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Extremely elongated tomato fruit controlled by four quantitative trait loci with epistatic interactions

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Abstract Cultivated tomato (*Lycopersicon esculentum*) encompass a wide range of fruit shape and size variants. This variation can be used to genetically dissect the molecular basis of ovary and fruit morphology. The cultivar Long John displays an extremely elongated fruit phenotype, while the wild relative *Lycopersicon pimpinellifolium* LA1589 produces fruit that are nearly perfect spheres, typical of wild tomatoes. Quantitative trait mapping of an F2 population between Long John and LA1589 revealed four fruit shape QTLs, located on chromosomes 2, 3, 7 and 11. The primary role of the fruit shape QTL located on chromosome 7, *ljfs7*, is to control pericarp elongation. The primary role of the fruit shape QTLs on chromosome 2, 3 and 11 (*ljfs2*, *ljfs3* and *ljfs11*, respectively) is to control pear shape, measured as the eccentricity index. QTL map position and the effect of the loci on fruit shape suggested that *ljfs2* and *ljfs7* are allelic to the well-studied fruit shape loci *ovate* and *sun*, respectively. *ljfs3* and *ljfs11* map near the previously identified, but less characterized, fruit shape loci *fs3.2* and *fs11.1*, respectively. This result suggests that most of the variation in tomato fruit shape is controlled by a few major QTLs. Although eccentricity and pericarp elongation were largely controlled by independent growth processes, significant interactions were detected between all four fruit shape loci in the control of eccentricity. This indicates that the three eccentricity loci, *ljfs2*, *ljfs3* and *ljfs11*, epistatically control the same developmental process, while *ljfs7* had a pleiotropic effect on eccentricity.

Keywords Tomato · Fruit shape · Development · QTL · Interaction

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Introduction

Tremendous variation in fruit morphology exists within cultivated tomato (*Lycopersicon esculentum* Mill.). While the wild relatives bear fruits that are small, round and inconspicuous, cultivated tomato bears fruits which are much larger and display a variety of shapes: from round to elongated and blocky, to pear and bell-pepper shaped. Our interests are to understand the nature of the variation in tomato fruit morphology. For example, we want to know how many loci control the major change in fruit morphology from small and round to large and variably shaped. Furthermore, we want to apply the knowledge gained from studies in tomato fruit morphology to fruit development in other crops.

The roles of the ovary and fruit, collectively called the gynoecium, are many fold. Before fertilization, the ovary protects developing ovules and mediates pollination. After fertilization, the fruit protects developing seeds and aids in their dispersal. In addition, fruit of tomato and all other vegetable and fruit-bearing crops is an essential component of the human and animal diet and, therefore, of great economic importance. Varietal differences in tomato gynoecium morphology occur after the floral meristem has committed itself to the formation of the ovary, during ovary development (Frary et al. 2000; Ku et al. 2000, 2001), and/or after pollination and successful fertilization, during fruit development (Van der Knaap and Tanksley 2001). Successful completion of gynoecium development requires that regional differentiation and growth of the different tissue types in the ovary and fruit are highly coordinated. The complexity of the regulation of gynoecium development is underscored by

intricate genetic interactions observed between *Arabidopsis* loci controlling ovary and fruit morphology (reviewed in Bowman et al. 1999; Ferrándiz et al. 1999; Sessions 1999). Although the *Arabidopsis* laboratory induced mutants and the genes affected in these mutants provide a basis for understanding gynoecium development, alternative genetic approaches, such as quantitative trait loci us (QTL) analyses, are necessary to gain a more-thorough insight into gynoecium developmental processes. Unlike *Arabidopsis*, domestication and repeated cycles of selection in tomato have resulted in a large number of fruit morphology variants from which extreme types can be selected as parental material for crosses. Recent years have shown that the ultimate identification of genes underlying quantitative variation is feasible (*e.g.*, Doebly et al. 1997; Frary et al. 2000; Fridman et al. 2000; Yano et al. 2000).

Using the approach of QTL mapping, many 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 and fine-mapped (Grandillo et al. 1996; Ku et al. 1999; Ku et al. 2000, 2001). The difference in round versus pear-shaped fruit, seen in the cultivar Yellow Pear, is due to the action of one major locus, *ovate*, located at the bottom of chromosome 2 (Ku et al. 1999). A novel fruit shape locus was identified in Sun 1642 (Van der Knaap and Tanksley 2001). The elongated fruit shape in Sun 1642 was due to the action of a single locus, *sun*, positioned on the top of chromosome 7; *sun* regulates pericarp elongation after fertilization (Van der Knaap and Tanksley 2001).

