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Identification and characterization of a novel locus controlling early fruit development in tomato

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Abstract Cultivated tomatoes (*Lycopersicon esculentum*) encompass a wide range of fruit size and shape variants. This variation provides the basis for dissecting the genetic and molecular pathways of ovary and fruit development. One fruit shape variant is displayed by the cultivar Sun 1642 (TA491). TA491 has an elongated fruit phenotype, while the wild relative *L. pimpinellifolium* LA1589 produces fruit that are nearly perfect spheres, a shape typical of wild tomatoes. Developmental studies indicated that the differences in fruit shape between TA491 and LA1589 are determined by events occurring immediately after pollination and extending to 14 days post-pollination. Quantitative trait mapping revealed a single major locus on chromosome 7 (named *sun*) to be responsible for the differential development of TA491 and LA1589 fruit. Other fruit shape loci characterized in tomato (e.g. *fs8.1* and *ovate*) exert their effects before anthesis and early in ovary development. *sun* is the first major locus identified in tomato controlling fruit shape through post-pollination events.

Keywords Tomato · Fruit shape · Development · Mapping · QTL

Introduction

Dramatic increases in fruit size and variation in fruit morphology have accompanied the domestication of tomato (*Lycopersicon esculentum*) and other fruit-bearing crops. While fruit within the non-domesticated *Lycopersicon* genus are generally round, small and inconspicuous, fruit of cultivated tomato display a wide range of sizes and shapes. The appearance of fruit ranges from round to elongated and blocky, from pear-shaped and oval, to a shape reminiscent of bell pepper fruits (Grandillo et al. 1996; Frary et al. 1998; Ku et al. 1999).

The development of the tomato seed-bearing structure commences with ovary development within the floral meristem. Regional identity is first established in the developing ovary followed by the differentiation of the tissue types. The differentiation of the epidermis, the pericarp, the placenta and the ovules is completed by anthesis (Gillaspy et al. 1993). After successful pollination and fertilization, the tomato ovary develops into a fruit which proceeds through a stage of cell division, followed by a rapid growth stage mainly due to cell expansion (Gillaspy et al. 1993). The final stage of fruit development, the ripening stage, occurs when seed maturation has been completed. This stage is characterized by changes in color, texture, flavor, aroma, softening, and changes in ethylene biosynthesis and perception (reviewed in Gray et al. 1994). While the ripening stage has been studied extensively, little is known about tomato ovary and early fruit development. Changes in fruit shape and size become apparent during ovary and fruit development. Therefore, variation in fruit shape and size can be used to gain information about processes that occur during ovary and fruit development.

Using the approach of quantitative trait loci (QTL) mapping, many of the loci controlling tomato fruit shape and size have been positioned on the genetic map (Grandillo et al. 1999). The molecular nature of a fruit size QTL, *fw2.2*, was recently identified and found to encode a novel, plant-specific protein that regulates cell number in the developing ovary (Frary et al. 2000). None of the genes controlling fruit shape have been cloned, but several loci have been characterized developmentally (Grandillo et al. 1996; Ku et al. 1999, 2000a, 2001). Two such loci, *fs8.1* and *ovate*, act early in ovary development since the final fruit shape is apparent at anthesis (Ku et al. 2000a, 2001). The processes these loci affect are likely to be in signaling pathways leading up to differences in regional identity and/or differentiation of tissue types in the developing ovary. In this paper, we

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describe the developmental characteristics and genetic basis of fruit shape in a processing tomato cultivar, TA491. We report for the first time the identity of a genetic locus controlling fruit shape and development through post-anthesis events.

Materials and methods

Plant materials

Parental plants were inbred stocks of *L. esculentum* TA491 (Sun 1642 from Harris-Moran), TA503 (Yellow Pear) and *L. pimpinellifolium* LA1589. For genetic analysis, 100 F_2 plants derived from a cross between LA1589 and TA491 were grown in the greenhouse at a day temperature of 27°C and a night temperature of 17°C, with supplemental lighting. In most cases, eight ripe fruits per plant were analyzed for the fruit shape index (length over diameter). Fruits containing no seeds were eliminated from the analyses.

