

1.15 Fruit Quality

For processing tomato, fruit soluble solids content, pH, and paste viscosity are the major quality traits. According to distributors and retailers, fruit quality is essentially defined by shelf-life and firmness. During recent years, these criteria have been taken into account for breeding but have led to flavorless fruit. For consumers, quality is defined by the traits governing fruit attractiveness and fruit flavor. Nutritional quality (e.g., antioxidants, vitamins) is also important (See Sect. 1.14) but cannot be directly evaluated by consumers. Fruit size, shape, color and firmness are the first quality traits which attract consumers by visual and tactile stimulation. When eaten, the fruit expresses its organoleptic quality which involves the senses of taste and smell. Organoleptic quality is complex as it results from a combination of aroma, taste and texture components. These traits are often difficult to measure by methods other than sensory analysis. Some of the quality components are associated with each other, which makes the analysis even more complex. However, some of the major components of tomato flavor can be assessed by physical or chemical measurements. For example, flavor depends on the ratio of sugars and acids, and aroma is related to certain volatile compounds (Baldwin et al. 1998).

The large diversity in fruit size and shape of tomato illustrates the genetic variability available in this species. Each cultivar is characterized by a particular aroma profile, and a specific range of taste and texture. Genetic variation is the major source of fruit quality variation (Stevens 1986; Causse et al. 2003), but fruit organoleptic quality is also influenced by external factors such as the environment (Dorais et al. 2001) and conditions during fruit storage (Stern et al. 1994).

Identifying “robust” quality QTLs is a prerequisite for molecular breeding or for their molecular characterization. This robustness can be assessed by experimental studies of their stability over years, over different external conditions and over genetic backgrounds. These “robust” QTLs can also be identified by comparing data from different experiments and/or obtained with different populations. Molecular characterization of QTLs to date has been performed by positional cloning, but new genomic tools are starting to be applied for identifying candidate genes related to QTL variation.

1.15.1 Gene/QTL Mapping of Fruit Quality

Most tomato fruit quality traits are quantitatively inherited. Many studies have been performed by the groups of S. D. Tanksley (Cornell University, USA) and D. Zamir (The Hebrew University of Jerusalem, Israel) to map QTLs controlling yield and fruit quality related traits (Paterson et al. 1988, 1990, 1991; Azanza et al. 1994; Eshed and Zamir 1995; Goldman et al. 1995; Grandillo and Tanksley 1996b; Tanksley et al. 1996; Fulton et al. 1997, 2000, 2002a; Bernacchi et al. 1998b; Chen et al. 1999; Doganlar et al. 2002c; Frary et al. 2004). These studies were all performed on progeny derived from interspecific crosses between wild tomato species and processing tomato inbreds. Some quality traits of interest for processing tomato are common to fresh market tomato (e.g., sugar content, soluble solids content, pH, acidity, firmness) and QTL locations can be compared across the progenies. In most of the studies QTLs were detected, sometimes with strong effects. A few QTLs explaining a large fraction (20 to 50%) of the phenotypic variation, acting in concert with minor QTLs, are usually detected. Most of the QTLs act in an additive manner, but dominant and overdominant QTLs were detected (Paterson et al. 1988, 1991; de Vicente et al. 1993; Semel et al. 2006). Epistasis (interaction among QTLs) is rarely detected unless a specific experimental design is used (Eshed and Zamir 1996).

Fruit Weight and Fruit Shape QTLs

Grandillo et al. (1999) summarized the results of QTL mapping for fruit weight obtained in 17 studies based on progeny of various types and involving seven wild species. According to the studies, three to more than 18 QTLs were detected. Six QTLs explained more than 20% of the phenotypic variation. A common set of 28 QTLs could be identified that frequently segregated in at least two populations. Nevertheless only QTL cloning and complementation permits determination of whether each consensus QTL location corresponds to a single gene. Lippman and Tanksley (2001) studied progeny based on a cross between two genotypes of extreme fruit size. None of the detected six QTLs mapped to a novel location, but this was the first time that these six QTLs were detected together.

For fruit shape, Grandillo et al. (1999) identified a common set of 11 QTLs from the six studies where the fruit length:diameter ratio was segregating. In another study, three major QTLs were identified, *ovate*

on chromosome 2, *sun* on chromosome 7 and *fs8.1* on chromosome 8 (van der Knapp et al. 2002). Locule number is another major component of fruit size. Several QTLs have been mapped for this trait (Lippman and Tanksley 2001; van der Knaap and Tanksley 2003; Barrero and Tanksley 2004) the major two corresponding to the mutations *fasciated* on chromosome 11 and *lc* on chromosome 2. A strong epistatic interaction between these two genes was shown, with locule number considerably increasing when both loci were homozygous for the alleles increasing locule number (Lippman and Tanksley 2001).