The objectives of the present study were to identify existing and novel loci controlling fruit shape in the extremely elongated fruit of the tomato cultivar Long John (see Fig. 1a, b). The shape of Long John fruits bore resemblance to that of Yellow Pear and Sun 1642 (van der Knaap and Tanksley 2001). We therefore addressed the question whether *ovate* and *sun* as well as other hitherto unknown loci, controlled the extremely elongated fruit characteristic of Long John. Furthermore, we were interested in identifying possible epistatic interactions between the fruit shape loci detected in this study. To this end, we analyzed the fruit shape and genotype of an F2 population derived from a cross between Long John and a wild relative of tomato, *L. pimpinellifolium* LA1589. The QTL analyses resulted in the identification of four fruit shape QTLs, three of which controlled pear shape, measured as eccentricity index, while the remaining QTL controlled pericarp elongation. The results suggested that one of the fruit shape loci controlling pear shape was allelic to *ovate*, and that the QTL controlling pericarp elongation was allelic to *sun*. This then suggested that the evolution of the elongated fruit type from the spherical fruit type may have been due to the action of a few major QTLs. Although eccentricity and pericarp elongation were largely controlled by independent growth processes, significant epistatic interactions were obtained between all four loci, indicating that these four QTLs play a role in the same developmental process controlling fruit shape.

Materials and methods

Plant materials and phenotypic measurements

Parental plants were inbred stocks of *L. esculentum* Long John (LA791) and *L. pimpinellifolium* LA1589 obtained from TGRC tomato stock center: http://tgrc.ucdavis.edu. For genetic analysis, 85 F2 plants derived from a cross between LA1589 and Long John were grown in the field in Ithaca, N.Y., in the summer of 1999. In most cases, eight ripe fruits per plant were analyzed for the fruit shape index (total length divided by the diameter of the fruit at its widest point), pericarp elongation index (length of pericarp, the region surrounding the seeds, divided by the diameter of the fruit at its widest point) and eccentricity index (total length divided by the pericarp length of the fruit), as shown in Fig. 1c.

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 97 markers, covering the entire tomato genome, showed a RFLP (restriction fragment length polymorphism) between LA1589 and Long John with at least one of the following restriction enzymes: *Bst*NI, *Dra*I, *Eco*RI, *Eco*RV, *Hae*III, *Hin*dIII, *Sca*I and *Xba*I. The markers on chromosome 1 were *CT233, TG67, TG125, CT149, TG273, TG59, TG460, CT191, TG465, TG245, TG260, TG580*. The markers on chromosome 4 were *CD59, TG483, CT157, CT178, CT194, TG500, TG163*. The markers on chromosome 5 were *CT101, CT93, TG96, TG619, CT172, TG351, TG185*. The markers on chromosome 6 were *CT216, TG590, CT83, TG356, TG365, TG253, 24C3, CT206, TG314*. The markers on chromosome 8 were *TG176, CT92, TG349, TG302, TG330, CT265, CT68*. The markers on chromosome 9 were *GP39, CT143, TG291, TG551, CT74, TG421*. The markers on chromosome 10 were *CT16, CT234, TG560, CT20, CT240, TG233*. The markers on chromosome 12 were *TG180, TG68, CT211 A, TG360, TG565, TG111, CT156, CT276*. The markers on the remaining chromosomes, 2, 3, 7 and 11, are shown in Fig. 3. These markers were present on the high-density molecular map (Pillen et al. 1996).