Fruit development analysis

For the measurement of the shape index of ovaries at anthesis, flowers that had been opened less than 24 hours were harvested. Flowers were cut longitudinally to expose the ovaries and viewed using a Zeiss dissecting stereomicroscope. Images were captured by a CCD camera. For the fruit developmental analysis in TA491, individual flowers were tagged and all petals, stamens and three sepals were removed 1 day prior to anthesis. Stigmas were pollinated 2–3 days post-emasculation, which was then counted as 0 days after pollination. Due to a severe incidence of blossom-end rot in TA491, only eight fruits were used for the analysis of fruit development. For LA1589, stamens and petals were removed on the day of anthesis and pollination. Sepals were not removed to expose the developing fruit because this resulted in either fruit abortion or severely retarded growth. Pictures of each developing fruit were taken twice a week with an Olympus digital camera 2500L. All images were viewed and analyzed using NIH image software (http://rsb.info.nih.gov/nih-image/).

Molecular analyses

DNA isolation, genomic gel blot analyses and autoradiography were performed as described by Bernatzky and Tanksley (1986) and Fulton et al. (1995). A total of 106 markers showed a RFLP (restriction fragment length polymorphism) between LA1589 and TA491 with one or more of the following restriction enzymes: *Bst*NI, *Dra*I, *Eco*RI, *Eco*RV, *Hae*III, *Hind*III, *Sca*I and *Xba*I. Of these, 104 markers were present on the high-density molecular map (Tanksley et al. 1992), while *T42* (AI485360) and *21J7* (AI488457) are tomato expressed sequence tags (ESTs). Two additional markers were mapped as single nucleotide polymorphisms (SNPs). Primers for *TG418* were: TG418F, 5´-TCAGCTGAAGAACAGCGAGA-3´ and TG418R2, 5´-GGGACGTGATTGAGTGGAAG-3´. Primers for *TG131* were: TG131RR1, 5´-CCTTGGGTTCCAATTCAGAG-3´ and TG131RF1, 5´-ATCCGAAAACCCAAAGATCA-3´. Sequence analysis with primers TG418R2 and TG131RR1 revealed two and one SNP between the alleles of LA1589 and TA491, respectively. To map *TG418* and *TG131*, we performed polymerase chain reaction (PCR) amplification of these markers, and subsequent sequence analysis was only performed on F2 plants recombinant in the interval expected to contain these markers.

Statistical analyses

Student's *T*-tests for shape index differences between TA491 and LA1589 were performed for both ovaries at anthesis and ripe fruits. For the fruit development study, fruit shape indices were averaged for the developing fruits at 0, 4, 7, 11, 14, 21, 28, 35, 42, 49 or 56 days after anthesis, and standard errors were derived. To detect significant differences in fruit shape index within each F_3 family, the average fruit shape index per plant in the recombinant versus non-recombinants classes were contrasted in unpaired *T*-tests.

Linkage analysis of 108 markers on the 12 tomato chromosomes was performed using the software package MAPMAKER v2.0 (Lander et al. 1987). Markers and their corresponding distances were included within the framework map only if the LOD score for the ripple was >3, unless otherwise indicated. The Kosambi mapping function was used to convert recombination frequencies to map distances in centiMorgans (Kosambi 1944). Distortion of allele segregation was determined using the *chi*-square test. Genome-wide QTL analysis was performed by both a single-point linear regression model and by interval analysis using QGENE software version 3.06d (Nelson 1997). The LOD threshold was set at 2.4. The degree of dominance =D/A, where D=Aa–(AA+aa)/2, and A=(AA–aa)/2.

Results and discussion

Comparison of fruit developmental characteristics between TA491 and LA1589

To determine whether the elongated fruit shape characteristic of TA491 (Fig. 1c) is apparent at anthesis, we took length over diameter measurements of ovaries at anthesis and compared these to that of its round-fruited closest wild relative *L. pimpinellifolium* LA1589 (Fig. 1a, b). At the time of anthesis, the shape index (length over diameter ratio) for LA1589 and TA491 were not significantly

