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ORIGINAL PAPER

Characterization of *fs10.1*, a major QTL controlling fruit elongation in *Capsicum*

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Abstract We previously identified *fs10.1* as a major QTL controlling fruit shape (index of length to width) in an interspecific F_2 cross of *Capsicum annuum* (round fruit) × *C. chinense* (elongated fruit) in pepper. To more precisely map and characterize the QTL, we constructed near-isogenic lines for *fs10.1* and mapped it in a BC_4F_2 population. In this population, *fs10.1* segregated as a Mendelian locus and mapped 0.3 cM away from the closest molecular marker. We further verified the effect of *fs10.1* in an F_2 population from an independent cross between elongated- and conical-fruited parents. To identify additional allelic variation at fruit shape loci, we screened an EMS-mutagenized population of the blocky-fruited cv. Maor and identified the mutant E-1654 with elongated fruit. This fruit shape mutation was mapped to the *fs10.1* region and was determined to be allelic to the QTL. By measuring fruit shape of near-isogenic lines for *fs10.1* during fruit development, we found that the shape of the fruit is determined primarily in the first 2 weeks after anthesis. Histological measurements of cell size and cell shape in pericarp sections of fruits of the isogenic lines throughout fruit development indicated that the shape of the fruit is determined primarily by cell shape and that the development of fruit shape is correlated with cell shape.

Introduction

Pepper (*Capsicum* spp.) was domesticated in South and Central America about 6,000 years ago (Perry et al. 2007). The wild progenitor of *C. annuum*, the main cultivated species, is thought to be the bird pepper, which was domesticated in Mexico (Eshbaugh 1993). The fruit of wild bird pepper is small (about 1 cm in length), erect, red colored, pungent, deciduous (falls off the plant when ripe), and soft-fleshed. These traits contribute to good adaptation for seed dispersal by birds (Paran and van der Knaap 2007). The shape of the wild pepper fruit can be round, oval, or elongated; however, continued selection during domestication and breeding resulted in a large increase in shape variation which, together with size and color, are the major determinants of fruit morphology in this species.

Fruit shape in pepper is typically inherited as a quantitative trait with high heritability (Ben Chaim and Paran 2000). Early studies indicated that fruit shape (ratio of length to width), although quantitatively inherited, is controlled by a single or a few major genes (Kaiser 1935; Khambanonda 1950; Peterson 1959). The first linkage study of genes controlling fruit shape was reported by Peterson (1959) who found linkage among *A*, *O*, and *G* loci, controlling purple immature fruit color, fruit shape, and yellow immature fruit color, respectively. Years later, the linkage between *A* and *O* was verified, and the loci were assigned to chromosome 10 (Ben Chaim et al. 2003a).

Quantitative trait locus (QTL)-mapping studies have identified several loci that control fruit shape in pepper (Ben Chaim et al. 2001; Rao et al. 2003; Zygier et al. 2005; Barchi et al. 2009). These and subsequent studies identified two major QTLs, *fs3.1* and *fs10.1*, which control most of the shape variation in *Capsicum* (Ben Chaim et al. 2003a, b). *fs3.1* controls the difference between blocky and elongated fruit in an intraspecific cross of *C. annuum* and explains 67% of the total phenotypic variation for fruit shape in this cross (Ben Chaim et al. 2001). *fs3.1* was also detected as a major QTL in crosses of *C. annuum* × *C. frutescens*

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(Rao et al. 2003) and *C. annuum* × *C. chinense* (Ben Chaim et al. 2003b). *fs10.1* controls the difference between round and elongated fruit in an interspecific cross of *C. annuum* × *C. chinense* and explains 44% of the total phenotypic variation for fruit shape in the cross (Ben Chaim et al. 2003a). This QTL is likely to be identical to the completely dominant *O* gene described by Peterson (1959) that controls fruit shape. However, whereas round fruit was dominant over elongated fruit in Peterson's (1959) study, *fs10.1* exhibited an additive mode of action (Ben Chaim et al. 2003a).

In continuation to the initial mapping study in which *fs10.1* was detected in an F_2 cross of *C. annuum* 5226 (round fruit) × *C. chinense* PI 159234 (elongated fruit) (Ben Chaim et al. 2003a), our objectives in the present study were to (1) construct and characterize near-isogenic lines (NILs) for *fs10.1*, (2) fine-map *fs10.1* in an F_2 population derived from crossing the QTL-NILs, (3) verify the effect of *fs10.1* in additional genetic backgrounds, and (4) determine the developmental and cellular basis of fruit shape variation conferred by *fs10.1*.

