Theor Appl Genet (2003) 106:889–894
DOI 10.1007/s00122-002-1132-9

A. B. Chaim · Y. Borovsky · W. De Jong · I. Paran

Linkage of the *A* locus for the presence of anthocyanin and *fs10.1*, a major fruit-shape QTL in pepper

Received: 8 May 2002 / Accepted: 15 August 2002 / Published online: 30 October 2002

Abstract The purple color of the foliage, flower and immature fruit of pepper (*Capsicum* spp.) is a result of the accumulation of anthocyanin pigments in these tissues. The expression of anthocyanins is controlled by the incompletely dominant gene *A*. We have mapped *A* to pepper chromosome 10 in a *Capsicum annuum* (5226) × *Capsicum chinense* (PI 159234) F_2 population to a genomic region that also controls anthocyanin expression in two other Solanaceous species, tomato and potato, suggesting that variation for tissue-specific expression of anthocyanin pigments in these plants is controlled by an orthologous gene(s). We mapped an additional locus, *Fc*, for the purple anther filament in an F_2 population from a cross of IL 579, a *C. chinense* introgression line and its recurrent parent 100/63, to the same position as *A*, suggesting that the two loci are allelic. The two anthocyanin loci were linked to a major quantitative trait locus, *fs10.1*, for fruit-shape index (ratio of fruit length to fruit width), that also segregated in the F_2 populations. This finding verified the observation of Peterson in 1959 of linkage between fruit color and fruit-shape genes in a cross between round and elongated-fruited parents. The linkage relationship in pepper resembles similar linkage in potato, in which anthocyanin and tuber-shape genes were found linked to each other in a cross of round and elongated-tuber parents. It is therefore possible that the shape pattern of distinct organs such as fruit and tuber in pepper and potato is controlled by a similar gene(s).

Communicated by J. Dvorak

A.B. Chaim · Y. Borovsky · I. Paran (✉)
Department of Plant Genetics and Breeding,
Agricultural Research Organization, The Volcani Center,
P.O. Box 6, Bet Dagan, 50250, Israel
e-mail: iparan@volcani.agri.gov.il
Fax: +972-3-9669642

W. De Jong
Department of Plant Breeding, 252 Emerson Hall,
Cornell University, Ithaca, NY 14853, USA

Keywords *Capsicum* · Fruit color · Fruit shape · Solanaceae

Introduction

Anthocyanins are flavonoid compounds responsible for a range of colors in a variety of plant organs such as fruit, flower, stem and leaf. In pepper (*Capsicum* spp.), some lines have a purple color in the immature fruit, flower and foliage. The organ distribution of the purple color varies among genotypes from plants with colored fruit, flowers, stems and leaves, to plants with only few colored flower organs such as the filament or the anther. In addition to the qualitative variation in the presence and distribution of anthocyanins, there is quantitative variation in the intensity of the purple color among genotypes. For example, some genotypes such as *Capsicum frutescens* BG 2816 have light purple immature fruit, while others such as *Capsicum annuum* 5226 used in this study have very dark purple fruit.

The presence of anthocyanin in pepper organs is controlled by the incompletely dominant *A* locus (Daskalov and Poulos 1994). A second locus, *MoA*, was characterized as a modifier of *A*, i.e., it intensifies the purple color in the presence of *A* (Daskalov and Poulos 1994). The inheritance of pepper flower color was studied by Odland (1960) in crosses that differed for color of the petal, anther, filament and style. He concluded that flower color is conditioned by three genes *S*, *W*, and *A*.

The map locations of pepper anthocyanin genes are unknown, although some linkage information exists from previous studies. Peterson (1959) reported linkage of 6.5 cM between *A* and the *O* locus conditioning round fruit shape in *C. annuum*. Pochard (1977) localized several morphological mutations in pepper by trisomic analysis. The *MoA* locus was localized to the trisomic BR which was subsequently identified as chromosome 11 by sharing linkage with *L* that confers resistance to TMV (Lefebvre et al. 1997; Ben Chaim et al. 2001). The *A* gene was assigned to the trisomic Rouge (RO); however,

unlike other trisomic lines that were aligned with the pepper genetic and molecular map (Lefebvre et al. 1997), the chromosome identification of the RO trisomic is unknown. The gene *fc* controlling anther-filament color was found to co-segregate with the RFLP marker CD5 by Prince et al. (1993); CD5 was subsequently assigned to pepper chromosome 10 by Livingstone et al. (1999).

