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fw 2.2: a major QTL controlling fruit weight is common to both red- and green-fruited tomato species

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Abstract We have shown that a major QTL for fruit weight (*fw2.2*) maps to the same position on chromosome 2 in the green-fruited wild tomato species, *Lycopersicon pennellii* and in the red-fruited wild tomato species, *L. pimpinellifolium.* An introgression line F_2 derived from *L. esculentum* (tomato) × *L. pennellii* and a backcross 1 (BC_1) population derived from *L. esculentum* × *L. pimpinellifolium* both place *fw2.2* near TG91 and TG167 on chromosome 2 of the tomato high-density linkage map. *fw2.2* accounts for 30% and 47% of the total phenotypic variance in the *L. pimpinellifolium* and *L. pennellii* populations, respectively, indicating that this is a major QTL controlling fruit weight in both species. Partial dominance (d/a of 0.44) was observed for the *L. pennellii* allele of *fw 2.2* as compared with the *L. esculentum* allele. A QTL with very similar phenotypic affects and gene action has also been identified and mapped to the same chromosomal region in other wild tomato accessions: *L. cheesmanii* and *L. pimpinellifolium.* Together, these data suggest that *fw2.2* represents an orthologous QTL (i.e., derived by speciation as opposed to duplication) common to most, if not all, wild tomato species. High-resolution mapping may ultimately lead to the cloning of this key locus controlling fruit development in tomato.

Key words *Lycopersicon esculentum* · RFLP Mapping · Domestication

Introduction

While macromutations play an important part in the expression of traits that exhibit a major phenotype, continuous variation is more common in nature. Continuous variation represents the collective action of polygenes or quantitative trait loci (QTLs) in concert with environmental variation (Johanssen 1909; Nilsson-Ehle 1909; East 1915). Much of the phenotypic diversity observed among plants and animals is a result of polygenes. Tomato fruit size is considered a classic example of a quantitative trait displaying continuous variation (MacArthur and Butler 1938). The analysis of quantitative traits has recently been investigated by the association of quantitative trait loci (QTLs) with molecular markers (Edwards et al. 1987, 1992; Stuber et al. 1987, 1992; Paterson et al. 1988, 1990, 1991; Miura et al. 1992; de Vicente and Tanksley 1993; Xiao et al. 1995).

The genus *Lycopersicon*, which includes the cultivated tomato (*Lycopersicon esculentum* Mill.) and related wild species, was originally divided into two subgenera based on fruit color (Muller 1940): (1) Eulycopersicon – red fruited species and (2) Eriopersicon – green-fruited species. Rick (1976) further divided the genus based on those species which are cross-compatible with the cultivated tomato (esculentum-complex) and those which are not (peruvianum-complex). Although cross compatibility and fruit color are used to distinguish tomato species, one common factor which all wild species share is small fruit size as compared with the domesticated tomato.

In this paper we report on the presence of a major QTL controlling fruit size (hereafter called *fw2.2*) mapping to the same position on chromosome 2 in the green-fruited wild tomato species, *L. pennellii*, and the red-fruited wild tomato species, *L. pimpinellifolium.* These data, together with other published reports, suggest that the cultivated tomato is differentiated from both its red-fruited and green-fruited wild relatives by a major allelic substitution at *fw2.2.*

Materials and methods

L. pimpinellifolium population

L. esculentum cv M82-1-7 was crossed as the pistillate parent to the small red-fruited wild species *L. pimpinellifolium* (LA1589; hereafter

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called Pp) from Peru. A single F_1 plant was backcrossed to *L. esculentum* cv E6203 using the F_1 as the female parent. Two hundred sixty four BC_1 plants, as well as 20 of each parental control, were transplanted to the field in Ithaca, N. Y., in a completely randomized design (Grandillo and Tanksley 1995).

L. pennellii population

Seed for the *L. pennellii* F_2 introgression line population (hereafter called Pn) was provided by Dr. D. Zamir, Hebrew University of Jerusalem, and was generated as described by Eshed and Zamir (1994). Through repeated backcrossing and selection based on molecular markers, a series of 50 introgression lines were produced, each carrying a single chromosomal segment from the *L. pennellii* genome in an otherwise *L. esculentum* background (Eshed and Zamir 1994). One of these introgression lines (IL2-5), containing the distal portion of chromosome 2, was crossed to *L. esculentum* cv M82-1-8 and selfed to produce the F_2 population used in this study (see Fig. 1).

