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ORIGINAL PAPER

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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

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Abstract Quantitative trait locus (QTL) mapping for fruit weight and shape in pepper (*Capsicum* spp.) was performed using *C. chinense* and *C. frutescens* introgression lines of chromosomes 2 and 4. In chromosome 2, a single major fruit-weight QTL, *fw2.1*, was detected in both populations that explained 62% of the trait variation. This QTL, as well as a fruit-shape QTL, *fs2.1*, which had a more minor effect, were localized to the tomato fruit-shape gene *ovate*. The cloned tomato fruit-weight QTL, *fw2.2*, did not play a major role in controlling fruit size variations in pepper. In chromosome 4, two fruit-weight QTLs, *fw4.1* and *fw4.2*, were detected in the same genomic regions in both mapping populations. In addition, a single fruit-shape QTL was detected in each of the mapping populations that co-localized with one of the fruit-weight QTLs, suggesting pleiotropy or close linkage of the genes controlling size and shape. *fw2.1* and *fw4.2* represent major fruit-weight QTLs that are conserved in the three *Capsicum* species analyzed to date for fruit-size variations. Co-localization of the pepper QTLs with QTLs identified for similar traits in tomato suggests that the pepper and tomato QTLs are orthologous. Compared to fruit-shape QTLs, fruit-weight QTLs were more often conserved between pepper and tomato. This implies that different modes of selection were employed for these traits during domestication of the two Solanaceae species.

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Introduction

Comparative mapping studies in plants have found an overall high conservation of gene content and order in different taxa, such as the Brassicaceae, Poaceae, and Solanaceae (reviewed by Paterson et al. 2000). Most comparative mapping studies, however, determine the syntenic relationship between genomes but do not assess the degree of conservation of gene function in controlling similar traits. Because most traits related to the quality and yield of crop plants are quantitatively inherited and because the identity of most of the genes that control these traits is not known, a mapping approach that delineates a quantitative trait locus (QTL) to a specific chromosomal region could provide the basis for comparing the genetic control of similar traits between diverged species.

In the Solanaceae, comparative maps between tomato and potato (Tanksley et al. 1992), tomato and pepper (Livingstone et al. 1999) and, most recently, tomato and eggplant (Doganlar et al. 2002a) have established the syntenic relationships between the genomes of these vegetable crops. Whereas tomato and potato are differentiated from each other by only a few paracentric inversions, the genomes of tomato, eggplant, and pepper, although sharing large blocks of collinear chromosomal regions, have been much more extensively rearranged during speciation by means of translocations and inversions.

Studies comparing the genetic control of similar phenotypes in the Solanaceae have focused mainly on disease resistance and, more recently, on fruit characters. Resistance genes in tomato, potato, and pepper are often located at corresponding genomic positions, although in most cases the resistance genes have altered pathogen specificity (Grube et al. 2000). Comparative mapping analysis of genes from the carotenoid biosynthesis pathway has indicated that fruit-color variation in tomato and pepper is partly controlled by corresponding genes (Thorup et al. 2000).

The fruit is the main commodity of important Solanaceae crops such as tomato, eggplant, and pepper. Fruit size and fruit shape were among the major traits under selection during domestication of these crops. Whereas the wild fruits are typically small and round, the cultivated plants bear large fruits of diverse shapes. The genetic control of fruit size and fruit shape has been studied most extensively in tomato, and QTLs controlling these traits have been identified in several crosses involving cultivated and wild parents (Grandillo et al. 1999; Lecomte et al. 2004; reviewed by Tanksley 2004). These studies enabled the recent positional cloning of two major QTLs controlling fruit weight (*fw2.2*) and fruit shape (*ovate*) in tomato (Frary et al. 2000; Liu et al. 2002). In addition to tomato, fruit-related QTLs have been mapped in eggplant, and comparative QTL mapping in tomato and eggplant has revealed an overall high conservation of gene function for the major QTLs for these traits (Doganlar et al. 2002b).

In pepper, QTLs for fruit-related traits were identified in two recent mapping studies involving crosses of the same blocky-type parent, cv. Maor (*Capsicum annuum*), with small-fruited *C. annuum* and *C. frutescens* accessions (Ben Chaim et al. 2001; Rao et al. 2003). The inclusion of restriction fragment length polymorphism (RFLP) markers common to tomato in the pepper maps allowed a comparison of QTL conservation in these two Solanaceae species. A genome-wide comparison of fruit size and shape QTLs mapped in the two pepper populations and in two tomato introgression line (IL) populations of *Solanum pennellii* and *Solanum hirsutum* has identified three genomic regions in chromosomes 2, 3, and 4 that contain QTLs for fruit weight in all four pepper and tomato populations. These QTLs are therefore primary targets for putative orthology of fruit-weight QTL in pepper and tomato (Ben Chaim 2002).

To more accurately assess the possibility of QTL orthology in these chromosomes, we constructed ILs of pepper chromosomes 2 and 4 using two *Capsicum* species, *C. chinense* and *C. frutescens*. The goals of the present study were: (1) to use the pepper ILs to map QTLs for fruit size and shape in chromosomes 2 and 4; (2) to determine the degree of QTL conservation in the two *Capsicum* species; (3) to more vigorously test the hypothesis that QTLs in these regions are orthologous in pepper and tomato.