Sugar and Acid Content QTLs

Chromosomal regions carrying QTLs for sugar content or related traits (Brix°, fructose, glucose, or sucrose content), based on 14 populations involving eight different species (Paterson et al. 1988, 1990, 1991; Azanza et al. 1994; Eshed and Zamir 1995; Goldman et al. 1995; Grandillo and Tanksley 1996b; Tanksley et al. 1996; Fulton et al. 1997, 2000, 2002a; Bernacchi et al. 1998b; Chen et al. 1999; Saliba-Colombani et al. 2001; Doganlar et al. 2002c; Causse et al. 2004; Frary et al. 2004) are summarized in Fig. 7. From three to 19 QTLs were detected per progeny, with a total of 95 QTLs concentrated in 56 chromosomal regions. For the majority of QTLs the wild species alleles increased the trait value. In 28 regions, QTLs were detected in more than one population, and may possibly correspond to the same QTL. But the large number of regions involved suggests that many mechanisms are responsible in increasing fruit sugar content. The same results were obtained for acid content (Causse et al. 2002, 2004; Fulton et al. 2002a), with only a few regions common to acid and sugar content. In contrast, frequent colocations between QTLs for sugar content and fruit weight (Grandillo et al. 1999) with opposite allelic effects could be detected, suggesting pleiotropic effects of some common QTLs.

Levin et al. (2000) described a locus, *Fgr*, that modulates the fructose-glucose ratio in mature fruit, with a *S. habrochaites* allele yielding a higher ratio. More recently, Levin et al. (2004) showed that alleles of *S. habrochaites* at two loci interacted to increase this ratio. These loci remain to be characterized.

Fruit Firmness QTLs

Firmness is an important trait for fruit quality. It is related to shelf-life and to fruit texture, and thus has been frequently measured in genetic studies. Several

long shelf-life mutants have contributed to the understanding of fruit maturation (Giovannoni 2001, 2004; Seymour et al. 2002). The first to be described, *Never ripe* (*Nr*, Rick 1956) was the first cloned (Wilkinson et al. 1995). The *Nr* gene encodes a protein homologous to ETR1 in *Arabidopsis*. ETR1 is an ethylene receptor, explaining the phenotype of the *Nr* mutant, which is insensitive to ethylene. The mutants ripening-inhibitor (*rin*, Robinson and Tomes 1968) and non-ripening (*nor*, Tigchelaar et al. 1973) are defective in ethylene biosynthesis. The corresponding genes encode MADS-box transcription factors (Vrebalov et al. 2002). The *Colourless nonripening* (*Cnr*) mutation, modified in cell-to-cell adhesion, is an epigenetic mutation in a SQUAMOSA promoter binding protein box (SBP-box) transcription factor (Manning et al. 2006).

Firmness has also been used in quantitative genetic studies. Figure 8 presents a summary of QTLs controlling fruit firmness in nine populations (Tanksley et al. 1996; Fulton et al. 1997, 2000; Bernacchi et al. 1998b; Causse et al. 2002; Doganlar et al. 2002c; Frary et al. 2003b, 2004; Walley and Seymour 2006). Forty-six QTLs controlling firmness were mapped using seven different populations. Firmness was measured by touching (30 QTLs), by mechanical instrumentation (11 QTLs), or by taste (5 QTLs). In some cases the QTLs obtained by these three different methods co-localized. More than half of the QTLs were grouped in clusters of three to four QTLs. These clusters were localized on chromosomes 1, 2, 4, 5, and 9–11. On chromosomes 2, 5, and 10, the genes *rin*, *nor*, and *Cnr* co-localized with firmness QTLs. It would be interesting to discover whether these QTLs are controlled by *rin*, *nor* and *Cnr*.

Volatile Compounds QTLs

QTLs for volatile compounds have been mapped in two populations. Saliba-Colombani et al. (2001) detected QTLs for 12 volatile compounds among 18 that were quantified in the progeny of a cross between cherry tomato inbred line Cervil and larger-fruited inbred line Levovil. Tieman et al. (2006) identified QTLs for 23 volatiles in the population of ILs derived from *S. pennellii*. Twenty-five loci altered in content of one or more volatiles were identified. Although ten volatiles were analyzed in both studies, only three QTLs were detected in the same regions, for phenylacetaldehyde on chromosome 8 (confirming the effect of the QTL *Malodorous*, named by Tadmor et al. 2002), on chromosome 9 for 2-methylbutanol, and