Five hundred four IL-2-5-F_2 seeds were sown in flats and further subjected to RFLP analysis (see next section for markers utilized). Based on this analysis, 86 F_2 plants were identified which contained recombinants in the introgressed region of chromosome 2. These recombinants were transplanted to the greenhouse in Ithaca, N. Y., for further phenotypic evaluation.

Phenotypic analysis

Individual plants were evaluated for fruit weight (FW) by weighing ten representative fruits from each plant (including controls).

Parental polymorphism survey and RFLP analysis of the Pp and Pn populations

For the Pp population, parental DNA was digested with seven restriction enzymes (*Eco*RI, *Hin*dIII, *Dra*I, *Eco*RV, *Sca*I, *Xba*I and *Bst*NI) and subjected to Southern-blot analysis as described by Bernatzky and Tanksley (1986). Four hundred thirty DNA clones (cDNA and genomic) from the tomato high-density linkage map were surveyed (Tanksley et al. 1992). A minimum of two of the seven restriction enzymes chosen were tested per probe. The probes were labeled with ^{32}P-dCTP by primer extension (Feinberg and Volgelstein 1983). One hundred sixteen informative RFLP markers were chosen for QTL mapping, ensuring a coverage of the tomato genome at intervals of 10–20 cM (Grandillo and Tanksley 1995). Of the 116 informative RFLP markers, 12 were chosen for *fw 2.2* analysis in the Pp population (see Fig. 1).

Segregation analysis of the Pn population (86 IL2-5-F2s) followed the same procedures except that the restriction enzymes *Bst*NI, *Eco*RI and *Eco*RV were used with 14 informative RFLP markers in the vicinity of *fw2.2* (see Fig. 1).

Statistical analysis

Statistical analyses of the Pp and Pn populations were performed using JMP version 2.0 for the Macintosh (SAS Institute 1989). The expected segregation ratios for RFLP markers in the Pp (1 : 1) and Pn (1 : 2 : 1) populations were tested for distortion by chi-square analysis. Normality for average fruit weight was found to be skewed towards the smaller-fruited parent using the Shapiro-Wilk W test ($P < 0.01$) within the "Distribution of Ys" command; the $\log_{10}$ of fruit weight was used in the quantitative analyses to improve normality.

Linkage analysis of the 257 BC_1 and 86 IL2-5-F_2 plants was performed using the software package MAPMAKER V2.0 (Lander et al. 1987). In order to include a locus in a linkage group, a minimum LOD ($\log_{10}$ of the likelihood odds ratio) threshold of 3.0 and a maximum recombination fraction of 0.35 were used in the two-point analyses. The "orders" and "ripples" commands were then used, respectively, to establish and verify the framework order of markers within groups. Markers and their corresponding distances (cM) were included within the framework map only if the LOD value for the ripple was > 3. Once the correct linear arrangement of marker loci along the chromosome was determined, multi-point analyses were used to estimate recombination frequencies between markers. The Kosambi mapping function was used to convert recombination frequencies to map distances in cM (Kosambi 1944).

To identify the position of *fw2.2*, one-way ANOVAs were performed in which marker-genotype groups were used as class variables. Significant ($P < 0.001$) differences in marker class means were interpreted to indicate linkage of *fw2.2* to the marker locus. The results were confirmed by interval regression using the program QGene (Nelson 1994). To estimate the percentage of the total phenotypic variation explained (PVE) by *fw2.2*, one-way ANOVAs were performed; the PVE is equivalent to a R^2 value.

Results and discussion

Marker analysis

Marker segregation ratios

A total of 22 polymorphic RFLP markers on chromosome 2 were utilized for the QTL analysis of fruit weight in the Pp and Pn populations (Fig. 1). None of the markers in either population showed distorted segregation ratios ($P > 0.01$).