Materials and methods

Plant material

For the construction of *Capsicum chinense* chromosome 2 and 4 ILs, we used the small-fruited accession PI 152225 as a donor and the *C. annuum* blocky-type inbred 100/63 as a recurrent parent. By a series of backcrossing and marker-assisted selections, we generated BC_2S_3 homozygous lines IL-37 and IL-315, which contain introgressions of most of chromosomes 2 and 4, respectively (Fig. 1a). Except for the targeted chromosomes, these lines are isogenic to100/63. We then crossed these ILs with 100/63 and constructed F_2 populations of 68 and 125 individuals for IL-37 and IL-315, respectively. For IL-315, additional selfing and marker-assisted selection resulted in fixed F_4 lines that contain small overlapping introgressions useful for verification and high-resolution mapping of fruit size and shape QTLs.

The *C. frutescens* populations were derived from advanced backcross progenies of the cross of Maor and the wild *C. frutescens* accession BG 2816 (Fig. 1b; Rao et al. 2003). Based on the BC_2 map of this cross, two BC_2 plants, BC_2-117 and BC_2-29, were selected as containing chromosome 2 and 4 introgressions, respectively. These plants contained an additional five introgressions that, based on the advanced backcross QTL analysis, did not affect fruit size or shape and were therefore ignored in the QTL analyses. Selfed progenies of 99 and 123 plants of the BC_2S_1-117 and BC_2S_1-29 populations, respec-

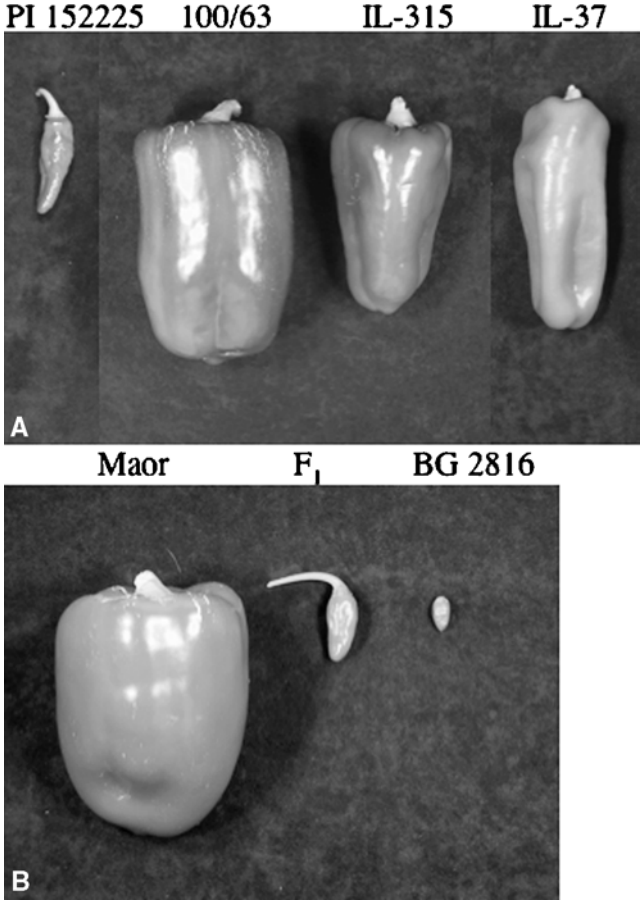

Fig. 1 Fruits of the parents used for QTL mapping. **a** PI 152225 (*Capsicum chinense*) and 100/63 (*C. annuum*) are the donor and recurrent parents, respectively, used to construct IL-315 and IL-37. **b** BG 2816 (*C. frutescens*) and Maor (*C. annuum*) are the donor and recurrent parents, respectively, used to construct the BC_2S_1 populations

tively, were used to construct RFLP maps and perform QTL analyses.

Field trial and trait measurements

The parents, F_2, and BC_2S_1 progenies for chromosome 2 were grown in a net-house in Bet Dagan in 2001; the parents, F_2 and BC_2S_1 progenies for chromosome 4 were grown in a net-house in Mivhor in 2002. The F_4 homozygous lines were grown along with IL-315 and 100/63 in the open field at the Mivhor and Lachish experimental farms in 2003. For both trials, ten plants from each line were grown in a randomized complete block design with five replications, two plants per replication. For all experiments, three fruits from each plant were harvested at maturity and measured for weight and shape index (length/width) as described by Ben Chaim et al. (2001).

Mapping, QTLs, and data analyzes

Procedures for RFLP analysis and genetic mapping were as described by Ben Chaim et al. (2001). Genetic maps were constructed using MAPMAKER software (Lander et al. 1987). Map distances were computed with the Kosambi mapping function. Interval-mapping QTL analyses in the segregating populations were performed with QGENE ver. 3.04 software (Nelson 1997). Significance threshold levels for QTL detection were computed by permutation tests for each trait with 1,000 iterations at $P < 0.01$ and an LOD range between 2.8 and 3.0. For the analysis of fruit weight in the BC_2S_1-29 population, composite interval mapping (MQM analysis) was employed using MAPQTL 4.0 (Van Ooijen et al. 2002) because distinct peaks could not be determined by interval mapping. Correlation coefficients were determined by QGENE.

