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REVIEW ARTICLE

Genetic and molecular regulation of fruit and plant domestication traits in tomato and pepper

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Abstract

Tomato and pepper are two Solanaceous fruit crops that display an enormous diversity in fruit morphology. In this review, we will present an overview of the history of tomato and pepper and discuss key plant traits that were specifically selected during domestication of the two species. The traits discussed are fruit weight, shape, colour, ripening, pungency and plant architecture. We will review these characteristics as well as the genetic loci or genes that control these features, questioning whether mutations at orthologous loci occurred independently in these two species or whether unique plant and fruit features resulted in selection at different genes.

Key words: Domestication, orthology, pepper, tomato.

Introduction

Domestication is defined as he selection of wild plants and animals for adaptation to cultivation and human use. The domestication process involves the selection of beneficial alleles at a collection of loci underlying yield and quality of the cultivated plant compared to its wild relative. These beneficial alleles were either present in the wild germplasm or arose during the domestication process via spontaneous mutations. For grain crop species, some of the genes underlying domestication traits like yield, shattering, and inflorescence structure have been identified (Doebley *et al*., 2006) and their role in domestication and plant development is currently being investigated. Less is known about the genes underlying domestication and selection in fruit-bearing crops such as those found in the Solanaceae family.

Tomato (*Solanum lycopersicum* L.) and pepper (*Capsicum* spp) are two important Solanaceous fruit crops whose wild forms occupy similar geographic areas and display a similar domestication history. This review covers what is known about key genetic loci and the underlying genes, when known, that were targets for selection during the parallel domestication processes in these two species. In addition, key loci and underlying genes that were not critical for domestication *per se*, but were discovered during the last several hundred years of variety improvements, will be described as well. These findings are reviewed with two questions in mind. (i) To what extent were orthologous genetic loci selected during domestication and variety improvement in tomato and pepper? (ii) Did common and unique attributes of fruit and plant development of tomato and pepper affect the targets of selection in these species? Before the regulation of domestication traits is discussed, a brief overview of the history of tomato and pepper cultivation is provided as well as the key features that were selected by man from the beginnings of agriculture.

Tomato domestication and variety improvement

Tomato originated in the Andes region of South America in an area largely encompassing Peru. Domestication of tomato traces to a Mexican origin of cultivation, although a Peruvian origin has also been proposed (Jenkins, 1948). Through the Spanish conquistadors, tomato was brought to Europe and other parts of the world starting in the early part of the 16th century. The first written record of an early cultivated type appeared in Italy in 1544 as a short paragraph in a manuscript describing a poisonous distant

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relative of tomato, the mandrake. The paragraph details the human consumption of the fruit with oil and salt, thus tomato was already being established in the Italian cuisine at that time (Matthiolus, 1544). In addition, the fruit was described as flattened, segmented, and of yellow colour, hence its Italian name pomi d'oro (golden apple) (Matthiolus, 1544). Other fruit types were documented following Matthiolus's original publication, most notably describing variations in colour as well as size and shape. In North America, tomato became more common in the early part of the 19th century. As in most of Europe, tomato was considered to be poisonous until its acceptance around 1840 as a nutritious vegetable (Gould, 1983).

The fruit of one of tomato's closest wild relatives, *S. pimpinellifolium,* is red, round, and small weighing only a few grams. Fruit from this species is edible and referred to as the currant tomato. The plant exhibits reduced apical dominance and prostrate growth habit resulting in a large shrub with inflorescences carrying many flowers and fruit. The fruit of *S. lycopersicum* subspecies *cerasiforme* is larger than that of *S. pimpinellifolium*, and is, commonly, round and red. This subspecies of tomato is referred to as the cherry tomato and is thought to be the direct ancestor of cultivated tomato because of its diversity, its wide spread occurrence in Central America, and its close genetic relationship with cultivated tomato (Rick, 1995).

Some of the most important features that were selected during domestication and varietal improvement of tomato were fruit appearance and quality, as well as plant architecture and, within the last 100 years, ease of mechanical harvest. Compared with their wild relatives, cultivated *S. lycopersicum* bear fruit that is much larger in size and exhibits an array of shapes: spherical, elongated, pear-shaped, squared, squat, blocky, bumpy, oxheart, and bell pepper shaped (Fig. 1). In addition to the wild-type red, fruit colours range from green and pale yellow to nearly purple in the cultivated germplasm.

Domestication and selection of tomato was also accompanied by changes in plant stature from an unruly shrub to a more erect (upright), apical dominant, and thick-stemmed plant. One especially noticeable feature of plant stature is exhibited by processing tomato varieties compared with the fresh market types (see below).

Pepper domestication and variety improvement

Hot chile pepper was one of the first plants that were domesticated in the Americas. Archeological microfossils derived from pepper found in South and Central America are estimated to be up to 6000 years old (Perry *et al.*, 2007). In the early days of cultivation, chile was used mainly for seasoning and as a medicinal plant whose effect was attributed to the pungency or hotness of the fruit. Today, peppers are consumed fresh or processed as

Fig. 1. Phenotypic diversity of tomato fruit. This figure was kindly supplied by Dr DM Francis.

vegetables and spice. Peppers are also valued as ornamental plants and for extracts used in various pharmaceutical and cosmetic products.