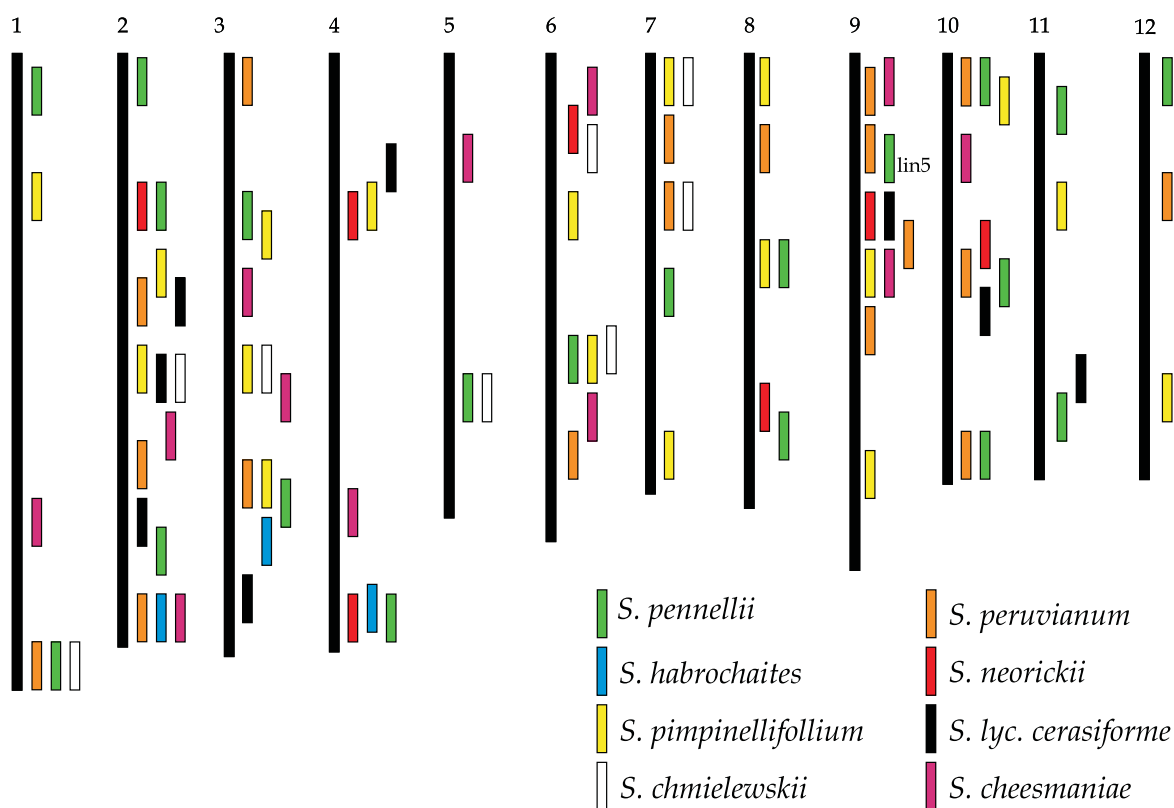


Fig. 7. Summary of QTL for sugar content or related traits (Brix° or hexose content) in one of the following progeny: *S. lycopersicum* × *S. cheesmaniae* F₂ population (Paterson et al. 1991); *S. lycopersicum* × *S. cheesmaniae* recombinant inbred population (Goldman et al. 1995); *S. lycopersicum* × *S. chmielewskii* F₂ and advanced backcross lines (Paterson et al. 1988, 1990; Azanza et al. 1994); *S. lycopersicum* × *S. habrochaites* advanced backcross population (Bernacchi et al. 1998b); *S. lycopersicum* × *S. neorickii* advanced backcross population (Fulton et al. 2000); *S. lycopersicum* × *S. pimpinellifolium* advanced backcross population (Tanksley et al. 1996; Doganlar et al. 2002c); *S. lycopersicum* × *S. pimpinellifolium* backcross populations (Grandillo and Tanksley 1996b; Chen et al. 1999); *S. lycopersicum* × *S. pennellii* introgression lines (Eshed and Zamir 1995; Causse et al. 2004); *S. lycopersicum* × *S. pennellii* advanced backcross population (Frery et al. 2004); *S. lycopersicum* × *S. peruvianum* advanced backcross population (Fulton et al. 1997); *S. lycopersicum* cv *cerasiforme* × *S. lycopersicum* recombinant inbred line population (Saliba-Colombani et al. 2001). The data concerning the advanced backcross involving *S. pimpinellifolium*, *S. peruvianum*, *S. neorickii* and *S. habrochaites* were summarized by Fulton et al. (2002a). The QTLs were positioned on the tomato reference map (Tanksley et al. 1992), based on the nearest marker

on chromosome 12 for pentanol. The content of some volatile compounds appeared strongly variable across years or environments (Tieman et al. 2006). This could partly explain the small number of QTLs common to the two studies. In both studies, QTLs for several volatiles were frequently in clusters. In a few cases these clusters corresponded to volatiles derived from the same metabolic pathway (related to fatty acid, carotenoid or amino acid degradation), suggesting the action of a gene within a single pathway. More frequently, co-localizations of QTLs for volatiles derived from various metabolic pathways were shown, suggesting a regulatory gene acting on several pathways.

Sensory Traits QTLs

Certain cherry tomato accessions have been shown to be most flavorful among tomato cultivars. In order to study organoleptic quality through all of its components, a QTL experiment was designed using the progeny of a cherry tomato line (Cervil, with high quality fruit) and a classical inbred line for fresh market (Levovil, producing large fruit with a common taste) (Causse et al. 2001, 2002; Saliba-Colombani et al. 2001). A population of 144 RILs was developed from crossing these two lines. Progeny were characterized for physical and chemical traits such as color, weight, firmness, pH and titratable acidity, sugars and soluble solids content, concentration of

Vegetables

Kole, C. (Ed.)

2007, XXVIII, 380 p. 55 illus., 5 illus. in color., Hardcover

ISBN: 978-3-540-34535-0