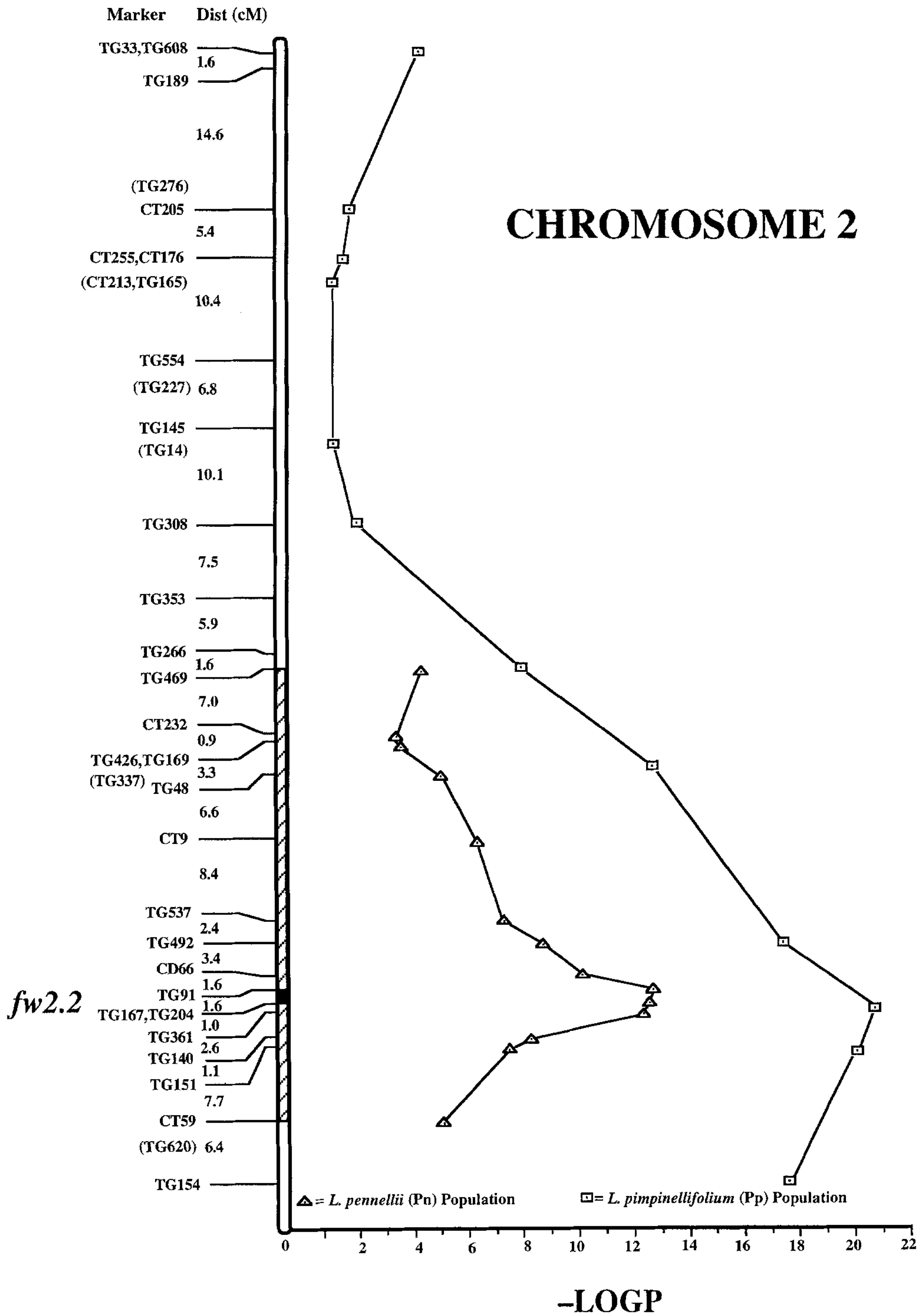
Marker order and recombination values

The linear order for 21 of the 22 RFLP markers studied in both the Pp and Pn populations agreed with the previously published high-density linkage map (Tanksley et al. 1992). The only exception was TG91 which was originally placed on the short arm of chromosome 2 (Zamir and Tanksley 1988). As part of the current study, we re-mapped this clone on the high-density mapping population consisting of 67 F_2 plants (Tanksley et al. 1992) and report that TG91 actually maps to a position 1.6 cM from both CD66 and TG167 on the long arm of chromosome 2 (Fig. 1). The re-positioning of TG91 within the interval flanked by CD66 and TG167 has also been independently confirmed by Eshed and Zamir (personal communication).

Recombination frequencies for the Pp and the Pn populations differ in several instances from those reported for the high-density linkage map (Table 1). In the Pn population, the segment spanning TG469 and CT59 consists of approximately 12 cM, as compared to approximately 48 cM on the high-density map (Fig. 1). This represents a 75% reduction in the recombination frequency. This reduced recombination, however, is highly heterogeneous across chromosome 2. For example, the greatest suppression in the Pn population was observed between markers TG151 and CT59 (88%), while the least was between markers TG167 and TG361 (10%). Furthermore, in the interval directly adjacent to TG167 and TG361, the region spanning markers TG91 and TG167 had a suppression rate of 81%.