It is generally accepted that the *Capsicum* genus originated in Bolivia and consists of 25–30 species (Eshbaugh, 1993). Five of these *Capsicum* species were domesticated: *C. annuum*, *C. baccatum*, *C. chinense*, *C. frutescens*, and *C. pubescens*. The largest group of varieties is found among the *C. annuum* spp. which are grown worldwide. The wild progenitor of *C. annuum* is thought to be the bird pepper, whose domestication occurred in Mexico (Eshbaugh, 1993). The fruit of wild bird pepper is small (about 1 cm in length), erect, red-coloured, pungent (hot), deciduous (falls of the plant when ripe), and soft-fleshed. These traits contribute to good adaptation for seed dispersal by birds. Moreover, capsaicin, the secondary metabolite responsible for pungency in chile pepper, has been shown to discourage herbivores, but has no repelling effect on more beneficial seed dispersers such as birds (Tewksbury and Nabhan, 2001).

Two of the key traits that were selected during domestication of pepper were non-deciduous fruit that remained on the plant until harvest and the change in position from erect to pendant fruit. This latter change may be associated with an increase in fruit size, better protection from sun exposure, and predation by birds. Other changes associated with domestication and variety improvement were fruit appearance and reduced pungency. While wild peppers can be found in several basic shapes including oval, spherical, or elongated, continued selection resulted in a large increase of shape variation and tremendous increases in fruit mass (Fig. 2). Selection also resulted in yellow, orange, and brown fruit colours in addition to the wild-type red, which occurs in all cultivated pepper species (Fig. 2). Lastly, another important selection was that of non-pungent fruits. Today, fresh

Fig. 2. Phenotypic diversity of pepper fruit.

non-pungent peppers, generally of the bell-types, are economically the most important peppers and are part of the human diet throughout the world (Bosland and Votava, 2000). Bell peppers were first described approximately 500 years ago and the earliest variety used for cultivation was described in 1774 (Boswell, 1937). Non-pungent peppers mostly belong to *C. annuum*. However, sources of non-pungency can be found in the other pepper species (Votava and Bosland, 2002).

Comparative mapping in tomato and pepper

Domestication traits often seem to be controlled by independent mutations at orthologous loci (Paterson *et al*., 1995), although this observation does not hold true in all cases (Li and Gill, 2006). The lack of detailed genome sequences and functional analysis of genes at the selected loci limits a thorough investigation as to whether orthologous genes were indeed selected during the parallel domestication processes of closely related species. However, when two genomes show a high level of synteny (order of genes on the chromosome), orthologous loci and genes are proposed based on colocalization of related quantitative trait loci (QTL) along the chromosomes. Due to a sufficiently high level of gene sequence conservation in pepper and tomato, many molecular linkage map markers that were initially developed for tomato were successfully employed to construct a pepper linkage map, thus facilitating the analysis into the colinearity of these two genomes (Livingstone *et al*., 1999). Although up to 30 break points differentiate the tomato and pepper genomes, the marker conservation is high within each of the chromosomal segments or even entire chromosomes (Livingstone *et al*., 1999). Therefore, within each of the conserved segments, colocalizing loci that control similar traits in the two species are likely to underlie orthologous genes.

Fruit weight

The progenitor species of tomato and pepper bear fruit of much smaller size compared with the cultivated counterparts, and thus, increased fruit size was a major selection criterion in both species. Fruit weight is a quantitatively inherited character and is controlled by many genetic loci, some with a large effect and others with a small effect. The quantitative inheritance of fruit weight has made it challenging to identify the underlying genes, despite extensive studies into the genetics of the trait in tomato and pepper as well as other Solanaceous fruit crops (Grandillo *et al*., 1999*a*; Doganlar *et al*., 2002; Ben-Chaim *et al*., 2006). In tomato, 28 QTL were identified in two or more independently conducted studies (Grandillo *et al*., 1999*a*). Seven QTL explained more than 20% of the phenotypic variance (Grandillo *et al*., 1999*a*; Tanksley, 2004). To date, *fw2.2*, i.e. the second fruit weight QTL on chromosome 2, is the only locus for which the underlying gene has been identified (Frary *et al*., 2000) (Table 1). The large-fruited *fw2.2* allele is present in most, if not all, cultivated tomatoes, and appears to have been present in the wild germplasm prior to the domestication of this crop (Nesbitt and Tanksley, 2002). The function of the protein is proposed to be a regulator of cell division since larger fruit size is associated with more cells per unit tissue (Frary *et al*., 2000). This observation is further supported by the finding that the FW2.2 protein is found at the plasma membrane where it interacts with the beta subunit of CKII kinase, postulated to be involved in the cell cycle signalling pathway (Cong and Tanksley, 2006). In addition to cell number, cell size and ploidy levels are also positively correlated to larger fruit mass (Cheniclet *et al*., 2005). Interestingly, whereas pericarp cell number and cell size does not vary dramatically at the time of anthesis, at the onset of ripening these two parameters vary significantly among cultivated tomatoes carrying different size fruit (Cheniclet *et al*., 2005). This result shows that regulators of cell division and cell size acting predominantly after anthesis underlie the differences in fruit mass observed in tomato varieties.