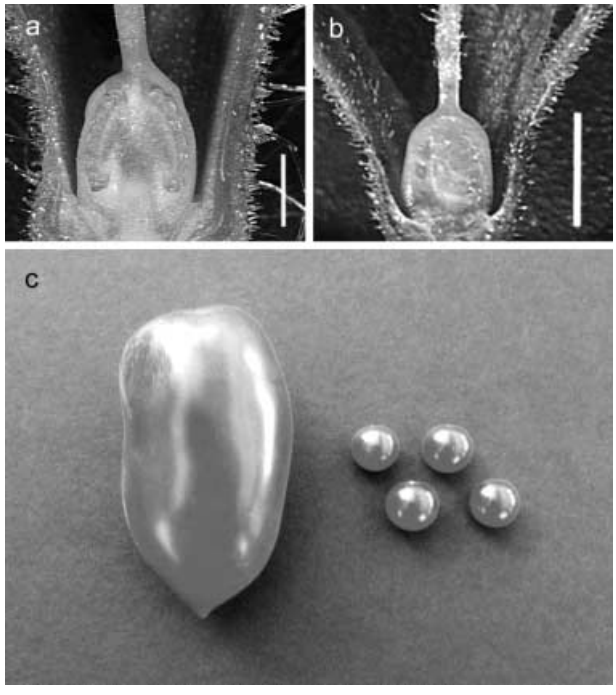

Fig. 1a–c Ovary and fruit shape of TA491 and LA1589. **a** TA491 ovary at anthesis. (*bar*=1 mm). **b** LA1589 ovary at anthesis (*bar*=1 mm). Petals and stamens were removed in (**a, b**). (**c**) TA491 ripe fruit on the *left* and four LA1589 fruit on the *right*

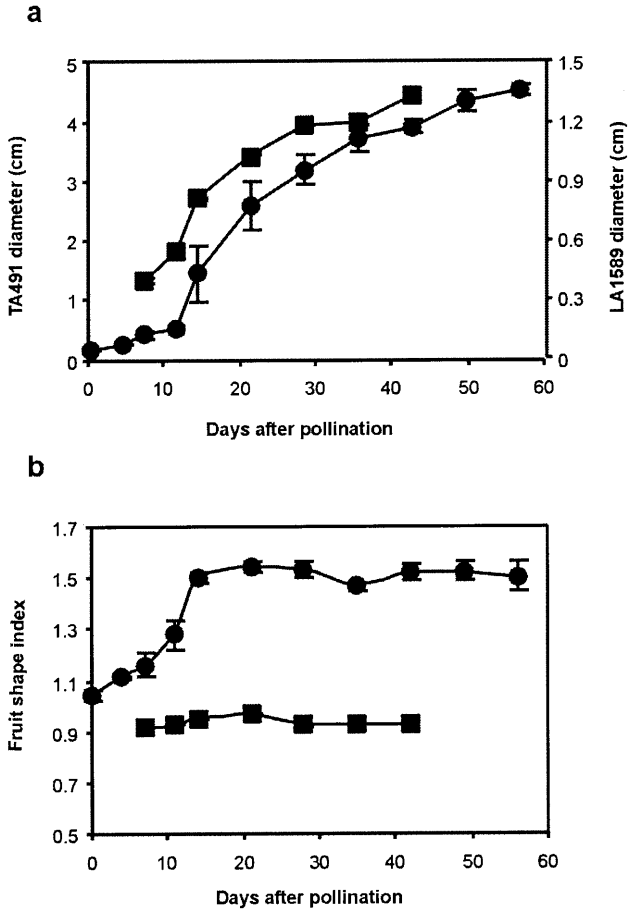

Fig. 2a, b Tomato fruit development. **a** Fruit growth curve of TA491 (*closed circles*) and LA1589 (*closed squares*). *Bars* indicate standard error. **b** Fruit shape index curve during development of TA491 (*closed circles*) and LA1589 (*closed squares*) fruit. *Bars* indicate standard error