Recombination was also suppressed in the Pp population as compared to the high-density map. In the Pp

Fig. 1 The association between reduced fruit weight and tomato chromosome-2 markers in the Pn population (*triangles*) and Pp population (*squares*). The F statistic was used to determine the corresponding *P* value for each marker which was converted to $-\log P$ for simplicity. The kosambi mapping function was used to convert recombination frequencies to map distances in centiMorgans, cM (Kosambi 1944). Map distances are based on the previously published tomato high-density linkage map (*L. esculentum* × *L. pennellii*; Tanksley et al. 1992). Markers with *tick marks* were ordered with LOD > 3. Markers enclosed in *parentheses* were located to corresponding intervals with LOD < 3. The *hatched box* corresponds to the *L. pennellii* region of chromosome 2 contained in the introgression line (IL2–5). the *black box* indicates the likely position of *fw2.2*



population, the segment spanning TG608 and TG154 consists of approximately 98 cM, while in the high-density linkage map it consists of approximately 118 cM (Fig. 1). This represents a 17% reduction in the recombination frequency. The interval spanning TG151 and TG154 in the Pp population had the greatest reduction (69%) as compared to the high-density map. Interestingly, three intervals in the Pp population had an increase in the recombination rate as compared to the high-density linkage map (CT205–CT176, TG308–TG469 and TG167–TG151).

Phenotypic analysis

Frequency distribution of fruit weight

The mean fruit weights for the Pp and Pn populations were 33.6 g ± 10.3 and 36.8 g ± 13.9, respectively. In

Table 1 A comparison of chromosome-2 interval distances in the *L. pimpinellifolium* (Pp) and *L. pennellii* (Pn) populations. The map distances (cM) for the *L. pimpinellifolium* (Pp) and *L. pennellii* (Pn) populations are compared to the previously published tomato high-density map (Tanksley et al. 1992). Intervals without distances in the Pp and Pn populations are a result of markers on the tomato high-density map that were located with LOD < 3, or to markers that were not polymorphic. The percent (%) difference in recombination indicates a decrease (−) or increase (+) in recombination relative to the high-density map in the Pp and Pn populations

Interval	High-density map	Pp	Pn	% Difference in recombination
TG608–CT205	16.2	14.0		−14
CT205–CT176	5.4	6.1		+13
TG308–TG469	15.0	15.2		+1
TG469–CT232	7.0		1.9	−73
CT232–TG426	0.9		0.5	−44
TG426–TG48	3.3		1.6	−52
TG48–CT9	6.6		1.6	−76
CT9–TG537	8.4		1.4	−83
TG537–TG492	2.4		0.3	−88
TG492–TG167	6.6	4.4		−33
TG492–CD66	3.4		0.8	−76
CD66–TG91	1.6		0.7	−56
TG91–TG167	1.6		0.3	−81
TG167–TG361	1.0		0.9	−10
TG167–TG151	4.7	6.9		+47
TG361–TG140	2.6		0.6	−77
TG140–TG151	1.1		0.3	−73
TG151–TG154	14.1	4.4		−69
TG151–CT59	7.7		0.9	−88