In pepper, several fruit weight QTLs were detected in crosses of large blocky cultivars with small-fruited accessions (Ben Chaim *et al*., 2001; Rao *et al*., 2003). To date, none of the genes underlying fruit size in pepper have been identified. However, the use of molecular markers that are shared between tomato and pepper allowed comparison of QTL locations in these two species (Zygier *et al*., 2005; Ben Chaim *et al*., 2006). On pepper chromosome 2, a single major QTL, *fw2.1*, maps in the syntenic region as *fw2.1* of tomato (Ben Chaim *et al*., 2006). By contrast, the locus syntenic to *fw2.2* does have

Table 1. *Genes selected during domestication and varietal improvement of tomato and pepper*

Locus	Chromosome	Crop	Trait	Function/underlying gene	Reference
fw2.2	2	Tomato	Fruit weight	Regulation of cell division	Frary *et al*., 2000
ovate	2	Tomato	Fruit shape	Negative regulation of plant growth	Liu *et al*., 2002
r	3	Tomato	Fruit colour	Phytoene synthase1	Fray and Grierson, 1993
Delta	12	Tomato	Fruit colour	Lycopene δ-cyclase	Ronen *et al*., 1999
tangerine	10	Tomato	Fruit colour	Carotenoid isomerase	Isaacson *et al*., 2002
Beta	6	Tomato	Fruit colour	Chromoplast-specific lycopene β-cyclase	Ronen *et al*., 2002
old-gold	6	Tomato	Fruit colour	Chromoplast-specific lycopene β-cyclase	Ronen *et al*., 2002
high pigment-1	2	Tomato	Fruit colour	UV damaged DNA binding protein	Liu *et al*., 2004
high pigment-2	1	Tomato	Fruit colour	Homologue of *deetiolated1*	Mustilli *et al*., 1999
c2	4	Pepper	Fruit colour	Phytoene synthase	Thorup *et al*., 2000
y	6	Pepper	Fruit colour	Capsanthin capsorubin synthase	Lefebvre *et al*., 1998
A	10	Pepper	Fruit colour	Anthocyanin2	Borovsky *et al*., 2004
rin	5	Tomato	Fruit ripening	MADS box protein	Vrebalov *et al*., 2002
Green-ripe	1	Tomato	Fruit ripening	Unknown	Barry and Giovannoni, 2006
Never ripe	9	Tomato	Fruit ripening	Ethylene receptor	Wilkinson *et al*., 1995
Pun1	2	Pepper	Pungency	AT3 acyltransferase	Stewart *et al*., 2005
S	10	Pepper	Fruit ripening	Polygalacturonase	Rao and Paran, 2003
self pruning	6	Tomato	Plant architecture	Homologue of *terminal flower1*	Pnueli *et al*., 1998
jointless	11	Tomato	Plant architecture	MADS box protein	Mao *et al*., 2000

an effect on fruit weight variation in pepper, albeit minor. On pepper chromosome 4, two fruit-weight QTLs, *fw4.1* and *fw4.2*, are present. The latter QTL, *fw4.2* maps to the syntenic location of *fw4.2b* in tomato (Monforte *et al*., 2001). Additional pepper QTLs, *fw1.1*, *fw3.1*, *fw8.1*, *fw11.1*, and *fw11.2*, are putative orthologues of tomato fruit weight QTLs. However, detailed comparative mapping of these syntenic loci has not been performed yet to confirm this overlap (Ben Chaim *et al*., 2006). Nevertheless, the significant degree of overlap of fruit weight QTLs in pepper and tomato suggests that selection during domestication for this trait occurred frequently at common genes in both species, even though the magnitude of the effect at the syntenic loci differs. The latter notion is likely due to genetic background effects between varieties and species.

Fruit shape

Like fruit size, shape is also a quantitative inherited character. However, whereas a major fruit weight QTL such as *fw2.2* can contribute up to 30% of the variance in certain populations, major shape QTL can contribute as much as 67% of the variance (Brewer *et al*., 2007), which is particularly helpful when the map-based cloning of the underlying gene is concerned. In tomato, the major loci affecting fruit shape are *ovate*, *sun, fruit shape chr 8.1* (*fs8.1*), *fasciated* (*f*), and *locule number* (*lc*), (Tanksley, 2004). Several minor fruit shape QTLs have been detected as well (Grandillo *et al*., 1999*a*; Van der Knaap and Tanksley, 2003; Brewer *et al*., 2007). Elongated fruit shape is controlled by *ovate*, *sun*, and *fs8.1*. Locule number which also greatly affects fruit shape is controlled by *f* and *lc*. The *ovate* locus imparts pear and elongated-shaped tomato and has been found in several QTL studies (Ku *et al*., 1999; Van der Knaap *et al*., 2002). The gene encodes a protein that negatively regulates plant growth (Liu *et al*., 2002) (Table 1). The pear and elongated-shaped tomatoes carrying *ovate* share the same mutation, suggesting one common progenitor allele (MJ Gonzalo and E Van der Knaap, unpublished data). The *OVATE* gene is cloned from the *S. lycopersicum* subspecies *cerasiforme* variety 'Yellow Pear', which is interesting because it implies that this mutation arose in the progenitor species and was maintained in the cultivated germplasm pool. Over-expression of wild-type *OVATE* in pear-shaped tomato resulted in round fruit and altered plant morphology, but did not affect fruit size and seed set (Liu *et al*., 2002).