Dunnett's test ($P \leq 0.05$) was employed by means of JMP ver. 4.0 software (SAS Institute 2000) to contrast the means of the IL-315 F_4 lines with the control (100/63). An IL was considered to contain a QTL only if significant effects were detected in both experiments. When a QTL was detected in two overlapping ILs, the location of the QTL was assumed to be in the overlapping region. Percentage difference from the isogenic control was calculated as 100(IL-control)/control.

Results

The parents used in this study varied considerably with respect to the size and shape of their fruits (Table 1, Fig. 1). The *C. annuum* inbred line 100/63, used as a recurrent parent for the construction of the *C. chinense* ILs, has a very large blocky fruit weighing 256 g and a shape index of 1.5. Maor has a typical bell-type fruit that weighs 165 g and has a shape index of 1.0. The fruit of *C. chinense* PI 152225 is small (4.3 g) and elongated (shape index 2.8), whereas that of *C. frutescens* BG 2816 is very small (0.2 g) with an oval shape. The fruits of IL-37 and IL-315 weigh less than one-half of that of the recurrent parent 100/63 (91.6 and 109.1 g, respectively, vs. 256 g). The fruit shape of IL-315 is similar to that of 100/63 (shape index of 1.2), whereas the fruit of IL-37 is narrower than that of 100/63, with a shape index of 2.3.

Table 1 Means and standard errors (SE) of fruit weights and shapes in the parents

Trait	Parent	Species	Mean	SE
Fruit weight (g)	100/63	*Capsicum annuum*	256	9.5
	Maor	*C. annuum*	165	3.2
	PI 152225	*C. chinense*	4.3	0.1
	BG 2816	*C. frutescens*	0.2	0.02
	IL-37		91.6	2.2
	IL-315		109.1	4.4
Fruit shape	100/63	*C. annuum*	1.5	0.1
	Maor	*C. annuum*	1.0	0.1
	PI 152225	*C. chinense*	2.8	0.1
	BG 2816	*C. frutescens*	1.9	0.1
	IL-37		2.3	0.04
	IL-315		1.2	0.04

QTL mapping in chromosome 2

In the F_2 cross of IL-37 and 100/63, a single major QTL, *fw2.1*, was detected for fruit weight (Fig. 2b). The most significant marker in the QTL region was *ovate*, which explained 62% of the phenotypic variation for the trait (Table 2). Plants homozygous for the *C. chinense* allele at *ovate* had fruits that were 58.2% smaller than those of plants homozygous for the recurrent parent allele. There was no significant correlation between fruit weight and shape in this population, and no QTL was detected for fruit shape.

A single major fruit-weight QTL, *fw2.1*, at *ovate* was also detected in the BC_2S_1-117 population, explaining 62% of the phenotypic variation for the trait (Fig. 2c, Table 2). Plants homozygous for the *C. chinense* alleles at *fw2.1* had fruits that were 64.1% smaller than those of plants homozygous for the recurrent parent allele at this locus.

A single fruit-shape QTL, *fs2.1*, at *ovate* was detected in the BC_2S_1-117 population, explaining 18.5% of the phenotypic variation for the trait. The fruits of plants homozygous for the *C. frutescens* allele at *ovate* were 9.7% less elongated than those of homozygous plants with the *C. annuum* allele. Unlike *fw2.1*, which segregated in this population and exhibited additive gene action, *fs2.1* showed an over-dominance effect ($d/a = 2.2$; Table 2). The significant positive correlation between fruit weight and shape ($r = 0.29$) was manifested by a common QTL at *ovate* for the two traits.

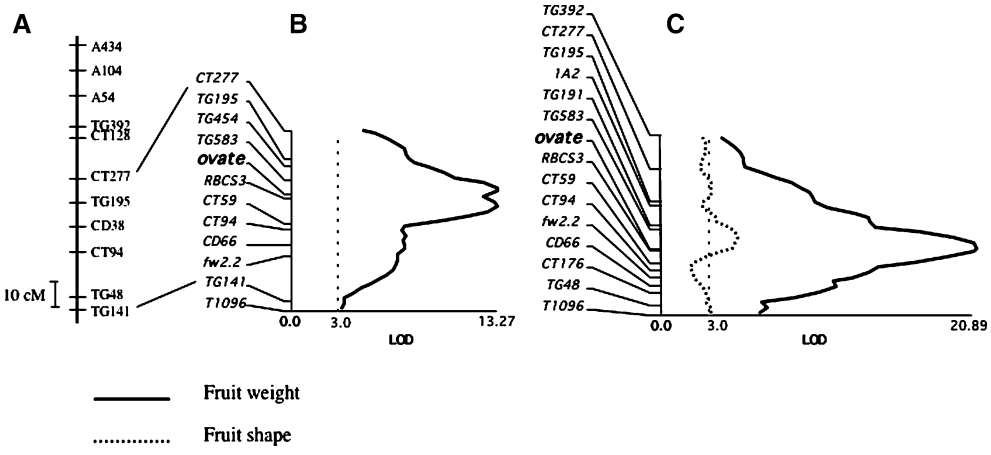

Fig. 2 QTL mapping in chromosome 2. **a** Map of chromosome 2 constructed by Livingstone et al. (1999). **b** Interval QTL mapping for fruit weight in the F_2 population of IL-37. **c** Interval QTL mapping for fruit weight and shape in the BC_2S_1-117 population. LOD scores are shown on the *x-axis*, and marker order and scaled distances are shown on the *y-axis*

