomes, identification of region-specific DNA markers, and discovery and characterization of genes or QTLs underlying important qualitative and quantitative characteristics [290]. The first developed IL population of tomato consisted of 50 lines, each containing a single introgression from *L. pennellii* LA716 in the background of processing tomato cultivar M-82 [238, 291, 292]. Since 1995, however, the number of ILs in this population has increased to 76, which totally represent the entire genome of *L. pennellii* LA716 in homozygous or heterozygous conditions. This IL population delimits 107 marker-defined mapping bins, each bin having an average length of 12 cM [293–

295]. In addition to this IL population, a total of 99 NILs and BILs derived from a cross between processing tomato cultivar E6203 and a single plant of *L. hirsutum* accession LA1777 have been developed [236]. In this population, most of the lines contain a single-defined introgression from the *L. hirsutum* parent in the *L. esculentum* genetic background, and together the lines provide a coverage of more than 85% of the genome of the LA1777 plant used as the donor parent (note that LA1777 is not an inbred accession and thus the plant used for developing this population does not represent the total variation within LA1777). More recently, an IL population containing introgressions from *S. lycopersicoides* in the background of *L. esculentum* has been developed [296].

The permanent mapping populations have been used for identification and mapping of genes and QTLs for many important tomato traits (see Tables 2 and 4; <http://zamir.sgn.cornell.edu>), including fruit weight, shape, SS content, pH and yield [236, 238, 290, 297, 298], carotenoid content in relation to fruit color [294, 299], antioxidants [300], and disease resistance [282]. The mapping power of ILs is generally greater than traditional QTL mapping populations and as a result often larger number of QTLs is detected by such populations [238]. Furthermore, although ILs are mainly used for low-resolution mapping, they also can be used for high-resolution mapping by developing F₂ populations of crosses between targeted ILs and the recurrent parent. Using this strategy, ILs have been used to develop NILs for fine-mapping and map-based cloning of several genes and QTLs controlling various traits, including *self pruning* [170], color mutants [299, 301], fruit soluble solids content [98, 302–304], fruit weight [305], fruit shape [304, 306], stigma exertion [307], and a few other traits as shown in Table 7. Moreover, the IL populations can be used for MAS pyramiding of important QTLs, as it has been done in case of tomato yield and soluble solids QTLs [308].

The use of BILs and ILs also allows development of NILs for particular genes, QTLs or segments of a chromosome, which can be used for further analyses such as validation of individual effects of QTLs in uniform *L. esculentum* background, marker-assisted transferring of individual or combination of QTLs to different genetic backgrounds, determination of the presence and nature of association (linkage or pleiotropy) between different traits, determination of QTL × QTL, QTL × genetic background and QTL × environment interactions, and fine-mapping and possible cloning and characterization of underlying genes or QTLs. To date, NILs have been developed for QTLs controlling many important traits in tomato, including various disease resistance and fruit quality characters (see Tables 2, 4, and 7).

3.2. Disease resistance genes and QTLs

In tomato, mapping disease resistance genes and QTLs has been the focus of many mapping activities. Identification of genetic markers associated with disease resistance in tomato started in 1970s with the pioneering work of Charles M. Rick and his co-workers who identified an association between root-knot nematode resistance and a form of isozyme acid phosphatase, *Aps-1^l* [372]. At the time, resistance to

TABLE 2: Summary of disease (fungal, bacterial, viral, and nematode) and insect resistance genes and QTLs (Q) mapped on tomato chromosomes.

Disease	Gene/QTL	Pathogen	Resistance source	Mapping population	Chromosomal location	References
Alternaria stem canker	<i>Asc</i>	<i>Alternaria alternata</i> f. sp. <i>lycopersici</i>	<i>L. pennellii</i>	F ₂	3	[309, 310]
Anthracnose ripe rot	<i>Anthracnose</i> (Q)	<i>Colletotrichum coccodes</i>	<i>L. esculentum</i>	F ₂	Various Chromosomes	[67]
Aphid (potato)	<i>Meu-1</i>	<i>Macrosiphum euphorbiae</i>	<i>L. peruvianum</i>	NIL F ₂	6	[38, 311, 312]
Bacterial canker	<i>Rcm 1.0–10.0</i> (Q)	<i>Calvibacter michiganensis</i> ssp. <i>michiganensis</i>	<i>L. peruvianum</i>	BC ₁	1,6,7,8,9,10	[313]
	<i>Rcm5.0, Rcm7.1, Rcm9.0</i> (Q)	<i>Calvibacter michiganensis</i> ssp. <i>michiganensis</i>	<i>L. peruvianum</i>	F ₂	5,7,9	[314]
	<i>Rcm2.0, Rcm5.1</i> (Q)	<i>Calvibacter michiganensis</i> ssp. <i>michiganensis</i>	<i>L. hirsutum</i>	BC ₂ S ₅	2,5	[287, 315]
Bacterial speck	<i>Pto</i>	<i>Pseudomonas syringae</i> pv. <i>Tomato</i> (<i>Pst</i>)	<i>L. pimpinellifolium</i>	NIL F ₂	5	[57, 316]
	<i>Prf</i>	Required for resistance to <i>Pst</i>	<i>L. pimpinellifolium</i>	NIL F ₂	5	[317]
Bacterial spot	<i>Rx-1, Rx-2, Rx-3, Rx-4</i> (Q) <i>Bs4, Xv4</i>	<i>Xanthomonas euvesicatoria</i> , <i>X. vesicatoria</i> , <i>X. perforans</i> , <i>X. gardneri</i>	<i>L. esculentum</i> <i>L. pennellii</i>	BC ₁ , F ₂ , BC ₃	1,3,4,5	[68, 69, 318, 319]
Bacterial wilt	<i>Rrs 3.0–12.0</i> (Q)	<i>Ralstonia solanacearum</i>	<i>L. pimpinellifolium</i> <i>L. peruvianum</i>	F ₂ , F ₃	3,4,6,7,10	[320–324]
Blackmold	<i>Blackmold</i> (Q)	<i>Alternaria alternata</i>	<i>L. cheesmanii</i>		2,3,9,12	[288]
Corky root rot	<i>Py-1</i>	<i>Pyrenochaeta lycopersici</i>	<i>L. peruvianum</i>	NIL F ₂	3	[325]
Cucumber mosaic virus	<i>Cmr</i>	CMV	<i>L. chilense</i>	BC ₁ -inbred	12	[326]
Early blight	<i>11</i> (Q)	<i>Alternaria solani</i>	<i>L. hirsutum</i>	BC ₁	1,2,5,8,9,10,11,12	[242]
	<i>13</i> (Q)	<i>Alternaria solani</i>	<i>L. hirsutum</i>	BC ₁ S ₁	1,2,3,5,8,9,10,11,12	[242]
	<i>7</i> (Q)	<i>Alternaria solani</i>	<i>L. hirsutum</i>	BC ₁	1,2,3,5,8,9,10,11,12	[243]
	<i>7</i> (Q)	<i>Alternaria solani</i>	<i>L. pimpinellifolium</i>	RILs	1,3,4,5,6,9,11	Foolad et al. (unpubl.)
Fusarium crown and root rot	<i>Frl</i>	<i>Fusarium oxysporum</i> f. sp. <i>radidicis-lycopersici</i>	<i>L. peruvianum</i>	F ₂	9	[327]
Fusarium wilt	<i>I, I1, I2, I2C, I3</i>	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	<i>L. pimpinellifolium</i> <i>L. pennellii</i>	Different populations	7,8,11	[328–336]
Gray leaf spot	<i>Sm</i>	<i>Stemphylium</i> spp.	<i>L. pimpinellifolium</i>	F ₂	11	[337]
Late blight	<i>Ph-1, Ph-2, Ph-3</i>	<i>Phytophthora infestans</i>	<i>L. pimpinellifolium</i>		7,9,10	[338–340]
	<i>lb1-lb12</i> (Q)	<i>Phytophthora infestans</i>	<i>L. hirsutum</i> <i>L. pimpinellifolium</i>		All 12 Chromosomes	[341–343]
Leaf mould	<i>Cf-1, Cf-2, Cf-4, Cf-5, Cf-9, Cf-ECP2</i>	<i>Cladosporium fulvum</i>	<i>L. hirsutum</i> <i>L. pimpinellifolium</i>	F ₂ , NIL F ₂ , BC ₁	1,6	[218, 344–347]
Nematode (potato cyst)	<i>Hero</i>	<i>Globodera restochiensis</i>	<i>L. pimpinellifolium</i>	NIL F ₂	4	[348]
Nematode (root knot)	<i>Mi, Mi-1, Mi-2, Mi-3, Mi-9</i>	<i>Meloidogyne</i> spp.	<i>L. peruvianum</i>	F ₂ , F ₃ , NIL F ₂ , BC ₁ , BC ₂	6,12	[312, 349–355]

TABLE 2: Continued.

Disease	Gene/QTL	Pathogen	Resistance source	Mapping population	Chromosomal location	References
Potyriviruses	<i>pot-1</i>	Potyriviruses	<i>L. hirsutum</i>	ILs	3	[356]
	<i>Lv</i>	<i>Leveillula taurica</i>	<i>L. chilense</i>	F ₂	12	[357]
Powdery mildew	<i>Ol-1, Ol-2</i>	<i>Oidium lycopersicum</i>	<i>L. esculentum</i> <i>L. hirsutum</i>	F ₂	4,6	[219, 358, 359]
	<i>Ol (Q)-1, Ol (Q)-2, Ol (Q)-3</i>	<i>Oidium lycopersicum</i>	<i>L. parviflorum</i>	F ₂	6,12	[360]
Tobacco mosaic virus	<i>Tm-1, Tm-2</i> ^(a)	TMV/ToMV	<i>L. hirsutum</i> <i>L. peruvianum</i>	F ₂ , NILs	2,9	[327, 361–364]
Tomato mottle virus	One Gene	ToMoV	<i>L. chilense</i>	F ₂	6	[365]
Tomato spotted wilt virus	<i>Sw-5</i>	TSWV	<i>L. peruvianum</i>	NILs, F ₂	9	[366]
Tomato yellow leaf curl virus	<i>Ty-1 (Q), two other Q</i>	TYLCV	<i>L. esculentum</i> <i>L. chilense</i> <i>L. pimpinellifolium</i> <i>L. hirsutum</i>	BILs, F ₂ , F ₃ , F ₄	6,11	[289, 367, 368]
	<i>Ty-2</i>	TYLCV	<i>L. hirsutum</i>	F ₆ RILs	11	[369]
	<i>Ty-3</i>	TYLCV	<i>L. chilense</i>	F ₂ NILs	6	[370]
Verticillium wilt	<i>Ve</i>	<i>Verticillium dahliae</i>	<i>L.cheesmanii</i> <i>L. esculentum</i> <i>L. pennellii</i>	F ₂ , RILs, ILs	9	[282, 371]

root-knot nematodes was known to be genetically inherited and controlled by a single dominant gene, known as *Mi*, located on the long arm of chromosome 6 [373]. Since 1970s, however, genetic markers, in particular DNA markers, have been used extensively to tag or map major genes for vertical (a.k.a. race-specific) resistance and QTLs for horizontal (a.k.a. field or race-nonspecific) resistance to many fungal, bacterial, viral, and nematode diseases in tomato. In Table 2, all known mapped disease resistance genes and QTLs in tomato together with information on gene/QTL symbols, the causal agents of the diseases (pathogens), genetic source(s) of the resistance, chromosomal locations of the resistance genes/QTLs and the cited references are displayed. The space limitation in this review article does not allow for discussion of procedures or methodologies used for mapping of genes or QTLs for resistance to different diseases. However, not withstanding that the procedures and methodologies used for different diseases vary, some general comments can be made as to the mapping of resistance genes and QTLs as follows.

(1) With some exceptions (e.g., [64–69, 374, 375]), most genes and QTLs for disease resistance have been identified in the related wild species of tomato and mapped using inter-specific segregating populations (see Table 2).

(2) For some diseases, often multiple gene resources have been employed to identify and map resistance genes and QTLs. The identification of multiple resistance genes/QTLs for each disease may provide the opportunity to pyramid resistance in selected lines and cultivars using a MAS approach.