Materials and methods

Plant material

NILs for *fs10.1* were developed by using the parents of the original population used to map *fs10.1* (Ben Chaim et al. 2003a). Line 5226 with round fruit was used as a recurrent parent, and line PI 159234 with elongated fruit was used as a donor parent in a series of four backcross generations. In each generation, plants were selected for elongated fruit, and for the alleles of PI 159234 at two markers that flank *fs10.1*, i.e., absence of anthocyanin controlled by the *A* locus (Ben Chaim et al. 2003a), and the molecular marker CT11. Morphological markers such as orange fruit color and *fasciculate* growth habit that resemble the recurrent parent phenotype were used for background selection of the recurrent parent. In the BC_4 generation, heterozygous plants were selfed, and BC_4F_2 plants that were homozygous for alternate alleles at *fs10.1* were fixed. This pair of NILs was used to create an F_2 population of 147 individuals that segregates for *fs10.1*. Additional selfing to create BC_4F_3 lines was performed to determine that the fruit shape phenotype is fixed in the NILs.

To test the effect of *fs10.1* and to detect additional fruit shape QTLs in other genetic backgrounds, we constructed a mapping population from an interspecific cross of line 1154 (*C. annuum* accession A44750157, Nijmegen Botanical Garden, The Netherlands, with conical fruit shape) and PI 152225 (*C. chinense* with short elongated fruit). An F_2 population of 182 individuals was used to create the map with molecular markers and for measuring fruit shape.

To find additional allelic variation at the *fs10.1* locus, we searched an EMS-mutagenized population constructed from the blocky-fruited *C. annuum* cv. Maor for alterations in fruit shape (Paran et al. 2007). Visual screening was performed for 1,650 M_2 families (10 plants in each family) in the open field during the summer seasons of years 2004–2005. This screen allowed the identification of E-1654 with elongated fruit. E-1654 was further crossed to Maor, and mutant plants were selected from the F_2 population and advanced to F_3.

Trait measurement

Fruit shape index, ratio of length (from the proximal end to the distal end) to width (at the middle of the pericarp), was measured for at least three mature fruits per plant in each segregating population as described by Ben Chaim et al. (2001). Segregating populations plus parents and F_1 were grown in the open field in the experimental farm at the Volcani Center during the summer seasons of 2007 and 2009.

QTL mapping

RFLP markers in the *fs10.1* region were converted to CAPS markers for genotyping the BC_4F_2 population (Table 2). To map the 1154 × PI 152225 population, we used a total of 200 AFLP, RFLP, and COSII markers. The AFLP markers (contributed by Nunhems Netherlands B.V.) were chosen as a subset of approximately 450 markers distributed throughout the genome. Procedures for RFLP and AFLP analyses and genetic mapping were as previously described (Ben Chaim et al. 2001). The genetic map was constructed using MAPMAKER software (Lander et al. 1987). Map distances were computed with the Kosambi mapping function. Chromosome numbers were assigned to linkage groups based on known markers previously mapped to pepper chromosomes. For QTL analysis, interval mapping were performed by QGENE software (Nelson 1997). The experiment-wide significance level for interval analysis (LOD $\geq$ 3.2) was calculated by performing 1,000 permutations at $P < 0.05$.

Fruit development studies

Flower buds and fruits from the BC_4F_3 NILs (two flowers and fruits per plant, 10 plants per line) were used for measurements of length, width, and shape index at pre-and post-anthesis stages as described above. Measurements with a digital caliper were done on flowers estimated to be at 3 days before anthesis by harvesting flower buds and

isolating their ovaries. Starting from anthesis, measurements were taken on developing fruits on the plant at intervals of approximately 3 days until 21 days after anthesis in which thereafter fruit shape did not change. The length, width, and fruit shape values were plotted to create a growth curve of the fruits for each line.

Light microscopy and histological analysis

To measure cell shape and cell size in NILs differing for *fs10.1,* we used longitudinal and transverse sections of three fruits per genotype throughout fruit development. Each fruit was cut through the middle of the pericarp. Fruit samples were fixed in FAA (1.85% formaldehyde, 5% glacial acetic acid, 63% ethanol), dehydrated through an ethanol series (70, 80, 90, and 100%, 30 min each), embedded in paraffin, sectioned in a microtome (Leica RM2245), and stained with Safranin-O/Fast-green. The sectioned material was visualized by a Leica DMLB light microscope equipped with a DC200 camera. At least 50 cell measurements were made for each fruit in the layer of up to ten parenchyma cells in the mesocarp tissue. Cell width, length, and area were measured using the IM 1000 Image Manager software (Leica).