QTL mapping in chromosome 4

Two fruit-weight QTLs, *fw4.1* and *fw4.2*, were detected in the F_2 population of IL-315, explaining 17.1% and 25.3% of the phenotypic variation for the trait, respectively (Fig. 3a, Table 3). Plants homozygous for the *C. chinense* allele at these loci had fruits that were 34.7% and 35.1% smaller, respectively, than those of plants homozygous for the *C. annuum* alleles. A single fruit-shape QTL, *fs4.1*, was detected at the same interval as *fw4.1* (T819-TG208), which explained 16.5% of the phenotypic variation for the trait. The co-incidence of the fruit-weight and -shape QTLs was reflected by the significant correlation ($r = 0.44$) between these two traits.

In the BC_2S_1-29 population, two fruit-weight QTLs, *fw4.1* and *fw4.2*, were detected in the same intervals as in the IL-315 population (Fig. 3b). These QTLs had greater effects than in the IL-315 population, explaining 30.2% and 28.3% of the phenotypic variation for the trait, respectively (Table 3). Plants homozygous for the *C. frutescens* alleles at these loci had fruits that were 49% and 43.8% smaller, respectively, than those of plants homozygous for the *C. annuum* alleles.

A single fruit-shape QTL, *fs4.2*, was detected in the BC_2S_1-29 population. Unlike *fs4.1* detected in the IL-315 population, which was mapped to the same interval as *fw4.1*, *fs4.2* was mapped to the same interval as *fw4.2* (TG500-TG22). *fs4.2* explained 26.1% of the phenotypic variation for the trait, and fruits of homozygous plants for the *C. frutescens* allele were 17.2% less elongated than those of plants homozygous for the *C. annuum* allele. There was no significant correlation between fruit weight and shape in this population.

Verification of QTLs in sub-ILs of chromosome 4

To verify the QTL positions in IL-315, we constructed nine smaller overlapping introgressions by selecting recombinants in the F_2 progenies of IL-315 and obtaining homozygous F_4 lines (Fig. 4). Comparison of the phenotypic effects of the sub-ILs and their parents in two field trials enabled us to identify fruit-weight and -shape QTLs in positions similar to those detected in the F_2 population of IL-315 (Fig. 5).

The fruits of line 37-6 were significantly smaller (by 27–37%) than those of 100/63 in both replications (Fig. 5a, b), indicating a QTL effect corresponding to that of *fw4.1* detected in the F_2. Similarly, the fruits of line 66-1 were significantly smaller (by 22–35%) than those of 100/63 in both replications, consistent with a QTL effect corresponding to that of *fw4.2* detected in the F_2. Lines 45-2 and IL-315, which contain both QTLs, had fruits that were 55% smaller than those of 100/63. Lines 90-7 and 97-1, which do not contain *fw4.1*, had fruits that were significantly smaller than those of 66-1 and close in size to the fruit of IL-315. This suggests the existence of an additional QTL in the TG574-T819

Table 2 QTLs for fruit weight and shape in chromosome 2 of pepper

Population	Trait[a]	QTL	Interval	Mean AA[b]	Mean aa[c]	Mean Aa[d]	Difference[e] (%)	LOD	R^2 (%)	d/a[f]
F_2 IL-37	FW	*fw2.1*	*ovate*-RBCS3	141	58.9	93.5	−58.2	13.3	62.1	−0.15
BC_2S_1-117	FW	*fw2.1*	*ovate*-RBCS3	71.6	25.7	47.1	−64.1	20.9	62.2	−0.07
	FS	*fs2.1*	*ovate*-TG583	1.03	0.93	1.09	−9.7	4.4	18.5	2.2

[a]FW, Fruit weight; FS, fruit shape
[b]Mean of the homozygous class for the cultivated parent (Maor and 100/63) allele
[c]Mean of the homozygous class for the alleles of PI 152225 and BG 2816
[d]Mean of the heterozygous class
[e]Calculated by subtracting the mean of the aa class from the mean of the AA class divided by the mean of AA and multiplying by 100. A negative sign indicates a reduced effect of the aa class relative to the control
[f]Gene action