(3) For most field (horizontal) resistance traits, often multiple QTLs have been identified in each study. In many cases, it has been difficult to determine the precise location or actual effect or importance of each QTL in the original studies. Many studies have suggested development of NILs and sub-NILs to obtain such necessary information.

(4) In most cases, early filial and backcross populations, such as F₂ and BC₁, have been used for mapping. More recently, however, advanced segregating populations such as RILs, BILs, and ILs have been utilized (see Table 2). Such populations have provided better mapping resolution.

Knowledge of the linkage between molecular markers and resistance genes or QTLs can facilitate an effective, and in some cases rapid, transfer of resistance to various tomato genetic backgrounds through MAS. As described below, MAS has been employed for disease resistance breeding in tomato, in particular by many seed companies. In fact, the utility of MAS for disease resistance breeding has superseded its utility for any other trait in tomato breeding.

3.3. Insect resistance genes and QTLs

There are fewer reports of genes or QTLs identified for insect resistance in tomato than those for disease resistance. It is generally very challenging to set up controlled experiments on insect resistance to identify underlying genetic factors. However, over the years some research has been conducted toward this goal. Much of the insect resistance

mapping experiments in tomato have been conducted using *L. pennellii* accession LA716 as a resistance parent. The multiple pest resistance of this accession is mediated by acylsugars exuded by type-IV glandular trichomes on the leaf surface of these plants [73]. The acylsugars act as feeding deterrents for tomato pests, including potato aphid, green peach aphid, tomato fruitworm, and beet armyworm, as feeding and oviposition deterrents for the leafminer and silverleaf whitefly. In one study, an F₂ population of an *L. esculentum* × *L. pennellii* (LA716) was surveyed for acylsugar accumulation, and a total of five QTLs were detected on *L. pennellii* chromosomes 2, 3, 4, and 11 with association with one or more aspects of acylsugar production [73]. In a follow-up study, attempts were made to transfer these QTLs via MAS to an *L. esculentum* genetic background [376]. However, resulting BC₃ progeny plants with complementary subsets of 3–5 QTLs were found to accumulate only low levels of acylsugars, prompting the authors to speculate presence of other yet unidentified genetic factors controlling acylsugar accumulation. Furthermore, the derived lines exhibited high levels of linkage drag. This research clearly demonstrated the complexity of the trait and difficulties in developing tomato plants with improved insect resistance. In another study, an F₂ population of an intraspecific cross between two *L. pennellii* accessions (LA716 and LA1912) was employed to study the genetic basis of acylsugar fatty acid composition [377]. A total of six QTLs were detected which together could explain 23–60% of the variation for each of nine fatty acid constituents. These QTLs were different from those which had been detected in an *L. esculentum* × *L. pennellii* F₂ population [73], further suggesting complexity of the genetic control of acylsugar production [377].

Based on most research reports, specific insect resistance genes often confer resistance to only one insect species or to a closely related species within the same genus. However, the *Mi* gene, which originally was identified as a dominant gene for resistance to a root-knot nematode [269] is an interesting exception. After the *Mi* gene had been cloned [312, 388] it was determined that it was the same locus as *Meu1*, which confers resistance to the potato aphid, *Macrosiphum euphorbiae* [38]. Currently, *Meu1* (*Mi*) is the only insect resistance gene that has been cloned from a plant species. This gene is a member of leucine zipper, nucleotide binding, leucine-rich repeat family of plant resistance genes [389], many members of which have been found to confer isolate-specific resistance to viruses, bacteria, fungi, and nematodes [390]. However, the *Mi* gene is the first example of a plant resistance gene active against two such distantly related organisms belonging to different phyla. A later study revealed that several isolates of potato aphid and green peach aphid (*Myzus persicae*) can overcome the resistance mediated by *Mi* (*Meu1*), limiting the use of this gene for aphid control in tomato [391]. In a more recent study, two tomato BI populations, derived from crosses between two different aphid susceptible *L. esculentum* lines and two aphid resistant accessions of *L. pennellii* and *L. hirsutum*, were evaluated for resistance to both potato aphid and green peach aphid [80]. Field screening over two years resulted in the identification of seven BILs (BC₂S₃ to

BC₂S₆) with resistance to both types of aphid. These BILs can be useful for breeding tomatoes for aphid resistance using PS and/or MAS.

In conclusion, unlike in the case of disease resistance, there has been rather limited research progress in identification, mapping or transfer of genes/QTLs for insect resistance in tomato. Although there are several reasons for these shortcomings, difficulties in phenotypic screening for insect resistance, problems with linkage drag, and the ease of insect control by pesticides are probably the main ones. However, with the increasing restrictions on the use of pesticides and the advancements in marker development, it is expected that more research will be devoted to the identification and use of makers for insect resistance breeding in tomato.

3.4. Abiotic stress resistance genes and QTLs

In most crop species, traditional breeding protocols for improved abiotic stress resistance/tolerance has been generally unrewarding mainly due to the very complex nature of such traits. Thus, identification of genetic markers that are associated with tolerance traits and their use in marker-assisted breeding is regarded a promising approach. The challenge is to improve the efficiency of selection for stress tolerance by integrating marker technology with the conventional protocols of plant genetics and breeding [81]. In tomato, while significant efforts have been devoted to the identification and mapping of QTLs conferring tolerance to environmental stresses such as salinity, drought and low temperatures, less mapping research has been conducted on other stresses, including high temperatures (for a review see [81]). It should be noted, however, that some heat-tolerant inbred lines and commercial cultivars of tomato have been successfully developed using traditional breeding protocols [33, 90, 392]. In fact, it seems that in tomato more progress has been made in breeding for heat tolerance than breeding for tolerance to any other environmental stresses. This could be due to a greater emphasis that has been placed on breeding for heat tolerance. Below, the recent mapping activities on different abiotic stresses in tomato are briefly reviewed and discussed.

Salt tolerance

More mapping research has been conducted on tomato salt tolerance (ST) than tolerance to any other environmental stresses [81]. Also, because ST is a developmentally regulated, stage-specific phenomenon, efforts have been made to identify contributing genetic components at specific developmental stages. For example, QTLs have been identified for ST during seed germination, vegetative growth and later stages in tomato (see Table 3). The identified QTLs for tolerance at different stages can potentially be transferred to desirable genetic backgrounds through a pyramiding approach using MAS to develop tomatoes with improved ST throughout the plant ontogeny.

More efforts have been made to identify QTLs for ST during seed germination than any other stage. For example, QTLs have been identified in different tomato wild species and under different levels of salt stress. Comparisons of the

TABLE 3: Summary of abiotic stress tolerance/resistance QTLs mapped on tomato chromosomes.

Stress	Specific trait ^(a)	Number of QTLs	Tolerance source	Mapping population	Chromosomal location	References
Cold (low temp.)	SG	3	<i>L. pimpinellifolium</i>	BC ₁ S ₁	1,4	[378]
		5	<i>L. pimpinellifolium</i>	RILs	1,2,3,8,12	Foolad et al. (unpubl.)
	VG	3	<i>L. hirsutum</i>	BC ₁	6,7,12	[275]
	Sht. wlt., RAU	10	<i>L. hirsutum</i>	BC ₁	1,3,5,6,7,9,11,12	[379]
Drought	SG	4	<i>L. pimpinellifolium</i>	BC ₁ S ₁	1,8,9,12	[86]
		8	<i>L. pimpinellifolium</i>	RILs	1,2,3,4,8,9,12	Foolad et al. (unpubl.)
	WUE	3	<i>L. pennellii</i>	BC ₁ S ₁ , F ₃	Undetermined	[380]
Salt		5	<i>L. pennellii</i>	F ₂	1,3,7,8,12	[381]
	SG	8	<i>L. pennellii</i>	F ₂	1,2,3,7,8,9,12	[382]
		8	<i>L. pennellii</i>	F ₂	1,3,5,6,8,9	[383]
		7	<i>L. pimpinellifolium</i>	BC ₁ S ₁	1,2,5,7,9,12	[95]
		8	<i>L. pimpinellifolium</i>	RILs	1,2,3,4,8,9,12	Foolad et al. (unpubl.)
	VG	4	<i>L. pimpinellifolium</i>	BC ₁ S ₁	1,5,9	[384]
		5	<i>L. pimpinellifolium</i>	BC ₁	1,3,5,6,9	[385]
		7	<i>L. pimpinellifolium</i>	RILs	1,3,4,5,7,8,9	Foolad et al. (unpubl.)
	Ion accumulation	6	<i>L. pennellii</i>	F ₂	1,2,4,5,6,12	[386].
	FN, FW, FY	Several	<i>L. pimpinellifolium</i>	F ₂	Undetermined	[387]

^(a) FN: fruit number; FW: fruit weight; FY: fruit yield; RAU: root ammonium uptake; SG: seed germination; Sht. wlt.: shoot wilting; VG: vegetative growth; WUE: water use efficiency.

QTLs identified for ST in different interspecific populations of tomato, including those derived from *L. esculentum* × *L. pennellii* and *L. esculentum* × *L. pimpinellifolium* crosses, indicated that some QTLs were conserved across species whereas others were species-specific [378, 382, 383]. Comparisons of the QTLs identified in different populations of the same cross indicated stability of QTLs across populations and generations. Furthermore, it has been determined that often same QTLs contribute to tolerance at different levels of salt stress [393].

ST during vegetative growth in tomato is more important and more complex than ST during seed germination, and numerous physiological components may affect tolerance at this stage (see [281] for a detailed review). Although a good progress has been made in mapping QTLs for ST during the vegetative stage in tomato (see Table 3 for references), more research is needed for a better understanding of the underlying genetic components. The overall results of the mapping studies support a previous suggestion [394, 395] that ST during the vegetative stage in tomato is controlled by more than one gene and is highly influenced by environmental variation. However, most studies indicate the presence of some major QTLs, suggesting the potential utility of MAS for improving tomato ST during the vegetative stage.

In comparison to the research conducted during seed germination and the vegetative stage, limited research has been conducted to identify QTLs for ST during reproduction in tomato [387, 396–398], and the reported QTLs have not been verified in independent studies or populations. A few QTL mapping studies also have examined relationships among ST at different developmental stages [93, 399]. The overall results support the suggestion that different genetic

and physiological mechanisms contribute to ST during different stages of plant development. In theory, simultaneous improvement of ST at different plant stages should be possible through the use of marker-assisted breeding and pyramiding of various tolerance components. In practice, however, for improving tomato ST via MAS, a good knowledge of carefully identified and verified QTLs at all stages of plant development is required.

Cold tolerance

The physiology and genetics of tomato cold tolerance (CT) has been investigated at different developmental stages (see [81] for a review). However, compared to that for ST, much less research has been conducted to identify markers that are associated with genes/QTLs contributing to CT at different developmental stages in tomato. For CT during seed germination, the only published research is that of [378] in which a few QTLs were identified using backcross progeny of an interspecific cross between *L. esculentum* and *L. pimpinellifolium*. More recently two additional studies were conducted to identify QTLs for CT during seed germination in tomato. While in one study a selective genotyping approach was used in a large *L. esculentum* × *L. pimpinellifolium* BC₁ population ($N = 1000$), the second study used an F₉ RIL population ($N = 145$) of the same cross Foolad et al. (unpubl.). These two studies verified all of the QTLs that were identified in the original study [378] and further detected a few new QTLs. The combined results of these studies suggest that CT during seed germination in tomato is a quantitative character controlled by more than one gene. A comparison of QTLs in different populations of the same cross indicates that most

QTLs are stable across populations and generations, whereas a few are population specific.

QTL mapping studies for CT during vegetative growth and reproduction are scarce. This is unfortunate, as the value of QTLs for tolerance at these stages would be much greater than that for CT during seed germination. This is because most field tomato productions are based on the use of transplants that are often produced in warm greenhouses. Tomatoes with CT during seedling stage, in contrary, can facilitate early field planting, which may lead to early harvest and huge economic incentives. Similarly, tomato production in temperate climates with frequent cold spells during the season can be more successful by the use of cold-tolerant cultivars. To the author's knowledge, there are only two reports of QTLs for CT during the vegetative stage in tomato. In one study, using BC₁ population of an interspecific cross between a cold-sensitive *L. esculentum* line and a cold-tolerant *L. hirsutum* accession, [275] identified three QTLs responsible for growth at low temperatures. In another study, several QTLs were identified associated with shoot wilting and root ammonium uptake under chilling temperatures in an *L. esculentum* × *L. hirsutum* BC₁ population [379]. However, extensive research is needed to determine the actual value of these QTLs from *L. hirsutum* and to identify and validate other potentially useful QTLs for CT breeding in tomato. Because of the natural complexity of CT characteristics, molecular marker technology is expected to be useful in identifying critical genetic components leading to development of cold-tolerant tomatoes.