Results

Fine mapping of *fs10.1*

To verify the map location of *fs10.1* and to eliminate confounding effects of other segregating fruit shape QTLs, we constructed an F_2 population from a pair of NILs differing for *fs10.1* (Fig. 1a, b). Fruit shape segregated as a single Mendelian gene in this population (χ^2 value for single gene segregation $= 2.3$; $0.5 < P < 0.1$). Furthermore, the fruit shape phenotype was clearly distinguished among the three genotypic classes of linked flanking markers, indicating that no additional fruit shape gene differed between the NILs (Fig. 1c; Table 1).

To map *fs10.1* in the BC_4F_2 population, we scored *fs10.1* as a codominant gene by visually assessing the fruit

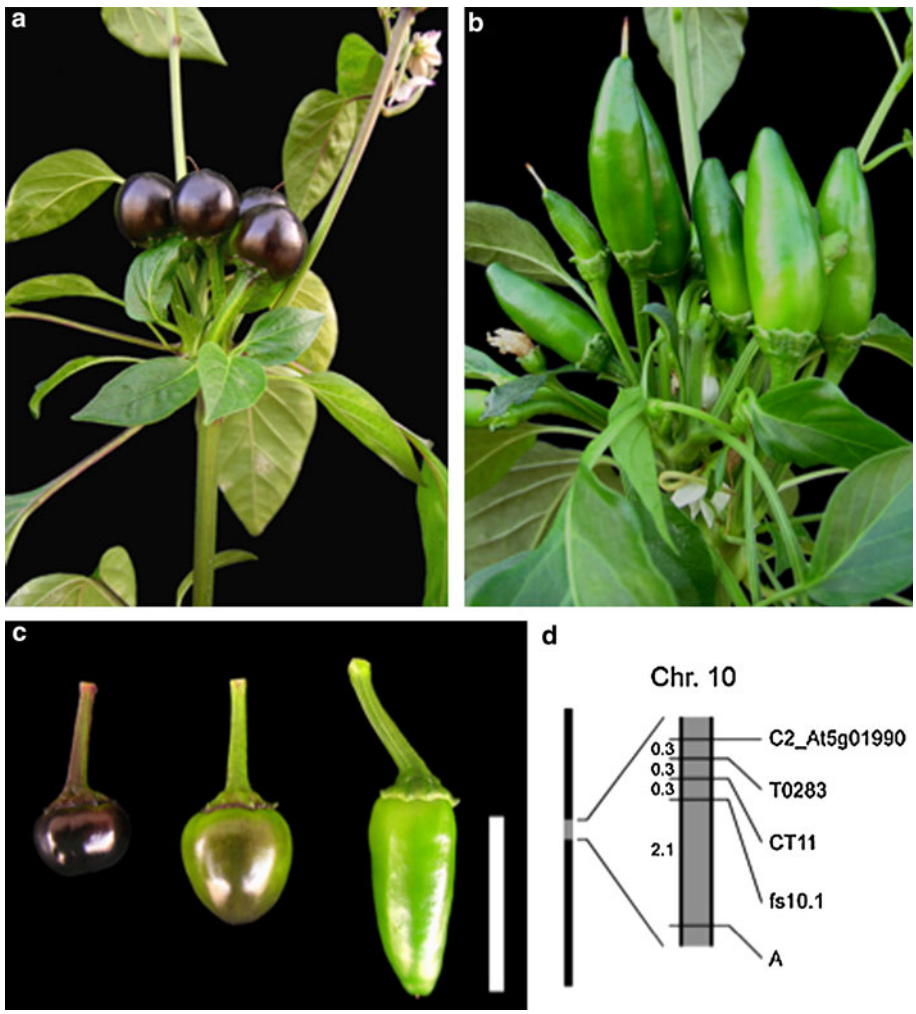

Fig. 1 Fruits of parents used in this study for QTL mapping and QTL map. **a** *fs10.1* QTL-NIL with *round and purple* fruit. **b** *fs10.1* QTL-NIL with *elongated and green* fruit. **c** Mendelian segregation of *fs10.1* in the BC_4F_2 population showing the fruit shape of three genotypic classes at the QTL. From *left* to *right*: homozygous for the round parent allele, heterozygous, homozygous for the elongated parent allele. **d** Map of chromosome 10 region containing *fs10.1* derived from the BC_4F_2 population. Numbers to the *left* of the linkage group represent genetic distances in cM. *Scale bar* in **c** 5 cm