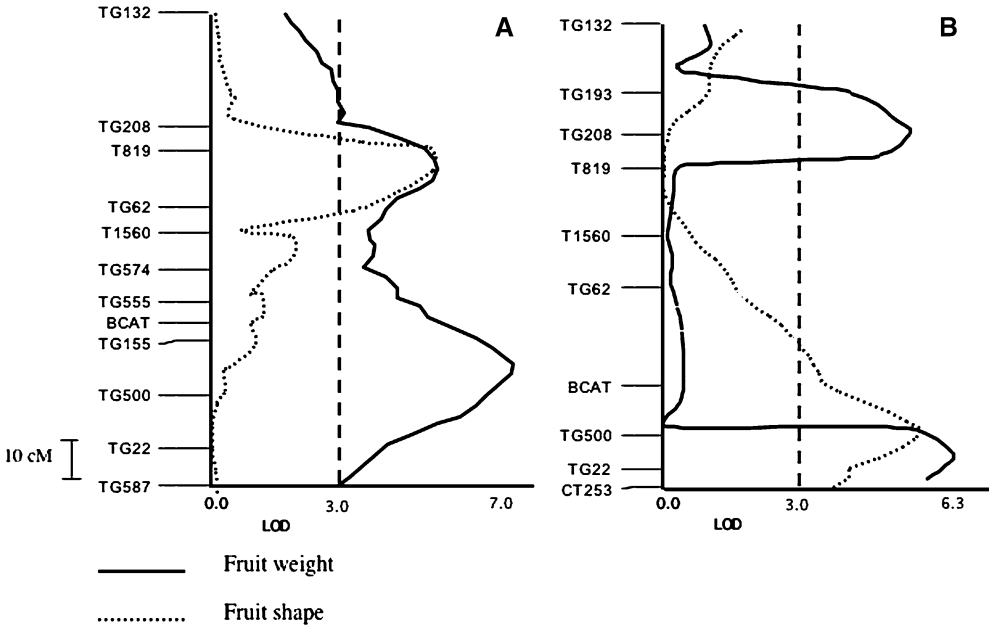

Fig. 3 QTL mapping in chromosome 4. **a** Interval QTL mapping for fruit weight and shape in the F_2 population of IL-315. **b** Interval QTL mapping for fruit weight and shape in the BC_2S_1-29 population. LOD scores are shown on the *x-axis*, and marker order and scaled distances are shown on the *y-axis*

interval that was not detected in the F_2. However, because sub-ILs containing only this region were not available, it was not possible to verify the effect of this putative QTL.

The fruit of line 37-6 was less elongated (by 17–26%) than that of 100/63, which is consistent with the fruit-shape QTL effect detected with *fs4.1* in the F_2 (Fig. 5c, d). The significant shape effect in line 97-1 delineates *fs4.1* to the interval between T819 and TG62; this in comparison to its location in the interval between T819 and TG208 in the F_2. The fruit of line 66-1 was also significantly less elongated than that of 100/63; however, because lines 123-1-1 and 90-7, which have the region contained in 66-1, did not deviate from the control, we conclude that there is no fruit-shape QTL in 66-1.

Discussion

Previous QTL mapping in pepper identified major QTLs for fruit weight in chromosomes 2 and 4 in an intra-specific cross of *C. annuum* and in the inter-specific cross of *C. annuum* × *C. frutescens* (Ben Chaim et al. 2001; Rao et al. 2003). An additional fruit-shape QTL was identified in chromosome 4 in the latter cross. However, because the mapping populations segregated for additional QTLs throughout the genome, the confidence QTL intervals were large, and it was not possible to determine whether single or multiple QTLs exist in these chromosomes. The present study allowed the mapping of fruit-weight and -shape QTLs in chromosomes 2 and 4 without the interference of other segregating QTLs and with improved chromosome coverage by molecular markers. In addition, QTL mapping was performed in a previously non-analyzed cross of *C. annuum* × *C. chinense*, thereby allowing a determination of the degree of QTL conservation in the *Capsicum* genus.

Conservation of QTLs in chromosome 2 in pepper and tomato

A single QTL, *fw2.1*, with a very large effect (accounting for 62% of the total phenotypic variation), was detected

Table 3 QTLs for fruit weight and shape in chromosome 4 of pepper

Population	Trait[a]	QTL	Interval	Mean AA[b]	Mean aa[c]	Mean Aa[d]	Difference[e] (%)	LOD	R^2 (%)	d/a[f]
F_2 IL-315	FW	*fw4.1*	T819-TG208	186.5	121.8	164.2	−34.7	4.6	17.1	0.3
	FW	*fw4.2*	TG500-TG22	186.2	120.8	146.8	−35.1	5.3	25.3	−0.2
	FS	*fs4.1*	T819-TG208	1.3	1.1	1.3	−15.4	4.5	16.5	1.0
BC_2S_1-29	FW	*fw4.1*	T819-TG208	71.2	36.3	61.7	−49	8.5	30.2	0.5
	FW	*fw4.2*	TG500-TG22	74.3	41.8	61.5	−43.8	7.5	28.3	0.2
	FS	*fs4.2*	TG500-TG22	1.7	1.4	1.4	−17.2	4.1	26.1	−1.0

[a]FW, Fruit weight; FS, fruit shape
[b]Mean of the homozygous class for the cultivated parent (Maor and 100/63) allele
[c]Mean of the homozygous class for the alleles of PI 152225 and BG 2816
[d]Mean of the heterozygous class
[e]Calculated by subtracting the mean of the aa class from the mean of the AA class divided by the mean of AA and multiplying by 100. A negative sign indicates a reduced effect of the aa class relative to the control
[f]Gene action

