6 Molecular Mapping and Identification of QTLs and Genes for Economically Important Traits in the *Capsicum* Genome

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Abstract

Pepper exhibits large phenotypic variation for economically important traits that are mostly quantitatively inherited. In this chapter, we review the quantitative trait locus (QTL) mapping studies focused on plant growth and fruit yield and quality traits. We further review recent developments of genomic resources and genotyping techniques and their utilization for construction of ultra-high-density maps of pepper including newly developed maps established for the less explored *Capsicum* species *Capsicum baccatum*. These studies allowed a comprehensive understanding of the genetic basis for regulation of these traits in pepper and the development of molecular markers linked to favorable genes and their introgression to elite backgrounds.

6.1 Introduction

Pepper consists of a vast variation in morphological traits such as fruit color, size, and shape (Fig. 6.1), fruit quality traits such as metabolic contents of phytonutrients, yield-related traits such as response to biotic and abiotic stresses and shoot growth traits such as flowering time and plant architecture. Mapping the loci governing this variation and identification of the causative genes has been done in the last thirty years by exploiting natural variation that exists within several *Capsicum* species and in a more limited scale by induced variation mostly for flowering and shoot architecture traits. Early mapping studies in pepper have been summarized by Paran et al. (2006) and by Paran (2013). More recent review focused on mapping of economically important traits in the perspective of translational research (Ramchiary et al. 2014). The present chapter will focus on recent mapping studies that utilized newly developed genomic tools as well as on QTL studies for mapping major plant growth and fruit-related traits.

6.2 Ultra-High-Density Maps

With the advent of reference genome sequences of pepper (Kim et al. 2014; Qin et al. 2014) and affordable genomic tools such as single-nucleotide polymorphism (SNP) arrays and low-coverage next-generation sequencing (NGS)-based methods,

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Fig. 6.1 Natural variation of fruit morphology in pepper

several high-density maps have been constructed and used for mapping in pepper in recent years which are described below.

In the study of Han et al. (2016), an ultra-high-density bin map was constructed in a *Capsicum annuum* intraspecific recombinant inbred line (RIL) population from the cross of Perennial and Dempsey. SNP markers were detected by low-coverage (1X) resequencing of the RILs. Over 1 million SNPs were detected between the parents and used to construct a bin map in which all SNPs within a window of defined size were regarded as a bin using the sliding window approach. Using this approach, 2578 bins were used to construct the map that spans 1372 cM. Each of the 12 chromosomes consisted of 154–370 bins per chromosome in an average density of 1 bin/0.5 cM, thus providing a highly saturated map for efficient QTL mapping. A total of 18 plant architecture, leaf, flower, and fruit traits were measured, and a total of 86 QTLs were detected in multiple environments. This study confirmed the results from other QTL analyses for the occurrence of major fruit weight and fruit shape QTLs in chromosomes 2 and 3 (Ben Chaim et al. 2001; Barchi et al. 2009; Chunthawodtiporn et al. 2018).

Two RIL populations, an intraspecific cross of *C. annuum* Early Jalapeno × CM 334 (NM) and an interspecific *Capsicum frutescens* BG2814-6 × *C. annuum* NuMex RNaky (FA) cross, were used to construct ultra-high-density maps (Hill et al. 2015). Polymorphism detection was done using a pepper GeneChip containing 31,196 unigene expressed sequence tags (EST; Ashrafi et al. 2012). In total, 3878 and 16,167 EST markers were mapped in the NM and FA populations, respectively. The markers in the two maps were clustered into 783 and 2105 bins (markers with zero recombination were considered as a single bin) in the NM and FA populations, respectively. Because the maps were based on gene-based markers, they allowed syntenic comparison between pepper and other Solanaceae species and comparative mapping of common traits. Similar to other pepper interspecific

crosses, translocation between chromosomes 1 and 8 was observed in the FA map and the high-density map allowed to precisely locate the translocation breakpoint to a specific bin in the chromosome. The use of a high number of common markers in both maps allowed to compare recombination rate and markers' distortion in an intraspecific cross compared to an interspecific cross.

A more recent SNP Illumina Infinium array consisting of 16,000 SNPs was developed as a public tool to aid pepper breeding and mapping (Hulse-Kemp et al. 2016). The SNPs were selected based on resequencing of 22 pepper lines representing chili and bell-fruited types. The utility of the array was tested by constructing a high-density map from an interspecific cross of *C. frutescens* Tabasco × *C. annuum* blocky-type P4. A total of 5546 markers were mapped into 12 linkage groups and arranged in 1362 genetic bins. The present map and the above-mentioned FA map were compared using a common set of 822 markers and found to be highly similar. Important advantages of the Infinium SNP array are low rate of missing data, accurate calling of heterozygotes, and rapid downstream processing of the raw data.

A second Illumina Infinium SNP array was developed and utilized for mapping and diversity analysis in pepper (Cheng et al. 2016). A set of 15,000 SNPs was selected based on resequencing of the cultivars, BA3 and B702, of which approximately 8200 loci were anchored to the Zunla genome assembly (Qin et al. 2014) and scored in various populations. An interspecific cross of BA3 (*C. annuum*) × YNXML (*C. frutescens*) was used to construct an F_2 mapping population. The population was genotyped with 5828 SNPs and phenotypically scored for erect/pendant fruit orientation controlled by the *up* locus which has been previously assigned to chromosome 12 (Lefebvre et al. 1995). A major locus, *Up12.1*, that controls the trait was mapped to a 4.5 Mb region containing 65 genes in the latter chromosome. Furthermore, the SNP array was used to evaluate the genetic diversity of a panel of 399 *C. annuum* elite and landrace pepper lines originated from China. The relative low genetic diversity level found within this panel indicates the need to broaden the genetic variation of the germplasm used for breeding.

Genomewide association study (GWAS) was conducted in a diverse collection of 94 *C. annuum* accessions to identify significant genomic regions affecting capsaicinoids content and fruit weight (Nimmakayala et al. 2016). SNPs' discovery and genotyping were done by the genotyping-by-sequencing (GBS) method (Elshire et al. 2011). A total of 66,960 SNPs were identified among the accessions and mapped to the reference genome of CM334 (Kim et al. 2014), of which a set of 7331 SNPs was used for the QTL study. For both traits, multiple genomic regions with relatively small effects were found to contain significant SNPs. Several significant SNPs were found in candidate genes that have related biological function in other species. For capsaicinoid content, 30 and 56 SNPs were found to be associated with capsaicin and dihydrocapsaicin, respectively; 14 SNPs were common for both traits. Both capsaicinoid content and fruit weight are important traits for pepper domestication. In accordance, many significant SNPs for these traits were located within regions in the genome that exhibits selective sweep signatures.

6.3 Genetic Mapping in *C. baccatum*

Most mapping populations in pepper have been constructed in *C. annuum* intraspecific crosses or in interspecific crosses between *C. annuum* and *Capsicum chinense* or *C. frutescens*. Few genetic studies have been performed in the other cultivated species *Capsicum baccatum* and *Capsicum pubescens*. *C. baccatum* consists of both cultivated and wild subspecies and possesses high variability of fruit-related traits and sources for resistance to diseases such as anthracnose and powdery mildew. Therefore, mapping efforts have been performed in the latter species to aid in mapping and introgression of the resistance genes and other traits for use in breeding (Kim et al. 2010; Lee et al. 2010; Eggink et al. 2014;

Mahasuk et al. 2016). To determine the genome structure of *C. baccatum* and its comparison to *C. annuum*, an intraspecific *C. baccatum* cross was used to map 395 SNPs identified by resequencing the two mapping parents (Lee et al. 2016). Comparison of the map to the *C. annuum* reference genome of CM334 revealed translocations between chromosomes 1 and 8 as previously shown in interspecific crosses in *Capsicum*. Furthermore, additional reciprocal translocations were detected between chromosomes 3 and 5 and between chromosomes 3 and 9. These translocations may act as genetic barriers between *C. baccatum* and *C. annuum* and explain the difficulties in crossing these species.