Statistical analyses

Linkage analysis of the 97 markers on the 12 tomato chromosomes was performed using the software package MAPMAKER 2.0 (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. The Kosambi mapping function was used to convert recombination frequencies to map distances in centiMorgans (cM, Kosambi 1944). 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 3 for interval analysis and $p<0.005$ for single-point linear regression analysis. The degree of dominance of the alleles at a given locus was expressed as D/A, where D=Aa−(AA+aa)/2, and A=(AA−aa)/2. AA=phenotypic value for homozygous *L. esculentum*, aa=phenotypic value for homozygous *L. pimpinellifolium*, Aa=phenotypic value for the heterozygote. Additive gene action will result in a D/A value of 0; gene action of −1 or 1 indicates complete dominance of the *L. pimpinelli-*

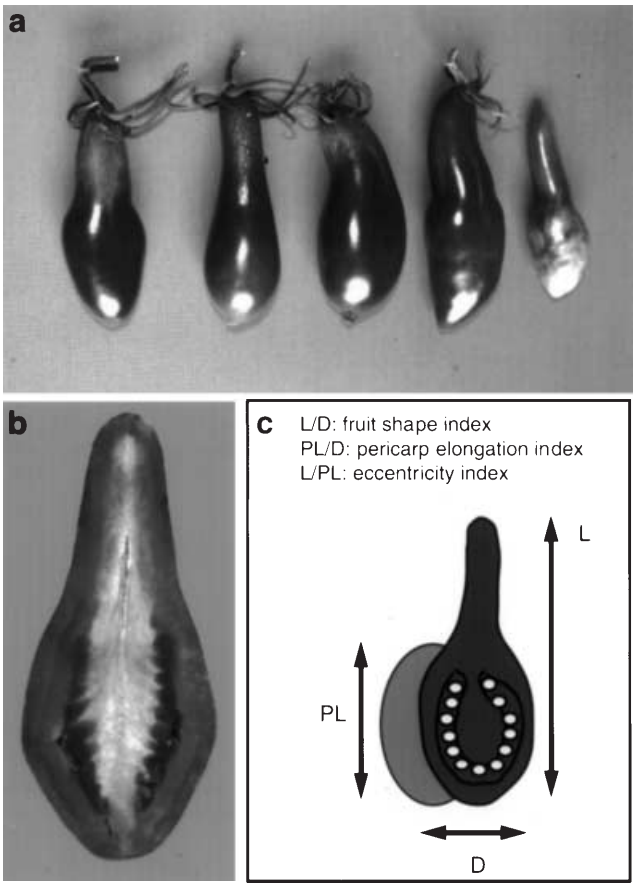

Fig. 1 a Long John fruit. **b** Longitudinal section of a Long John fruit. **c** Schematic representation of fruit shape index, pericarp elongation index; and eccentricity index measurements performed in the phenotypic analysis of the F2 population derived from a cross between Long John and *L. pimpinellifolium* LA1589

folium or *L. esculentum* allele, respectively. Gene action of 1<D/A <–1 indicates overdominance. Interaction between fruit shape and eccentricity loci was determined via two-way analysis of variance (ANOVA) using StatView (SAS Institute Inc).

Results

Fruit shape in the *L. esculentum* cultivar Long John was expressed as the ratio of the total length of the fruit to the diameter at its widest point (fruit shape index). However, the elongated fruit shape in Long John was the result of growth processes regulating pericarp elongation and pear shape (Fig. 1a, b). Therefore, in addition to the fruit shape index, Long John fruit was measured for pericarp elongation and pear shape (Fig. 1b). The region surrounding the seeds was considered the the pericarp, and pericarp elongation index was the ratio of the pericarp length to the diameter of the fruit at its widest point. As an indirect measure of pear shape, we indicated the relative position of the seeds in the fruit by calculating the eccentricity. The eccentricity index was the ratio of the total length of the fruit to the pericarp length (Fig. 1c).