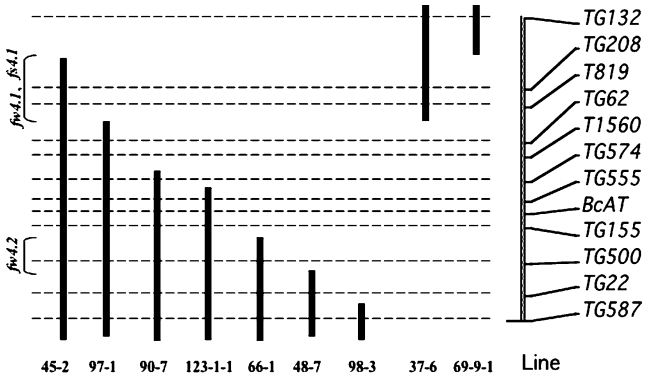

Fig. 4 Sub-introgression lines (ILs) derived from IL-315. A *black bar* indicates the introgressed segment in each line. QTLs identified by the F_2 of IL-315 and sub-ILs are indicated to the *left* of the *lines*

in the same genomic region of chromosome 2 in both mapping populations. The gene action of *fw2.1* was determined to be mostly additive in both populations. The localization of *fw2.1* to the same genomic region in both crosses supports the conclusion that the same QTL is segregating in both populations. A fruit-weight QTL was also detected in chromosome 2 in the *C. annuum* intra-specific cross of Maor × Perennial (Ben Chaim et al. 2001), indicating the possible conservation of a fruit-weight QTL in chromosome 2 across three *Capsicum* species. A single fruit-shape QTL, *fs2.1*, with a smaller effect than *fw2.1*, was detected in only one population (BC_2S_1-117) and coincided with *fw2.1*. The co-incidence of fruit-weight and -shape QTLs may result from pleiotropy of a single gene or from the action of distinct, linked ones.

In both mapping populations, *ovate*, a fruit-shape QTL recently cloned in tomato (Liu et al. 2002), was the most closely linked marker to the fruit-weight QTL. In tomato, five fruit-weight QTLs have been detected in chromosome 2 (Fig. 6a), of which three (*fw2.1*, *fw2.2*, and *fw2.3*) have been fine-mapped in the distal portion of the long arm of the chromosome (Eshed and Zamir 1995). Pepper *fw2.1*, although co-localized with *ovate*, could correspond to the tomato *fw2.1* (Fig. 6a). However, one cannot rule out the possibility that pepper *fw2.1* is encoded by *ovate*, which affects cell division during early carpel development in tomato. While *ovate* may affect the polarity of cell division in tomato, it may