The tomato *sun* locus controls fruit elongation and has also been found in several populations (Van der Knaap and Tanksley, 2001; Van der Knaap *et al*., 2002; Brewer *et al*., 2006). The locus affects fruit shape primarily after pollination and fertilization. The elongated shape, measured by calculating the ratio of height to width, is final at 2 weeks post-pollination, suggesting a role in the early stages of fruit set (Van der Knaap and Tanksley, 2001). Detailed fruit shape QTL analysis using a newly developed software program called Tomato Analyzer showed that this locus affects many features of shape including the distal end angle and the proximal indentation area in addition to fruit elongation (Brewer *et al*., 2007).

The locus *fs8.1* is responsible for the elongated and blocky fruit that is characteristic of processing tomatoes (Grandillo *et al*., 1996). In addition, this locus causes pleiotropic fruit shape phenotypes such as increased fruit elongation as well as enhanced fruit bumpiness (Van der Knaap and Tanksley, 2003). The *fs8.1* locus is segregating in many populations, suggesting that the allele at *fs8.1* was selected early during cultivar improvement of tomato (Brewer *et al*., 2007; MJ Gonzalo and E Van der Knaap, unpublished data).

The *f* and *lc* loci control locule number and map to chromosome 11 and 2, respectively (Lippman and Tanksley, 2001; Van der Knaap and Tanksley, 2003; Barrero and Tanksley, 2004; Barrero *et al*., 2006). Interestingly, *lc*, which is also known as *lcn2.1*, maps near *ovate*. However, the *ovate* allele that gives rise to the pear-shaped fruit is not present in those populations, suggesting that *lc* is another allele of *ovate* or encodes a tightly linked gene.

The genetic analyses of elongated fruit shape in pepper identify several QTLs that control this trait. Two major QTLs, *fs3.1* and *fs10.1* that account for up to 67% and 44% of the phenotypic variation, respectively, are detected in multiple populations (Ben Chaim *et al*., 2001, 2003; Rao *et al*., 2003).

Unlike the high level of conservation of QTLs controlling fruit weight in tomato and pepper, only one pepper elongated fruit shape QTL, *fs8.1*, was found in common genomic positions in both species (Ben Chaim *et al*., 2006). The lack of common loci that control fruit shape in pepper and tomato may reflect differences in organ structure and development in the two species. In tomato fruit, the seeds are surrounded by a gelatinous and juicy matrix (gel) whereas in pepper fruit, the seeds are in a hollow and dry area of the fruit. In addition, the placenta to which the seeds are attached forms a central column in the tomato fruit (the septum), whereas in pepper the placenta is attached to the pericarp or valves of the fruit and a central column is lacking. An alternative explanation is that the shape of the fruit can be perturbed by many genes, only a few of which were selected in each crop species. It is known that shape features are more pronounced in larger fruit (Van der Knaap and Tanksley, 2003). Therefore, selection for interesting and novel shapes could only occur after alleles conferring larger fruit were fixed in the population. Thus, this could mean that the shape features exhibited by both species are the result of different trajectories during the last several hundred years of crop improvement. In support of the latter scenario, QTL analysis involving a tomato 'Yellow Stuffer' cultivar with fruit characteristics that are very similar to that of bell pepper did not identify common fruit shape QTLs with the exception of *fs8.1* (Van der Knaap and Tanksley, 2003). In summary, the combined results from the fruit weight and shape studies imply that fruit shape features of tomato and pepper were largely independently derived, whereas fruit size loci arose via mutation at mostly orthologous genes.

Fruit colour

To a large extent, the variation in colour of tomato and pepper fruit is controlled by mutations in the enzymes of the carotenoid biosynthetic pathway. These mutations give rise to easy scorable phenotypes which greatly facilitates the identification of the underlying genes. Moreover, unlike fruit shape and size, for which the biochemical pathways leading to the trait variation are largely unknown, carotenoid biosynthetic proteins can often be predicted based on biochemical studies. The wild-type red colour of the mature fruit of tomato and pepper results from the accumulation of carotenoid pigments. Green unripe fruits contain chlorophyll and carotenoid pigments such as lutein, β-carotene, and violaxanthin, which are also present in leaves. Upon ripening, the chloroplasts are converted into chromoplasts giving rise to the red colour of the ripening fruit. While the red tomato colour is due to the accumulation of lycopene, the red pepper colour results from the accumulation of the xanthophylls capsanthin and capsorubin. These xanthophylls are products that are downstream of lycopene (Fig. 3). Consequently, the differences in the carotenoid biosynthesis pathway in