To study population diversity in *C. baccatum*, a panel of 283 and 94 accessions of *C. baccatum* and *C. annuum*, respectively, was genotyped by genotyping by sequencing (GBS; Elshire et al. 2011) and assessed for population structure, linkage disequilibrium (LD) and QTL mapping by GWAS analysis. Approximately 13,000 SNPs were detected in the *C. baccatum* panel (Nimmakayala et al. 2016). The population was phenotyped for peduncle length that differentiates cultivated and wild accessions. Significant associations were detected in 10 out of the 12 chromosomes, cumulatively explaining 21% of the variation for the trait.

The potential of using *C. baccatum* for the improvement of fruit quality was tested by introgressing multiple chromosome segments into *C. annuum* backgrounds. Multi-parent backcrossing coupled with embryo rescue allowed the construction of BC_2S_1 population from an interspecific cross of *C. annuum* and *C. baccatum* which was evaluated for attributes of fruit quality and subjected for QTL mapping (Eggink et al. 2014). Fruit phenotyping included volatile profiling, chemical composition, morphology, and sensory attributes. Subsequently, near-isogenic lines were developed to confirm QTLs detected in the BC_2S_1 population. The QTL with the strongest effect (LOD = 40.1) was detected for immature fruit color. This QTL likely corresponds to *GOLDEN2-like* (*CaGLK2*) that was identified as controlling chlorophyll content in the immature fruit (Brand et al. 2014). Sensory and metabolomic analyses allowed the identification of a QTL allele originated from *C. baccatum* that confers a strong effect on volatile content and flavor in chromosome 3. Since this QTL is mapped to a small introgression without apparent linkage drag, it is an important candidate for use in breeding for improved flavor. Additional potential sources for improved flavor are a QTL for increased content of sugars in chromosome 3 that does not coincide with reduced fruit size. Furthermore, QTLs for increased content of terpenoids were detected in chromosomes 1 and 10; their phenotypic effect on plant adaptation is yet to be determined.

6.4 QTLs for Economically Important Traits

High yield, early flowering, biotic and abiotic stress tolerance, enriched metabolite content, desired fruit size and shape and reduced postharvest water loss have been major targets for pepper improvement mostly by classical breeding efforts. More recently, molecular breeding techniques such as QTL mapping and introgression, identification of causative genes, and molecular marker development have been utilized for breeding enhancement. A compilation of QTL data for various economical traits associated with plant and fruit growth is presented in Table 6.1, and the major results are summarized in the following paragraphs.

6.4.1 Plant Growth

Shoot architectural components such as the length of the primary stem, internode length, leaf size, degree of lateral branching, and timing of flowering initiation determine the overall plant growth. QTLs for plant development in a cross of Yolo Wonder × Criollo de Morelos 334 RIL population were identified by Barchi et al. (2009). Colocalization of QTLs affecting flowering time, primary axis (stem) length, internode length, axis growth speed, and internode growth time was observed in chromosomes P2, P4, P9,

Table 6.1 List of QTLs for plant growth and fruit traits in pepper

Trait	Population	No. of QTLs	Major effect QTLs[a]	References
Plant architecture				
Axis growth speed	YW (*C. annuum*) × CM334 (*C. annuum*)	4		Barchi et al. (2009)
Internode growth time	YW (*C. annuum*) × CM334 (*C. annuum*)	2		Barchi et al. (2009)
Internode length	YW (*C. annuum*) × CM334 (*C. annuum*)	3		Barchi et al. (2009)
Internode length	Perennial (*C. annuum*) × Dempsey (*C. annuum*)	5		Han et al. (2016)
Primary axis length	YW (*C. annuum*) × CM334 (*C. annuum*)	5		Barchi et al. (2009)
Main stem length	Perennial (*C. annuum*) × Dempsey (*C. annuum*)	6		Han et al. (2016)
Plant height	CW (*C. annuum*) × LCA235 (*C. annuum*)	1	*Qpht.iivr.5.1*	Dwivedi et al. (2015)
Plant height	Perennial (*C. annuum*) × Dempsey (*C. annuum*)	6		Han et al. (2016)
Plant width	Perennial (*C.annuum*) × Dempsey (*C. annuum*)	2		Han et al. (2016)
Branching	2814-6 (*C. frutescens*) × NuMexRNAKY (*C. annuum*)	6		Yarnes et al. (2012)
Lateral branch number	Perennial (*C. annuum*) × Dempsey (*C. annuum*)	2	*LBN-2.1, LBN-2.2*	Han et al. (2016)
Trichome density	CM334 (*C. annuum*) × Chilsungcho (*C. annuum*)	11	*Ptel1, Ptel2, Ptel9,*	Kim et al. (2011)
Flowering time	YW (*C. annuum*) × CM334 (*C. annuum*)	5		Barchi et al. (2009)
Flowering time	2814-6 (C. frutescens) × NuMexRNAKY (C. annuum)	8	*2.6, 2.8*	Yarnes et al. (2012)
Flowering time	PI 527325 (*C. annuum*) × PI 511887 (*C. annuum)*	1	*Flw2.1*	Borovsky et al. (2015)
Number of leaves	CW (*C. annuum*) × LS2341 (*C. annuum*)	2	*Nle1.1, Nle12.1*	Mimura et al. (2010)
Number of leaves	YW (*C. annuum*) × CM334 (*C. annuum*)	2		Alimi et al. (2013)
Number of leaves	BA3 (*C. annuum*) × YNXML (*C. frutescens*)	6	*Nle2.2*	Tan et al. (2015)
Yield				
Number of fruits/plant	CW (*C. annuum*) × LCA235 (*C. annuum*)	1		Dwivedi et al. (2015)
Ten fruits weight	CW (*C. annuum*) × LCA235 (*C. annuum*)	1	*Qtfw.iivr-2.1*	Dwivedi et al. (2015)
Total fruit weight	CW (*C. annuum*) × LCA235 (*C. annuum*)	3	*Qtofw.iivr-1.1*	Dwivedi et al. (2015)
Fruit size/weight				
Fruit size	Maor (*C. annuum*) × Perennial (*C. annuum*)	5		Ben Chaim et al. (2001)
Fruit size	Maor(*C. annuum*) × BG 2816 (*C. frutescens*)	8		Rao et al. (2003)
Fruit weight	PI 152225 (*C. chinense*) × 100/63 (*C. annuum*)	3	*fw2.1, fw4.1, fw4.2*	Zygier et al. (2005)
Fruit weight	NuMex Rnaky (*C. annuum*) × BG 2814-6 (*C. frutescens*)	2	*fw2.1, fw3.1*	Ben Chaim et al. (2006)
Fruit weight	YW (*C. annuum*) × CM334 (*C. annuum*)	7		Barchi et al. (2009)
Fruit weight	PEN45 (*C. baccatum)* × SM,GNM (*C. annuum*)	3	*LG1_8*	Eggink et al. (2014)
Fruit weight	CW (*C. annuum*) × LCA235 (*C. annuum*)	1	*Qfw.iivr-2.1*	Dwivedi et al. (2015)
Fruit weight	94 accessions of *C. annuum*	16		Nimmakayala et al. (2016)
Fruit weight	Perennial (*C. annuum*) × Dempsey (*C.annuum*)	6		Han et al. (2016)