Drought tolerance

Comparatively, less mapping research has been conducted on tomato drought tolerance (DT) than tomato ST or CT. There may be only one published report on QTLs for DT during seed germination [86], in which four QTLs were identified in backcross progeny of an *L. esculentum* × *L. pimpinellifolium* cross. In a more recent study, F₉ RILs of the same cross were evaluated for germination rate under drought stress and a composite interval mapping detected several QTLs for DT on different tomato chromosomes Foolad et al. (unpubl.), consistent with results of the original study. The combined results indicated presence of stable QTLs for DT during seed germination across populations of the same cross, suggesting the usefulness of these QTLs for improving tomato DT during seed germination by MAS. The stability of these QTLs across other populations and interspecific crosses, however, should be examined before considering them for MAS transfer to the cultivated tomato.

Similar to the situations with tomato ST and CT, limited research has been undertaken to characterize the genetic control of, or to develop tomatoes with, improved DT during the vegetative or reproductive stage. In one study, to facilitate selection for low ffl (¹³C/¹²C discrimination), 3 QTLs associated with this trait were identified using progeny of a cross between *L. esculentum* and *L. pennellii* [380]. However, subsequently it has not been determined whether selection for these QTLs would increase water use efficiency or DT in tomato. There is no published research on QTLs for DT dur-

ing the reproductive stage. Yet again, if we expect using MAS technology for improving DT in tomato, the first and most important step is to identify reliable QTLs for DT-related characteristics during important growth stages. To the author's knowledge, unfortunately, no such effort is currently underway.

Relationship among tolerances to different stresses

Although several studies have investigated physiological and genetic relationships among tolerances to different abiotic stresses in tomato, only a few studies have used QTL mapping as a tool for such investigations and which focused only on the seed germination stage [94, 400–403]. The overall results of these studies have indicated the presence of genetic relationships among cold, salt, and DT during seed germination. For example, a few QTLs were identified with effects on seed germination under two or three stresses; such QTLs were referred to as stress-nonspecific QTLs. Comparatively, a few other QTLs were identified with effects on germination rate only under specific stress conditions, referred to as stress-specific QTLs. In summary, the results suggest that some genes affect tomato seed germination under different stress conditions while other genes are more specific. Further research is necessary to identify and compare genes/QTLs for tolerance to different stresses at different developmental stages. Such information will not only be scientifically intriguing, but also may be useful for developing plants with tolerance to different environmental stresses.

3.5. Genes and QTLs for flower- and fruit-related characteristics

Molecular markers have been used to map genes or QTLs for many flower- and fruit-related characteristics in tomato, including exerted stigma, petal and sepal characters, fruit size, shape, color, soluble solids content, pH, lycopene, acidity, flavor, ripening, and many others. Table 4 summarizes the genes and QTLs that have been identified and/or mapped on tomato chromosomes for such characteristics during the past 2-3 decades. It can be seen from the table that often several groups have conducted research on the same or similar characteristics, or the same traits have been studied using different interspecific populations of tomato. The status of marker development for some major fruit characteristics in tomato is briefly discussed.

Fruit size

This trait has been studied very extensively, as can be seen from Table 4. Although there is variation in fruit size within the cultivated tomato, differences are much greater when comparing wild species (with fruit size as small as 1 g with 2 locules) with the cultivated species (with fruit size as large as 1000 g with 10 or more locules). Thus, most QTL mapping experiments have been based on the use of interspecific populations. Traditional breeding studies had suggested that the genetic control of this trait was not very complex, as the trait could be easily manipulated through PS and breeding

TABLE 4: Summary of flower, fruit, and yield-related characteristics for which genes or QTLs have been identified and mapped in tomato.

Trait ⁽¹⁾	Wild species used	Mapping population	Genes (G) or QTLs (Q)	Chromosome	References
Anther-tube width	<i>L. pimpinellifolium</i>	BC ₁	2 Q	6,7	[208]
Anther-tube length	<i>L. pimpinellifolium</i>	BC ₁	2 Q	2,7	[208]
Carotenoid biosynthesis candidate genes	<i>L. pennellii</i>	ILs	23 G	Most chromosomes	[294]
Corolla indentation	<i>L. hirsutum</i>	BC ₁	2 Q	2,8	[235]
Flwr., exerted stigma	<i>L. pennellii</i>	BC ₁	4 Q	1,2,7	[274]
	<i>L. hirsutum</i>	BC ₁	1 Q	12	[235]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	2 Q	2,9	[240]
Flwr., petal apex angle	<i>L. pennellii</i>	F ₂	1 Q	11	[404]
Flwr., petal length	<i>L. pennellii</i>	F ₂	2 Q	7,12	[404]
Flwr., petal number	<i>L. pennellii</i>	F ₂	1 Q	11	[404]
Flwr., petal surf. area	<i>L. pennellii</i>	F ₂	1 Q	12	[404]
Flwr., petiolule length	<i>L. pennellii</i>	F ₂	2 Q	7,12	[404]
Flwr., sepal apex angle	<i>L. pennellii</i>	F ₂	2 Q	5,9	[404]
Flwr., sepal D/L ratio	<i>L. pennellii</i>	F ₂	3 Q	5,8,11	[404]
Flwr., sepal number	<i>L. pennellii</i>	F ₂	2 Q	2,11	[404]
Flwr., sepal surf. area	<i>L. pennellii</i>	F ₂	1 Q	3	[404]
Flwr., sepal width	<i>L. pennellii</i>	F ₂	1 Q	3	[404]
Flwr., sepal W/L ratio	<i>L. pennellii</i>	F ₂	2 Q	5,8	[404]
Fr. antioxidant capacity	<i>L. pennellii</i>	ILs	5 Q	3,6,7,10	[300]
Fr. ascorbic acid	<i>L. pennellii</i>	ILs	6 Q	3,5,10,12	[300]
Fr. citric acid content	<i>L. pennellii</i>	ILs	7 Q	4,5,8,9,10	[297]
Fr. color	<i>L. pimpinellifolium</i>	BC ₁	2 Q	2,6	[208]
	<i>L. pimpinellifolium</i>	BC ₂ , BC ₃	5 Q	2,3,4,7,8	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	8 Q	1,6,7,8,9,10,12	[240]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	15 Q	1,2,4,5,7,8,9,10,11	[283]
	<i>L. hirsutum</i>	subNILs	1 Q	1	[405]
	<i>L. parviflorum</i>	BC ₃	9 Q (visual test)	1,2,4,5,7,8,11,12	[234]
			4 Q (spec. test)	4	[234]
	<i>L. chmielewskii</i>	NILs	1 Q	1	[406]
	<i>L. hirsutum</i>	NILs	1 Q	1	[406]
<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	1 Q	12	[239]	
Fr. color (β -carotene)	<i>L. cheesmannii</i>				[131, 220, 407–409]
	<i>L. hirsutum</i> <i>L. pennellii</i>	F ₂ , ILs	1 G (B)	6	
	<i>L. parviflorum</i>	BC ₃	6 Q	2,4,8,9,10,11	[234]
	<i>L. pennellii</i>	ILs	1 G (B)	6	[220, 299]
	<i>L. pennellii</i>	ILs	2 Q	6	[300]
Fr. color (carotene content)	<i>L. esculentum</i>	RIL	3 Q	2,3,8	[410]
Fr. color (crimson)	<i>L. esculentum</i>	F ₂	1 G (<i>ogc</i> , <i>cr</i>)	6	[131–133, 299, 411]

TABLE 4: Continued.

Trait ⁽¹⁾	Wild species used	Mapping population	Genes (G) or QTLs (Q)	Chromosome	References
Frt. color (external)	<i>L. parviflorum</i>	BC ₃	9 Q	1,2,4,5,7,8,11,12	[234]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	2 Q	3,11	[231]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	2 Q	5,12	[239]
Frt. color (high pigment 1)	<i>L. esculentum</i> , <i>L. cheesmannii</i>	F ₂	1 G (<i>hp-1</i>)	2	[120, 412]
Frt. Color (high pigment 2)	<i>L. esculentum</i> , <i>L. pennellii</i>	BC ₁	1 G (<i>hp-2</i>)	1	[121, 413]
Frt. color (internal)	<i>L. parviflorum</i>	BC ₃	15 Q	1,2,4,5,7,8,9,10,11,12	[234]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	3 Q	3,11	[231]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	1 Q	12	[239]
	<i>L. pennellii</i>	ILs	16 Q	Most chromosomes	[294]
Frt. color (lycopene)	<i>L. pimpinellifolium</i>	BC ₁ S ₁	8 Q	1,4,5,6,7,10,12	[414]
	<i>L. parviflorum</i>	BC ₃	5 Q	2,3,5,8,12	[234]
	<i>L. esculentum</i>	RIL	2 Q	4,11	[410]
	<i>L. pennellii</i>	ILs	2 Q	3,6	[300]
Frt. color (orange)	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	2 Q	11,12	[239]
Frt. color (yellow)	<i>L. parviflorum</i>	BC ₃	1 Q	12	[234]
Frt. cracking	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	5 Q	2,5,8,10,12	[239]
Frt. cracking (concentric)	<i>L. pimpinellifolium</i>	BC ₂ F ₆	3 Q	2,8,9	[231]
Frt. cracking (radial)	<i>L. pimpinellifolium</i>	BC ₂ F ₆	2 Q	2,9	[231]
Frt. diameter	<i>L. pimpinellifolium</i>	BC ₁	3 Q	1,2,8	[208]
	<i>L. pimpinellifolium</i>	BC ₁ S ₁	8 Q	1,2,3,6,7,11	[414]
	<i>L. pimpinellifolium</i>	F ₂	7 Q	1,2,3,4,7,11	[40]
	<i>L. esculentum</i>	RIL	5 Q	2,3,11,12	[410]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	12 Q	2	[231]
Frt. elasticity	<i>L. esculentum</i>	RIL	5 Q	1,2,3,4,9	[410]
Frt. epidermal reticulation	<i>L. parviflorum</i>	BC ₃	4 Q	4,6,8,12	[234]
Frt. firmness	<i>L. pimpinellifolium</i>	BC ₂ , BC ₃	4 Q	2,3,4,8	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	6 Q	1,3,4,6,9,11	[240]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	3 Q	2,5,11	[283]
	<i>L. parviflorum</i>	BC ₃	12	1,3,5,6,8,9,10,11,12	[234]
	<i>L. esculentum</i>	RIL	2 Q	4,9	[410]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	2 Q	6	[231]
	<i>L. chmielewskii</i>	NILs	1 Q	1	[406]
Frt. fructose content	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	3 Q	2,10	[239]
	<i>L. pennellii</i>	ILs	4 Q	4,5,7,9	[297]

TABLE 4: Continued.