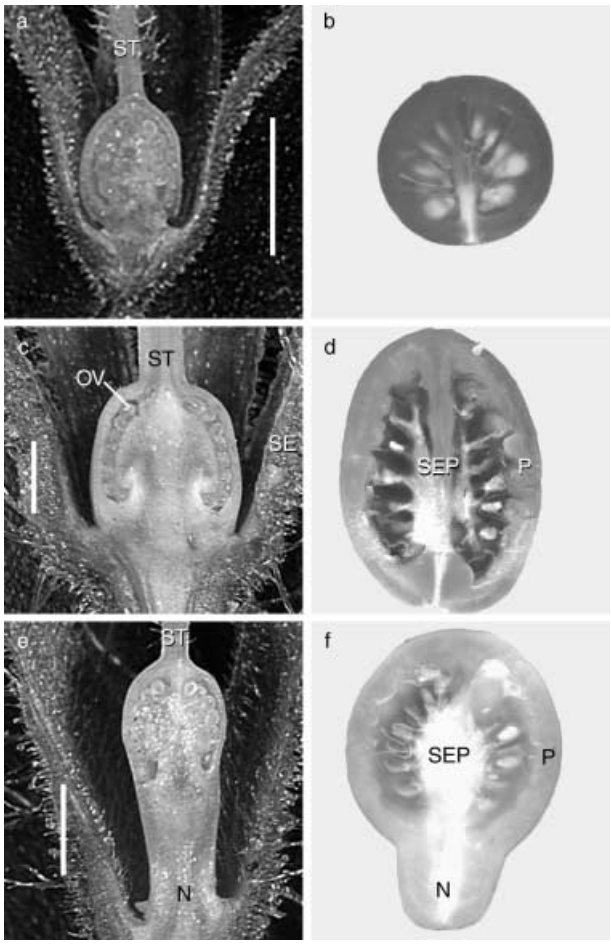

Fig. 3a–f Comparison of ovary and fruit shape between LA1589, TA491 and TA503: **a, b** LA1589, **c, d** TA491, **e, f** TA503. **a, c, e** Ovaries at anthesis (*bar*=1 mm). **b, d, f** Mature fruit displayed in the same orientation as the ovaries. *N*, Neck, *P* pericarp, *SEP* septum, *SE* sepal, *ST* style, *OV* ovule

Table 1 Fruit shape index of ovaries at anthesis and of ripe fruit

	Ovaries		Ripe fruit	
	TA491	LA1589	TA491	LA1589
Shape index	1.22	1.14	1.53	0.93
Standard error	0.032	0.002	0.036	0.001
n	25	27	8	10
P	0.07		0.00002	

different ($P>0.05$, Table 1). However, fruit shape index of ripe fruit was significantly different between TA491 and LA1589 ($P<0.0001$, Table 1). These results indicate that the difference in fruit shape index between LA1589 and TA491 manifests itself after anthesis.

To more accurately assess when, during fruit development, the change in fruit shape in TA491 compared to LA1589 becomes apparent, fruit growth and shape was monitored from anthesis until mature fruit. Growth after pollination followed a sigmoidal curve for both TA491 and LA1589 (Fig. 2a). Immediately following pollination, TA491 developing fruits grew more in length than in width, resulting in an increase in fruit shape index (Fig. 2b). In contrast, the fruit shape index remained constant in LA1589 (approx. 0.93) throughout development. These results indicate that the differences in fruit shape between LA1589 and TA491 are the result of developmental events occurring immediately following pollination and extending for approximately 2 weeks. The changes in fruit shape observed for TA491 coincided with the cell division phase, but preceded the rapid growth phase of fruit development (Fig. 2a, b; Gillaspy et al. 1993; Joubès et al. 1999). Therefore, fruit shape may be mediated by the differential regulation of cell division.

Fruit shape appearance in TA491 after anthesis contrasts that of other tomato cultivars, whose final fruit shape index is apparent at anthesis (Houghtaling 1935; Yeager 1937; Ku et al. 2000a, 2001). As can be seen in TA503, which contains the major fruit shape locus *ovate*, final fruit shape is apparent at anthesis (Fig. 3e, f; Ku et al. 2000b). An additional difference between TA491 and TA503 is that the increase in length over width ratio in TA491 fruit appears to be the result of increased

Table 2 Molecular linkage map of tomato. RFLP markers were used to map the position of the major fruit shape locus in TA491. The map was derived from the F_2 of a cross between LA1589×TA491