(continued)

Table 6.1 (continued)

Trait	Population	No. of QTLs	Major effect QTLs[a]	References
Pericarp				
Pericarp thickness	YW (*C. annuum*) × CM334 (*C. annuum*)	8		Barchi et al. (2009)
Pericarp thickness	2814-6 (*C. frutescens*) × NuMexRNAKY (*C. annuum*)	10	*4.4*	Yarnes et al. (2012)
Pericarp thickness	Early Jalapeno (*C. annuum*) × CM334 (*C. annuum*)	1	*3.1*	Naegele et al. (2014)
Pericarp thickness	CW (*C. annuum*) × LCA235 (*C. annuum*)	1	*Qpt.iivr-2.1*	Dwivedi et al. (2015)
Pericarp area	2814-6 (*C. frutescens*) × NuMexRNAKY (*C. annuum*)	8		Yarnes et al. (2012)
Fruit shape				
Fruit diameter	YW (*C. annuum*) × CM334 (*C. annuum*)	12		Barchi et al. (2009)
Fruit diameter	Perennial (*C. annuum*) × Dempsey (*C. annuum*)	5	*FD-1, FD-3.2*	Han et al. (2016)
Fruit width	PEN45 (*C. baccatum*) × SM,GNM (*C. annuum*)	7	*LG1_8, LG9*	Eggink et al. (2014)
Fruit length	YW (*C. annuum*) × CM334 (*C. annuum*)	4	*Frl4.1*	Barchi et al. (2009)
Fruit length	TF68 (*C. annuum*) × Habanero (*C. chinense*)	5	*3.1*	Lee et al. 2011
Fruit length	PEN45 (*C. baccatum*)X SM,GNM (*C. annuum*)	4	*LG10.1*	Eggink et al. (2014)
Fruit length	CW (*C. annuum*) × LCA235 (*C. annuum*)	2	*Qfl.iivr.3.2*	Dwivedi et al. (2015)
Fruit length	Perennial (*C. annuum*) × Dempsey (*C. annuum*)	6	*FL-3.1, FL-3.2, FL-3.3*	Han et al. (2016)
Fruit shape index	Maor (*C. annuum*) × Perennial (*C. annuum*)	3	*fs3.1*	Ben Chaim et al. (2001)
Fruit shape index	Maor (*C. annuum*) × BG 2816 (*C. frutescens*)	5	*fs3.1*	Rao et al. (2003)
Fruit shape index	5226 (*C. annuum*) × PI 159234 (*C. chinense*)	1	*fs10.1*	Ben Chaim et al. (2003a)
Fruit shape index	PI 152225 (*C. chinense*) × 100/63 (*C. annuum*)	3	*fs4.2*	Zygier et al. (2005)
Fruit shape index	YW (*C. annuum*) × CM334 (*C. annuum*)	7		Barchi et al. (2009)
Fruit shape index	1154 (*C. annuum*) × PI 152225 (*C. chinense*)	3	*fs1.1, fs10.1*	Borovsky and Paran (2011)
Fruit shape index	2814-6 (*C. frutescens*) × NuMexRNAKY (*C. annuum*)	51	*2.5, 2.6,2.8, 2.10, 4.4, 11.4*	Yarnes et al. (2012)
Fruit shape index	Early Jalapeno (*C. annuum*) × CM334 (*C. annuum*)	5	*4.1*	Naegele et al. (2014)
Fruit shape index	PEN45 (*C. baccatum*) × SM,GNM (*C. annuum*)	5	*LG1_8*	Eggink et al. (2014)
Fruit shape index	Perennial (*C. annuum*) × Dempsey (*C. annuum*)	4	*FS-3.1, FS-3.2*	Han et al. (2016)
Fruit color				
Color ripe	PEN45 (*C. baccatum*) × SM,GNM (*C. annuum*)	3		Eggink et al. (2014)
Color unripe	PEN45 (*C. baccatum*) × SM,GNM (*C. annuum*)	3	*LG10.1*	Eggink et al. (2014)
Immature fruit color	Perennial (*C. annuum*) × Dempsey (*C. annuum*)	6	*IFC-10.2*	Han et al. (2016)
Metabolites				
Biochemical composition	PEN45 (*C. baccatum*) × SM,GNM (*C. annuum*)	8	*LG1_8, LG10.1*	Eggink et al. (2014)
Capsaicin	*NB1 (C. annuum)* × Bhut Jolokia (*C. chinense*)	3	*Qcap3.1, qcap6.1*	Lee et al. (2016)
Capsaicin	NuMex Rnaky (*C. annuum*) × BG 2814-6 (*C. frutescens*)	5	*cap7.2*	Ben Chaim et al. (2006)

(continued)

Table 6.1 (continued)

Trait	Population	No. of QTLs	Major effect QTLs[a]	References
Capsaicinoid	2814-6 (*C. frutescens*) × NuMexRNAKY (*C. annuum*)	12	*4.2, 4.14, 4.15*	Yarnes et al. (2012)
Capsaicinoid	Maor (*C. annuum*) × BG 2816 (*C. frutescens*)	1	*cap*	Blum et al. (2003)
Capsaicinoids	94 accessions of *C. annuum*	14		Nimmakayala et al. (2016)
Dihydrocapsaicin	*C. annuum* 'NB1' × *C. chinense* 'Bhut Jolokia'	2	*Qhdc2.1, qdhc2.2*	Lee et al. (2016)
Dihydrocapsaicin	NuMex Rnaky (*C. annuum*) × BG 2814-6 (*C. frutescens*)	4	*dhc4.1*	Ben Chaim et al. (2006)
Nordihydrocapsaicin	NuMex Rnaky (*C. annuum*) × BG 2814-6 (*C. frutescens*)	1	*ndhc7a.1*	Ben Chaim et al. (2006)
Total capsaicinoids	NuMex Rnaky (*C. annuum*) × BG 2814-6 (*C. frutescens*)	5	*total7.2*	Ben Chaim et al. (2006)
Chlorophyll content	1154 (*C. annuum*) × PI 152225 (*C. chinense*)	2	*pc8.1*	Brand et al. (2012)
Metabolites	AC1979 (*C. annuum*) × No. 4661 (*C. chinense*)	279		Wahyuni et al. (2014)
Other fruit traits				
Number of locules	YW (*C. annuum*) × CM334 (*C. annuum*)	9	*NloLG25.1*	Barchi et al. (2009)
Pedicel length	YW (*C. annuum*) × CM334 (*C. annuum*)	6		Barchi et al. (2009)
Fruit firmness	Early Jalapeno (*C. annuum*) × CM334 (*C. annuum*)	1	*12.1*	Naegele et al. (2014)
Fruit position	Perennial (*C. annuum*) × Dempsey (*C. annuum*)	6	*FP-12.1,FP-12.2, FP-12.3*	Han et al. (2016)
Fruit orientation	BA3 (*C. annuum*) × YNXML (*C. frutescens*)	1	*Up12.1*	Cheng et al. (2016)
Postharvest water loss	1154 (*C. annuum*) × PI 593611 (*C. chinense*)	3	*PWL10.1, PWL10.2*	Popovsky-Sarid et al. (2017)

[a]QTL with effect larger than 20% explained phenotypic variation

and LG47 which may indicate pleiotropic effects of these QTLs. Twelve QTLs for several plant growth traits were detected in an intraspecific *C. annuum* doubled haploid (DH) population, explaining 14–34% of the phenotypic variability for various plant architectural traits (Mimura et al. 2010). The strongest QTL effect was detected for flowering time in *LG8* that was not conclusively assigned to a specific chromosome. QTLs for pepper growth traits such as leaf size, plant height, flowering time, days to breaker fruit stage, and branching were also mapped in an RIL population from an interspecific cross of 2814-6 (*C. frutescens*) × NuMex RNaky (*C. annuum*). A total of 23, 15 and 17 QTLs mostly with minor effects were identified for leaf traits, floral traits, and whole plant morphology, respectively (Yarnes et al. 2012). Additionally, a major QTL for plant height was reported in *LG5* (Dwivedi et al. 2015), and two major QTLs for lateral branch number were reported in chromosome 2 (Han et al. 2016).