Trait ⁽¹⁾	Wild species used	Mapping population	Genes (G) or QTLs (Q)	Chromosome	References
Fr. fructose:glucose ratio	<i>L. hirsutum</i> <i>L. pennellii</i>	F ₂ , F ₃ , BC ₁ , ILS	1 G (<i>Fgr</i>)	4	[141]
Fr. glucose content	<i>L. pennellii</i>	ILS	4 Q	4,5,9,12	[297]
Fr. graywall	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	1 Q	12	[239]
Fr. green gel	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	3 Q	1,5,8	[239]
Fr. length	<i>L. pimpinelli-folium</i>	BC ₁ S ₁	9 Q	1,2,3,6,7,9,12	[414]
	<i>L. pimpinelli-folium</i>	F ₂	7 Q	1,2,3,4,9,11	[40]
	<i>L. pimpinelli-folium</i>	BC ₂ F ₆	5 Q	2,3,8,9,11	[231]
Fr. locule number	<i>L. pimpinelli-folium</i>	BC ₁	2 Q	1,3	[208]
	<i>L. pimpinelli-folium</i>	F ₂	3 Q	2,11	[40]
	<i>L. pimpinelli-folium</i>	F ₂	5 Q	2,3,4,10,12	[404]
Fr. malic acid content	<i>L. pennellii</i>	ILS	5 Q	3,4,8,12	[297]
Fr. maturity	<i>L. pimpinelli-folium</i>	BC ₂ , BC ₃	7 Q	2,3,5,7,8,9	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	5 Q	3,5,7,8,9	[240]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	6 Q	3,5,7,8,9,12	[283]
	<i>L. parviflorum</i>	BC ₃	16	1,2,3,5,6,7,8,9,10,12	[234]
	<i>L. pimpinelli-folium</i>	BC ₂ F ₆	1 Q	7	[231]
Fr. organoleptic quality	<i>L. esculentum</i>	RIL	Many Q	Various chromos.	[143, 410, 415]
Fr. ostwald	<i>L. parviflorum</i>	BC ₃	1 Q	6	[234]
Fr. pericarp thickness	<i>L. pimpinelli-folium</i>	BC ₁	4 Q	2,8,10	[208]
	<i>L. parviflorum</i>	BC ₃	7 Q	1,6,7,8,9,10	[234]
	<i>L. chmielewskii</i>	NILs	1 Q	1	[406]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	2 Q	10,12	[239]
	<i>L. chmielewskii</i>	BC ₁ , BC ₂	5 Q	3,6,7,8,10	[167]
Fr. pH	<i>L. cheesmanii</i>	F ₂ , F ₃	9 Q	1,3,4,6,7,8,10	[232]
	<i>L. chmielewskii</i>	BILs/BC ₂ F ₅	1 Q	7	[101, 416]
	<i>L. pimpinelli-folium</i>	BC ₂ , BC ₃	5 Q	1,3,5,7,12	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	6 Q	2,3,9,10,12	[240]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	10 Q	1,2,3,4,6,8,9,10,12	[283]
	<i>L. pimpinelli-folium</i>	BC ₁ S ₁	6 Q	1,2,4,5,9,12	[414]
	<i>L. parviflorum</i>	BC ₃	10 Q	2,3,4,5,6,7,9,12	[234]
	<i>L. esculentum</i>	RIL	2 Q	11,12	[410]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	2 Q	3,12	[239]
	<i>L. pennellii</i>	ILS	11 Q	2,4,5,8,9,10,11,12	[297]
Fr. phenolic content	<i>L. pennellii</i>	ILS	9 Q	3,5,6,7,8,9	[300]

TABLE 4: Continued.

Trait ⁽¹⁾	Wild species used	Mapping population	Genes (G) or QTLs (Q)	Chromosome	References
Frt. puffiness	<i>L. pimpinellifolium</i>	BC ₂ , BC ₃	5 Q	2,8,9,11	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	1 Q	9	[240]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	1 Q	4	[283]
	<i>L. parviflorum</i>	BC ₃	13 Q	2,3,4,5,7,8,9,10,11,12	[234]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	3 Q	8,9	[231]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	4 Q	2,3,10	[239]
Frt. reducing sugar	<i>L. pennellii</i>	ILs	13 Q	1,2,4,5,7,8,9,10,11,12	[297]
Frt. ripening	<i>L. esculentum</i>	F ₂	2 Q	5,12	[417]
	<i>L. pennellii</i>	F ₂	Many loci	All chromosomes	[160, 418]
	<i>L. pimpinellifolium</i>	BC ₁	3 Q	2,8,9	[208]
	<i>L. pimpinellifolium</i>	BC ₂ , BC ₃	4 Q	2,4,7,8	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	4 Q	2,3,8,9	[240]
Frt. ripening (<i>alcobaca</i>)	<i>L. esculentum</i>	F ₂	<i>alc</i>	10	[159]
	<i>L. pimpinellifolium</i>	BC ₁	<i>alc</i>	10	[160]
Frt. ripening (<i>colorless nonripening</i>)	<i>L. esculentum</i> , <i>L. cheesmanii</i>	F ₂	<i>Cnr</i>	2	[419, 420]
Frt. ripening (<i>never ripe</i>)	<i>L. esculentum</i> , <i>L. cheesmanii</i>	F ₂	<i>Nr</i>	9	[421–423]
Frt. ripening (<i>nonripening</i>)	<i>L. pennellii</i> <i>L. cheesmanii</i>	F ₂	<i>nor</i>	10	[153, 155, 158, 424, 425]
Frt. ripening (<i>polygalacturonase</i>)	<i>L. pimpinellifolium</i>	BC ₁	TOM6	10	[160]
Frt. ripening (<i>ripening-inhibitor</i>)	<i>L. pennellii</i> <i>L. cheesmanii</i>	F ₂	<i>rin</i>	5	[153, 155, 158, 424, 425]
Frt. ripening (<i>uniform ripening</i>)	<i>L. pimpinellifolium</i>	BC ₁	<i>u</i>	10	[160]
Frt. rotten	<i>L. pimpinellifolium</i>	BC ₂ F ₆	4 Q	2,8,9	[231]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	5 Q	3,5,8,9,12	[239]
Frt. sensory attributes	<i>L. esculentum</i>	RIL	Many Q	Various chromosomes	[143, 415]
Frt. set (fertility)	<i>L. pimpinellifolium</i>	BC ₂ F ₆	3 Q	4,5,7	[231]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	3 Q	3,9,12	[239]
Frt. shape	<i>L. pimpinellifolium</i>	BC ₂ , BC ₃	4 Q	1,2,8	[286]
	<i>L. pimpinellifolium</i>	BC ₁	2 Q	2,8	[208]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	12 Q	1,2,6,7,8,9,10,12	[240]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	9 Q	2,3,7,8,9,11,12	[283]
	<i>L. pimpinellifolium</i>	BC ₁ S ₁	4 Q	1,9,10,12	[414]
	<i>L. hirsutum</i>	subNILs	1 Q	1	[405]

TABLE 4: Continued.

Trait ⁽¹⁾	Wild species used	Mapping population	Genes (G) or QTLs (Q)	Chromosome	References
Frt. shape	<i>L. parviflorum</i>	BC ₃	16 Q	All 12 chromosomes	[234]
	<i>L. pimpinelli-folium</i>	F ₂	1 Q	11	[40]
	<i>L. pimpinelli-folium</i>	BC ₂ F ₆	2 Q	1,9	[231]
	<i>L. pimpinelli-folium</i>	F ₂	4 Q	2,3,7,11	[426]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	4 Q	2,8,10,12	[239]
Frt. shape (bumpiness)	<i>L. pimpinelli-folium</i>	F ₂	3 Q	8,9,11	[427]
Frt. shape (bell pepper)	<i>L. pimpinelli-folium</i>	F ₂	3 Q	2,8	[427]
	<i>L. pennellii</i>	F ₂	1 Q	2	[428]
Frt. shape (blossom-end blockiness I)	<i>L. pimpinelli-folium</i>	F ₂	1 Q	2	[427]
Frt. shape (elongated)	<i>L. pimpinelli-folium</i>	F ₂	2 Q	6,9	[427]
Frt. shape (heart)	<i>L. pimpinelli-folium</i>	F ₂	4 Q	1,2,3,7	[427]
Frt. shape (pear)	<i>L. pimpinelli-folium</i>	F ₂	2 Q	2,10	[428]
Frt. shape (stem-end blockiness)	<i>L. pimpinelli-folium</i>	F ₂	6 Q	1,2,3,7,8,12	[427]
Frt. shoulder pigmentation	<i>L. hirsutum</i>	subNILs	1 Q	1	[405]
	<i>L. parviflorum</i>	BC ₃	1 Q	10	[234]
Frt. size	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	4 Q	2,3,10,12	[239]
Frt. skin reticulation	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	4 Q	2,4,5,8	[239]
Frt. soluble solids (SS)	<i>L. chmielewskii</i>	NIL F ₂	1 Q	Undetermined	[429]
	<i>L. chmielewskii</i>	BC ₁ , BC ₂	4 Q	3,4,6,7	[167, 430]
	<i>L. cheesmanii</i>	F ₂ , F ₃	7 Q	2,3,6,7,9	[232]
	<i>L. chmielewskii</i>	BILs/BC ₂ F ₅	3 Q	7,10	[101]
	<i>L. pennellii</i>	ILs	3 Q	1,5,7	[298]
	<i>L. chmielewskii</i>	BC ₂ F ₅	1 Q	7	[101, 416]
	<i>L. cheesmanii</i>	F ₈ RIL	12 Q	1,2,3,4,5,6,9,10	[279]
	<i>L. pennellii</i>	ILs	23 Q	Most chromosomes	[238]
	<i>L. pimpinelli-folium</i>	BC ₂ , BC ₃	12 Q	2,3,4,5,6,7,8,11,12	[286]
	<i>L. pimpinelli-folium</i>	BC ₁	3 Q	3,6,9	[208]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	9 Q	1,2,7,8,9,10	[240]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	5 Q	3,5,6,9	[283]
	<i>L. pimpinelli-folium</i>	BC ₁ S ₁	13 Q	1,2,3,7,10,12	[414]
	<i>L. hirsutum</i>	subNILs	1 Q	1	[405]
	<i>L. parviflorum</i>	BC ₃	5 Q	4,5,6,9	[234]
	<i>L. esculentum</i>	RIL	3 Q	2,9	[410]
<i>L. pimpinelli-folium</i>	BC ₂ F ₆	2 Q	8,9	[231]	
<i>L. chmielewskii</i>	NILs	1 Q	1	[406]	
<i>L. hirsutum</i>	NILs	1 Q	1	[406]	

TABLE 4: Continued.

Trait ⁽¹⁾	Wild species used	Mapping population	Genes (G) or QTLs (Q)	Chromosome	References
Frt. soluble solids (SS)	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	3 Q	4,9,12	[239]
	<i>L. pennellii</i>	ILs	9 Q	1,3,4,5,7,9,10,12	[297]
Frt. SS × red yield	<i>L. pennellii</i>	ILs	14 Q	Most chromosomes	[238]
	<i>L. pimpinelli-folium</i>	BC ₂ , BC ₃	4 Q	3,7,9	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	9 Q	1,2,5,7,8,9,10,12	[240]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	9 Q	1,2,3,4,6,8,11,12	[283]
	<i>L. parviflorum</i>	BC ₃	2 Q	5,8	[234]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	4 Q	3,5,12	[239]
Frt. stem release (%)	<i>L. pimpinelli-folium</i>	BC ₂ , BC ₃	5 Q	1,2,3,10	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	5 Q	2,6,9,12	[240]
	<i>L. parviflorum</i>	BC ₃	6	2,6,7,8,10	[234]
Frt. stem retention (%)	<i>L. hirsutum</i>	BC ₂ , BC ₃	6 Q	2,8,9,10,11	[283]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	9 Q	2,3,4,6,9,10,11,12	[239]
Frt. stem scar size	<i>L. parviflorum</i>	BC ₃	11 Q	2,3,4,5,6,7,8,9,10,11	[234]
	<i>L. pimpinelli-folium</i>	BC ₂ F ₆	7 Q	1,2,3,4,6,7,8	[231]
	<i>L. chmielewskii</i>	NILs	1 Q	1	[406]
	<i>L. hirsutum</i>	NILs	1 Q	1	[406]
Frt. stem scar penetration (veins)	<i>L. parviflorum</i>	BC ₃	2	1,6	[234]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	2 Q	4,8	[239]
Frt. sugar content	<i>L. esculentum</i>	RIL	5 Q	2,3,10,11	[410]
	<i>L. esculentum</i> var. <i>cerasifomee</i>	F ₂	6 Q	ND	[112]
Frt. sunscald	<i>L. pimpinelli-folium</i>	BC ₂ , BC ₃	2 Q	7,8	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	4 Q	2,3,8,9	[240]
Frt. titratable acidity	<i>L. esculentum</i>	RIL	6 Q	1,2,3,9,12	[410]
	<i>L. pennellii</i>	ILs	15 Q	2,3,4,5,7,8,9,10,11,12	[297]
Frt. total acid	<i>L. parviflorum</i>	BC ₃	4 Q	3,4,7,8	[234]
Frt. total organic acid	<i>L. parviflorum</i>	BC ₃	2 Q	9,12	[234]
Frt. viscosity	<i>L. pimpinelli-folium</i>	BC ₂ , BC ₃	1 Q	9	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	4 Q	1,2,8,9	[240]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	2 Q	2,10	[283]
	<i>L. parviflorum</i>	BC ₃	3 Q	2,9,10	[234]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	4 Q	2,3,9,12	[239]
Frt. weight	<i>L. pennellii</i>	BC ₁	5 Q	2,4,8	[274]
	<i>L. chmielewskii</i>	BC ₁ , BC ₂	6 Q	1,4,6,7,9,11	[167, 430]
	<i>L. cheesmanii</i>	F ₂ , F ₃	11 Q	1,2,3,4,6,7,9,11,12	[232]
	<i>L. cheesmanii</i>	F ₈ RIL	13 Q	1,2,3,4,6,7,9,12	[279]
	<i>L. pennellii</i>	ILs	18 Q	Many chromosomes	[238]

TABLE 4: Continued.