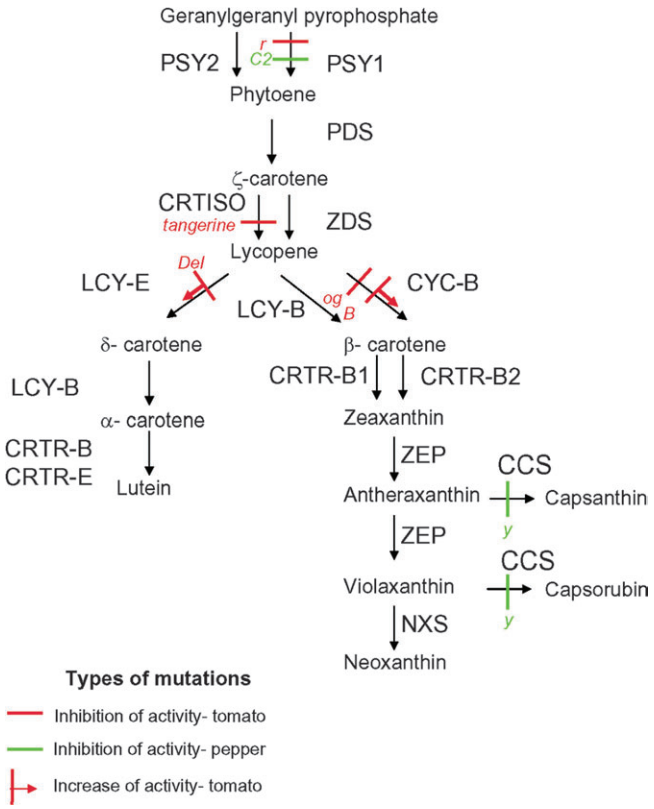

Fig. 3. Carotenoid biosynthesis pathway in tomato and pepper. Genes that are impaired in tomato and pepper fruit colour mutants are indicated by the red and green bars, respectively. The names of the mutant loci are similarly coloured and in italics. The enzymes of the pathway are as follows: PSY1, chromoplast-specific phytoene synthase; PSY2, chloroplast-specific phytoene synthase; PDS, phytoene desaturase; ZDS, ξ-carotene desaturase; CRTISO, carotenoid isomerase; CYC-B, chromoplast-specific lycopene β-cyclase; LCY-B, chloroplast-specific lycopene β-cyclase; CRTR-B1, chloroplast-specific β-ring hydroxylase; CRTR-B2, chromoplast- specific β-ring hydroxylase; ZEP, zeaxanthin epoxidase; CCS, capsanthin capsorubin synthase; NXS, neoxanthin synthase; LCY-E, lycopene δ-cyclase; CRTR-E, δ-ring hydroxylase. This figure has been modified from Galpaz *et al.* (2006), copyrighted by the American Society of Plant Biologists and is reprinted with permission.

chromoplast-containing tissues resulted in the selection of different genes controlling colour variation in these two species.

Yellow-coloured tomato fruit is controlled by the locus *yellow flesh* (*R*) (Table 1). The recessive *r* genotypes carry a mutation in the phytoene synthase1 gene (*PSY1*) resulting in a truncated protein that is unable to convert geranylgeranyl diphosphate to phytoene (Fray and Grierson, 1993). The yellow colour is thought to result from low amounts of yellow carotenoids such as lutein which are normally found in green tissues, and from flavonoids in the skin.

The yellow pepper fruit colour is the result of a mutation in an entirely different enzyme in the carotenoid biosynthesis pathway. The yellow colour is recessive to red and is controlled by the *Y* locus. Linkage analyses showed that *Y* cosegregates with the gene coding for capsanthin capsorubin synthase (CCS) that is responsible for the synthesis of the red carotenoid pigments capsanthin and capsorubin (Lefebvre *et al*., 1998).

Multiple genetic loci control orange fruit colour of tomato. The locus *delta* underlies a gene encoding lycopene δ-cyclase (Ronen *et al*., 1999). The dominant allele confers increased expression of the lycopene δ-cyclase which results in δ-carotene accumulation at the expense of lycopene. The orange *delta* allele originated from the wild species *S. pennellii* (Ronen *et al*., 1999). Another locus that controls orange-coloured tomato fruit is *tangerine*. In the *tangerine* background, *cis*-lycopene and other carotenoids accumulate instead of all-*trans*-lycopene found in the wild-type fruit (Isaacson *et al*., 2002). *TANGERINE* encodes a carotenoid isomerase (indicated as CRTISO in Fig. 3) and its expression is abolished in the mutant (Isaacson *et al*., 2002).

Whereas orange fruit is uncommon in the *S. lycopersicum* germplasm pool, it is the colour exhibited by *S. cheesmaniae* fruit, a wild relative of cultivated tomato that is indigenous to the Galapagos Islands. Introgression of the dominant *beta* allele from *S. cheesmaniae* into *S. lycopersicum* results in orange-coloured fruit that contain 5–10-fold more β-carotene than wild-type fruit. *BETA* encodes a chromoplast specific lycopene β-cyclase (CYC-B) that is expressed during fruit ripening (Ronen *et al*., 2000). A recessive allele of *beta* is allelic to *old-gold* (*og*). This null allele of *beta* results in a complete absence of β-carotene accumulation in fruit, in comparison to 5–10% β-carotene of the total carotenoid pool in wild-type fruit. The *og* mutants exhibit a significant increase in lycopene resulting in deep red tomato fruit (Ronen *et al*., 2000).

The orange fruit colour of pepper is also controlled by multiple loci. One major locus is *C2* which, via linkage analysis, is suggested to encode the gene *PSY*, the orthologue of *PSY1* that confers yellow fruit colour in tomato when mutated (Huh *et al*., 2001; Thorup *et al*., 2000). Whereas the distribution of the carotenoid types in orange Habanero pepper (*C. chinense*) is the same as in red pepper, i.e. capsanthin is the major carotenoid, the quantity of the carotenoids in orange fruit is reduced six times compared with that of the red fruit (Huh *et al*., 2001). The low level of carotenoids in the *c2* mutant may be due to a second *PSY* gene, perhaps a homologue of *PSY2* in tomato that is typically expressed in leaves but also at low levels in ripening fruit. A pepper orthologue of *PSY2* has not been found yet, but, based on the conservation of the pathway in tomato and pepper, it is postulated that such a gene exists in pepper and may contribute to carotenoid synthesis in the ripe fruit as it does in tomato. Orange fruit colour of pepper can result from the accumulation of other carotenoids such as β-carotene and zeaxanthin as major pigments. However, detailed genetic analysis of the loci controlling this variation has not yet been conducted.