We recently performed genetic and molecular analyses of fruit shape in pepper and mapped several quantitative trait loci (QTLs) controlling fruit shape in different *Capsicum* species (Ben Chaim et al. 2001, 2002; Rao et al. 2003). The objectives of the present study were: (1) to localize the genes that control the presence of anthocyanins in various plant organs on the genetic linkage map of pepper, (2) to determine their allelic relationships, and (3) to examine the linkage between these genes and fruit-shape QTLs.

Materials and methods

Plant material

IL 579 is one of a series of introgression lines developed from a cross between the recurrent parent 100/63 (a *C. annuum* bell-type inbred line obtained from Dr. Chen Shifriss, The Volcani Institute, Israel) and the donor parent *Capsicum chinense* PI 152225 (Tanyolac and Paran, unpublished). By marker-assisted selection, this cross was used to construct a set of near-isogenic lines (BC_3S_2 NILs) containing one or two introgressions from *C. chinense* in an otherwise uniform genetic background. An F_2 population of 195 plants resulting from a cross between IL 579 and 100/63 was used to map the purple filament and fruit-shape genes.

A second F_2 population of 100 plants was constructed from an inter-specific cross of *C. annuum* 5226 × *C. chinense* PI 159234. Line 5226 (obtained from Dr. Chen Shifriss, The Volcani Institute, Israel) has small round purple fruit (Fig. 1) as well as purple flowers, stem and foliage. PI 159234 has elongated green fruit, green stem and foliage, and white flowers.

Trait measurements

The F_2 population from the cross of 100/63 × IL 579 and the two parents (20 plants each) were grown in the open field in Qiryat Gat during the summer of 2001. Growing practices were described by Ben Chaim et al. (2001). The color of the filament was recorded visually as purple or white from three flowers per plant. Fruit length, width and shape (ratio of length to width) were measured from three mature fruits as described by Ben Chaim et al. (2001).

The F_2 population from the cross of 5226 × PI 159234 as well as the two parents were grown in the greenhouse in The Volcani Institute during the winter of 2001/2002. Although the F_2 plants segregated for purple color in their fruit, flower, stem and foliage, we chose to score the putative *A* locus by visually assessing the presence or absence of color only in the stem and in the flower petals because the scoring of these tissues allowed the clearest distinction between the presence and absence of purple color. Because some F_2 plants did not set fruits because of male sterility, we pollinated 3–5 flowers in each plant to ensure full development of the fruit. We measured fruit length, width and shape twice from three fruits per plant in December 2001, and again in April 2002 after the plants were trimmed and allowed to set fruit a second time.

Mapping, QTL and data analyses

Procedures for RFLP analysis and genetic mapping were described by Ben Chaim et al. (2001). Genetic maps were constructed by using MAPMAKER software (Lander et al. 1987). Map distances were computed using the Kosambi mapping function. Interval and single-marker QTL analyses were performed by QGENE software (Nelson 1997). The experimental-wise significance levels for interval analysis (LOD ≥ 2.4 and LOD ≥ 2.8 for 100/63 × IL 579 and 5226 × PI 159234 populations, respectively) were calculated by doing 1,000 permutations at $P < 0.01$. The degree of dominance (D/A) of the alleles of codominant loci was calculated with the software program QGENE. Student's *t* test ($P \leq 0.01$) was used to contrast the means of IL 579 and 100/63 for the measured traits by JMP v.3 software (SAS Institute, 1994). The percent difference between the two lines was calculated by subtracting the mean of IL 579 from the mean of 100/63, dividing by the mean of 100/63 and multiplying by 100.

Results

The phenotype of introgression line IL 579, which has a single 16 cM introgression in chromosome 10, first suggested to us that chromosome 10 may harbor a gene(s) controlling anthocyanin pigmentation in pepper. IL 579 has a purple anther filament, similar to the donor parent PI 152225, and unlike the white filaments of its recurrent parent 100/63. The F_1 from the cross 100/63 × IL 579 also had purple filaments, indicating a dominant inheritance pattern for this trait. The segregation of the purple filament in the F_2 fitted a 3:1 ratio for a single dominant gene (chi square = 2.5, $0.1 < P < 0.25$). Prince et al. (1993) assigned the symbol *Fc* to the gene controlling the filament-color trait.