Table 1 Fruit shape index (ratio of length to width) of QTL-NILs and BC_4F_2 genotypic classes at *fs10.1*

	Genotype				
	NIL-round*	NIL-elongated	BC_4F_2-A[a]	BC_4F_2-H	BC_4F_2-B
Fruit shape ± SD	0.87 ± 0.04	2.54 ± 0.3	0.87 ± 0.08[C]	1.29 ± 0.13[B]	2.23 ± 0.18[A]

* Significant difference between the NILs as determined by Student's *t* test at $P < 0.0001$

[a] *A* homozygous for the round parent allele, *H* heterozygous, *B* homozygous for the elongated parent allele

shape as round, elongated, or intermediate (Fig. 1c). The *A* locus for anthocyanin accumulation was scored visually as a codominant marker by the presence or absence of purple color in the flower petal. Heterozygotes were clearly distinguished from dominant homozygotes by having a thin ring of purple color in the petals compared to fully colored petals in the homozygous plants. In addition, we mapped one COSII and two RFLP markers that were converted to CAPS markers as detailed in Table 2. The closest marker to *fs10.1* was CT11, 0.3 cM away from the fruit shape locus (Fig. 1d). The genetic distance between *fs10.1* flanking markers C2_At5g01990 and *A* was 3 cM, compared to 16.5 cM in the original F_2 used to map *fs10.1* (Ben Chaim et al. 2003a, unpublished), a 5.5-fold reduction in recombination frequency in the more advanced population.

Change of shape during fruit development

The shape of ovaries and fruits of BC_4F_3 NILs for *fs10.1* was compared throughout fruit development. The shape of ovaries from flower buds differed between the NILs already 3 days before anthesis (Fig. 2). However, starting 3 days after anthesis, rapid elongation occurred in the fruits of the elongated NIL until 10 days after anthesis reaching a fruit shape index of 3.5. From 10 to 21 days after anthesis, the fruit shape index was reduced to 2.7 because of widening of the fruit without substantial further elongation. In contrast, the fruit shape index of the round NIL remained constant at about 1.0 throughout fruit development.

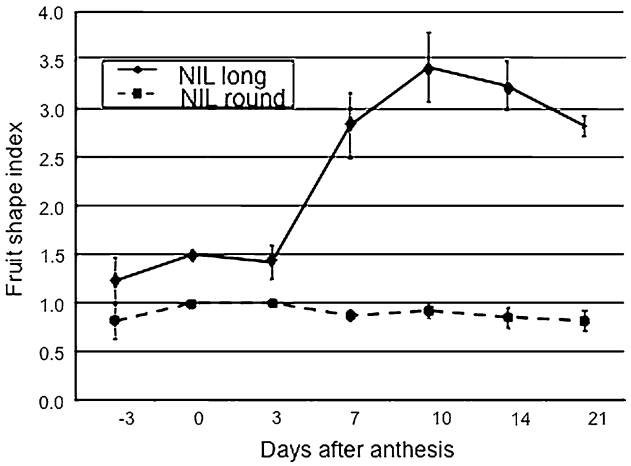

Fig. 2 Fruit shape index of two BC_4F_2 isogenic lines differing for *fs10.1* at different stages of fruit development starting 3 days before anthesis until 21 days after anthesis. *Bars* SDs

Detection of *fs10.1* in additional genetic backgrounds

To test whether *fs10.1* controls fruit shape in additional genetic backgrounds in pepper, we analyzed an F_2 population from a cross of *C. chinense* PI 152225 with an elongated fruit shape (fruit shape index 2.3 ± 0.3) and *C. annuum* 1154 with a conical fruit shape (fruit shape index 1.3 ± 0.1; Fig. 3). We detected three fruit shape QTLs in chromosomes 1, 3, and 10 (Fig. 3; Table 3). The most significant marker for the QTL in chromosome 10 was CT11, indicating that this QTL corresponds to *fs10.1*

Table 2 Markers used to genotype the BC_4F_2 population

Marker	Type	Primers (5′→3′)	Restriction enzyme
fs10.1	Morphological		
Anthocyanin (*A*)	Morphological		
T0283	CAPS	TGAAACACAACAGGGAATATTTG	*Hae*III
		AACCACTTCCATCCTTGTCA	
C2_At5g01990	COSII	CTTTGGACGGCTGTGTTTGG	*Hpa*II
		TCCTTCCCACACCCTCTCAA	
CT11	CAPS	TGTGCGTGGTGTTGATTGC	*Hae*III
		AGAGAGAGACAACGGCACGA	