Chr 1		Chr 2		Chr 3		Chr 4		Chr 5		Chr 6		Chr 7		Chr 8		Chr 9		Chr 10		Chr 11		Chr 12	
CT233	*0*[a]	TG608	*0*	TG114	*0*	TG15	*0*	CT101	*0*	CT216	*0*	TG342	*0*	TG176	*0*	GP39	*0*	TG122	*0*	TG497	*0*	TG180	*0*
TG67	*17*	CT205	*14*	TG130	*5*	TG483	*12*	TG441	*8*	TG590	*25*	CT52	*9*	CT47	*5*	TG18	*10*	CT234	*11*	TG508	*19*	TG68	*6*
TG125	*40*	TG165	*25*	TG138	*14*	CT157	*36*	CT167	*12*	TG356	*46*	CD57	*44*	CT92	*9*	CT143	*18*	CT11	*33*	TG147	*48*	CT211A	*18*
CT62	*42*	TG14	*40*	CT141	*22*	CT178	*62*	CT93	*30*	TG365	*54*	TG174	*64*	TG349	*28*	TG291	*44*	CT203	*42*	TG384	*54*	TG360	*29*
CT149	*67*	CT244	*58*	TG520	*36*	CT194	*69*	TG96	*36*	TG253	*61*	TG183	*67*	TG302	*38*	TG551	*65*	TG403	*71*	TG546	*71*	TG565	*44*
TG273	*86*	TG645	*68*	CT82	*59*	CT50	*85*	TG100A	*49*	CT206	*76*	TG20A	*94*	TG330	*49*	CT74	*77*	TG63	*83*	TG36	*78*	TG111	*50*
TG59	*95*	TG537	*78*	CD51	*68*	TG163	*101*	CT118A	*68*	TG314	*80*	TG499	*105*	CT265	*66*	TG421	*86*			TG393	*92*	CT156	*72*
TG460	*100*	TG167	*85*	TG129	*78*			TG185	*96*					CT68	*78*	TG328	*103*					CT276	*80*
CT191	*105*	TG151	*88*	TG246	*84*																		
TG465	*115*	TG154	*98*	CT85	*92*																		
TG245	*119*			TG214	*111*																		
TG260	*121*																						
TG255	*137*																						
TG580	*147*																						

[a] The number in italics indicates the position of the marker on the chromosome

length of the pericarp and septum, while in TA503 this increase appears to be the result of an increase in neck length (Fig. 3d, f). The different temporal and spatial appearance of fruit shape in TA491 and TA503 suggest that elongated fruit shape can be mediated by independent developmental pathways.

Construction of the genetic map and identification of a major locus for post-anthesis control of fruit shape

To explore the genetic basis of the elongated fruit shape in TA491, we grew 100 F_2 plants, derived from a cross between TA491 and LA1589, in the greenhouse. A total of 106 RFLP and two SNP markers were placed on the map (Table 2). The linkage map spanned 1,174 cM with an average distance between markers of 12.2 cM. The maximum map distance between two adjacent markers observed in this population was less than 30 cM (Table 2, Fig. 5).

Ripe fruit from each F_2 plant was evaluated for the shape index, and this trait showed a continuous distribution, typical of a quantitative trait (Fig. 4). The distribution was highly skewed towards plants with a low value for shape index, *i.e.* displaying rounder fruits. Phenotypic and molecular marker analyses identified one major QTL on the short arm of chromosome 7, near *CT52* (Table 3). This region on chromosome 7 showed distorted segregation at the expense of the homozygous *L. esculentum* class ($P<0.0001$ for markers *CT52* and *TG342*, Table 3), which explains, in part, the skewness towards round fruit in the F_2 population (Fig. 4). The major fruit shape locus, which we have named *sun*, accounted for 58% of the phenotypic variance for fruit shape index. The degree of dominance (D/A=–0.39) indicated that the round-fruited allele from LA1589 is partially dominant over that of TA491 (Table 3). This finding suggests that the effect of the locus on fruit shape is not modulated by a loss-of-function allele but by a change in regulation or differential activity of the allelic gene products. A loss-of-function allele would likely be completely recessive. Similar partial dominance of round over elongated shape has been noted for other fruit shape loci, *ovate* and *fs8.1*, which are located on chromosome 2 and 8, respectively (Grandillo et al. 1996; Ku et al. 1999). No additional QTL for fruit shape were detected at a significance level of $P<0.01$, LOD>2.4. This strongly indicates that the *sun* locus mediates the formation of elongated fruit shape as shown in the parental line TA491 (Fig. 2).

Refining the map position of the *sun* locus

The position of *sun* on the short arm of chromosome 7 was refined by the addition of molecular markers (Fig. 5). Five of the markers (*CP52*, *TG418*, *TG131A*, *TG113A* and *CD57*) were from the high-density molecular linkage map (Tanksley et al. 1992). Two additional markers, *T42* and *21J7*, were tomato clones derived from sequenced cDNA libraries. An ongoing large-scale Tomato-*Arabidopsis* synteny project in our laboratory

Table 3 QTL analysis of fruit shape index. Data analyzed by single-point linear regression. The CT52 marker showed the most significant association with the fruit shape index