Several studies have focused specifically on mapping flowering time QTLs. A major QTL for flowering time was identified in chromosome 2 in a cross of *C. annuum* blocky-fruited type accession (early flowering) and *C. annuum* var. *glabriusculum* wild accession (late flowering) (Fig. 6.2, Borovsky et al. 2015). This QTL was co-localized with the flowering suppressor gene *CaAPETALA2* that is disrupted in the EMS (ethylmethane sulfonate)-induced early flowering mutant. The same genomic region has been detected as a major flowering time QTL in an independent study in a *C. annuum* × *C. frutescens* cross (Tan et al. 2015). Additional five minor QTLs were detected in the latter study. In addition to these QTLs, several flowering

promoter and suppressor genes that also control shoot architecture were identified by using EMS-induced mutants including *CaJOINTLESS* (Cohen et al. 2012), *CaBLIND* (Jeifetz et al. 2011), *CaS* (Cohen et al. 2014) and *CaFASCICULATE* (Elitzur et al. 2009).

Trichome density on the plant stem and flower calyx varies among accessions and are often present in wild accessions and landraces. QTL mapping for the trait was performed in intraspecific *C. annuum* populations involving CM334 as a trichome-rich parent. A major QTL, *Ptel1*, controlling trichome density in the main stem and in the calyx was detected in LG24 corresponding to Chromosome 10 (Kim et al. 2011). Additional 10 minor QTLs were detected in other chromosomes. Recently, an RIL population from a cross of CM334 × Maor was analyzed for several fruit and growth traits including the degree of stem pubescence that was scored by a visual scan (Chunthawodtiporn et al. 2018). Three QTLs were detected in chromosomes 2, 10, and 11, the QTL in chromosome 10 having the largest effect on the trait which likely corresponds to *Ptel1*. Two candidate genes, *TRICHOME BIREFRINGENCE-LIKE 5* and a *C2H2* zinc-finger transcription factor which are putatively involved in the formation of trichomes based on Arabidopsis studies, were located in the vicinity of the QTL.

6.4.2 Fruit Traits

6.4.2.1 Fruit Size and Yield

Fruit size/weight QTLs have been identified in multiple studies (Table 6.1 and summarized by Paran and van der Knaap 2007; Hill et al. 2017). Several QTL studies in mapping populations consisting of crosses of a common blocky-fruited cv. Maor (*C. annuum*) with small-fruited *C. annuum*, *C. frutescens,* and *C. chinense* accessions have been carried out. Two major QTLs for fruit weight, *fw2.1* and *fw4.2,* are conserved in the three *Capsicum* species. *fw2.1* had the most significant effect in multiple populations (Ben Chaim et al. 2001; Rao et al. 2003; Zygier et al. 2005). A putative tomato orthologous fruit weight QTL, *fw2.2*, is located in a syntenic region in chromosome 2 (Frary et al. 2000). The gene that underlies *fw2.2* in tomato is *CELL NUMBER REGULATOR* (*CNR*). However, the syntenic region in pepper consists of multiple genes associated with organ size regulation including the ortholog of *OVATE*, a fruit shape gene in tomato (Hill et al. 2017). Therefore, high-resolution mapping will be required to precisely map this QTL and identify the underlying gene.

Another possible orthologous fruit weight QTL in pepper and tomato is *fw3.2* that is associated with the gene *KLUH*, a P450 coding enzyme in both species (Chakrabarti et al. 2013). A cluster of minor QTLs for fruit weight, fruit shape, fruit diameter, and pericarp thickness is located in *P11* and *P12* (Barchi et al. 2009). 16 significant SNPs associated with fruit weight were identified in a GWAS study of 94 accessions (Nimmakayala et al. 2016). Except for chromosome 7, all other chromosomes had at least one significant SNP. Out of the 16 SNPs, seven were located in known genes that control organ size such as *STYLOSA*, *FASCIATED*, *WUSCHEL*, and *CLAVATA1*.

The yield of pepper is affected by parameters such as number of fruits per plant, fruits weight, and total fruit yield. QTL mapping for these traits was performed in a *C. annuum* intraspecific RIL population (Dwivedi et al. 2015). A total of 10 QTLs were detected for yield-related traits. Colocalization of five QTLs in chromosome 2 (*Qtofw.iivr-2.1*, *Qtfw.iivr-2.1*, *Qfw.iivr-2.1*, *Qnfp.iivr-2.1,* and *Qpt.iivr-2.1*) with significant additive effects was identified which might be due to the linkage of different QTLs or pleiotropic effects of the same genes. Other QTL studies for fruit-related traits in pepper reported clustering of QTLs for fruit traits in the same region of chromosome 2 (Ben Chaim et al. 2001; Rao et al. 2003; Zygier et al. 2005; Barchi et al. 2009; Chunthawodtiporn et al. 2018).

Pericarp thickness is positively correlated with fruit weight (Ben Chaim et al. 2001), and therefore, QTLs for both traits are often located in common genomic positions. Two major QTLs for pericarp thickness were identified in different

intraspecific populations of *C. annuum* in chromosomes 2 and 3 (*Qpt.iivr-2.1, 3.1*). *Qpt.iivr-2.1* is located in the same genomic region in chromosome 2 that contains a QTL for fruit weight (Dwivedi et al. 2015; Naegele et al. 2014). Several linked QTLs for pericarp thickness were identified in chromosome 4 in a cross of *C. annuum* and *C. frutescens* (Yarnes et al. 2012). Several minor QTLs for pericarp thickness were also identified by Barchi et al. (2009).

An additional factor that may be associated with fruit size is locule number. The locule number locus, *lcn2.1,* in tomato affects fruit size via changing carpal numbers (Lippman and Tanksley 2001). Only limited data is available for mapping this trait in pepper. Low positive correlation between fruit weight and locule number was reported by Barchi et al. (2009). Few minor QTLs for locule number were identified in this cross; the strongest QTL being *NloLG25.1*.