Trait ⁽¹⁾	Wild species used	Mapping population	Genes (G) or QTLs (Q)	Chromosome	References
Frt. weight	<i>L. pimpinellifolium</i>	BC ₁	7 Q	1,2,8,11	[208]
	<i>L. pimpinellifolium</i>	BC ₂ , BC ₃	8 Q	2,3,4,5,7,9	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	10 Q	1,2,3,7,8,9,10,12	[240]
	<i>L. hirsutum</i>	BC ₁	3 Q	1,3	[235]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	3 Q	2,3,4	[283]
	<i>L. pimpinellifolium</i>	BC ₁ S ₁	12 Q	1,2,3,4,6,7,8,9,11,12	[414]
	<i>L. parviflorum</i>	BC ₃	8 Q	2,3,6,7,10,11,12	[234]
	<i>L. esculentum</i>	F ₂	2 Q	4,6	[417]
	<i>L. pimpinellifolium</i>	F ₂	6 Q	1,2,3,11	[40]
	<i>L. esculentum</i>	RIL	5 Q	2,3,11,12	[410]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	2 Q	2,3	[231]
	<i>L. pimpinellifolium</i>	F ₂	7 Q	1,2,3,5,6,7,11	[427]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	3 Q	3,10,12	[239]
	<i>L. pennellii</i>	ILs	13 Q	2,3,4,5,6,7,9,10,11,12	[297]
	Frt. yield (total yield)	<i>L. chmielewskii</i>	BILs/BC ₂ F ₅	1 Q	7
<i>L. pennellii</i>		ILs	11 Q	Various chromosomes	[238]
<i>L. pimpinellifolium</i>		BC ₂ , BC ₃	6 Q	2,3,7,9	[286]
<i>L. peruvianum</i>		BC ₃ , BC ₄	10 Q	1,2,6,7,8,9,10,12	[240]
<i>L. hirsutum</i>		BC ₂ , BC ₃	12 Q	1,2,3,4,5,6,7,8,12	[283]
<i>L. hirsutum</i>		subNILs	1 Q	1	[405]
<i>L. parviflorum</i>		BC ₃	5 Q	1,2,3,6,8	[234]
<i>L. pennellii</i>		BC ₂ /BC ₂ F ₁	6 Q	3,5,8,9,12	[239]
Frt. yield (red yield)	<i>L. pimpinellifolium</i>	BC ₂ , BC ₃	2 Q	2,7	[286]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	12 Q	1,2,3,5,7,8,9,10,12	[240]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	11 Q	1,2,3,5,7,8,10,11,12	[283]
	<i>L. parviflorum</i>	BC ₃	4 Q	2,5,8	[234]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	4 Q	3,5,12	[239]
Frt. yield (green yield)	<i>L. hirsutum</i>	BC ₂ , BC ₃	11 Q	2,3,7,8,11,12	[283]
	<i>L. pennellii</i>	BC ₂ /BC ₂ F ₁	3 Q	8,9,12	[239]
Jointless	<i>L. cheesmanii</i>	F ₂	<i>j</i>	11	[176, 431]
	<i>L. cheesmanii</i>	F ₂	<i>j-2</i>	12	[432]
Phytochrome genes	<i>L. esculentum</i> <i>L. pennellii</i>	BC ₁	5 G (<i>PhyA</i> , <i>PhyB1</i> , <i>PhyB2</i> , <i>PhyE</i> , <i>PhyF</i>)	1, 2, 5, 7, 10	[121]

⁽¹⁾ D = distance; Flwr. = flower; Frt. = fruit; L = length; W = width.

TABLE 5: Summary of other characteristics for which genes or QTLs have been identified and mapped in tomato chromosomes.

Trait ⁽¹⁾	Wild species used	Mapping population	Genes (G) or QTLs (Q)	Chromosome	References
Branch number	<i>L. cheesmanii</i>	F ₈ RIL	7 Q	2,3,4,5,7,11	[280]
Bud type	<i>L. hirsutum</i>	BC ₁	7 Q	1,2,7,12	[235]
Curly leaf	<i>L. pimpinellifolium</i>	BC ₂ F ₆	7 Q	2,3,5,6,8,9,11	[231]
Days to emergence	<i>L. pimpinellifolium</i>	BC ₁	3 Q	1,2,3	[208]
Days to 1st flower	<i>L. pimpinellifolium</i>	BC ₁	2 Q	1,2	[208]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	2 Q	3,4	[231]
Days to 1st ripe fruit	<i>L. pimpinellifolium</i>	BC ₁	2 Q	2,4	[208]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	2 Q	1,7	[231]
Days to 3rd leaf	<i>L. pimpinellifolium</i>	BC ₁	3 Q	1,2,3	[208]
Flwr., number/plant	<i>L. hirsutum</i>	BC ₁	1 Q	1	[235]
	<i>L. pimpinellifolium</i>	BC ₁	3 Q	3,6,9	[208]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	5 Q	1,7,9,10,11	[231]
	<i>L. pimpinellifolium</i>	F ₂	9 Q	1,2,3,4,5,7,9	[426]
Flwr. node number	<i>L. cheesmanii</i>	F ₈ RILs	5 Q	4,8,9,11	[280]
Hort. acceptability	<i>L. parviflorum</i>	BC ₃	3	1,5,9	[234]
Inflores. raquis length	<i>L. hirsutum</i>	BC ₁	3 Q	1,5,7	[235]
Inflores. veg. meristem	<i>L. hirsutum</i>	BC ₁	2 Q	4,12	[235]
Leaf, length	<i>L. cheesmanii</i>	F ₈ RIL	5 Q	2,3,4,6,11	[280]
Leaflet, apex angle	<i>L. pennellii</i>	F ₂	4 Q	4,5,7	[404]
Leaflet, D/L ratio	<i>L. pennellii</i>	F ₂	1 Q	5	[404]
Leaflet, length	<i>L. pennellii</i>	F ₂	4 Q	2,11,12	[404]
Leaflet, number	<i>L. pennellii</i>	F ₂	2 Q	1,5	[404]
Leaflet, surface area	<i>L. pennellii</i>	F ₂	3 Q	10,11	[404]
Leaflet, width	<i>L. pennellii</i>	F ₂	2 Q	17,12	[404]
Leaflet, W/L ratio	<i>L. pennellii</i>	F ₂	2 Q	1,4	[404]
Male sterility	<i>L. pimpinellifolium</i>	F ₂	ms-10	2	[271]
Node number	<i>L. cheesmanii</i>	F ₈ RIL	6 Q	1,2,3,6,8	[280]
	<i>L. peruvianum</i>	BC ₃ , BC ₄	8 Q	1,2,3,5,8,9,10	[240]
	<i>L. hirsutum</i>	BC ₂ , BC ₃	6 Q	2,3,6,7,8	[283]
	<i>L. parviflorum</i>	BC ₃	19	1,2,3,4,5,6,8,9,10,11,12	[234]
Plant fresh mass	<i>L. cheesmanii</i>	F ₈ RIL	8 Q	2,3,4,6,9,11	[280]
Plant growth habit	<i>L. peruvianum</i>	BC ₃ , BC ₄	6 Q	1,2,3,7,8,9	[240]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	4 Q	2,3,9,11	[231]
Plant height	<i>L. pennellii</i>	ILs	16 Q	Many chromosomes	[238]
	<i>L. pimpinellifolium</i>	BC ₁	1 Q	2	[208]
	<i>L. hirsutum</i>	BC ₁	4 Q	1,2,5,11	[235]
	<i>L. cheesmanii</i>	F ₈ RIL	7 Q	2,3,4,6,7	[280]
	<i>L. pimpinellifolium</i>	BC ₁	4 Q	4,6,7,12	[208]
Seed number	<i>L. pimpinellifolium</i>	F ₂	2 Q	1,11	[40]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	4 Q	5,6,8	[231]
	<i>L. pimpinellifolium</i>	F ₂	10 Q	1,2,3,4,6,7,9,11,12	[426]
	<i>L. pennellii</i>	BC ₁	5 Q	1,2,4,7,8	[274]
Seed weight	<i>L. cheesmanii</i>	F ₈ RILs	14 Q	1,2,3,4,6,7,9,11,12	[279]

TABLE 5: Continued.

Trait ⁽¹⁾	Wild species used	Mapping population	Genes (G) or QTLs (Q)	Chromosome	References
Seed weight	<i>L. pimpinellifolium</i>	BC ₁	4 Q	2,4,10,12	[208]
	<i>L. pimpinellifolium</i>	F ₂	4 Q	1,2,4	[40]
	<i>L. pimpinellifolium</i>	BC ₂ F ₆	5 Q	1,4,5,7	[231]
Self incompatibility	<i>L. peruvianum</i>	Reciprocal F ₁ s	S locus	1	[272]
	<i>L. peruvianum</i>	F ₁	S locus	1	[433]
	<i>L. hirsutum</i>	BC ₁	S locus	1	[235]
Self pruning	<i>L. esculentum</i>	F ₂	<i>sp</i>	6	[407]
	<i>L. chmielewskii</i>	BC ₁	<i>sp</i>	6	[167]
	<i>L. pimpinellifolium</i>	BC ₁	<i>sp</i>	6	[166]
Stem vascular morphology	<i>L. hirsutum</i>	BC ₂ S ₅	1 Q	2	[434]
Transgressive Segregation	<i>L. pennellii</i>	F ₂	74 Q for 8 traits	All 12 chromosomes	[237]
Unilateral incongruity	<i>L. hirsutum</i>	BC ₁	6 Q	1,2,3,11,12	[235]
Various frt. and plant characteristics	<i>L. pimpinellifolium</i>	F ₂	Many Q	Undetermined	[276]

⁽¹⁾ D = distance; Flwr. = flower; Frt. = fruit; L = length; W = width.

due to its high heritability. Molecular mapping studies have revealed presence of about a couple dozens of QTLs for fruit size in tomato, which have been mapped to all 12 chromosomes (see Table 4), some of which with very large effects [414]. Many studies have identified QTLs in the same chromosomal locations, and the most recent studies have not identified novel QTLs for tomato fruit size that were not previously reported. For example, in an F₂ population of a cross between an *L. pimpinellifolium* accession (LA1589), with average fruit weight of 1 g, and the *L. esculentum* cultivar Giant Heirloom, with fruit size as large as 1000 g, no novel QTLs were identified [40]. This study detected all major QTLs for fruit size that were previously identified in other studies, including *fw1.1* (explaining ~17% of the variation), *fw1.2* (~13%), *fw2.1* (~12%; previously known as *locule number*, *lc*), *fw2.2* (~23%), *fw3.1* (~12%) and *fw11.3* (~37%; previously known as *fasciated*, *f*). Of these QTLs, *fw2.1* (*lc*) and *fw11.3* (*f*) are associated with an increase in locule number. It has been suggested that exceptionally large-fruited fresh market tomato varieties, such as Giant Heirloom, were evolved as a result of novel combinations of all these major QTLs, whereas medium-size processing tomatoes (with 2–4 locules) were evolved from QTLs *fw1.1*, *fw2.1*, *fw2.2*, *fw3.1*, *fw3.2*, and *fw11.3*, none of which affecting locule number [40].