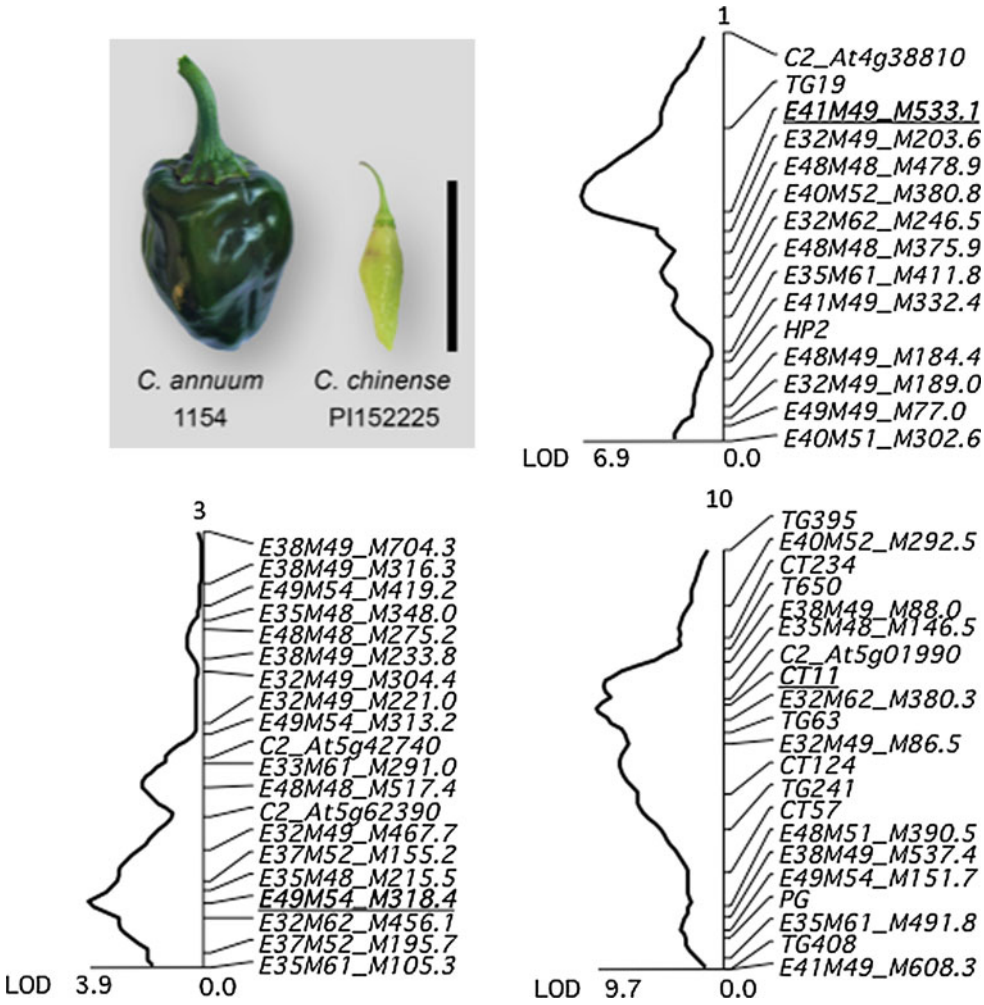

Fig. 3 Parents of the PI 152225 × 1154 cross and fruit shape QTL maps of chromosomes 1, 3, and 10 in the F_2 population. The LOD values at the QTL peaks are presented at the *axis* in each plot. *Scale bar* in the picture of the parents = 5 cm

Table 3 QTLs for fruit shape in the 1154 × PI 152225 population

QTL	Interval[a]	Direction	Means[b]			R^2	LOD
			AA	Aa	aa		
fs1.1	E41M49_M533.1-TG19	1154	2.5	1.9	2.0	20	6.9
fs3.1	E49M54_M318.4-E35M48_M215.5	PI 152225	1.7	2.1	2.3	12	3.9
fs10.1	CT11-C2_At5g01990	PI 152225	1.7	2.1	2.7	26	9.7

R^2 represents the proportion of phenotypic variation attributed to the QTL

[a] The most significant marker in the interval is underlined

[b] *AA* homozygous 1154, *Aa* heterozygous, *aa* homozygous PI 152225

detected in the BC_4F_2 population. In contrast to *fs3.1* and *fs10.1* for which the allele contributing to an elongated fruit at the QTLs originated from the elongated-fruited parent (PI 152225), the allele contributing to an elongated fruit at *fs1.1* originated from the conical-fruited parent (1154; Table 3). The appearance of transgressive F_2 segregants with fruit shape index up to 4.1 confirmed that QTL alleles for elongated fruit originated from both parents (data not shown).