In addition to mutations directly affecting carotenoid biosynthesis, mutations in genes from other pathways influence the intensity of fruit colour. For example, the brown colour of mature tomato and pepper fruits results from the accumulation of red carotenoids and green chlorophyll pigments. During ripening, chlorophyll is normally degraded, but in the tomato and pepper mutants *green flesh* (*gf*) and *chlorophyll retainer* (*cl*), respectively, chlorophyll degradation is inhibited (Smith, 1950; Kerr, 1956). The loci *gf* and *cl* could correspond to orthologous genes as suggested by common chromosomal assignment (Kerr, 1958; Efrati *et al*., 2005). Future comparative mapping and gene cloning will reveal whether the two genes are indeed orthologous.

Purple fruits of tomato and pepper accumulate higher than usual anthocyanin pigments. In tomato, purple colour is controlled by *Anthocyanin fruit* (*Aft*), a dominant mutation, introgressed from *S. chilense* (Jones *et al*., 2003). Similarly, in pepper, purple colour is controlled by a single dominant gene *A*. The *A* locus was identified as the homologue of *ANTHOCYANIN2* from *Petunia*, a transcription factor controlling the expression of genes in the anthocyanin biosynthesis pathway (Borovsky *et al*., 2004). Recently, *Aft* was shown to be the orthologue of *A* (Levin *et al*., 2007).

Fruit epidermal cells harbour yellow flavonoids as their major pigments (Laguna *et al*., 1999). Pink-coloured tomato fruit is due to the absence of these pigments in the cells of the peel tissue and is conditioned by the *y* locus (Rick and Butler, 1956). When the mutation of *y* is combined with *r*, conferring yellow flesh colour, a pale yellow to almost white tomato fruit is obtained (Rick and Butler, 1956).

Other loci of special interest are conferred by the tomato *high-pigment* (*hp*) mutations in which the production of carotenoids, flavonoids, and vitamins are elevated. The *hp-1* and *hp-2* underlie mutations in proteins active in light signal transduction. *HP-2* encodes the tomato

orthologue of the *Arabidopsis* nuclear protein DEETIOLATED1 (DET1) (Mustilli *et al*., 1999), while *HP-1* encodes the tomato orthologue of the *Arabidopsis* UV DAMAGED DNA BINDING protein (DDB1) that interacts with DET1 (Lieberman *et al*., 2004; Liu *et al*., 2004). Enhancement of carotenoid accumulation in both mutants probably results from increased number of plastids. Because of their enhanced nutritional quality such as high content of vitamins A and C, varieties containing *hp* mutations have been developed (Wann, 1997). However, the *hp* mutations are also associated with negative horticultural effects. Therefore, success in cultivar development has been restricted to processing tomatoes and lycopene-enriched varieties to carry the *hp* alleles. Although variation in colour intensity is known in pepper, the genes controlling this variation have not been characterized and mutations in the pepper *HP* genes are not known. The list of the cloned genes that affect colour is shown in Table 1.

Despite the differences in the carotenoid pathways of tomato and pepper fruits and, consequently, different genes that control fruit colour in these species, it is evident that selection acted on homologous genes. One example is yellow fruit colour in tomato and orange fruit colour in pepper that is conferred by PSY1 and C2 proteins, respectively. These orthologous proteins control the same biochemical function but lead to different colour outcomes. Another interesting example is offered by BETA protein of tomato that, when overexpressed, confers an orange fruit while the null allele confers a deep-red-coloured fruit. BETA is most similar to the chromoplast specific CCS from pepper (86% identical at the amino acid level while only 53% identical to LCY-B, a second chloroplast-specific tomato lycopene β-cyclase) which, when mutated, confers the yellow colour of pepper. The respective genes map to the syntenic region on chromosome 6. Therefore, it is likely that tomato *BETA* and pepper *CCS* are orthologous genes. However, while the tomato enzyme kept its original catalytic activity, the pepper enzyme acquired a new function allowing synthesis of capsorubin and capsanthin by a similar chemical mechanism to lycopene cyclization (Hugueney *et al*., 1995).

Ripening

Fruit ripening involves many biochemical processes leading to the production of carotenoids, aroma compounds, sugars, and fruit softening. Tomato fruit ripening is climacteric, i.e. it is characterized by a burst of respiration at the beginning of the process accompanied by the production of ethylene. In contrast, ripening in pepper is non-climacteric, therefore, tomato ripening mutations that are impaired for aspects of climacteric ripening discussed below have not been observed in pepper.