One of the major QTLs, *fw2.2*, which was detected in many QTL studies in tomato (see Table 4), has been cloned and characterized [305]. This QTL was reported to make the largest contribution to the difference in fruit size between most cultivated tomato genotypes and their small-fruited wild species counterparts [435]. In fact, many studies that used interspecific tomato populations for mapping identified *fw2.2*. As to other fruit size QTLs, a comparison of their map positions across studies indicates colocalization of their posi-

tions (see [414]), supporting the hypothesis that the majority of fruit size variation in the cultivated tomato is attributed to allelic variation at a rather limited number of loci [427]. Many studies also have indicated colocalization of QTLs for fruit size and solids contents (see [414]), confirming the negative correlation between these two traits in tomato reported in many studies (e.g., [112]).

Fruit shape

There are extensive variations in fruit shape in the cultivated tomato, including oblate, globe (round), ovate (blocky, square round), heart shaped, ellipsoid (plum-shaped), elongated (cylindrical, long oblong) and pear shaped (pyriform). Traditional genetic studies had identified several genes controlling fruit shape in tomato such as *pr* (pyriform), *o* (ovate), *bk* (beaked tomato), *n* (nipple-tip tomato), *f* (fasciated), and *lc* (for locule number) [436]. During the past two decades, a few of these genes and several other genes and QTLs affecting fruit shape in tomato have been located on tomato molecular linkage map and/or cloned and characterized at the molecular level (see Tables 4 and 7). For example, a major fruit-shape QTL (termed *fs8.1*) differentiating fresh market (round) and processing (blocky) tomatoes was mapped on tomato chromosome 8 [437] and later cloned and characterized [438]. *fs8.1* exerts its effect by changing the length of carpels during preanthesis resulting in longer and larger mature fruit. Similarly, another major fruit-shape QTL termed *ovate*, controlling the transition from round to pear-shaped fruit, was mapped [428] and cloned and characterized [439]. The overall results from different studies indicate that most of the variation in the cultivated tomato fruit shape is controlled by a few major loci and that the observed

variation is most likely due to allelic variation at these loci [427].

Fruit color

Because it is an important fruit quality characteristic in tomato, color has been the focus of numerous mapping studies. The attention to tomato fruit color has recently increased as the health benefits of lycopene, the major carotenoid in tomato that is responsible for the red fruit color, has become more obvious [114, 440–443]. As indicated earlier, several major genes with significant contribution to high contents of fruit lycopene (e.g., *hp-1*, *hp-2*, *dg* and *Og^c*) and other carotenoids (e.g., beta-carotene, *B*) were previously identified and mapped onto the classical linkage map of tomato [30, 444]. However, during the past two decades, numerous QTLs and candidate genes with significant effects on fruit color and/or lycopene content were identified and mapped onto tomato chromosomes along with the previously identified genes (see Table 4). While some of the identified QTLs mapped to the chromosomal locations of many of the known genes in the carotenoid biosynthesis pathway, many mapped to unknown locations (e.g., see [294]). Therefore, it was suggested that there might be more genes affecting fruit color in tomato than those known to affect based on the carotenoid biosynthesis pathway [294]. Currently, a few research programs in the U.S. and around the world are conducting research to identify, map, and possibly clone new genes involved in determining fruit color in tomato. In addition, there are numerous programs attempting to improve tomato nutritional quality either through traditional breeding or transgenic approaches [299, 409, 445].

Fruit soluble solids

As indicated earlier, fruit soluble solids content (SSC) has been the focus of numerous tomato genetics and breeding programs worldwide. However, due to a negative correlation between yield and SSC in tomato, breeders have had limited success in increasing SSC of high-yielding tomato cultivars using traditional phenotypic selection [113]. Although fruit size and yield have been increased substantially via traditional breeding, SSC has remained essentially unchanged. To facilitate alternative approaches to increasing SSC of high-yielding tomato cultivars, significant efforts have been devoted to identify QTLs for high SSC. The hope has been to identify SSC QTLs that may not have any adverse effect on fruit size. Currently, there are more than 20 published studies that have identified QTLs for high fruit SSC in tomato (see Table 4). Although these studies used different interspecific populations, there have been significant overlaps in the locations of the QTLs identified across studies (e.g., see [414]). Furthermore, many studies have revealed that QTLs that positively influence SSC are mostly at the same chromosomal locations as QTLs that negatively impact fruit weight [414]. Although a few studies have reported SSC QTLs with no apparent effect on fruit size (e.g., [98]), there is no verification of the effects of such QTLs via MAS experiments.

Fruit yield

Yield is a complex trait that is directly or indirectly affected by numerous genetic and nongenetic factors. For this reason, the heritability for yield is often very low in most crop species, including tomato. Technically it is difficult to identify QTLs that may be truly indicative of genetic yield potential and could be utilized in marker-assisted breeding. Nevertheless, many studies have conducted QTL mapping for fruit yield in tomato and identified QTLs for traits such as total yield, red yield, and green yield (see Table 4). Basically, QTLs for yield have been identified in different interspecific populations of tomato and mapped to all 12 chromosomes. However, unlike QTLs for fruit weight and SSC that were rather consistent across studies, there is limited concordance across studies in regard to yield QTLs (see Table 4). This is not surprising considering the very complex nature of the trait and its low heritability. Furthermore, there is no published report of the use of fruit yield QTLs for MAS in tomato, and it is not expected that at least in the near future such QTLs would have wide utility for improving tomato fruit yield.

Fruit ripening

As indicated earlier, traditional genetics and breeding research had resulted in the identification and manipulation of several ripening-related genes. During the past two decades, molecular biology techniques facilitated characterization of such genes and identification and mapping of many other ripening-related genes, loci, and QTLs (see Table 4). Furthermore, a few ripening-related genes have been genetically characterized, fine mapped and cloned using map-based cloning techniques (see Table 7, [155, 424]). More detailed lists of genes with effects on fruit ripening in tomato can be found in [151, 153, 446]. Among the major ripening genes, at least one (*rin*) has been used in marker-assisted breeding (see Table 6).

Other traits

In addition to the traits described above, genes or QTLs have been identified for numerous other flower- and fruit-related characteristics as well as traits such as self incompatibility, unilateral incongruity, transgressive segregation, self-pruning (determinate type plants), jointless pedicel, and seed size and number among others, as shown in Tables 4 and 5. The available mapping information may be useful for basic research such as identifying and cloning genes underlying these traits as well as for breeding purposes. The limited space here does not allow discussion of these traits.

4. MARKER-ASSISTED SELECTION

MAS can be defined as selection for a trait based on the genotype of an associated marker rather than the trait itself. In essence, the associated marker is used as an indirect selection criterion. The potential of MAS as a tool for crop improvement has been extensively explored [448–450]. In theory, MAS can reduce the cost and increase the precision and

TABLE 6: Known traits for which marker-assisted selection and breeding are done in tomato.

Trait	Source species	Gene/QTL (Q)	Reference
Bacterial canker	<i>L. peruvianum</i>	3 Q	Seed companies
	<i>L. hirsutum</i>	<i>Rcm2.0, Rcm5.1(Q)</i>	[287]
Bacterial speck	<i>L. pimpinellifolium</i>	<i>Pto</i>	Seed companies, [447]
Bacterial spot	<i>L. esculentum</i>	<i>Rx-3 (Q)</i>	[447]
Bacterial wilt	<i>L. esculentum</i>	2 Q	Seed companies
Blackmold	<i>L. cheesmanii</i>	Few Q	[288]
Corky root rot	<i>L. peruvianum</i>	<i>Py-1</i>	Seed companies
Fusarium wilt	<i>L. pimpinellifolium</i>	<i>I-2C, I-3</i>	Seed companies, public breeders
Jointless	<i>L. cheesmanii</i>		Seed companies
Late blight	<i>L. pimpinellifolium</i>	<i>Ph-3</i>	Seed companies, public breeders
	<i>L. hirsutum</i>	4 Q	[342]
Lycopene	<i>L. esculentum</i>	<i>Og^c, cr</i>	Seed companies
Powdery mildew	<i>L. chilense, L. hirsutum</i>	<i>Lv, Ol-1, Ol-2</i>	Seed companies
Ripening inhibitor	<i>L. cheesmanii</i>	<i>rin</i>	Seed companies
Root-knot nematode	<i>L. peruvianum</i>	<i>Mi</i>	Seed companies, public breeders
Self pruning	<i>L. esculentum</i>	<i>sp</i>	Seed companies, public breeders
Soluble solids	Not known	Q	Seed companies
Tomato spotted wild virus	<i>L. peruvianum</i>	<i>Sw-5</i>	Seed companies
Tomato yellow leaf curl virus	Different species	Few Q	Seed companies
Tobacco mosaic virus	<i>L. peruvianum</i>	<i>Tm-2^a</i>	Seed companies
Verticillium wilt	<i>L. esculentum</i>	<i>Ve</i>	Seed companies, public breeders

efficiency of selection and breeding. It may offer unique opportunities to circumvent many potential problems associated with PS, and thus may be more useful. MAS has been possible, if not always practical, for a wide range of plant traits since the early 20th century. However, with recent development of molecular tools and genetic maps, MAS has become more attractive and practical than before. MAS may allow selecting for a trait in seasons or locations where PS is not feasible or is costly or ineffective, thus increasing the efficiency of selection and flexibility of a breeding program. MAS may be less time consuming for traits whose expressions are developmentally regulated and are phenotypically obvious only late in the season. Markers are independent of variation caused by genetic or environmental factors and this offers the advantage of permitting selection for traits such as resistance in the absence of pathogen, which is otherwise required to identify useful segregants. Trait heritability is the most important factor influencing the utility of MAS. It is suggested that MAS is most useful for traits with low-to-moderate heritability, for which PS may be less effective. However, this is true only if reliable markers for the low-heritability traits can be identified.

Gene pyramiding is a useful approach to maximize utilization of existing gene resources. MAS is an effective approach for pyramiding genes or QTLs from different sources and for different traits into elite germplasm. It has been shown that in backcross breeding programs MAS can be effective in reducing linkage drag and optimizing population size by selecting against the donor genome (i.e., background selection) while selecting for allele(s) to be introgressed from

the donor parent (i.e., foreground selection). In other words, the use of MAS in a backcross breeding program can expedite transfer of desirable traits from the donor parent as well as fast recovery of the recurrent genome by breaking the undesirable linkages between traits following gene introgression from the wild species. In addition, MAS can expedite backcross breeding by allowing strict backcrossing in each generation rather than modified backcrossing (i.e., selfing after each generation of backcrossing), which is often necessary when transferring genes with recessive or additive effects. With MAS it is also possible to conduct multiple rounds of selection in a year, a gain of time of about two backcross generations per year compared to one in PS. Furthermore, MAS can speed up the breeding process by allowing seedling assays, simultaneous selection for multiple traits, and increasing the efficiency of selection by eliminating difficult trait assays.

Although the utility of MAS for manipulating single-gene traits is straightforward and has been well documented, its usefulness for complex traits also has been recognized [451–463]. However, it should be realized that MAS for polygenic trait improvement is in its infancy and transitory phase, and the field is on the verge of producing convincing results. Based on most simulation studies and empirical results, it appears that trait heritability (h^2) and the number-of-QTLs are the most important factors influencing the effectiveness of MAS. MAS seems to be most effective for traits with low h^2 (0.1–0.3) and which are controlled by rather small numbers of QTLs with large effects. It is generally accepted that, in most cases, for a low-heritability trait MAS will give

better selection results than phenotypic selection [457]. In particular, for many quantitative traits, MAS should be useful for pyramiding individual components comprising the complex trait. Thus, it would be more efficient to partition complex traits into their contributing components and identify QTLs for each component before attempting marker-assisted breeding.