The fruit of IL 579 was narrower than that of 100/63, while the lengths of both fruits were similar (Fig. 1, Table 1), resulting in a 48% increase of fruit-shape index for IL 579 compared to 100/63. Fruit shape was highly correlated with both fruit length and fruit width in the F_2 population ($r = 0.67$ and –0.81, respectively). Interval and single-marker QTL mapping analyses of fruit length, fruit width and fruit shape revealed a significant association between all the markers and intervals within the introgression for fruit width and fruit shape, but not for fruit length (Fig. 2B). TG63 was mapped 3 cM away from *Fc* and had the most significant association with

Table 1 Means, standard errors (SE), significance level and percentage of control of three traits for the introgression line IL 579 and its isogenic control 100/63

Trait	Parent	Mean	SE	*P* value[a]	% From control
Fruit length (mm)	100/63	140.7	3.8	NS	–
	IL 579	141.1	4.2		
Fruit width (mm)	100/63	87.2	2.1	<0.0001	–32.2
	IL 579	59.1	2.2		
Fruit shape (index)	100/63	1.61	0.07	<0.0001	47.8
	IL 579	2.38	0.07		

[a] NS = not significant

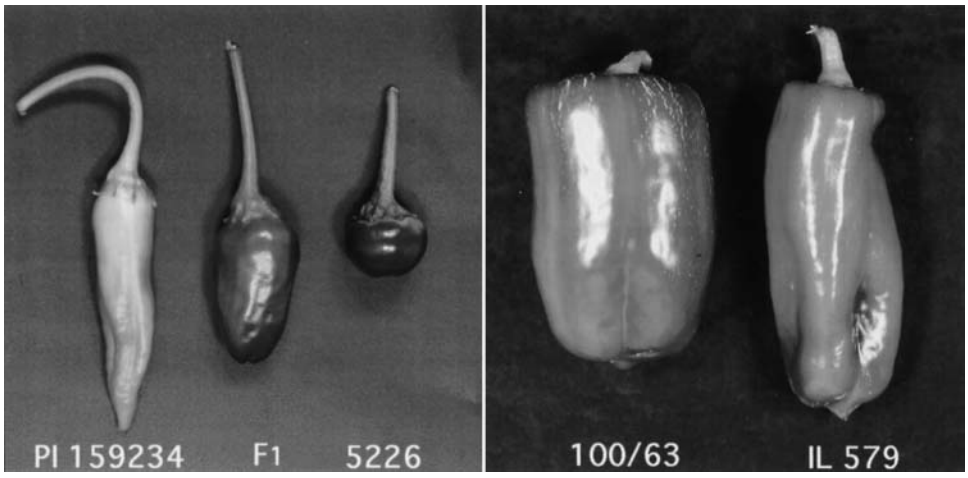

Fig. 1 Fruits of the parents and F_1 used in this study

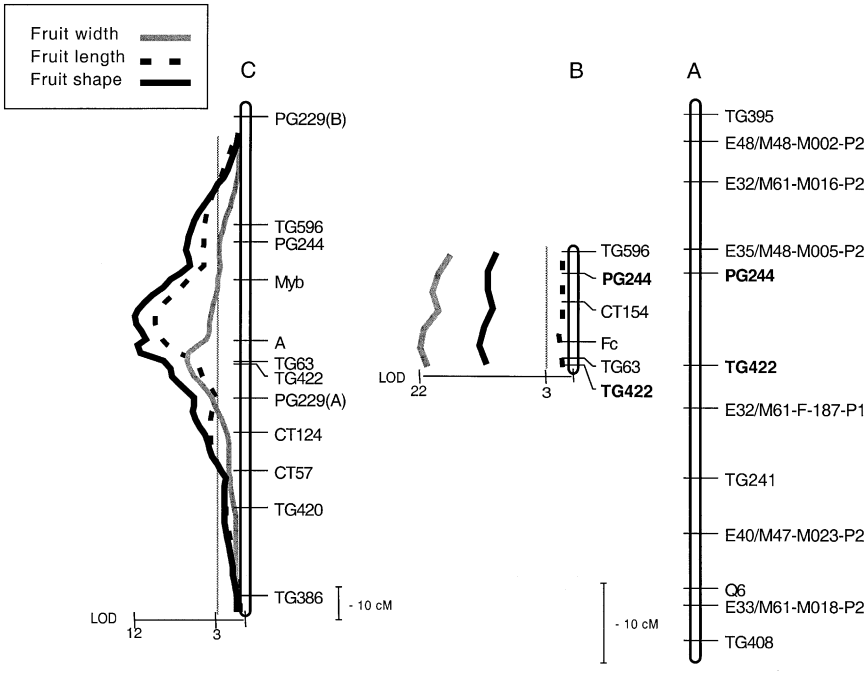

Fig. 2A–C Linkage maps of chromosome 10 and interval QTL analyses for fruit length, fruit weight and fruit shape. **A** Map of chromosome 10 in the 100/63 × PI 152225 BC_1 cross used to develop IL 579. **B** Map and QTL analysis of IL 579. Markers common to the two maps are *highlighted in bold type*. **C** Map and QTL analysis in the F_2 population of 5226 × PI 159234 in 2001

Table 2 Correlation coefficients for fruit shape, fruit length and fruit width in the 5226 × PI 159234 cross

Trait	Fruit shape 2002	Fruit shape 2001	Fruit width 2001	Fruit width 2002	Fruit length 2001