Detection of new allelic variation at *fs10.1*

In addition to mapping fruit shape QTLs in segregating populations from crosses of parents exhibiting natural variation for fruit shape, we screened an EMS-mutagenized population constructed from the blocky-fruited *C. annuum* cv. Maor for alteration in fruit shape. We detected the recessive mutant E-1654 with an elongated fruit shape (fruit shape index 3.25 compared to 1.1 for Maor; Fig. 4a).

We did not observe shape changes in other plant organs between the mutant and Maor. To test whether E-1654 is mutated at the *fs10.1* locus, we crossed this mutant with *C. annuum* 5226 with round and purple fruit to test the possibility that the fruit shape mutation is linked to the *A* locus controlling anthocyanin accumulation, as had been found for *fs10.1*. Single marker analysis (one-way ANOVA) of fruit shape by *A* in an F_2 population of 132 plants indicated that two loci are significantly linked at $P < 0.0001$, $R^2 = 0.55$ (Fig. 4b). To further test the possibility that the mutation in E-1654 and *fs10.1* are allelic, we crossed E-1654 and the elongated BC_4F_3 NIL derived from the original mapping population. The fruit of the F_1 was elongated with a fruit shape index of 4.3 ± 0.2 (Fig. 4c), higher than the fruit shape index of the parents of the cross (2.54 ± 0.3 for the elongated BC_4F_3 NIL and 3.25 ± 0.4 for E-1654, respectively), indicating that the mutation in E-1654 is allelic to *fs10.1*.

Effect of *fs10.1* on cell shape and cell area

To determine whether *fs10.1* influences fruit shape by changing cell shape or cell area, we measured cell shape (length-to-width ratio) and cell area in sections of mesocarp tissues from three representative fruits of Maor and E-1654 at intervals of 1 week starting at anthesis (Fig. 5; Table 4). The cells in the longitudinal fruit pericarp sections of E-1654 were significantly more elongated than those of Maor at all developmental stages (Fig. 5a, c, d; Table 4). The degree of cell elongation during fruit development in E-1654 had a similar pattern as fruit elongation observed in Fig. 2, i.e., elongation occurred primarily between anthesis until 2 weeks after anthesis. No significant difference in cell shape between the parents was observed in the transverse sections except in 1 week after anthesis (Table 4). Cell area in both parents increased from anthesis until 3 weeks after anthesis (Fig. 5b; Table 4). In the longitudinal sections, no significant differences except for 1 week were observed in cell area between Maor and E-1654. In the transverse sections, no significant differences were observed in cell area between the parents until 1 week after anthesis. Between 2 and 3 weeks after anthesis, cells in Maor were significantly larger than in E-1654.

Discussion

Fruit shape is quantitatively inherited in pepper, and multiple QTLs have been detected in various genetic backgrounds in chromosomes 1, 2, 3, 4, 8, 10, and 11 (Ben Chaim et al. 2001; Rao et al. 2003; Zygier et al. 2005; Barchi et al. 2009). While most of these QTLs have minor effects and are detected in specific crosses, *fs3.1* and *fs10.1* have much larger effects and are detected across a wider range of germplasm. This situation resembles fruit shape variation in tomato, for which multiple QTLs have been detected, but most of the variation can be explained by a limited number of QTLs, in particular *ovate* and *sun* (Liu et al. 2002; Xiao et al. 2008). Despite the close relationship between tomato and pepper in the Solanaceae, fruit shape QTLs, except for *fs8.1*, do not map to similar genomic regions, implying an independent evolutionary origin (Paran and van der Knaap 2007). Interestingly, the only organ shape gene in other Solanaceae mapped to the syntenic region of pepper *fs10.1* is the potato *Ro* gene controlling elongated tuber shape (van Eck et al. 1994; Zhang 2009). The parallel linkage conservation of *fs10.1* and *Ro* raises the possibility of a common orthologous gene controlling organ shape in both species.