4.1. Use of MAS in tomato breeding

The use of MAS in tomato breeding is by no means a new idea. In the early 1980s, many tomato seed companies in the U.S. and abroad took advantage of the reported linkage association between nematode resistance and *Aps-1*¹ locus [270] and used the *Aps* marker for selecting for nematode resistance. More recently, however, MAS has become a reality and to some extent a routine practice in many seed companies for improving tomatoes for many simply-inherited traits as shown in Table 6. Unfortunately, however, most of these activities are not reported in public literature. A survey by the author of some major seed companies in the U.S., including Seminis Vegetable Seeds (now owned by Monsanto), Syngenta, Harris Moran, Sakata and Asgrow, and in Europe, including Nunhems Zaden, Vilmorin, Seminis Vegetable Seeds Holland, ENZA, RijkZwaan and DeRuiter, indicated that MAS was routinely employed for tomato improvement for many qualitatively inherited disease resistance traits. Examples include vertical resistance to diseases such as corky root, fusarium wilt, late blight, root-knot nematodes, powdery mildew, bacterial speck, tobacco/tomato mosaic virus, tomato spotted wilt virus, and verticillium wilt (see Table 6). Many of these seed companies indicated that for several of the resistance traits MAS was not only faster than PS but in some cases was also cheaper and more effective. Accordingly, MAS is also practiced for improvement of tomato for some other simple-inherited traits such as jointless, ripening, and carotenoid content (lycopene and beta carotene). However, there is very little indication of the use of MAS in seed companies for manipulating QTLs for complex traits, although it seems that it is being attempted to improve quantitative resistance to bacterial wilt, bacterial canker, bacterial wilt, powdery mildew and yellow leaf curl virus as well as to improve fruit soluble solids (°Brix).

The use of MAS is much less common in public tomato breeding programs, although it has been practiced to improve vertical resistance to a few diseases such as late blight (M Mutschler, Cornell University; R Gardner, NC State University; Foolad, Penn State University), bacterial canker, bacterial speck and bacterial spot (D Francis, Ohio State University; [287, 447], and horizontal resistance to blackmold [288] and late blight [342]. It also has been used infrequently for simple inherited traits such as self pruning (e.g., in a few tomato genetics and breeding programs in the US) and complex fruit quality traits [464]. However, based on the published research, in most cases where MAS was employed to transfer QTLs there were major problems associated with the derived lines in terms of their horticultural value. For example, in case of late blight resistance where three NILs were developed each containing one resistance QTL on an

introgressed interval of 6.9, 8.8, or 15.1 cM from *L. hirsutum*, while all three lines exhibited expected level of resistance, they also suffered from undesirable horticultural characteristics [342]. Further inspections of the NILs resulted in the detection of QTLs for other characteristics such as plant shape, canopy density, maturity, fruit yield, or fruit size in the same introgressed regions. The results prompted the authors to suggest further refining of the QTLs before transferring to adapted genetic backgrounds. Similar conclusions were made regarding MAS transfer of QTLs for blackmold resistance from *L. cheesmanii* to the cultivated tomato, as negative associations were found between introgressed QTL alleles and horticultural characteristics [288]. Such undesirable associations were reported for some other complex characteristics in tomato (e.g., [242, 465]), and in most cases it was not clear whether they were due to genetic linkage or pleiotropic effects. With the current state of QTL identification, it is not unexpected that similar problems would arise if practicing MAS for other complex traits in tomato. Before MAS becomes a routine procedure for improving complex traits in tomato, issues surrounding its utility must be addressed.

4.2. Issues in using MAS

For almost two decades, MAS has been claimed as an effective alternative to PS for crop improvement. As indicated earlier, the successful use of MAS for manipulating single-gene traits has been well documented. However, despite tremendous investment in finding markers associated with important genes and QTLs, MAS has not yet become a routine procedure in most plant breeding programs, in particular for improving complex traits. The associated problems/issues with the use of MAS are several fold, including: (1) elevated cost of high-throughput marker genotyping, which makes MAS not affordable by most breeding programs. However, with advancements in technology and availability of more ESTs, microarrays and DNA sequences, this does not seem to be a permanent problem. (2) Unavailability of closely-linked markers for many traits for which markers have been reported. Loosely linked markers are not useful because of crossovers between markers and the genes or QTLs of interest. This is particularly a serious problem when genes or QTLs to be transferred are found within wild species. (3) Unavailability of reliable PCR-based markers for many simple as well as complex traits. Markers that are expensive and need extensive work to determine, for examples, RFLPs or AFLPs, are not useful in most plant breeding programs where often large populations need to be screened. In tomato, PCR-based markers are available only for a handful of traits (mainly a few disease resistance traits). (4) Lack of validated QTLs for most complex traits. Generally, markers are as good as phenotypic screenings that are used to identify them. For low-heritability traits, for which MAS is claimed to be most helpful, identification of reliable QTLs is not easy unless replicated experiments are conducted across populations and environments. The utility of MAS for complex traits depends on the availability of reliable and precisely delineated QTL intervals. Despite the identification of QTLs

for many traits in tomato, only for a few traits the identified QTLs have been verified. (5) Large size of QTL intervals and association with undesirable traits due to “linkage drag.” This is in particular a major problem when transferring genes or QTLs from wild species into the cultigen. (6) Limited molecular marker polymorphism within the cultivated species of tomato. Many tomato breeding programs largely exploit variation within the cultivated tomato. Lack of sufficient marker polymorphism within the cultigen has hindered the use of marker technology. However, with advancements in the marker technology and identification of more resolving DNA markers, this is not expected to be a major problem in future. (7) Unfamiliarity of many traditional plant breeders, who in fact release most of the modern cultivars, with the use of markers, or their limited access to molecular marker laboratories. (8) Identification and mapping of genes and QTLs mainly by researchers who are not breeders or do not have inherent interest in crop improvement. It seems that better cooperation between basic researchers and plant breeders is needed to coordinate meaningful identification and usage of gene/QTL-linked markers. However, from among all these issues, a primary limiting factor in the use of MAS in tomato breeding is the lack of adequate marker polymorphism in the cultivated species or between the cultivated species and closely related species such as *L. pimpinellifolium* and *L. cheesmanii*. Many tomato breeders focus primarily on exploitation of genetic variation among the elite lines or within the cultigen. A good example is the case of resistance genes for tomato bacterial spot (caused by *Xanthomonas campestris* pv. *vesicatoria*) which have been identified either in *L. esculentum* or *L. esculentum* var. *cerasiforme* [68]. In such cases, MAS cannot be easily employed using traditional molecular markers such as RFLPs, CAPS, or AFLPs. However, the current and recent development in discovering SNPs within the cultivated species of tomato are expected to reduce or rectify this problem and facilitate the use of markers in tomato breeding programs exploiting intraspecific genetic variation.

5. POSITIONAL CLONING OF GENES

Positional cloning has been practical in tomato because of the rather low ratio of physical-to-genetic distance (average ~750 kb/cM). In fact, as most tomato genes are located in the euchromatic regions of the genome, which constitute only about one fourth of the tomato genome [484], this ratio is much smaller for the genetically active fraction of the genome. Tomato was the first plant species in which a disease resistance gene, *pto*, conferring resistance to bacterial speck caused by *Pseudomonas syringae* pv. *tomato* (*Pst*), was cloned using map-based cloning approach [56]. Further analysis of this gene indicated similarity of its ORF to serine-threonine protein kinases (see Table 7; [57, 468]). Subsequently, a similar map-based cloning strategy was employed and several other tomato genes were cloned, including *Prf*, which is required for *Pto* activity and tomato resistance to *Pst* and which also confers tomato susceptibility to organophosphate insecticide Fenthion [317, 485], *Sw-5*, conferring resistance to tospovirus [483], *sp* (*self prun-*

ing; [170]), members of *sp* gene family [169], and *j* and *j-2*, controlling jointless pedicel [476]. It should be noted that both *j* and *j-2* are recessive mutants that completely suppress the formation of pedicel abscission zones [176, 432, 476–478]. As indicated earlier, *jointless* pedicel is an essential character and widely used in the processing tomato industry as it aids mechanical harvesting and prevents physical wounding during transportation. *Jointless* pedicel is also becoming highly desirable in fresh market tomato cultivars. In addition, during the past decade, several other major genes in tomato have been fine-mapped and/or cloned via map-based cloning approach, as shown in Table 7. Large-insert DNA libraries are essential to isolate genes and QTLs by map-based cloning. Thus, large-insert bacterial artificial chromosome (BAC) or plant-transformation-competent binary BAC (BIBAC) libraries have been constructed for several genotypes of the cultivated tomato, including cv. Mogoer [53]; (<http://hbz7.tamu.edu>), cv. Heinz 1706 and cv. LA3023 [52]; (<http://www.genome.arizona.edu>; <http://www.genome.clemson.edu>), and *L. pennellii* accession LA716 and *L. cheesmanii* accessions LA166 (<http://hbz7.tamu.edu>) and LA438 (<http://www.genome.arizona.edu>). A complete list of available tomato libraries can be found at the SGN (<http://www.sgn.cornell.edu>). The large-insert libraries have been used for different purposes in tomato genomics research, including physical mapping, map-based cloning and sequencing.

6. POSITIONAL CLONING OF QTLs

Most QTL experiments often detect QTLs within rather large marker intervals, usually 10 cM or greater. The genetic and physical natures of most such QTLs are not known. For example, often it cannot be determined whether a detected QTL contains one gene or several tightly linked genes affecting the same trait. Also, detected QTLs may affect more than one trait and often it is unknown whether such effects are due to pleiotropic effects of the same gene or linkage of several independent loci. In tomato, for example, the lower part of chromosome 1 has been identified to affect many agriculturally important traits, including various morphological and fruit quality characteristics as well as resistance to many biotic and abiotic stresses [405, 406]. Similarly, the long arm of chromosome 4 contains QTLs for many horticulturally important traits such as fruit soluble solids content, shape and lycopene content [304]. Furthermore, it has been shown frequently that introduction of a small segment of DNA from a tomato wild species into the cultivated tomato results in significant changes in several characteristics [234, 238, 288, 342]. Earlier QTL studies were unable to determine how many genes would control each character or whether same genes could affect more than one trait. During the past several years, however, advancements in marker technology have facilitated physical characterization of QTL segments in tomato. For example, a NIL of tomato containing a 40-cM introgression at the bottom of chromosome 1 from *L. hirsutum* accession LA1777 was dissected by developing sub-NILs containing smaller introgression segments affecting different traits [405]. In a similar study, a series of

TABLE 7: Fine-mapped and/or cloned genes and QTLs in tomato.

Trait	Gene/QTL	Chromosome	Source species	Fine mapping population	Nature/activity/function	Reference
Aphid (potato) resistance	<i>Meu-1</i>	6	<i>L. peruvianum</i>	NIL F ₂	NBS-LRR	[38, 388, 389]
Bacterial speck resistance	<i>Pto</i>	5	<i>L. pimpinellifolium</i>	NIL F ₂	Serine-threonine protein kinase	[56, 466, 467]
Brix (soluble solids)	<i>Brix9-2-5, Lin5(Q)</i>	9	<i>L. pennellii</i>	NIL F ₂	Apoplasmic invertase	[98, 302, 303]
Fenthion resistance	<i>Prf</i>	5	<i>L. pimpinellifolium</i>	NIL F ₂	NBS-LRR Resistance gene	[317, 468]
Flower, exerted stigma	<i>se2.1 (Q)</i>	2	<i>L. pennellii</i>	NIL F ₂ and F ₃	Affects several aspects of floral morphology	[307]
<i>Fr. color (β-carotene)</i>	<i>B</i>	6	<i>L. pennellii</i>	NIL F ₂	Lycopene β-cyclase	[131, 299]
<i>Fr. color (crimson)</i>	<i>og^c, cr</i>	6	<i>L. esculentum</i>	NIL F ₂	Lycopene cyclase null allele	[131, 299]
<i>Fr. color (high-pigment-2)</i>	<i>hp-2</i>	1	<i>L. esculentum</i>	N/A	Homologue of deetiolated 1	[413]
<i>Fr. color (old gold)</i>	<i>og</i>	6	<i>L. esculentum</i>	NIL F ₂	Lycopene cyclase null allele	[131]
<i>Fr. color (tangerine)</i>	<i>CRISTO</i>	10	<i>L. esculentum</i>	NIL F ₂	Carotenoid isomerase	[301]
<i>Fr. ripening (colorless non-ripening)</i>	<i>Cnr</i>	2	<i>L. esculentum, L. cheesmanii</i>	F ₂ and FISH	ND	[420]
<i>Fruit ripening (never ripe)</i>	<i>Nr</i>	9	<i>L. esculentum</i>	NIL F ₂	Blocks ethylene perception	[421–423]
<i>Fruit ripening (nonripening)</i>	<i>nor</i>	10	<i>L. esculentum</i>	NIL F ₂	MADS-box transcription factor	[153, 424, 425]
<i>Fr. ripening (polygalacturonase)</i>	<i>TOM6</i>	10	<i>L. esculentum</i>	N/A	Pectin hydrolyzing	[157, 418, 469]
<i>Fruit ripening (ripening inhibitor)</i>	<i>rin</i>	5	<i>L. esculentum, L. cheesmanii, L. pennellii</i>	NIL F ₂	MADS-box transcription factor	[153, 424, 425]
Fruit shape	<i>fs8.1 (Q)</i>	8	<i>L. pimpinellifolium</i>	NIL F ₂	Imparts blocky, elongated shape	[438, 470]
	<i>Sun (Q)</i>	7	<i>L. esculentum</i>	NIL F ₂ and F ₃	Imparts oval shape	[306, 470, 471]
	<i>ovate (Q)</i>	2	<i>L. pimpinellifolium</i>	NIL F ₂	Plant-growth suppressor	[428, 439, 470]
Fruit weight	<i>fw2.2 (Q)</i>	2	<i>L. pennellii</i>	NIL F ₂	Controls carpel cell number	[305, 435, 470, 472–474]
Fusarium wilt resistance	<i>I2</i>	11	<i>L. esculentum</i>	NIL F ₂	Leucine zipper and LRR-NBS	[335]
Growth habit	<i>PW9-2-5 (Q)</i>	9	<i>L. pennellii</i>	F ₂	Semi-determinate growth	[303]
Iron uptake	<i>chloronerva</i>	1	<i>L. pennellii</i>	NIL F ₂	Nicotianamine synthase	[475]

TABLE 7: Continued.