Fruit shape 2001	0.88				
Fruit width 2001	–0.47	–0.52			
Fruit width 2002	–0.67	–0.56	0.69		
Fruit length 2001	0.77	0.87	–0.11	–0.31	
Fruit length 2002	0.91	0.81	–0.26	–0.39	0.84

fruit width and shape, explaining 45% and 30% of the phenotypic variation of these traits, respectively (Table 3). The gene action of this fruit-shape QTL, which we have designated *fs10.1*, was determined to be partly additive (D/A = 0.3).

In order to determine whether the *Fc* locus is allelic to the gene(s) that controls purple color in other plant organs, and to determine whether the same region of chromosome 10 has an effect on fruit shape in another genetic background, we evaluated a second *C. annuum* × *C. chinense* cross between line 5226 and PI 159234. The F_1 from this cross had purple organs similar to 5226, although the intensity of the purple color was decreased compared to 5226, indicating incomplete dominance for anthocyanin pigmentation in this cross. The segregation of the purple color in the F_2 progeny in the flower and in

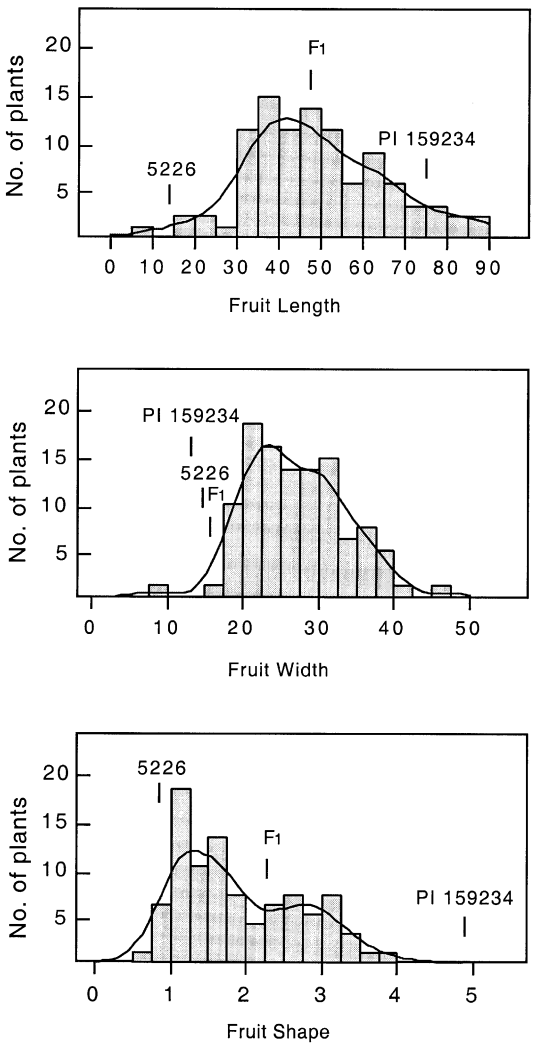

Fig. 3 Frequency distributions of fruit length, fruit width and fruit shape in the 5226 × PI 159234 F_2 population in 2001. The means of both parents and their F_1 are indicated by *lines*

the stem was identical, indicating that a single locus (*A*) (or two tightly linked loci) determines the presence of anthocyanin in these tissues. The segregation of pigmentation deviated significantly (chi square = 27.1, $P < 0.001$) from the expected 3:1 ratio for a single dominant gene, as did all the RFLP markers in the region because of skewed segregation against the homozygous class of the 5226 alleles. *A* mapped 5 cM away from TG63 in a similar position to where *Fc* mapped in the 100/63 × IL 579 cross.