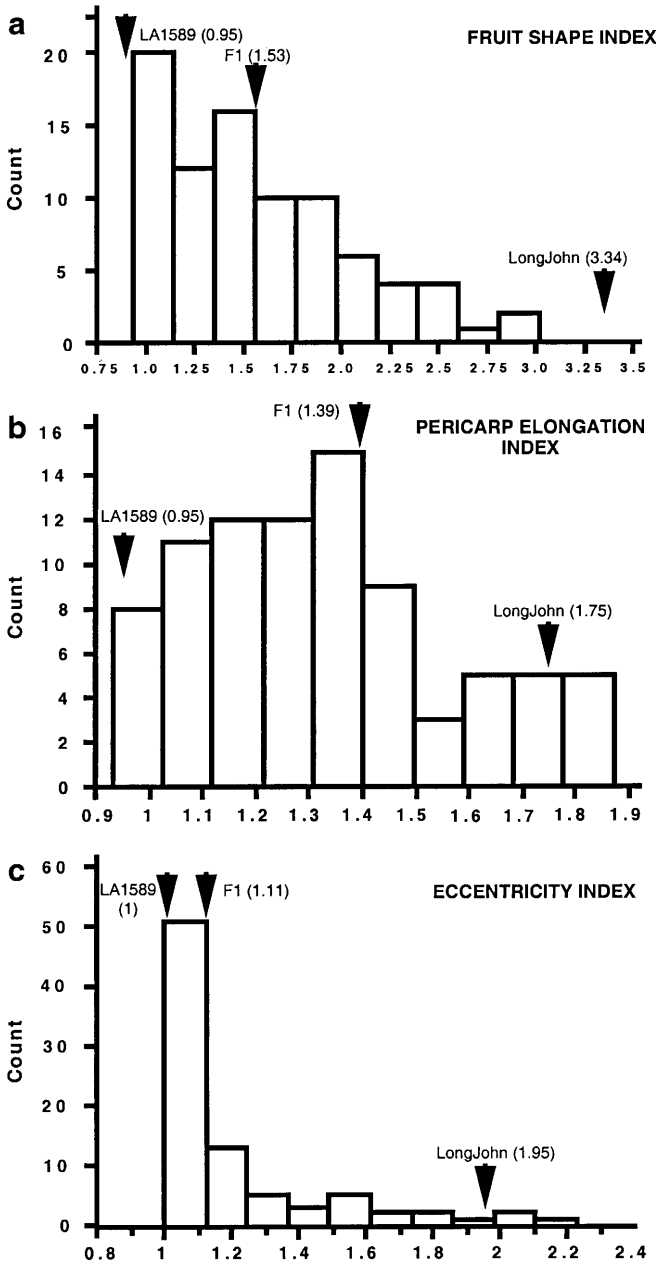

Fig. 2a–c Frequency distribution of a fruit shape index, **b** pericarp elongation index, and **c** eccentricity index. Arrows and *numbers in parentheses* indicate the value of the parents and the F1 for each trait

Identification of fruit shape QTLs

Measurements of individual fruit from 85 segregating F2 plants derived from a cross between Long John and *L. pimpinellifolium* LA1589 were taken. Frequency distributions showed that all three fruit measurements, *i.e.*, fruit shape index, pericarp elongation index, and eccentricity index displayed continuous variation, typical of quantitative traits (Fig. 2). As indicated by the fruit shape index value of the F1 (Fig. 2a) the wild parent, LA1589, was partially dominant over the cultivated

Long John parent. Nearly complete dominance of LA1589 was observed for the eccentricity index (Fig. 2c). On the other hand, the pericarp elongation index value for the F1 was between that of both parents (Fig. 2b). Fruit shape index and pericarp elongation index, as well as fruit shape index and eccentricity index, were positively correlated in a highly significant manner (Table 1). This is not surprising since both increases in pericarp elongation and eccentricity result in a higher value for the fruit shape index. Pericarp elongation and eccentricity were much less significantly correlated ($0.01<p<0.05$), which indicates that pericarp elongation and eccentricity are largely controlled by independent growth processes.

To identify genetic loci controlling fruit shape in Long John, 97 RFLP markers, covering the entire tomato genome, were mapped in the same F2 population derived from a cross between Long John and LA1589. The linkage map spanned a total of 1090 cM with an average map distance of 12.8 cM between adjacent markers. Interval analysis detected four significant QTLs control-

Table 1 Correlation coefficients for fruit shape, pericarp elongation and eccentricity indices

Trait[a]	L/D	PL/D
PL/D	0.703***	
L/PL	0.841***	0.218*

* $p<0.05$; ** $p<0.01$; *** $p<0.001$
[a] L/D, fruit shape index. PL/D, pericarp elongation index. L/PL, eccentricity index

Table 2 Linear regression analysis for fruit shape, pericarp elongation and eccentricity indices. *F*-value threshold was set at 5.66 and $p<0.005$