Trait	Gene/QTL	Chromosome	Source species	Fine mapping population	Nature/activity/function	Reference
Jointless	<i>j</i>	11	<i>L. esculentum</i>	F ₂ , NIL F ₂	Suppress formation of pedicel abscission zone	[176, 431, 476, 477]
	<i>j-2</i>	12	<i>L. cheesmanii</i>	F ₂	Suppress formation of pedicel abscission zone	[432, 478]
Leaf mould resistance	<i>Cf-2, Cf-4, Cf-5, Cf-9</i>	1,6	<i>L. peruvianum</i>	NIL F ₂	LRR	[479]
Nematode (rootknot) resistance	<i>Mi-1.1, Mi-1.2</i>	6	<i>L. peruvianum</i>	NIL F ₂	NBS-LRR	[38, 312, 388, 389]
Self pruning (<i>sp</i>)	<i>sp</i>	6	<i>L. esculentum</i>	NIL F ₂	Regulate cycle of vegetative and reproductive growth	[170]
<i>sp</i> gene family	<i>sp21, sp3D, sp5G, sp6A, sp9D</i>	2,3,5,6,9	<i>L. pennellii</i>	NIL F ₂	Not determined	[169]
Self incompatibility	<i>S</i>	1	<i>L. peruvianum</i>	N/A	RNase activity	[480]
Tomato spotted wilt virus	<i>Sw-5</i>	9	<i>L. peruvianum</i>	NIL F ₂	NBS-LRR Resistance gene	[481–483]

sub-NILs were developed for tomato chromosome 1 containing introgressions from *L. chmielewskii* to fine-map loci controlling a number of fruit quality characteristics important to processing tomato varieties [406]. By such substitution mapping studies, it was determined that in the lower part of tomato chromosome 1 independent genetic loci affected fruit soluble solids ($^{\circ}$ Brix), yield and fruit shape, whereas genetic factors affecting fruit weight, shoulder pigmentation, and external color coincided with the location of a $^{\circ}$ Brix locus. These results, combined with results of other studies, prompted the authors to conclude that the base of tomato chromosome 1, which exhibits significant effects on various agronomic and fruit quality characteristics, contains multiple QTLs whose effects can not be attributed to the pleiotropic effects of a single locus [405, 406]. In another study, NILs containing the lower part of chromosome 4 from either *L. peruvianum* or *L. hirsutum* were dissected by developing series of sub NILs containing small introgressions from either of the two wild species [304]. Results of this study indicated the presence of multiple, loci controlling soluble solids and fruit weight and other loci controlling fruit shape, fruit weight and epidermal reticulation which colocalized to the same portion of chromosome 4 and could be attributed to pleiotropy and/or gene-dense-area with low frequency of recombination. Many similar QTL coincidences have been observed in tomato and other crop species, however, in most cases the nature of such coincidences have yet to be determined.

During the past decade, efforts have been made to clone QTLs and determine whether QTLs have the same molecular basis as Mendelian genes [486]. Much of such efforts have been made in tomato as a model species. For example, the first map-based cloning of a QTL in plants was carried out in tomato for a fruit size QTL (*fw2.2*) by [305]. While tomato improvement for fruit size has been relatively easy due to its high heritability [487], the inheritance (e.g., [488]) and QTL mapping studies (e.g., [414, 465]) have revealed that this trait is controlled by many loci. To date, most, if not all, QTLs involved in the evolution of tomato fruit size (from small to large) have been identified and mapped (see Table 4). In many studies, one major QTL (known as *fw2.2*) was found to be associated with large phenotypic variation for fruit size [414, 465]. While the modern tomato cultivars carry large-fruit alleles at this locus, all wild *Lycopersicon* species examined contain small-fruit alleles [435]. Because of its large, consistently detectable effects, significant efforts were made to clone and characterize this QTL [305]. In a complementation test, when a cosmid obtained from *fw2.2* region of a small-fruited wild species (*L. pennellii*) was transformed into large fruited cultivars, it resulted in reduction in fruit size. By applying a map-based cloning approach, *fw2.2* was cloned, sequenced, and characterized [305, 473, 474]. Furthermore, it was determined that this gene was expressed early in floral development and controls carpel cell number. Following this remarkable advancement, similar strategy has been used in tomato to fine map and/or clone a few other QTLs affecting

traits such as soluble solids content, fruit shape, and exerted stigma, as shown in Table 7. However, it is expected that with advancements in marker technology and QTL identification, more and more QTLs will be fine-mapped and cloned using positional cloning strategy.

7. TOMATO GENOME ORGANIZATION AND SEQUENCING

The tomato nuclear genome comprises 12 chromosomes and approximately 950 Mbp of DNA, containing 59% non coding sequences, 28% coding sequences, 11% transposons, and 2% organellar sequences [484]. Approximately 77% of the chromosomal DNA is comprised of centromeric heterochromatic regions, which are devoid of genes [484, 489]. The tomato genome is estimated to encode ~35,000 genes, majority of which are populated at distal euchromatic regions of the chromosomes [8, 46, 490] with an approximate gene density of 6.7 kb/gene, similar to that of *Arabidopsis* and rice [484]. The latter study [484] also indicates that a significant portion of the tomato euchromatin is methylated in the intergenic spacer regions. Currently the 12 tomato chromosomes are being sequenced by an international consortium of 10 countries, including China (chr. 3), France (chr. 7), India (chr. 5), Italy (chr. 12), Japan (chr. 8), Korea (chr. 2), The Netherlands (chr. 6), Spain (chr. 9), United Kingdom (chr. 4), and the U.S. (chrs. 1, 10 and 11) (http://www.sgn.cornell.edu/help/about/tomato_sequencing.pl). This effort is part of a larger initiative known as the International Solanaceae Genome Project (SOL): Systems Approach to Diversity and Adaptation. Lunched in 2003, this project has set ambitious research goals for the next 10 years, including physical, evolutionary, and functional genomics of the family Solanaceae [491]; (<http://www.sgn.cornell.edu/solanaceae-project/index.pl>). The first cornerstone of the project, however, is to determine a high-quality sequence for the euchromatic portions of the tomato chromosomes as a reference for the Solanaceae. To date (March 2007), about 17% of the target regions have been sequenced (<http://sgn.cornell.edu>). Concomitantly, other genome organizations studies are being conducted in tomato, including efforts to expand EST database of tomato. To date, more than 214 000 ESTs have been developed (<http://compbio.dfci.harvard.edu/tgi/cgi-bin/tgi/gimain.pl?gudb=tomato>). Although the EST-derived unigene sets of tomato do not represent the entire gene repertoire of this species, analysis of the tomato EST database and several sequenced BAC libraries have led to the prediction that tomato genome encodes ~35 000 genes, largely sequestered in euchromatic regions of the 12 tomato chromosomes, which correspond to less than 25% of the total nuclear DNA in tomato [8, 484]. Recently, Syngenta has mapped 17 000 BACs to the *L. esculentum* × *L. pennellii* ILs and made the data available to the tomato sequencing project (ftp://ftp.sgn.cornell.edu/tomato_genome/bacs/syngenta).

8. CONCLUSION AND FUTURE PROSPECTS

During the past two decades, remarkable progress has been made in tomato molecular marker research, including development of markers and maps, mapping of genes and QTLs, comparative analysis, generation of large insert libraries, fine-mapping and map-based cloning of genes and QTLs, and genome sequencing and organization. A primary goal of molecular mapping has been to use markers as indirect selection criteria for crop improvement. Comparatively, however, little has been reported as to the actual use of markers in tomato breeding, in particular for improvement of complex traits. Potential reasons for this deficiency were discussed above. However, based on most recent discoveries and research progresses, it seems that the prospect for routine application of markers in tomato breeding in the future is good. Perhaps the most important factor is development of markers that are more resolving and easier to use in breeding programs. High-throughput marker systems that are easy to assay, PCR based, and can detect polymorphism between closely related genotypes are forthcoming. In particular, it is expected that more SNP markers will be available, which will detect polymorphism among elite tomato germplasm and will gain utility in marker-assisted breeding in tomato. It is also expected that with further advancements in molecular marker technology, the cost of marker development will continue to decline, making them more economical. Furthermore, as the sequencing of the tomato genome progresses, the information will be used to develop additional sequence-based high-resolving markers. It is also expected that a greater emphasis will be placed on development of functional markers, including PCR-based ESTs and candidate genes, which will be highly useful to both applied and basic research programs. Thus, it is not unlikely that in a near future MAS becomes a routine procedure in many tomato breeding programs, in particular for improvement of many simply inherited traits. Many breeders are convinced that even for many simple traits with high heritability MAS has an edge over PS because of various potential limitations in phenotypic screening. Current use of MAS for improvement of many such traits in commercial seed companies, where funding is often less limited than in public tomato breeding programs, supports this assessment.

Unlike for simple traits, there is little evidence of the use of markers for improving complex characteristics in tomato. Two major limiting factors are unreliability of QTLs and linkage drag, as discussed above. For many complex traits, such as yield or tolerance to abiotic stresses, obtaining reliable phenotypic data for QTL mapping is not straightforward, often leading to the identification of QTLs which may not be reproducible and thus of little value. Improvements ought to be made in our ability to identify more tractable QTLs for complex traits. One approach is to identify QTLs controlling individual components of complex genetic variation, rather than detecting QTLs based on the ultimate trait(s). For example, partitioning of the total genetic variation for a complex trait into its physiological and developmental components would lead to detection of QTLs for individual components, which may be more tractable and

useful. A subsequent necessary step to streamline the use of QTLs is to further refine QTL positions by development of NILs and sub-NILs. Such fine mapping may not only establish the actual value of individual QTLs, but also may determine whether any potential negative association with undesirable genes could be broken before transferring QTLs. In other words, fine mapping would allow detection of QTLs that are useful for marker-assisted breeding. The importance of such refinements is well recognized among geneticists and breeders and many research programs have initiated such activities. It is the author's expectation that in a not-too-distant future we will witness a greater application of marker technology to tomato crop improvement for simple as well as complex characteristics. Another reason to be optimistic is the increasing use of F₁ hybrid cultivars for commercial production. When developing hybrids, the use of MAS will not only be more practical but also more economical. However, despite all expected advancements in the marker technology, I do not anticipate that MAS will be a "silver bullet" solution to every breeding problem in tomato. Most likely, in future, a combination of traditional breeding protocols and marker-assisted breeding will become a routine procedure for tomato crop improvement.

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