6.4.2.2 Fruit Shape

Despite the large variation in fruit shape that exists in pepper, only few shape attributes were studied that include fruit width, fruit length, and fruit shape index (length/width). The two most significant QTLs for fruit shape index were *fs3.1* and *fs10.1* that have been identified as controlling fruit elongation (Ben Chaim et al. 2001, 2003a, b; Borovsky and Paran 2011). Both QTLs control most of the trait variation in *Capsicum*, explaining 67 and 44% of the phenotypic variation for *fs3.1* and *fs10.1*, respectively (Ben Chaim et al. 2003a, b). Major QTLs regulating fruit shape variation within *C. annuum* have been identified in multiple populations in chromosomes 1, 3, and 4 (Ben Chaim et al. 2001; Barchi et al. 2009; Naegele et al. 2014; Dwivedi et al. 2015; Han et al. 2016). Fruit shape QTLs were also identified in interspecific crosses between *C. annuum* and *C. chinense* in chromosomes 1, 3, 4, and 10 (Ben Chaim et al. 2003a; Zygier et al. 2005; Borovsky and Paran 2011). Four major QTLs in chromosome 4 and one QTL in each of the chromosomes 3, 4, and 11 were identified in a cross of *C. annuum* and *C. frutescens* (Yarnes et al. 2012). Fruit shape QTLs in chromosomes 10 and *LG1_8* have been identified in a cross of *C. annuum* and *C. baccatum* (Eggink et al. 2014). To-date, none of the genes underlying natural fruit shape variation in pepper has been identified. A pepper homolog of *OVATE,* a tomato fruit shape QTL (Liu et al. 2002), was shown to be associated with fruit shape variation by down regulation using virus-induced gene silencing (VIGS; Tsaballa et al. 2011), indicating the possibility that the pepper gene may regulate fruit shape variation in natural populations.

6.4.2.3 Fruit Color and Chlorophyll Content

Since the fruit pigments are associated with fruit color, nutrition, and flavor, pepper fruit color is important to the breeder and to the consumer. The color of the ripe fruits is determined primarily by carotenoids and that of the immature fruits by anthocyanins and chlorophyll. Mutations in genes in the carotenoid biosynthesis pathway result in change of color from red to yellow or to orange (Popovsky and Paran 2000; Thorup et al. 2000; Huh et al. 2001; Borovsky et al. 2013). Additional pepper fruit color variation is associated with chlorophyll catabolism, anthocyanin accumulation and chloroplast compartment size (Borovsky et al. 2004; Borovsky and Paran 2008; Pan et al. 2013).

Both qualitative and quantitative variation in fruit pigment content exists, however, its genetic control in largely unknown. QTL analysis for chlorophyll content in the immature fruit in a cross between a dark green-fruited *C. annuum* inbred 1154 and a light green-fruited *C. chinense* accession PI 152225 revealed the presence of two major QTLs, *pc8.1* and *pc10.1*, that control the trait (Fig. 6.3, Brand et al. 2012). One of the QTLs, *pc10*, was found to correspond to the pepper homolog of *GOLDEN2-like* transcription factor (*GLK2*) that controls chloroplast compartment size in the immature fruit (Brand et al. 2014). Major QTLs that regulates unripe fruit color were identified in chromosome 10 in an interspecific cross of *C. annuum* and *C. baccatum* and in an intraspecific *C. annuum* cross which likely correspond to *pc10.1* (Eggink et al. 2014; Han et al. 2016).

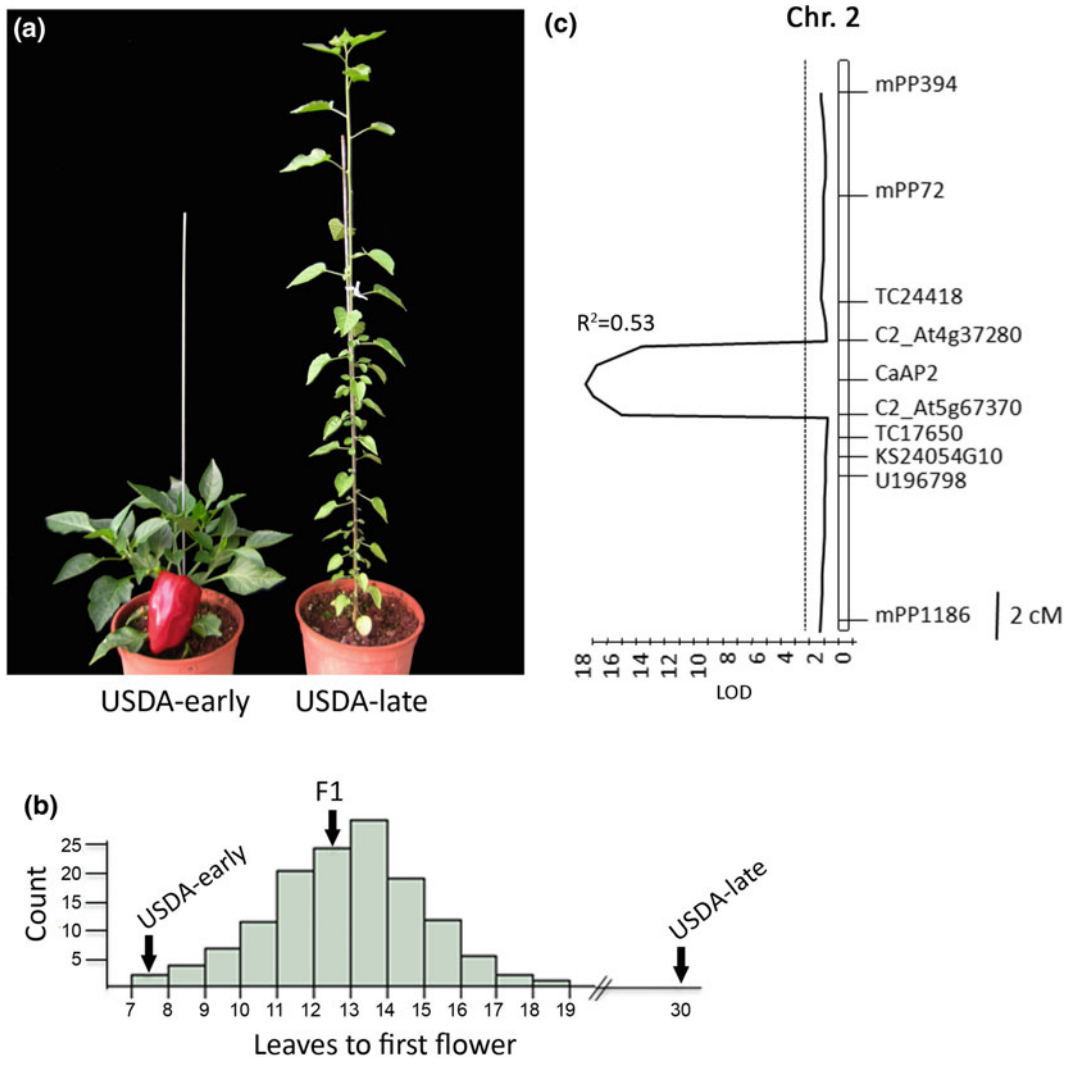

Fig. 6.2 QTL mapping of flowering time in a cross of *C. annuum* accession PI 527325 (USDA early) and *C. annuum* var. *glabriusculum* wild accession PI 511887 (USDA late). **a** Pictures of the early- and late-flowering parents used for QTL mapping. **b** Distribution of flowering time in the F_2 population. **c** Interval QTL mapping of flowering time in a region containing *CaAP2* in chromosome 2. Reprinted from Borovsky et al. (2015) by permission