Construction of the map for *fs10.1* using the BC_4F_2 NILs improved mapping accuracy compared to the original mapping study of *fs10.1* in an F_2 population of the same cross (Ben Chaim et al. 2003a). Whereas the distribution of fruit shape was continuous in the original F_2 cross, probably because other fruit shape genes segregated in the

Fig. 4 E-1654 and Maor differing at *fs10.1*. **a** Fruits of the wild-type Maor and of the elongated-fruited mutant E-1654. **b** Segregation and linkage of fruit shape and anthocyanin accumulation in fruits of an F_2 population from the cross of E-1654 with the round-fruited line 5226 (the parents are shown in the *upper right corner*). **c** Fruit of F_1 from a cross between an elongated BC_4F_3 NIL and E-1654. *Scale bars* 5 cm

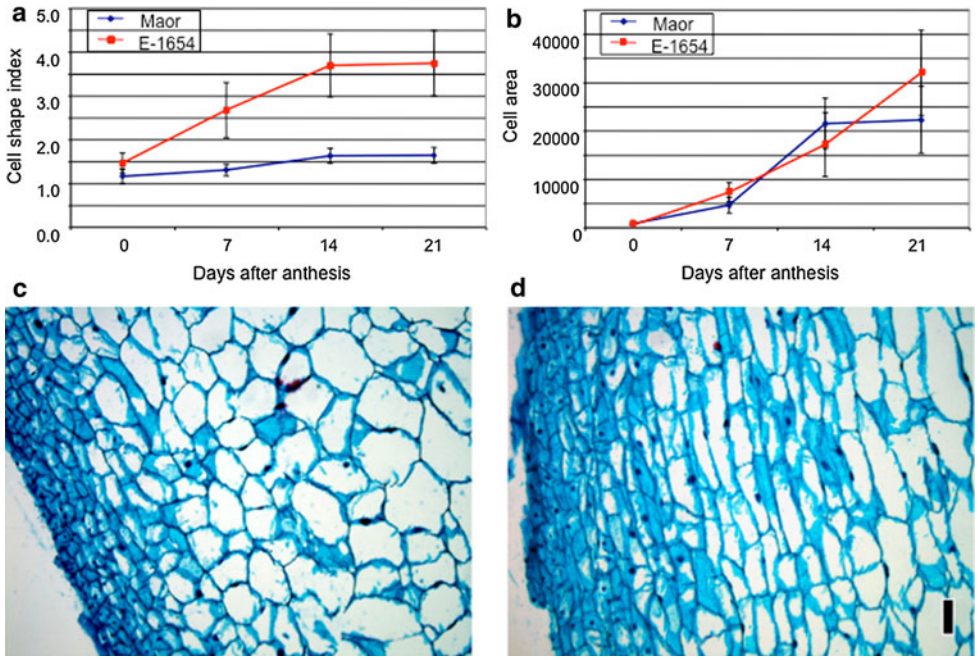

Fig. 5 Cell shape and cell area in isogenic lines for *fs10.1*. **a** Cell shape index in longitudinal mesocarp sections of fruits of Maor and E-1654 in different developmental stages. **b** Cell area in longitudinal mesocarp sections of fruits of Maor and E-1654 in different developmental stages. **c** Longitudinal mesocarp section of 2-week-old Maor fruit. **d** Longitudinal mesocarp section of 2-week-old E-1654 fruit. *Scale bar* 100 μm

Table 4 Cell shape (ratio of length to width) and cell area in pericarp sections of isogenic lines for *fs10.1*

Section	Fruit stage	Parent	Cell shape ± SD[a]	Cell area ± SD
Longitudinal	Anthesis	Maor	1.15 ± 0.16***	745 ± 188
		E-1654	1.45 ± 0.22	425 ± 69
	1 week	Maor	1.29 ± 0.13***	4,592 ± 1,603**
		E-1654	2.67 ± 0.63	7,234 ± 1,969
	2 weeks	Maor	1.62 ± 0.17***	21,469 ± 5,246
		E-1654	3.68 ± 0.72	17,135 ± 6,624
	3 weeks	Maor	1.63 ± 0.18***	22,229 ± 6,921
		E-1654	3.73 ± 0.72	31,938 ± 8,788
Transverse	Anthesis	Maor	1.12 ± 0.12	429 ± 92
		E-1654	1.14 ± 0.16	324 ± 65
	1 week	Maor	1.28 ± 0.14*	3,765 ± 1,003
		E-1654	1.05 ± 0.13	4,656 ± 1,270
	2 weeks	Maor	1.17 ± 0.17	19,803 ± 6,536**
		E-1654	1.24 ± 0.22	7,030 ± 1,789
	3 weeks	Maor	1.24 ± 0.21	23,892 ± 9,734**
		E-1654	1.14 ± 0.16	15,854 ± 4,426