QTL	Chrom.	Marker	*F*	RSq[a]	*P*	AA	N	aa	N	Aa	N	D/A[b]
Fruit shape index (L/D)												
ljfs2	2	TG337	21.66	0.35	<0.0001	2.1	20	1.32	26	1.52	39	–0.47
ljfs7	7	GP121	15.57	0.28	<0.0001	1.91	6	1.32	41	1.83	37	0.72
ljfs3	3	CT85	7.84	0.16	0.00077	1.76	15	1.29	25	1.7	44	0.67
ljfs11	11	TG546	7.43	0.16	0.00109	1.89	25	1.41	22	1.51	36	–0.54
Pericarp elongation index (PL/D)												
ljfs7	7	GP121	31.56	0.44	<0.0001	1.67	6	1.17	41	1.43	37	0
Eccentricity index (L/PL)												
ljfs2	2	TG337	37.69	0.48	<0.0001	1.54	20	1.05	26	1.13	39	–0.67
lljs11	11	TG546	13.27	0.25	<0.0001	1.41	25	1.07	22	1.13	36	–0.62
ljfs3	3	CT85	6.29	0.13	0.00287	1.3	15	1.05	25	1.25	44	0.58

[a] Phenotypic variance explained by the locus
[b] Degree of dominance

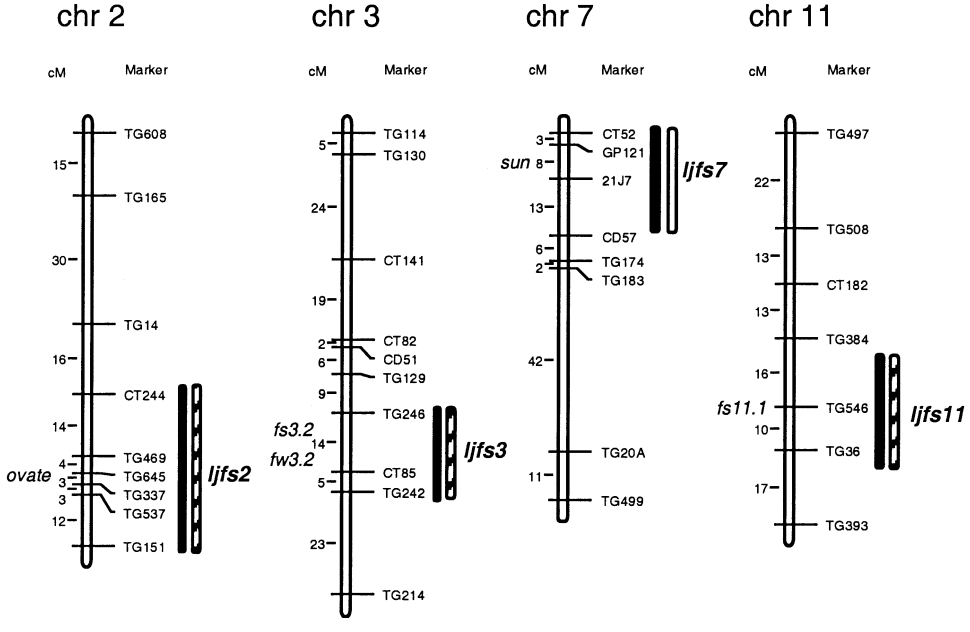

Fig. 3 Position of the fruit shape loci on the genetic map. *Numbers* on the left of each chromosome indicate the map distance between RFLP markers (in cM). *Black bars* on the right of each chromosome indicate the position of the fruit shape index QTL. The *open bar* indicates the position of the pericarp elongation index locus. *Hatched bars* indicate the position of the eccentricity index loci. The position of previously mapped fruit shape and fruit weight QTLs is indicated on the left of the chromosome

ling fruit shape index. Figure 3 shows the map positions of these four QTLs. The most significant QTL, *ljfs2* (*l*ong *j*ohn *f*ruit *s*hape chromosome *2*), was located on the bottom of chromosome 2, closest to RFLP marker *TG337* (Table 2). The locus *TG337* explained 35% of the variation in fruit shape index. The second most significant QTL, *ljfs7*, was found on the short arm of chromosome 7, closest to marker *GP121* (Table 2). The locus *GP121* explained 28% of the variation in fruit shape index. Two QTLs of smaller effect were found on chromosome 3, *ljfs3*, near marker *CT85*, and on chromosome 11, *ljfs11*, near marker *TG546*. The latter two QTLs each explained 16% of the phenotypic variance (Table 2).