6.4.2.4 Metabolites Content

A QTL study for metabolites content associated with flavor was performed in an interspecific cross between *C. annuum* and *C. baccatum* (Eggink et al. 2014). A strong effect on flavor was found in a small introgression of chromosome 3. This QTL explained 38.7% of the variation for odor and was associated with an intense odor of *C. baccatum.* NILs for this QTL showed an increase in intensity of the compound 6-methyl-4-oxo-5-heptenal and decrease of the compound (Z)-butanoic acid 3-hexenyl ester and 2-isobutyl-3-methoxypyrazine. Additional minor QTLs associated with sensory attributes were detected in different chromosomes. Two major QTLs that control variation in biochemical composition were identified in *LG1_8* and *LG10.1*. A significant QTL was found for brix,

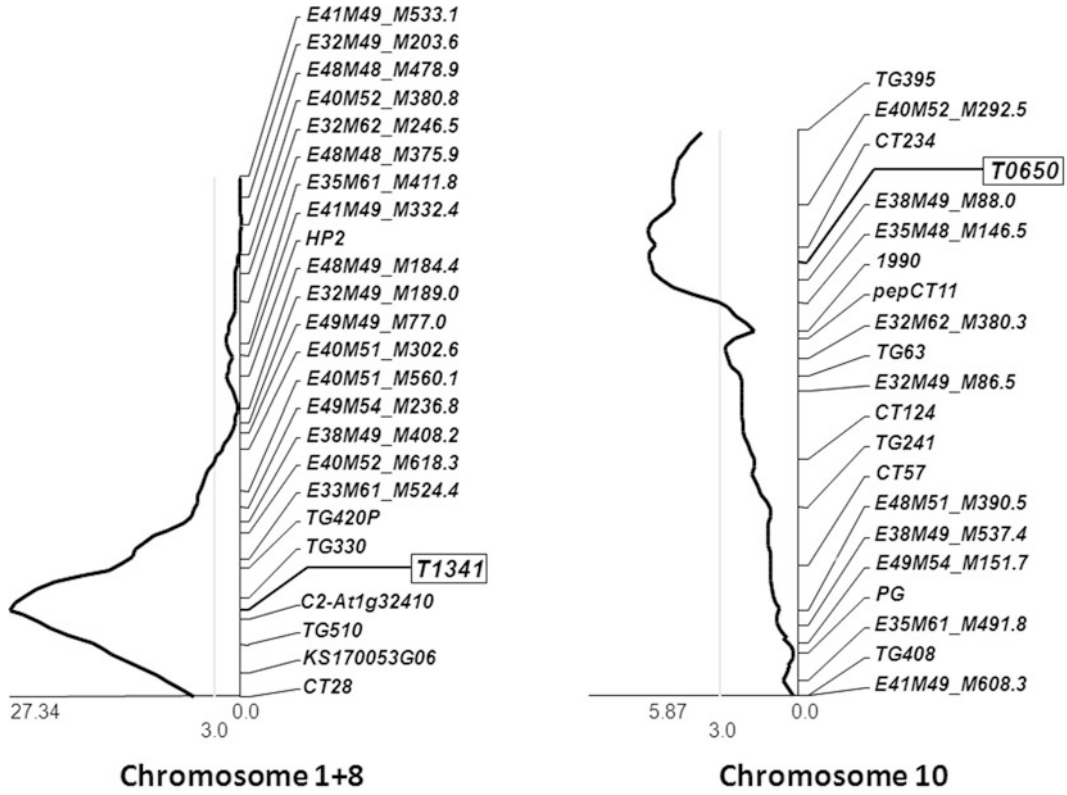

Fig. 6.3 Position of QTLs for pigment content in the F_2 of 1154 × PI 152225. The most significant markers at the two QTLs are boxed. Numbers on the horizontal axis represent LOD values. Reprinted from Brand et al. (2012) by permission

glucose, fructose, malate, and citrate in *LG1_8* that coincided with a major fruit size QTL. Because the *C. baccatum* allele was associated with an increased metabolite content and decreased fruit size, it was concluded that the increase in the metabolites concentration was a result of smaller fruits and not an effect of increased metabolism. In contrast, a QTL for increased BRIX value was detected in LG3 which was unaffected by fruit size. 46% of the variation in the metabolic content between the two parents was due to a group of 15 terpenoids controlled by QTLs in *LG10.1* and *LG1*.

The major QTL, *pc8.1*, affecting chlorophyll content in the immature fruit was also associated with an increase of other metabolites accumulated in the chloroplast such as tocopherols and carotenoids (Brand et al. 2012). This association is likely due to the effect of the QTL in modulating chloroplast compartment size. A QTL study was performed to dissect the molecular basis for variation in flavonoid content in a cross between *C. annuum* and *C. chinense* (Wahyuni et al. 2014). LCMS metabolic profiling of semi-polar metabolites allowed the identification of 52 annotated metabolites. A total of 279 mQTL were detected; however, most QTLs were clustered in few chromosomal regions creating QTL hotspots in chromosome 9. Furthermore, genes controlling flavonoids biosynthesis were mapped and some exhibited colocalization with mQTLs in chromosomes 1, 6, and 9.

6.4.2.5 Pungency

Pungency in pepper fruit is due to the unique accumulation of alkaloid compounds termed capsaicinoids. A single dominant gene at the *Pun1* locus in chromosome 2 is required for the

production of capsaicinoids (Stewart et al. 2005). In addition for the qualitative difference in the presence or absence of pungency, large variation in the capsaicinoid content exists which result in cultivars with varying degree of pungency. Several studies on QTL mapping for capsaicinoid content have been performed in diverse genetic backgrounds. Twelve QTLs were identified in six chromosomes by Yarnes et al (2012). Several QTLs were detected in chromosome 4, similar to Ben Chaim et al. (2006). A large effect QTL detected by bulked segregant analysis (BSA) was mapped in chromosome 7 (Blum et al. 2003). 14 significant SNPs scattered throughout the genome were associated with capsaicin and dihydrocapsaicin content in a GWAS study of 94 accessions (Nimmakayala et al. 2016). A QTL mapping study was also conducted in a cross of one of the hottest chili peppers 'Bhut Jolokia' (Lee et al. 2016). Two QTLs for capsaicin content were detected in chromosomes 3 and 6, while two different QTLs for dihydrocapsaicin content were detected in chromosome 2. A study conducted using a diversity panel of 40 lines consisting of 21 pungent and 19 non-pungent lines revealed several fixed regions for non-pungency (NP). Out of the 17 fixed regions for NP, 14 are overlapped with QTLs for fruit size or shape. The most significant fixed regions were located in chromosome 2, spanning *PUN1* and *CaOVATE*. In addition to *PUN1,* six genes regulating capsaicin biosynthesis were located in NP regions in chromosomes 1, 3, and 6, implicating their importance in breeding of non-pungent cultivars (Hill et al. 2017). The large variation in QTLs positions in different genetic backgrounds implicates the complexity of this trait and that markers used for selection in breeding programs will have to be developed in a genotype-specific manner.

6.4.2.6 Fruit Postharvest Water Loss

Fruit postharvest water loss (PWL) results in reduction in the overall fruit quality and thus affects the marketing of peppers. Based on screening of a wide germplasm for variation in the trait, two parents that exhibited large difference in PWL were selected for QTL mapping in an interspecific cross between *C. annuum* and *C. chinense*. Two linked QTLs, *PWL10.1* and *PWL10.2*, were identified for fruit PWL in chromosome 10 in multiple generations (Popovsky-Sarid et al. 2017). Several genes associated with cuticle biosynthesis, cell wall metabolism, and fruit ripening were identified as QTL candidates using transcriptome analysis of near-isogenic line (NILs) that differ for the QTL.