[a] Asterisks indicate significant differences between Maor and E-1654 by Student's *t* test. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

population, fruit shape in the BC_4F_2 population segregated as a Mendelian trait. Furthermore, while the closest marker to *fs10.1* in the original F_2 was the *A* locus, adding more markers to the map of the BC_4F_2 population allowed the identification of CT11 as the most closely linked marker to the QTL. Compared to the original F_2, a 5.5-fold reduction in recombination frequency was observed in the BC_4F_2 population. Suppression of recombination in interspecific introgressions has been frequently observed in tomato (Rick 1969; van der Knaap et al. 2004; Canady et al. 2006) and has been attributed to sequence divergence between the genomes which hampers crossing over. Based on the *Solanum lycopersicum* assembly 2.30 release (http://solgenomics.net/), the two markers CT11 and *ANT1* (the tomato ortholog of pepper *A*) that flank *fs10.1* are located 6.3 Mb apart from each other in tomato. This physical distance corresponds to 8.8 and 2.4 cM in the original F_2 population and the BC_4F_2 population, respectively. While the physical distance between these markers is currently not known in pepper, the tomato data imply that the *fs10.1* region is not highly recombinogenic.

In addition to the natural variation in fruit shape studied in pepper, we isolated an induced EMS mutant with an elongated fruit compared to the blocky fruit shape of the wild-type parent. The linkage of the fruit shape locus with the *A* locus and the allelism test indicated that E-1654 is mutated at *fs10.1*. Generation of a new mutant at *fs10.1* creates a new pair of isogenic lines in an independent genetic background of the BC_4F_2 NILs described above. These genetic materials will be instrumental for future identification of the gene encoded by the *fs10.1* locus.

In a previous QTL mapping study, involving a cross of Maor and *C. frutescens* BG 2816 with small oval fruit, we did not detect fruit shape QTL in the chromosomal region of *fs10.1*, probably because allelic variation did not exist at this locus (Rao et al. 2003). However, the generation of new variation by induced mutation and the detection of *fs10.1* in various genetic backgrounds and in crosses between parents with different fruit types indicates that

fs10.1 has a major role in controlling fruit shape in *Capsicum*. A more detailed examination of the role of *fs10.1* in determining fruit shape in pepper will require cloning the gene governing this QTL and studying its allelic diversity in a panel of lines with different fruit shapes.

Similar to pepper *fs3.1* (Ben Chaim et al. 2003b), *fs10.1* exerts its major effect on fruit elongation after anthesis. Although shape difference between the NILs was apparent already in anthesis, the major elongation phase in the elongated fruit occurred between 3 and 10 days after anthesis. This developmental pattern is similar to that found by Sinnott and Kaiser (1934) who studied the difference in fruit growth rate between elongated and round pepper fruits. Similarly, the *sun* locus that controls fruit elongation in tomato affects fruit shape primarily after anthesis (Van der Knaap and Tanksley 2001). In contrast, *OVATE* and *fs8.1* in tomato control fruit shape before anthesis (Ku et al. 2000; Liu et al. 2002). Similarly, in melon, fruit shape is controlled prior to anthesis (Perin et al. 2002). These patterns of shape development indicate that fruit shape may be determined by different developmental pathways within and among plant species or that genes within the same pathway, e.g., gibberellin biosynthesis are active in different developmental stages.

The histological analyses of pericarp tissues of Maor and E-1654 revealed that *fs10.1* exerts its effect mainly by regulating cell shape in the first 2 weeks of fruit development. This stage of development is characterized by cell division (Xiao et al. 2009); it is therefore possible that *fs10.1* is involved in this process. Among the known genes that control fruit size variation, *FW2.2* in tomato has been proposed to regulate cell division, as larger fruit size was associated with more cells per unit tissue (Frary et al. 2000). Similarly, the maize *Cell Number Regulator* (*CNR*) genes that are orthologous to tomato *FW2.2* control organ size by changing cell number (Guo et al. 2010). An association between fruit weight and cell number has also been observed for other QTLs (Prudent et al. 2009). In contrast, a cellular basis for fruit shape variation has not been reported to date. *OVATE*, which controls fruit elongation in tomato (Liu et al. 2002), was found to belong to a family of transcription factors in *Arabidopsis*, of which *Ovate Family Protein 1* (*AtOFP1*) has a role in suppressing cell elongation in *Arabidopsis* (Wang et al. 2007). Therefore, it is possible that tomato *OVATE* has a similar function in controlling fruit shape.

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