Marker	P	% of R2[a]	*F*-value	LOD	AA[b]	*n*[c]	aa[b]	*n*	Aa[b]	*n*	D/A[d]
CT52	<0.00001	58.3	63.62	17.85	1.38	8	0.91	41	1.05	45	–0.39

[a] % of R2, Fruit shape variance explained by the CT52 marker
[b] AA, Homozygous *L. esculentum*; Aa, heterozygous; aa, homozygous *L. pimpinellifolium*
[c] *n*, Number of plants per genotypic class
[d] D/A, Degree of dominance of the *L. esculentum* allele

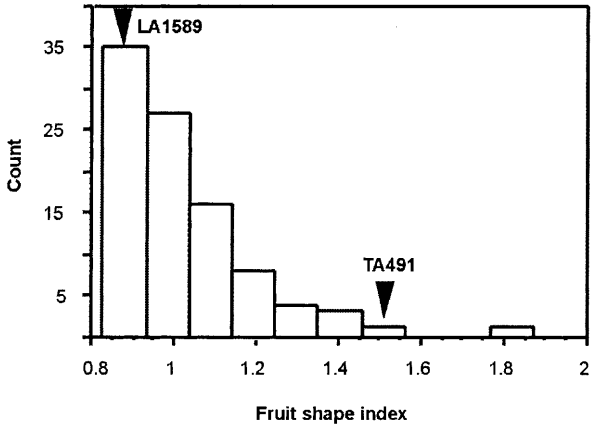

Fig. 4 Fruit shape index distribution in TA491×LA1589 F2. Shape index was calculated as the length over diameter ratio of mature fruit

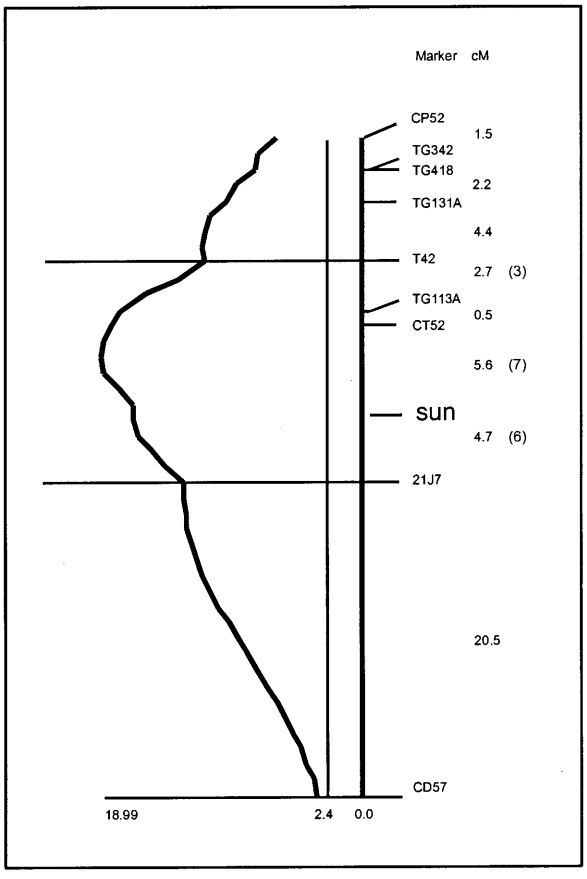

Fig. 5 Interval mapping analysis. The *Y-axis* indicates the map distance of the markers on the short arm of chromosome 7; the *X-axis* indicates the LOD score. The LOD curve was derived from F_2 analysis. The map position of *sun* was determined in the F_3 progeny of F_2 recombinants analyzed in Table 4. The *number in parenthesis* indicates the number of recombinants in the interval

had identified *T42* to map on the top of chromosome 7. In addition, tomato ESTs homologous to *Arabidopsis* genes involved in flower, ovary and fruit development were mapped as potential candidate genes for the *sun* locus. This resulted in the placement on chromosome 7 of *21J7*, which encodes a member of the Yabby family of transcription factors (Bowman, 2000). The LOD score for fruit shape using *21J7* as a marker is significantly lower than the LOD score for *CT52* indicating that, despite its linkage to *sun*, the protein encoded by *21J7* is not responsible for the elongated fruit shape in TA491 (Fig. 5). In all, the results from the F_2 analysis indicate that *T42* and *21J7* flank the *CT52* marker and delineate the region where the *sun* locus resides (Fig. 5).