The fruits of PI 159234 and 5226 were similar in their width but differed dramatically in their length, which resulted in a more than a 400% increase in the fruit-shape index for PI 159234 compared to 5226 (Fig. 1, Fig. 3). The fruit-shape index of the F_1 was intermediate to the two parents. The bi-modal segregation of fruit shape in the F_2 indicated that a single major gene controls the trait in this population. The distributions of fruit length and width were normal, showing transgressive segregation of fruit width. The fruit measurements in 2001 and in 2002 were very similar to each other ($r = 0.84$, 0.69 and 0.88 for length, width and shape, respectively, Table 2), consistent with the high heritability of these traits in pepper (Ben Chaim et al. 2000). Fruit shape in the F_2 population was highly correlated with fruit length, and to a lesser extent negatively correlated with fruit width (Table 2).

QTL analysis of the three traits in the F_2 population identified the A-Myb interval as containing a QTL for fruit length and shape, while for fruit width, a QTL was identified in the A-TG422 region (Fig. 2, Table 3). The *A* locus explained up to 44% of the phenotypic variation of fruit length and shape, while TG422 explained 36% of the phenotypic variation for fruit width.

Discussion

In this study we mapped two loci that control the presence of anthocyanin in pepper. The chromosome location determined for *Fc* is similar to the map position previously reported in a different *C. annuum* × *C. chinense* cross (Prince et al. 1993). The previous assignment of *A* to the RO trisomic by Pochard (1977), allows us to con-

Table 3 QTLs detected in the segregating populations

Trait	Cross	Year	Marker	Mean[a] AA	Mean[b] aa	Direction[c]	*P* value	R^2 (%)	LOD
Fruit length (mm)	5226 × PI 159234	2001	A	39.3	63.0	PI 159234	<0.0001	39	9.7
	5226 × PI 159234	2002	A	34.9	59.1	PI 159234	<0.0001	44	11.2
Fruit width (mm)	100/63 × IL 579	2001	TG63	69.2	56.0	100/63	<0.0001	45	21.7
	5226 × PI 159234	2001	TG422	36.7	23.5	5226	<0.0001	36	7.8
	5226 × PI 159234	2002	A	25.1	20.3	5226	<0.0001	18	3.8
Fruit shape	100/63 × IL 579	2001	TG63	2.1	2.5	IL 579	<0.0001	30	13.0
	5226 × PI 159234	2001	A	1.4	2.7	PI 159234	<0.0001	44	11.6
	5226 × PI 159234	2002	A	1.4	3.1	PI 159234	<0.0001	43	10.8

[a] Mean homozygous class for 100/63 and 5226 alleles. The mean for the dominant locus *A* was calculated for the AA/Aa class
[b] Mean homozygous class for the IL 579 and PI 159234 alleles
[c] Indicates the parent which contributes to the increase numeric value of the trait

clude that RO corresponds to chromosome 10. The map position of *A* was found to be identical with *Fc*, indicating that the two loci are allelic. Therefore, the differential accumulation of anthocyanin in various organs of the pepper plant is most probably controlled by a series of alleles at the same locus.

Pepper chromosome 10 is homologous (containing the same markers) to chromosome 10 in two other Solanaceous species, tomato and potato, although a parecentric inversion in the bottom part of chromosome 10 differentiates tomato from pepper and potato (Livingstone et al. 1999). In both tomato and potato, color mutations were mapped to the same region that corresponds to the *A* region in pepper. In tomato, the anthocyanin gainer (*ag*) mutation was mapped to the bottom of chromosome 10 linked to TG 63 and CD5 (Tanksley et al. 1992). In potato, the locus *F* that controls flower color was mapped as linked to TG63 (Van Eck et al. 1993). The common position of color genes in these Solanaceous species indicates that similar morphological variation for anthocyanin pigmentation in these species is controlled by the same genes. A similar situation exists for color genes associated with carotenoid biosynthesis in which the same genes control fruit color variation in both pepper and tomato (Thorup et al. 2000).