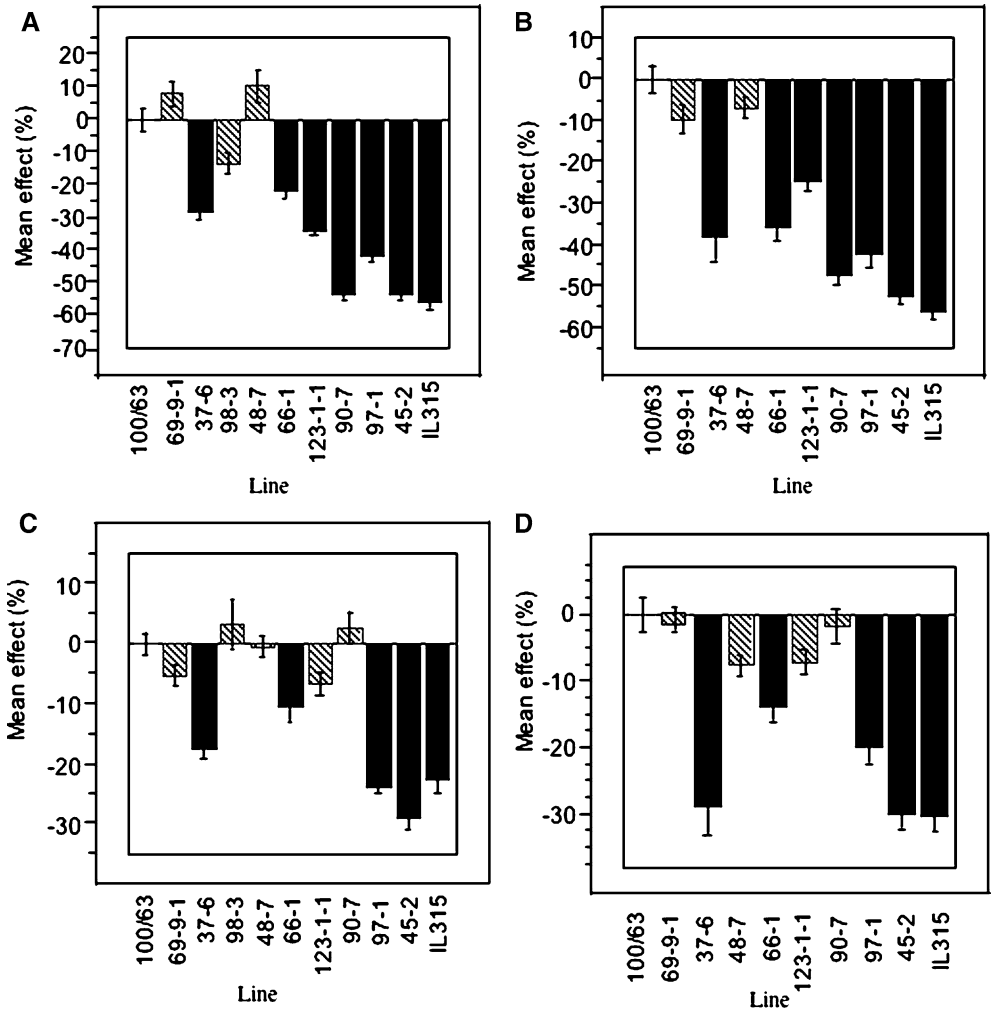

Fig. 5 The effect of sub-introgression lines (ILs) on fruit weight and shape. The effect is calculated by the percentage difference between the mean of the sub-IL from the mean of 100/63. *Black* and *hatched bars* represent significant and non-significant differences, respectively, from 100/63 in Dunnett's test ($P \leq 0.05$). **a** Fruit weight in Mivhor trial, **b** fruit weight in Lachish trial, **c** fruit shape in Mivhor trial, **d** fruit shape in Lachish trial

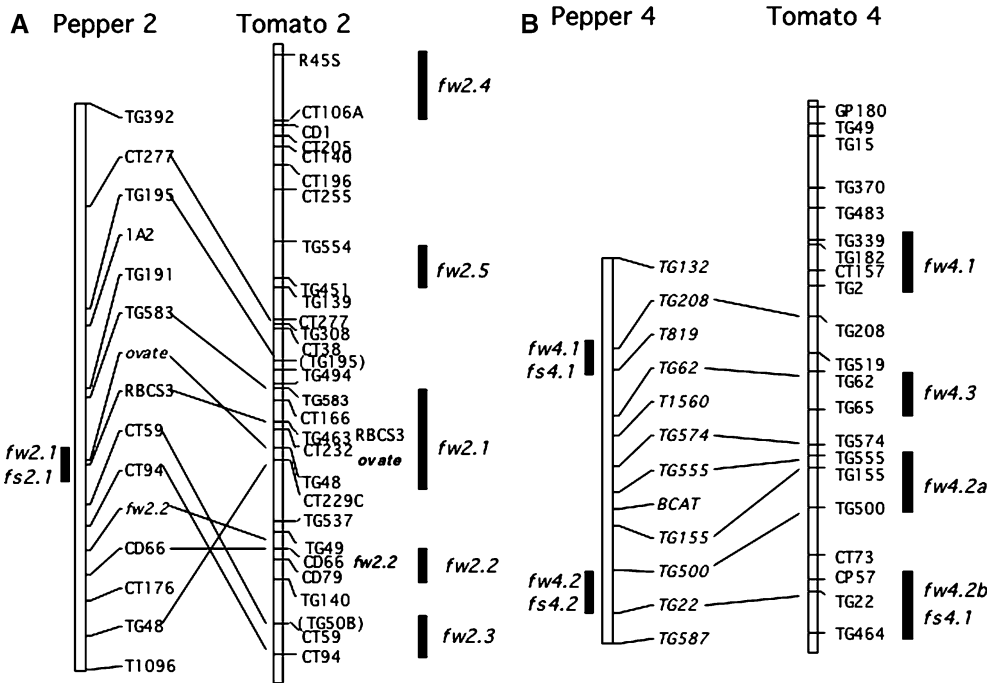

Fig. 6 Comparative QTL maps of pepper and tomato. **a** Comparison of QTL maps in chromosome 2. The pepper QTLs are presented on the map of BC_2S_1-117. *Black bar* to the *left* of the pepper chromosome represents QTLs identified in the present study. *Black bars* to the *right* of the tomato chromosomes represent fruit-weight QTLs according to Grandillo et al. (1999) and Eshed and Zamir (1995). Cloned QTLs (*ovate* and *fw2.2*) are indicated by *text*. *Solid lines* connect identical RFLP markers in the pepper and tomato maps. **b** Comparison of QTL maps in chromosome 4. The pepper QTLs are presented on the map of the F_2 of IL-315. *Black bars* to the *left* of the pepper chromosome represent QTLs identified in the present study. *Black bars* to the *right* of the tomato chromosomes represent fruit-weight and -shape QTLs according to Grandillo et al. (1999), Monforte et al. (2001), and Yates et al. (2004)

also affect other aspects of cell division in pepper that would account for the differences in fruit size. Alternatively, the co-localization of pepper *fw2.1* and *ovate* may reflect close linkage of these two genes. To discriminate between these two possibilities, high-resolution mapping (Fridman et al. 2002) or association studies (Wilson et al. 2004) using *ovate* as a candidate gene are required.

A comparison of the QTL maps in chromosome 2 of pepper and tomato indicates an inversion of the most distal part of the chromosome, which differentiates the two species (Fig. 6a). This inversion causes linkage of the chromosome region containing tomato *fw2.3* (CT59–CT94) to *fw2.1*. Therefore, the possibility of two tightly linked fruit-weight QTLs that account for the large phenotypic effect on the trait in pepper cannot be ruled out. Interestingly, tomato *fw2.2*, which has the most significant effect on fruit weight in tomato (Frary et al. 2000), does not play a major role in fruit size in pepper. In tomato, *fw2.2* is expressed mostly in the placental tissue and is only weakly expressed in the pericarp (Cong et al. 2002). Because the pepper fruit is comprised mostly of pericarp, the low expression of *fw2.2* in this tissue may account for the lack, or minor effect of this gene in pepper. In contrast to pepper, *fw2.2* was found to correspond to a major fruit-weight QTL in eggplant (Doganlar et al. 2002b), which, similar to tomato fruit, has a large placental tissue. Therefore, the anatomical differences between pepper fruits and those of tomato and eggplant may account for the differential impact of *fw2.2* on fruit size in these species. In tomato, the *locule-number* locus, which affects fruit size via changing carpel numbers, was identified in chromosome 2 (Lippman and Tanksley 2001). However, no change in locule number was observed in the pepper populations (data not presented), indicating that pepper fruit size is not affected by variations in locule number.