To determine whether *sun* is in the *T42–CT52* or in the *CT52–21J7* interval, we subjected F_3 progeny from 16 F_2 plants with a crossover in the *T42–21J7* interval to F_3 progeny testing (Table 4). From each F_3 family, three to five homozygous recombinants and three to five non-recombinants were identified via molecular marker-assisted selection. Due to segregation distortion in some F_3 families, the heterozygous recombinant class replaced the missing homozygous class. The recombinant and non-recombinant classes were contrasted for each F_3 family. If a significant difference ($P \leq 0.05$) between the recombinant and non-recombinant classes was observed within an F_3 family, we inferred that *sun* was heterozygous in the F_2. Likewise, if a non-significant difference between the classes was observed within an F_3 family, we inferred that *sun* was homozygous in the corresponding F_2 plant. The results of these F_3 analyses unambiguously place *sun* in the *CT52–21J7* interval, seven crossovers from *CT52* and six crossovers from *21J7* (Table 4, Fig. 5).

Conclusions

The major difference in fruit shape between the tomato cultivar TA491 and its wild relative, *L. pimpinellifolium* LA1589, is due to the action of a single, hitherto uncharacterized locus, *sun*, on the short arm of chromosome 7. While previously identified loci involved in fruit shape have been shown to exert their effect during ovary development prior to anthesis, *sun* is the first known locus in tomato which appears to exert its effect on fruit shape

Table 4 Fruit shape locus *sun* maps between CT52 and 21J7 on chromosome 7

F_2 parent						F_3 family				
	Shape index[a]	Marker[b]				Recombinant stock no.	Shape index rec. class[d]	Shape index non-rec. class[e]	Shape index het. rec. class[f]	Contrast *P* value
		T42	CT52	sun[c]	21J7					
98T473-2	1.87	2	1	1	1	TA2052	1.34 (5)[g]		1.22 (5)	0.27
98T473-15	1.17	2	2	2	1	TA2053	0.90 (4)	1.16 (4)		0.03
98T473-38	0.97	2	3	3	3	TA2054	0.92 (5)	0.92 (5)		0.94
98T533-7	1.05	2	2	2	3	TA2055		0.87 (3)	1.01 (4)	0.05
98T533-9	0.89	2	3	3	3	TA2056	0.90 (5)	0.89 (5)		0.57
98T533-25	1.06	2	2	1	1	TA2057	1.06 (4)		1.06 (4)	0.98
98T533-40	1.06	2	2	1	1	TA2058	0.98 (3)		1.00 (5)	0.63
98T473-8	1	3	3	2	2	TA2059	0.99 (5)	0.86 (5)		0.03
98T473-18	1	3	3	2	2	TA2060	1.02 (5)	0.87 (5)		<0.01
98T473-21	0.88	3	3	3	2	TA2061	0.89 (5)	0.85 (5)		0.29
98T473-27	0.91	3	3	3	2	TA2062	0.93 (5)	0.89 (5)		0.25
98T473-47	0.95	3	3	2	2	TA2063	1.05 (5)	0.88 (5)		0.01
98T473-49	0.98	3	3	2	2	TA2064	1.02 (5)	0.86 (5)		<0.01
98T473-50	1.09	3	3	2	2	TA2065	1.03 (5)	0.83 (5)		0.01
98T533-11[h]	0.91	3	2	2	1	TA2066	0.81[h] (5)	0.98[h] (5)		<0.01
98T533-30	0.9	3	3	3	2	TA2067	0.85 (5)	0.87 (5)		0.32

[a] Average fruit shape index of F_2 parent
[b] Marker score in F_2 parent: 1, homozygous *L. esculentum*; 2, heterozygous; 3, homozygous *L. pimpinellifolium*
[c] F_2 phenotype for *sun* deduced from F_3 data
[d] Average fruit shape index for homozygous recombinant class
[e] Average fruit shape index for homozygous non-recombinant class
[f] Average fruit shape index for heterozygous recombinant class
[g] Number in parenthesis indicates number of plants per class
[h] Data given for F_2 recombinant in CT52–21J7 interval

via a post-pollination mechanism. The effect of *sun* on fruit shape extends to approximately 2 weeks after fertilization and is the result of mainly elongation of the pericarp and septum. The future elucidation of the molecular nature of *sun* should provide new insights into post-pollination mechanisms controlling tomato fruit ontogeny and potentially that of other fruit-bearing species.

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