The genetics and biochemistry of anthocyanin biosynthesis in plants has been well characterized in *Antirrhinum*, maize and petunia (reviewed by Mol et al. 1998). Because the structural genes encoding the anthocyanin biosynthesis enzymes are conserved between different species, it is postulated that the variation in pigmentation pattern is controlled mainly by genes that regulate the biosynthesis pathway (Quattrocchio et al. 1998). Several anthocyanin regulatory genes have been isolated in petunia e.g. *an1, an2* and *an11* (De Vetten et al. 1997; Quattrocchio et al. 1999; Spelt et al. 2000), another member of the Solanaceae. The future cloning of these genes from pepper will allow us to determine whether any of these genes correspond to the *A* locus in this species.

Peterson (1959) reported linkage of 6.5 cM between *A* and *O*, the gene that controls round fruit shape in *C. annuum*. We verified this linkage in a *C. annuum* × *C. chinense* cross using round and elongated-fruited parents. In the study of Peterson as well as in additional early studies (Kaiser 1935; Khambanonda 1950), fruit shape was found to be controlled by a single major gene. Our recent molecular mapping studies support the existence of major genes that control this trait in pepper. In the *C. annuum* cross between blocky and elongated-fruited parents reported by Ben Chaim et al. (2001), a single QTL, *fs3.1*, was found to explain most (>60%) of the variation for fruit shape. A minor fruit-shape QTL explaining 10% of the phenotypic variation in the latter cross was also detected on chromosome 10 in the approximate position of *fs10.1* found in the present study. In a second cross between blocky and oval-fruited parents the same genomic region of *fs3.1* had the most effect on fruit shape, while no QTL effect was detected in the genomic region of *fs10.1* (Rao et al. 2003). The effect of *fs3.1* was further studied and verified in additional genetic backgrounds by Ben Chaim et al. (2002).

In the present study we identified a second major fruit-shape QTL in *Capsicum* that explained more than 40% of the phenotypic variation of this trait in the cross between round and elongated-fruited parents. Because we did not perform a genome-wide survey for the presence of additional fruit-shape QTLs in this cross, it is possible that other minor QTLs that affect this trait exist. Because *fs3.1* was identified previously as the QTL with the most effect on fruit shape in several pepper crosses, we tested whether it has an effect on the cross of 5226 × PI 159234. The RFLP marker TG130, that is tightly linked to *fs3.1*, detected polymorphism in this cross but in the F_2 population it was not significantly associated with fruit shape ($P = 0.06$ and 0.02 in 2001 and 2002, respectively).

In tomato, fruit-shape QTLs have been detected on several chromosomes (Grandillo et al. 1999); however, the few loci that were determined as having a major effect on this trait were mapped to different chromosomes than the pepper fruit-shape QTLs: *ovate* mapped to chromosome 2 (Ku et al. 2001) and *sun* mapped to chromosome 7 (Van der Knaap and Tanksley (2001). A possible orthology exits between tomato *fs8.1* (Ku et al. 2000) and pepper *fs8.1*, although the paucity of common markers in the two species precludes a precise comparison of this QTL (Ben Chaim et al. 2001). Interestingly, the potato *Ro* gene that controls tuber shape (round versus elongated) was found to be linked to tuber skin color and the RFLP marker TG63 on chromosome 10 (Van Eck et al. 1994). This linkage between an anthocyanin pigmentation gene and a gene conditioning a round tuber is exactly parallel to the linkage reported in pepper in this study. It is, therefore, possible that the shape pattern of distinct organs such as fruit and tuber in pepper and potato is controlled by the same gene(s). Comparative high-resolution mapping of the *fs10.1* and *Ro* regions in pepper and potato, and eventual cloning of these genes, will clarify whether they are orthologous.

Acknowledgements This research was supported by The United States–Israel Binational Agricultural Research and Development Fund Grant No. IS- 3225-01C, and by The Israel Science Foundation (Grant No. 643/00).