Several tomato mutants in which the major physiological and biochemical changes associated with ripening are lacking or greatly reduced have been reported. The *ripening inhibitor* (*rin*) and *non-ripening* (*nor*) mutants fail to produce ethylene and have low levels of carotenoids. These fruits remain firm with an extended shelf life. The *RIN* gene encodes a MADS-box protein that is required for climacteric fruit ripening (Vrebalov *et al*., 2002) (Table 1). Both *nor* and *rin* mutant alleles are dominant and operate upstream of ethylene biosynthesis. The role of these proteins is independent of ethylene suggesting that they have the potential to regulate ripening in non-climacteric fruits as well. Fruit softening in the above-mentioned tomato ripening mutants is greatly reduced. This particular feature leads to improved firmness and shelf life and thus, these mutants evoke considerable interest towards cultivar improvement of commercially grown tomatoes. The homozygous *rin* and *nor* plants display an extreme phenotype in that the fruit never ripens. Therefore, plants that are heterozygous at these loci (i.e. weaker phenotype) display delayed ripening which has been utilized for cultivar improvement. The effect of *nor* on ripening inhibition is stronger than *rin*. Therefore, while *rin* is used in large-fruited fresh-market tomatoes, the use of *nor* is restricted mainly to cherry tomatoes.

Additional dominant mutations in which inhibition of ripening is not as strong compared to *rin* and *nor* have been reported. These include *Never ripe* (*Nr*) which encodes an ethylene receptor (Wilkinson *et al*., 1995), and the allelic mutants *Green-ripe* and *Never-ripe2* (*Gr* and *Nr-2*) which display fruit-specific reduced ethylene sensitivity (Table 1). The underlying gene at the *Gr*/*Nr-2* locus is predicted to be membrane localized, evolutionary conserved, and of unknown function (Barry and Giovannoni, 2006). The *Nr* and *Gr* genes are components of the ethylene response pathway and, therefore, are not likely to function in controlling ripening of non-climacteric fruits such as pepper.

In pepper, two ripening-related traits played a significant role during the domestication of this crop. Plants were selected for reduced deciduousness and softness of fruit, which are both characteristics of wild pepper. These characters are controlled by a single locus, *S*. A candidate gene approach led to the identification of the *S* gene as the pepper homologue of the tomato fruit endopolygalacturonase (PG), as tomato *PG* mapped to the *S* in pepper (Rao and Paran, 2003). The tomato *PG* gene codes for a cell-wall modifying enzyme that has a role in changing the texture of the tomato fruit during ripening. In the pepper-mapping population, the soft flesh and deciduous fruit phenotypes were observed together in all segregating individuals, indicating a pleiotropic effect of *PG* on these two traits. Expression of *PG* was detected at the ripening stage in the fruit of wild pepper but not in the non-deciduous cultivars.

Pungency

Pungency results from the accumulation of the capsaicinoid alkaloids in the placenta of the fruit, and is unique to the *Capsicum* genus. The presence or absence of pungency is controlled by one locus, *Pun1* (formerly *C*). The candidate gene underlying *Pun1* was identified from genes that were differentially expressed in pungent versus non-pungent fruits. This candidate gene, *AT3*, encodes a protein with high homology to an acyltransferase and is tightly linked to *Pun1* (Stewart *et al*., 2005) (Table 1). Furthermore, all non-pungent accessions of *C. annuum* examined to date carry the recessive allele which contains a deletion spanning the promoter and first exon of the *AT3* gene. Moreover, virus-induced gene silencing of *AT3* resulted in reduced levels of capsaicinoids. Thus, *AT3* is very likely to underlie *Pun1*. Moreover, the wide distribution of the deletion in *AT3* across *C. annuum* indicates that it occurred early in the domestication of this species. The mechanism by which AT3 controls pungency is unknown. It is possible that AT3 is capsaicin synthase, the last enzyme in the capsaicinoid biosynthesis pathway, postulated to be an acyltransferase. Another gene, *CSY1,* is also suggested to be a candidate for capsaicin synthase despite its lack of similarity to acyltransferases (Prasad *et al*., 2006).

Pungent peppers differ greatly in their capsaicinoid content. A major QTL, *cap*, that controls this variation was detected on chromosome 7 (Blum *et al*., 2003). Because the known capsaicinoid biosynthesis genes do not colocalize with *cap*, this locus may represents a regulator of the pathway.

Plant architecture

For most crop species, plant growth habit changed dramatically as a result of domestication. This phenomenon is perhaps best described in corn where the wild progenitor teosinte exhibits branched shoots compared with modern corn which displays increased apical dominance (Clark *et al*., 2006). Contrary to the corn shoot which is monopodial, the tomato and pepper shoot is sympodial, displaying alternate vegetative and reproductive phases. Most cultivated tomato, including its wild relatives, display an 'indeterminate' growth habit, in which the primary and axillary shoot structure terminates in an inflorescence after which the vegetative shoot growth resumes from the axil of the youngest leaf below the terminated inflorescence and this process reiterates indefinitely (Pnueli *et al*., 1998).

There is substantial variation in the extent of vegetative growth and axillary branching in the cultivated germplasm pool. More extensive vegetative growth is found in the tomato's wild relatives that display highly branched and reduced apical dominance compared with its cultivated counterparts. However, very little is known about the genetic inheritance of this trait despite the fact that breeders select for increased reproductive and reduced vegetative growth. While the strategy of selecting against vegetative growth (resulting in less photosynthates for the developing fruit) often results in reduced total yield, this negative effect is easily offset by the ease of plant care, and reduction in space and nutrient requirements.