QTL analysis was performed on the components contributing to fruit shape in Long John, the pericarp elongation index and eccentricity index. Only one QTL was detected to control pericarp elongation. The pericarp elongation index QTL was located on the short arm of chromosome 7, corresponding to the fruit shape index QTL *ljfs7* (Table 2 and Fig. 3). The effect of *ljfs7* was more significant for the pericarp elongation index than for the fruit shape index: the *F*-value for marker *GP121* closest to *ljfs7* increased from 15.6 for the fruit shape index to 31.6 for the pericarp elongation index (Table 2). This indicates that the role of *ljfs7* in controlling fruit shape is mainly by regulating pericarp elongation.

Three QTLs were detected to control the eccentricity index (Table 2 and Fig. 3). These three QTLs were located on chromosomes 2, 3 and 11, corresponding to fruit shape index QTLs *ljfs2*, *ljfs3* and *ljfs11* (Table 2 and Fig. 3). When fitted simultaneously, the three QTLs explained 53% of the phenotypic variation. The *F*-value of marker *TG337*, near *ljfs2*, and marker *TG546*, near *ljfs11*, was higher for the eccentricity index than for the fruit shape index (Table 2). This indicates that the effect of both *ljfs2* and *ljfs11* is more significant for the eccentricity index than for the fruit shape index, and that the control of fruit shape by these loci is mainly by regulating eccentricity. On the other hand, the significance of marker *CT85*, near *ljfs3*, was slightly higher for the fruit shape index than for the eccentricity index (the *F*-value decreased from 7.8 to 6.3, respectively, Table 2). This suggests that *ljfs3* may have roles in addition to eccentricity to control fruit shape.

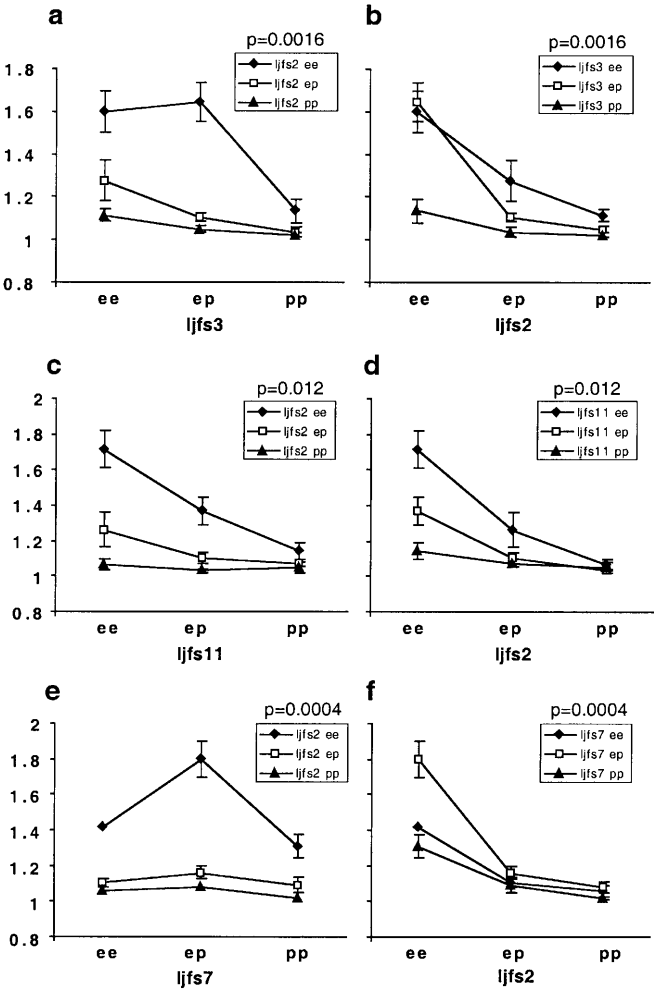

Fig. 4a–f Interaction plots for the eccentricity index. **a** Effect of genotype at loci *CT85* and *TG337* (*ljfs3* and *ljfs2*, respectively) on eccentricity. **b** Reciprocal plot of **a**. **c** Effect of genotype at loci *TG546* and *TG337* (*ljfs11* and *ljfs2*, respectively) on eccentricity. **d** Reciprocal plot of **c**. **e** Effect of genotype at loci *GP121* and *TG337* (*ljfs7* and *ljfs2*, respectively) on eccentricity. **f** Reciprocal plot of **e**. *Bars* indicate the standard error