References

Ben Chaim A, Paran I (2000) Genetic analysis of quantitative traits in pepper (*Capsicum annuum*). Proc Am Soc Hort Sci 125:66–70

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, Rao GU, Tanyolac B, Paran I (2002) *fs3.1*: a major fruit shape QTL conserved in *Capsicum*. Genome (in press)

Daskalov S, Poulos JM (1994) Updated *Capsicum* gene list. Capsicum and Eggplant Newslett 13:15–26

De Vetten N, Quattrocchio F, Mol J, Koes R (1997) The *an11* locus controlling flower pigmentation in petunia encodes a novel WD-repeat protein conserved in yeast, plants, and animals. Genes Dev 11:1422–1434

Grandillo S, Ku HM, Tanksley SD (1999) Identifying the loci responsible for natural variation in fruit size and shape in tomato. Theor Appl Genet 99:978–987

Kaiser S (1935) The factors governing shape and size in *Capsicum* fruits: a genetic and developmental analysis. Torrey Bot Club Bull 62:433–454

Khambanonda I (1950) Quantitative inheritance of fruit size in red pepper (*Capsicum frutescens* L.). Genetics 35:322–343

Ku H-M, Grandillo S, Tanksley SD (2000) *fs8.1*, a major QTL sets the pattern of tomato carpel shape well before anthesis. Theor Appl Genet 101:873–878

Ku H-M, Doganlar S, Tanksley SD (2001) Exploitation of Arabidopsis-tomato synteny to construct a high-resolution map of the ovate locus in tomato. Genome 44:470–475

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Lefebvre V, Caranta C, Pflieger S, Moury B, Daubeze AM, Blattes A, Ferriere C, Phaly T, Nemouchi G, Ruffinatto A, Palloix A (1997) Updated intraspecific maps of pepper. Capsicum and Eggplant Newslett 16:35–41

Livingstone KD, Lackney VK, Blauth J, Wijk VR Jahn MK (1999) Genome mapping in *Capsicum* and the evolution of genome structure in the Solanaceae. Genetics 152:1183–1202

Mol J, Grotewold E, Koes R (1998) How genes paint flowers and seeds. Trends Plant Sci 3:212–217

Nelson CJ (1997) QGENE: software for marker-based genomic analysis and breeding. Mol Breed 3:229–235

Odland ML (1960) Inheritance of flower color in *Capsicum annuum* L. Proc Am Soc Hort Sci 76:475–481

Peterson PA (1959) Linkage of fruit shape and color genes in *Capsicum*. Genetics 44:407–419

Pochard E (1977) Localization of genes in *Capsicum annuum* L. by trisomic analysis. Ann Amelior Plant 27:255–266

Prince JP, Pochard E, Tanksley SD (1993) Construction of a molecular linkage map of pepper and a comparison of synteny with tomato. Genome 36:404–417

Quattrocchio F, Wing JF, van der Woude K, Mol JMM, Koes R (1998) Analysis of bHLH and MYB domain proteins: species-specific regulatory differences are caused by divergent evolution of target anthocyanin genes. Plant J 13:475–488

Quattrocchio F, Wing JF, van der Woude K, Souer E, de Vetten N, Mol JNM, Koes R (1999) Molecular analysis of the *anthocyanin2* gene of petunia and its role in the evolution of flower color. Plant Cell 11:1433–1444

Rao GU, Ben Cahim 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 (in press)

SAS Institute (1994) JMP users guide: version 3. SAS Institute, Carry, North Carolina

Spelt C, Quattrocchio F, Mol JNM, Koes R (2000) *anthocyanin1* of petunia encodes a basic helix-loop-helix protein that directly activates transcription of structural anthocyanin genes. Plant Cell 12:1619–1632

Tanksley SD, Ganal MW, Prince JP, deVicente MC, Bonierbale MW, Broun P, Fulton TM, Giovanonni JJ, Grandillo S, Martin GB, Messeguer R, Miller JC, Miller L, Paterson AH, Pineda O, Roder MS, Wing RA, Wu W, Young ND (1992) High density molecular linkage maps of the tomato and potato genomes. Genetics 132:1141–1160

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 97:11,192–11,197

Van der Knaap E, Tanksley SD (2001) Identification and characterization of a novel locus controlling early fruit development in tomato. Theor Appl Genet 103:353–358

Van Eck HJ, Jacobs JME, van Dijk J, Stiekema WJ, Jacobsen E (1993) Identification and mapping of three flower colour loci of potato (*S. tuberosum* L.) by RFLP analysis. Theor Appl Genet 86:295–300

Van Eck HJ, Jacobs JME, Stam P, Ton J, Stiekema WJ, Jacobsen E (1994) Multiple alleles for tuber shape in diploid potato detected by qualitative and quantitative genetic analysis using RFLPs. Genetics 137:303–309