One of the most important cultivar improvements that took place in the last century is controlled by a locus that affects tomato plant stature, *SELF PRUNING* (*SP*) (Pnueli *et al*., 1998). In *sp* plants, the sympodial units are progressively terminated at an earlier stage than in the wild type, such that the number of leaves between inflorescences is reduced from three leaves to two leaves, and subsequently no leaves are produced between adjacent inflorescences. This termination results in a compact plant with near-simultaneous fruit set. The *sp* mutation is important for field and processing tomatoes because it allows for mechanical harvesting of the fruit. This allele, however, is not used in greenhouse varieties producing tomatoes for the fresh market. *SP* encodes the homologue of *TERMINAL FLOWER1* and *CENTRORADIALIS* from *Arabidopsis* and *Antirrhinum*, respectively, which maintain the indeterminate state of the apical meristem (Pnueli *et al*., 1998) (Table 1). The pepper orthologue of *SP* was cloned and shown to underlie the *fasciculate* mutation exhibiting a determinate growth habit, and these two loci map to syntenic positions on tomato chromosome 6 (Paran *et al*., 2005).

Other important mutations that permitted large-scale mechanical harvesting of field and processing tomato is at the *jointless* loci. When picked from the vine, wild-type tomato breaks off at the joint on the pedicel, between the proximal end of the fruit and the peduncle. This leaves a small stem segment capable of puncturing other fruit when mechanically harvested and packaged together. A jointless fruit results in separation of the fruit at the proximal end. The two *jointless* loci, *j* and *j2* which map to chromosomes 11 and 12, respectively, control the formation of the pedicel abscission zone. The gene underlying *J* is a member of the MADS box family of transcription factors (Mao *et al*., 2000) (Table 1). The *j* mutant has severe pleiotropic effects, most notably the vegetative reversion of its inflorescence and thus reduction in yield and has not been used in cultivar development. The *j2* locus on the other hand displays only a slight reduction in yield, which is easily offset by the greatly improved mechanical harvesting of varieties carrying this allele. This allele was introgressed from *S. cheesmanii* and maps to the centromere of chromosome 12 (Budiman *et al*., 2004). In combination with *sp*, *j2* has been bred into many processing varieties. This is because the *sp*/*j2* phenotype permits large-scale mechanical harvesting of the fruit, resulting in increases in the cultivation of field and processing tomatoes.

Conclusions

Significant progress has been made in the understanding of the genetic basis of many key fruit and plant traits that were selected during domestication and cultivar improvements of tomato and pepper. Whereas some of the selected traits were species-specific, i.e. pungency in pepper and ripening inhibition in tomato, other traits were selected in both species. Of the common traits, fruit size loci appear to colocalize between these two species, implying that similar genes were selected for domestication to act upon. However, additional studies are needed to confirm this notion. By contrast, fruit shape and colour variation appears to have arisen following different or only partly overlapping trajectories in the two species. Despite extensive studies into the genetic control of selected traits, the molecular bases of many fruit quality and plant architecture features are still largely unknown. Examples of these quality traits include fruit texture, aroma, taste (acids and sugars), yield, firmness, and soluble solids, despite significant efforts in these areas (Eshed and Zamir, 1995; Grandillo *et al*., 1999*b*; Fridman *et al*., 2002; Chaib *et al*., 2006, 2007).

Improvement of varieties will be achieved by the selection of spontaneous and induced mutations similar to the discovery of the *sp* and *rin* loci in tomato. Recently, a new tomato cultivar that displays delayed fruit deterioration (DFD) was described (Saladie *et al*., 2007). In the DFD mutant, fruit softening is greatly reduced while other aspects of ripening remain normal. The trait is associated with the absence of water loss in ripe fruit because of a change in the composition and structure of the cuticle (Saladie *et al*., 2007). It will be important to identify the gene that controls the reduction in water loss in order to improve the understanding of the trait and exploitation of this mutation in cultivar improvement. To identify additional phenotypic variants, large-scale mutagenesis projects are currently underway and will provide ample resources for new variation (Menda *et al*., 2004). Moreover, using reverse genetics tools such as TILLING would allow identification of homologous mutations presently known in tomato, but not in pepper, such as *hp*, *rin*, and *nor*, which would allow a comparison of gene function in both species.

Natural variation that exists within the cultivated germplasm pool will also continue to be exploited in the development of superior cultivars compared with the parental accessions. In addition, significant improvements will result from introgression of beneficial alleles from wild relatives, similar to the *beta* allele from *S. cheesmanii* (Ronen *et al*., 2000) and a brix allele from *S. pennellii* that improved soluble solid content of fruit (Fridman *et al*., 2000). A recent example of the latter is the Cuticular Water Permeability (*CWP1*) gene in tomato. The wild allele of this gene causes microfissures in the fruit cuticle resulting in rapid water loss during ripening (Hovav *et al*., 2007). Varieties containing the wild *CWP1* alleles can be exploited to develop new products such as vine-dried tomatoes. Characterization and exploitation of beneficial variation that exist in wild species remain one of the promising directions in plant breeding, despite the challenges that are associated with the introduction of unfavourable alleles that are linked to the trait of interest.

Future studies utilizing novel germplasm and genomic tools will allow the discovery of new genes important for cultivar improvement of tomato and pepper. Those genes will be used to develop novel value-added varieties and designer fruit to cater to the various industry and consumer needs. In addition, genes that control agriculturally important traits will also lead to further insights into the basic aspects of plant growth and development. Lastly, genes that underlie traits of importance to Solanaceous fruit crops will be of relevance to other plant families by providing a framework towards varietal improvement strategies in the other fruit crop species.

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