Conservation of QTLs in chromosome 4 in pepper and tomato

Two fruit-weight QTLs were detected in chromosome 4 in similar positions in both mapping populations. Both QTLs had a greater effect in the BC_2S_1-29 population than in the F_2 population of IL-315. This may result from the very small fruit of BG 2816 (0.2 g) compared to that of PI 152225 (4.3 g), although additional QTLs in other chromosomes contribute to the size differences between this accession and cv. Maor (Rao et al. 2003). In a previous mapping of the Maor × BG 2816 cross, only *fw4.2* was detected (Rao et al. 2003). The increased mapping resolution that allowed the detection of *fw4.1* in this study was made possible by the use of genetic material that eliminated the segregation of QTLs in other chromosomes. A fruit-weight QTL in the approximate position of *fw4.2* (a precise map comparison could not be made because of the lack of sufficient

common markers) was also detected in the intra-specific *C. annuum* population of Maor × Perennial (Ben Chaim et al. 2001). Therefore, it appears that *fw4.2* is conserved in the three *Capsicum* species analyzed to date for fruit-size variation.

One fruit-shape QTL was detected in each of the mapping populations that co-localized with one of the fruit-weight QTLs. While in the F_2 of the IL-315 population, the fruit-shape QTL *fs4.1* co-localized with *fw4.1*, in the BC_2S_1-29 population, the fruit-shape QTL *fs4.2* co-localized with *fw4.2*. Co-localization of fruit-weight and -shape QTLs has also been reported in chromosome 4 of tomato (Monforte et al. 2001) and may result from pleiotropy. In contrast to the conservation of the fruit-weight QTL in chromosome 4 in *Capsicum*, no such conservation was observed for fruit-shape QTLs. No fruit-shape QTL was detected in the intra-specific *C. annuum* population of Maor × Perennial (Ben Chaim et al. 2001). A fruit-shape QTL was detected in chromosome 4 in the BC_2 population of Maor × BG 2816 (Rao et al. 2003); however, its location did not fit the position of *fs4.2* detected in the BC_2S_1-29 population.

The cultivated alleles at both fruit-shape QTLs increased the degree of fruit elongation. However, the two fruit-shape QTLs differed in their mode of gene action. For *fs4.1*, there was complete dominance of the cultivated allele at the QTL ($d/a = 1.0$), whereas for *fs4.2*, the cultivated allele was completely recessive ($d/a = -1.0$).

In tomato, four fruit-weight QTLs have been were identified in chromosome 4 (Fig. 6b; Grandillo et al. 1999; Monforte et al. 2001; Yates et al. 2004). Of these, *fw4.1* has the greatest effect. However, according to Livingstone et al. (1999), the tomato chromosomal region containing *fw4.1* corresponds to pepper chromosome 5 and therefore did not segregate in the mapping populations. Pepper *fw4.2* is likely to correspond to tomato *fw4.2b*, whereas pepper *fw4.1* is mapped to the vicinity of tomato *fw4.3*, albeit not in the same genomic interval. In tomato, the fruit-shape QTL *fs4.1* was mapped in the same genomic interval as *fw4.2b* (Monforte et al. 2001; Yates et al. 2004), and it may correspond to the pepper *fs4.2* detected in the present study.

Different modes of selection for fruit size and shape during domestication of pepper and tomato

The wild progenitors of pepper and tomato bear fruit that are small and round (Tanksley 2004). In contrast, the cultivated species of these Solanaceae show very large variations in these traits because of the selection for alleles that have caused increases in size and changes in shape during domestication. The conservation of fruit-weight QTLs in chromosomes 2 and 4 in pepper and between pepper and tomato imply that these loci were under convergent selection during domestication. Additional fruit-weight QTLs identified in pepper (e.g., *fw1.1*, *fw3.1*, and *fw11.2*) are also potentially orthologous to tomato fruit-weight QTLs (Rao et al. 2003). In contrast to the conserved fruit-weight QTLs, fruit-shape QTLs in chromosomes 2 and 4, as well as in other pepper chromosomes (Rao et al. 2003), are not conserved in pepper and are only partly conserved between pepper and tomato. In pepper, the two major loci controlling fruit shape, *fs3.1* and *fs10.1* (Ben Chaim et al. 2003a; Ben Chaim et al. 2003b), do not correspond to tomato QTLs. Possible orthologous fruit-shape QTLs are pepper *fs8.1* and tomato *fs8.1* (Ben Chaim et al. 2001). However, the lack of enough common markers used to map these loci prevents substantiation of this hypothesis. The low level of QTL conservation controlling fruit shape in pepper and tomato implies that divergent selection for loci that control shape occurred during these species' domestication.

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