6.5 Concluding Remarks and Future Prospects

In recent years, numerous QTL studied have been conducted for economically important traits in pepper which can be exploited for introgression of beneficial QTL alleles into elite lines. The deciphering of the pepper genome sequence allowed searching for candidate genes that co-localize with the QTLs; however, only in few cases the causative genes underlying the QTLs were unequivocally identified. High-resolution mapping, expression studies, and functional assays for candidate genes will be required to expedite the discovery of such genes. One obstacle that hinders functional genomic studies in pepper is the lack of an efficient transformation system. The recent report on successful application of pollen-mediated transformation in pepper (Zhao et al. 2017) may open the way for a large-scale use of genome editing techniques in this species.

References

Alimi NA, Bink M, Dieleman JA, Magán JJ, Wubs AM et al (2013) Multi-trait and multi-environment QTL analyses of yield and a set of physiological traits in pepper. Theor Appl Genet 126:2597–2625

Ashrafi H, Hill T, Stoffel K, Kozik A, Yao J et al (2012) De novo assembly of the pepper transcriptome (*Capsicum annuum*): a benchmark for *in silico* discovery of SNPs, SSRs and candidate genes. BMC Genom 13:571

Barchi L, Lefebvre V, Sage-Palloix A-M, Lanteri S, Palloix A (2009) QTL analysis of plant development and fruit traits in pepper and performance of selective phenotyping. Theor Appl Genet 118:1157–1171

Ben Chaim A, Paran I, Grube R, Jahn M, van Wijk R, Peleman J (2001) QTL mapping of fruit related traits in pepper (*Capsicum annuum*). Theor Appl Genet 102:1016–1028

Ben Chaim A, Borovsky E, De Jong W, Paran I (2003a) Linkage of the *A* locus for the presence of anthocyanin and *fs10.1*, a major fruit-shape QTL in pepper. Theor Appl Genet 106:889–894

Ben Chaim A, Borovsky E, Rao GU, Tanyolac B, Paran I (2003b) *fs3.1*: a major fruit shape QTL conserved in *Capsicum*. Genome 46:1–9

Ben Chaim A, Borovsky Y, Falise M, Mazourek M, Kang BC et al (2006) QTL analysis for capsaicinoid content in *Capsicum*. Theor Appl Genet 113:1481–1490

Blum E, Mazourek M, O'Connell M, Curry J, Thorup T et al (2003) Molecular mapping of capsaicinoid biosynthesis genes and QTL analysis for capsaicinoid content in *Capsicum*. Theor Appl Genet 108:79–86

Borovsky Y, Paran I (2008) Chlorophyll breakdown during pepper fruit ripening in the *chlorophyll retainer* mutation is impaired at the homolog of the senescence-inducible stay-green gene. Theor Appl Genet 117:235–240

Borovsky Y, Paran I (2011) Characterization of *fs10.1*, a major QTL controlling fruit elongation in *Capsicum*. Theor Appl Genet 123:657–665

Borovsky Y, Oren Shamir M, Ovadia R, De Jong W, Paran I (2004) The *A* locus that controls anthocyanin accumulation in pepper encodes a MYB transcription factor homologous to *Anthocyanin2* of Petunia. Theor Appl Genet 109:23–29

Borovsky Y, Tadmor Y, Bar E, Meir A, Lewinsohn E, Paran I (2013) Induced mutation in *BETA-carotene hydroxylase* results in accumulation of beta-carotene and conversion of red to orange color in pepper fruit. Theor Appl Genet 126:557–565

Borovsky Y, Sharma VK, Verbakel H, Paran I (2015) *CaAP2* transcription factor is a candidate gene for a flowering repressor and a candidate for controlling natural variation of flowering time in *Capsicum annuum*. Theor Appl Genet 128:1073–1082

Brand A, Borovsky Y, Meir S, Rogachev I, Aharoni A, Paran I (2012) *pc8.1*, a major QTL for pigment content in pepper fruit, is associated with variation in plastid compartment size. Planta 235:579–588

Brand A, Borovsky Y, Hill T, Rahman KA, Bellalou A, Van Deynze A, Paran I (2014) *CaGLK2* regulates natural variation of chlorophyll content and fruit color in pepper fruit. Theor Appl Genet 127:2139–2148

Chakrabarti M, Zhang N, Sauvage C, Munos S et al (2013) A cytochrome 450 regulates a domestication trait in cultivated tomato. Proc Natl Acad Sci USA 110:17125–17130

Cheng J, Qin C, Tang X, Zhou H, Hu Y et al (2016) Development of a SNP array and its application to genetic mapping and diversity assessment in pepper (*Capsicum* spp.). Sci Rep 13:33293

Chunthawodtiporn J, Hill T, Stoffel K, Van Deynze A (2018) Quantitative trait loci controlling fruit size and other horticultural traits in bell pepper (*Capsicum annuum*). Plant Genome 11. https://doi.org/10.3835/plantgenome2016.12.0125

Cohen O, Borovsky Y, David-Schwartz R, Paran I (2012) *CaJOINTLESS* is a MADS-box gene involved in suppression of vegetative growth in all shoot meristems in pepper. J Exp Bot 63:4947–4957

Cohen O, Borovsky Y, David-Schwartz R, Paran I (2014) *Capsicum annuum* S (*Ca*S) promotes reproductive transition and is required for flower formation in pepper (*Capsicum annuum*). New Phytol 202:1014–1023

Dwivedi N, Kumar R, Paliwal R, Kumar U, Kumar S et al (2015) QTL mapping for important horticultural traits in pepper (*Capsicum annuum* L.). J Plant Biochem Biotechnol 24:154–160

Eggink PM, Tikunov Y, Maliepaard C, Haanstra JP, De Rooij H et al (2014) Capturing flavors from *Capsicum baccatum* by introgression in sweet pepper. Theor Appl Genet 127:373–390

Elitzur T, Nahum H, Borovsky Y, Pekker I, Eshed Y, Paran I (2009) Co-ordinated regulation of flowering time, plant architecture and growth by *FASCICULATE*: the pepper orthologue of *SELF PRUNING*. J Exp Bot 60:869–880

Elshire RJ, Glaubitz JC, Sun Q, Poland JA, Kawamoto K et al (2011) A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. PLoS ONE 6(5):e19379

Frary A, Nesbitt TC, Frary A, Grandillo S, van der Knapp E et al (2000) *fw2.2*: a quantitative trait locus key to the evolution of tomato fruit size. Science 289:85–88

Han K, Jeong HJ, Yang HB, Kang SM, Kwon JK (2016) An ultra-high-density bin map facilitates high-throughput QTL mapping of horticultural traits in pepper (*Capsicum annuum*). DNA Res 6:81–91

Hill T, Ashrafi H, Chin-Wo SR, Stoffel K, Truco MJ (2015) Ultra-high density, transcript-based genetic maps of pepper define recombination in the genome and synteny among related species. Gene Genet Genom 5:2341–2355

Hill TA, Chunthawodtiporn J, Ashrafi H, Stoffel K, Weir A, Van Deynze A (2017) Regions underlying population structure and the genomics of organ size determination in *Capsicum annuum*. Plant Genome 10:3. https://doi.org/10.3835/plantgenome2017.03.0026

Huh JH, Kang BC, Nahm SH (2001) A candidate gene approach identified phytoene synthase as the locus for mature fruit color in red pepper (*Capsicum* spp.). Theor Appl Genet 102:524–530