Interactions between fruit shape QTLs

To address the question of whether the four fruit shape loci identified in Long John interacted with each other, epistatic relationships between these loci were determined via two-way ANOVA. With regard to the eccentricity index, significant interactions were detected between markers *TG337* and *CT85*, near eccentricity loci *ljfs2* and *ljfs3* (Fig. 4a, b; p=0.0016), and markers *TG337* and *TG546*, near eccentricity loci *ljfs2* and *ljfs11* (Fig. 4c, d; p=0.012). No significant epistasis was detected between *CT85* and *TG546* (*ljfs3* and *ljfs11*), possibly due to the relatively low number of plants analyzed in this study and the lesser significance of these two QTLs with respect to eccentricity (Table 2). In the homozygous *L. pimpinellifolium* background at either *ljfs3* or *ljfs11*, the effect of *ljfs2* on eccentricity was detectable, albeit not significant (Fig. 4a, c). However, in the heterozygous and homozygous *L. esculentum* background of either *ljfs3* or *ljfs11*, the effect of *ljfs2* on eccentricity became much-more pronounced. A significant effect of *ljfs2* in the homozygous *L. pimpinellifolium* background of either *ljfs3* or *ljfs11* would most-likely have been observed if a larger population were analyzed and the genotype at the third eccentricity locus were fixed. Conversely, in the homozygous *L. pimpinellifolium* background of *ljfs2*, the effect of *ljfs3* on eccentricity was small but significantly detectable, while its effect synergistically increased in the heterozygous and homozygous *L. esculentum* background of *ljfs2* (Fig. 4b). In the homozygous *L. esculentum* background of *ljfs2*, the *L. esculentum* allele of *ljfs3*

was dominant over the *L. pimpinellifolium* allele in controlling eccentricity (Fig. 4a, b). By contrast, no effect of *ljfs11* on eccentricity was detected in the homozygous *L. pimpinellifolium* background of *ljfs2* (Fig. 4d). This indicates that for *ljfs11* to exert its effect on eccentricity, *L. esculentum* alleles at *ljfs2* are required.

The main role of *ljfs7* was in controlling pericarp elongation. However, a highly significant interaction was detected between markers *GP121* and *TG337* near *ljfs7* and *ljfs2*, respectively, in controlling eccentricity (p=0.0004, Fig. 4e, f). Since segregation at marker *GP121* was highly skewed against the homozygous *L. esculentum* class (see Table 2), two-way ANOVA was repeated with the homozygous *L. esculentum* class at *GP121* removed. Again, highly significant epistasis was detected between the loci *ljfs7* and *ljfs2* in controlling eccentricity (p<0.0001). The interaction was most strongly apparent in the homozygous *L. esculentum* background of *TG337*, where the heterozygous genotype at *GP121* significantly increased eccentricity. This indicates that, although the major effect of *ljfs7* is on pericarp elongation, this locus has a pleiotropic effect on eccentricity. No interaction was detected between *GP121* and the other two eccentricity loci in controlling eccentricity. Lastly, with respect to the control of the pericarp elongation index, no epistasis was detected between any of the four fruit shape loci. In all, the results from the interactions studies indicate that all four loci interact to control eccentricity and suggest that these loci are involved in the same developmental pathway controlling fruit morphology.