Hulse-Kemp AM, Ashrafi H, Plieske J, Lemm J, Stoffel K et al (2016) A HapMap leads to a *Capsicum annuum* SNP infinium array: a new tool for pepper breeding. Hort Res 3:16036

Jeifetz D, David-Schwartz R, Borovsky Y, Paran I (2011) *CaBLIND* regulates axillary meristem initiation and transition to flowering in pepper. Planta 234:1227–1236

Kim S, Kim KT, Kim DH, Yang EY, Cho MC et al (2010) Identification of quantitative trait loci associated with anthracnose resistance in chili pepper (*Capsicum* spp.). Korean J Hort Sci Technol 28:1014–1024

Kim HJ, Han JH, Kim S, Lee HR, Shin JS et al (2011) Trichome density of main stem is tightly linked to PepMoV resistance in chili pepper (*Capsicum annuum* L.). Theor Appl Genet 122:1051–1058

Kim S, Park M, Yeom SI, Kim YM, Lee JM, Lee HA et al (2014) Genome sequence of the hot pepper provides insights into the evolution of pungency in *Capsicum* species. Nat Genet 46:270–278

Lee J, Hong JH, Do JW, Yoon JB (2010) Identification of QTLs for resistance to anthracnose to two *Colletotrichum* species in pepper. J Crop Sci Biotechnol 13:227–233

Lee HR, Kim KT, Kim HJ, Han JH, Kim JH (2011) QTL analysis of fruit length using rRAMP, WRKY, and AFLP markers in chili pepper. Hort Environ Biotechnol 52:602–613

Lee J, Park SJ, Hong SC, Han JH, Doil C, Yoon JB (2016) QTL mapping for capsaicin and dihydrocapsaicin content in a population of *Capsicum annuum* 'NB1' × *Capsicum chinense* 'Bhut Jolokia'. Plant Breed 135:376–383

Lefebvre V, Palloix A, Caranta C, Pochard E (1995) Construction of an intraspecifc integrated linkage map of pepper using molecular markers and doubled-haploid progenies. Genome 38:112–121

Lippman Z, Tanksley S-D (2001) Dissecting the genetic pathway to extreme fruit size in tomato using a cross between the small fruited wild species *L. pimpinellifolium* and *L. esculentum* var. Giant Heirloom. Genetics 158:413–422

Liu J, Van Eck J, Cong B, Tanksley SD (2002) A new class of regulatory genes underlying the cause of pear-shaped tomato fruit. Proc Natl Acad Sci USA 99:13302–13306

Mahasuk P, Struss D, Mongkolporn O (2016) QTLs for resistance to anthracnose identified in two *Capsicum* sources. Mol Breed 36:10. https://doi.org/10.1007/s11032-016-0435-5

Mimura Y, Minamiyama Y, Sano H (2010) Mapping for axillary shooting, flowering date, primary axis length, and number of leaves in pepper (*Capsicum annuum*). J Jpn Soc Hort Sci 79:56–63

Naegele RP, Ashraffi H, Hill TA, Chin-Wo SR, Van Deynze A, Hausbeck MK (2014) QTL mapping of fruit rot resistance to the plant pathogen *Phytophthora capsici* in a recombinant inbred line *Capsicum annuum* population. Phytopathology 104:479–483

Nimmakayala P, Abburi VL, Saminathan T, Alparthi SB, Almeida A, Davenport B et al (2016) Genome-wide diversity and association mapping for capsaicinoids and fruit weight in *Capsicum annuum* L. Sci Rep 6:38081. https://doi.org/10.1038/srep3808

Pan Y, Bradley G, Pyke K, Ball G, Lu C et al (2013) Network inference analysis identifies an *APRR2-Like* gene linked to pigment accumulation in tomato and pepper fruits. Plant Physiol 161:1476–1485

Paran I (2013) Molecular linkage maps of *Capsicum*. In: Kang BC, Kole C (eds) Genetics, genomics and breeding of peppers and eggplants. CRC Press, Boca Raton, FL, USA, pp 40–55

Paran I, van der Knaap E (2007) Genetic and molecular regulation of fruit and plant domestication traits in tomato and pepper. J Exp Bot 58:3841–3852

Paran I, Ben Chaim A, Kang BC, Jahn M (2006) Capsicum. In: Kole C (ed) Genome mapping and molecular breeding, vol 5. Vegetables. Springer, Heidelberg, Berlin, New York, Tokyo, pp 209–226

Popovsky S, Paran I (2000) Molecular analysis of the *Y* locus in pepper: its relation to capsanthin-capsorubin synthase and to fruit color. Theor Appl Genet 101:86–89

Popovsky-Sarid S, Borovsky Y, Faigenboim A, Parsons EP, Lohrey GT et al (2017) Genetic and biochemical analysis reveals linked QTLs determining natural variation for fruit post-harvest water loss in pepper (*Capsicum*). Theor Appl Genet 130:445–459

Qin C, Yu C, Shen Y, Fang X, Chen L et al (2014) Whole-genome sequencing of cultivated and wild peppers provides insights into *Capsicum* domestication and specialization. Proc Natl Acad Sci USA 111:5135–5140

Ramchiary N, Kehie M, Brahma V, Kumaria S, Tandon P (2014) Application of genetics and genomics towards Capsicm translational research. Plant Biotechnol Rep 8:101–123

Rao GU, Ben Chaim A, Borovsky E, Paran I (2003) Mapping of yield related QTLs in pepper in an inter-specific cross of *Capsicum annuum* and *C. frutescens*. Theor Appl Genet 106:1457–1466

Stewart CJ, Kang BC, Liu K, Mazourek M, Moore SL et al (2005) The *Pun1* gene for pungency in pepper encodes a putative acyltransferase. Plant J 42:675–688

Tan S, Cheng JW, Zhang L, Qin C, Nong DG et al (2015) Construction of an interspecific genetic map based on InDel and SSR for mapping the QTLs affecting the initiation of flower primordia in pepper (*Capsicum* spp.). PLoS ONE 10:e0119389. https://doi.org/10.1371/journal.pone.0119389

Thorup TA, Tanyolac B, Livingstone KD, Popovsky S, Paran I, Jahn M (2000) Candidate gene analysis of organ pigmentation loci in the Solanaceae. Proc Natl Acad Sci USA 97:11192–11197

Tsaballa A, Pasentsis K, Darzentas N, Tsaftaris AS (2011) Multiple evidence for the role of an Ovate-like gene in determining fruit shape in pepper. BMC Plant Biol 11:46

Wahyuni Y, Stahl-Hermes V, Ballester AR, de Vos RC, Voorrips RE (2014) Genetic mapping of semi-polar metabolites in pepper fruits (*Capsicum* sp.): towards unravelling the molecular regulation of flavonoid quantitative trait loci. Mol Breed 33:503–518

Yarnes SC, Ashrafi H, Reyes-Chin-Wo S, Hill TA, Stoffel KM, Van Deynze A (2012) Identification of QTLs for capsaicinoids, fruit quality, and plant architecture-related traits in an interspecific *Capsicum* RIL population. Genome 56:61–74

Zhao X, Meng Z, Wang Y, Chen W, Sun C et al (2017) Pollen magnetofection for genetic modification with magnetic nanoparticles as gene carriers. Nat Plants 3:956–964

Zygier S, Chaim AB, Efrati A, Kaluzky G, Borovsky Y, Paran I (2005) QTLs mapping for fruit size and shape in chromosomes 2 and 4 in pepper and a comparison of the pepper QTL map with that of tomato. Theor Appl Genet 111:437–445