Discussion

Until recently, genetic analysis of fruit shape was difficult due to its quantitative nature. With the advent of molecular marker techniques and QTL mapping procedures, it is now possible to define genomic regions where QTLs controlling quantitative characters reside. By defining the components of fruit shape as the pericarp elongation index and the eccentricity index, and by careful measurements of these components, morphology in Long John and the F2 population derived from it was accurately analyzed. Genetic analysis indicated that two largely independent growth processes controlled fruit shape in Long John: pericarp elongation and eccentricity. The pericarp elongation index was controlled by a single locus, *ljfs7*. The map position of *ljfs7* was very close to that of the recently identified fruit shape locus, *sun*, and both *ljfs7* and *sun* regulate fruit shape via pericarp elongation (Van der Knaap and Tanksley 2001). The similar map position and effect on fruit shape strongly suggest that *ljfs7* and *sun* are allelic. Of the three loci detected to control the eccentricity index, *ljfs2* mapped to a similar position as the fruit shape locus *ovate*, on the bottom of chromosome 2 (Ku et al. 1999). Both *ljfs2* and *ovate* regulate fruit shape via eccentricity (Van der Knaap and Tanksley 2001). In this study, RFLP marker *TG337* was more-significantly correlated to *ljfs2* controlling eccentricity than *TG645* (*F*-value for *TG337* was 37.7; F-value for *TG645* was 26.6). However, fine-mapping studies have shown that RFLP marker *TG645* is closer linked to *ovate* than *TG337* (Ku et al. 2001). It is possible that an accurate QTL map position could not be obtained with the small F2 population analyzed in this study, or that *ljfs2* is comprised of two linked fruit shape loci. Nonetheless, the similarities in map position and effect on fruit shape suggest that *ovate* and *ljfs2* are allelic. Of the two remaining eccentricity loci, *ljfs3* mapped near *fs3.2*, identified in only one study (Fulton et al. 2000). The effect of *ljfs3* on fruit shape suggested that this locus may control fruit shape only in part by controlling eccentricity (Table 2). Interestingly, the map position of *ljfs3* overlaps with the map position of a fruit weight locus, *fw3.2*, identified in several studies (Grandillo et al. 1999). It is conceivable that fruit weight affects fruit shape, *i.e.*, larger fruits display more-extreme shapes. It is therefore possible that *ljfs3* corresponds to a previously identified fruit weight locus, which, in the right genotypic background, can affect fruit shape. Lastly, *ljfs11* mapped to a similar position as *fs11.1* (Grandillo et al. 1999). However, whether *fs11.1* affects fruit shape via eccentricity or pericarp elongation is not known. Therefore, inferences on allelism between *ljfs11* and *fs11.1* cannot be made.

Tomato has been domesticated and subject to selection for over many years. During that time, small and subtle as well as large-effect nucleotide changes have been at the heart of the extensive variation present in the cultivated germplasm. Not surprisingly, the changes in fruit appearance from round, like in the wild *L. pimpinellifolium*, to eccentric and elongated, like in Long John, were all due to the action of the *L. esculentum* allele at the four fruit shape loci identified in this study. For *TG337*, near *ljfs2*, and *TG546*, near *ljfs11*, the *L. pimpinellifolium* allele was partially dominant, suggesting a partial loss-of-function or else reduced activity of the protein product of the *L. esculentum* allele (Table 2). If so, this would suggest that both *ljfs2* and *ljfs11* are negative regulators of fruit eccentricity. *CT85* near *ljfs3* showed partial dominance of the *L. esculentum* allele over that of the *L. pimpinellifolium* allele (Table 2), suggesting a gain-of-function of the *L. esculentum* allele at this locus. If so, this would suggest that the *L. esculentum* allele at *ljfs3* is constitutively active and has lost its capacity to be down-regulated. The gene action at *GP121* near *ljfs7* indicated partial dominance of the *L. esculentum* allele for the fruit shape index (D/A=0.72) and additivity for the pericarp elongation index (D/A=0, Table 2). Epistatic interactions between *ljfs7* and *ljfs2* indicated a pleiotropic role for *ljfs7* in eccentricity, and was controlled by overdominance at the *ljfs7* locus (the heterozygote outperforms both parents, Fig. 4e, f). Therefore, the combination of overdominance for the eccentricity index and additivity for the pericarp elongation index may have resulted in partial dominance in the fruit shape index; the latter is the combined value of pericarp elongation and eccentricity.

This study represents one of the few cases of epistasis between several QTLs controlling a quantitative trait

(Tanksley 1993). This is especially remarkable considering the small F2 population used in the study. From a developmental point of view, the four fruit shape loci can be viewed as functionally related in that they control one aspect of fruit morphology: eccentricity. This study also suggested that most of the major variation in elongated fruit shape appears to be controlled by a limited number of loci and that these loci represent the key switches from round to elongated fruit. The identification of the gene present at the *ovate* locus (Ku et al. 2001) and *sun* locus (Van der Knaap and Tanksley 2001, unpublished results) in the near future will greatly enhance our knowledge of how tomato fruit morphological processes occur at the molecular level. The identification of the two additional fruit shape loci, *ljfs3* and *ljfs11*, and the eventual map-based cloning of genes underlying fruit shape variation at these loci will provide essential information to understand fruit development not only in tomato but in all fruit-bearing crops.

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