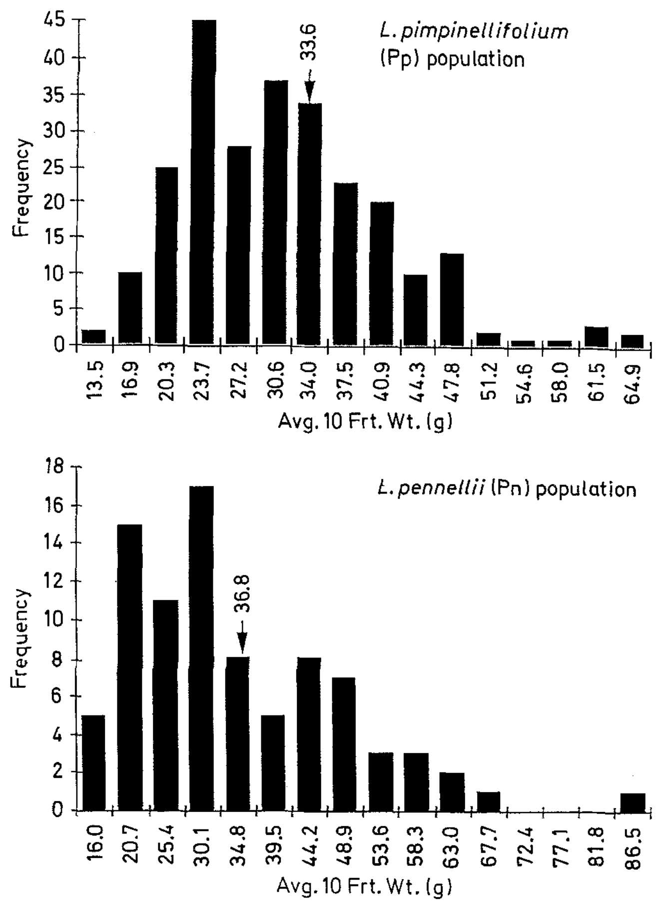


Fig. 2 Fruit-weight (g) histograms of the *L. pennellii* (Pn) and *L. pimpinellifolium* (Pp) populations. The *arrows* indicate the mean fruit weights for the Pp and Pn populations. In both populations normality for average fruit weight was found to be skewed towards the smaller-fruited parent using the Shapiro-Wilk W test ($P < 0.01$). The $\log_{10}$ of fruit weight was, therefore, used in the quantitative analyses to improve normality

both populations the frequency distribution for fruit weight showed continuous variation but was significantly skewed (Shapiro-Wilk W test; $P < 0.01$) towards the small-fruited wild species (Fig. 2). The observed continuous variation is consistent with previous studies (MacArthur and Butler 1938) and is suggestive of polygenic inheritance. Skewness towards the small-fruited parent has been previously reported and suggests that partial dominance is associated with small fruit (MacArthur and Butler 1938; Khalf-Allah and Mousa 1972; Banerjee and Kalloo 1989; Paterson et al. 1991).

fw2.2 localization

A major fruit-weight QTL (*fw 2.2*) was localized to the same chromosome-2 region in both the Pn and Pp populations (Fig. 1). In the Pn population, TG91 showed the most significant association with reduced fruit weight ($-\log P = 12.8$); in the Pp population the adjacent RFLP marker, TG167 (1.6 cM away), had the most significant association ($-\log P = 20.7$). TG91 was not scored in the Pp population because it was not polymorphic. However, the fact that TG91 and TG167 are tightly linked (1.6 cM) suggests that the same QTL (*fw 2.2*) is present in both Pn and Pp. In a comparative mapping study using another red-fruited wild tomato species *L. cheesmanii*, Paterson et al. (1991) identified a fruit-mass QTL localized to the same region on chromosome 2. Furthermore, in a study aimed at mapping earliness QTLs derived from the red-fruited (*L. pimpinellifolium*) and green-fruited (*L. parviflorum*) wild tomato species, Lindhout et al. (1994) identified an earliness QTL from *L. pimpinellifolium* which was associated with small fruit and mapped to the same region as *fw*2.2 on chromosome 2. Together, these data suggest that *fw2.2* may represent an orthologous (i.e., derived by speciation as opposed to duplication) fruit-weight QTL broadly distributed in green-fruited and red-fruited wild tomato species.

A comparison of fruit-weight effects between genotypes

The genotypic fruit-weight (g) means for the Pn and Pp populations are shown in Fig. 3. The mean fruit weights reported are for the chromosome-2 markers TG91 and TG167, which were found to have the greatest $-\log P$ value associated with reduced fruit weight. When com-

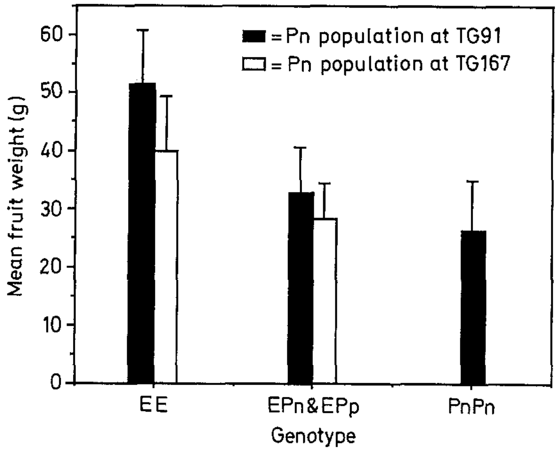


Fig. 3 *L. pennellii* (Pn) and *L. pimpinellifolium* (Pp) genotypic fruit-weight means. The symbol *EE* represents the homozygote, *L. esculentum*. The mean fruit weight for the homozygous (*EE* and *PnPn*) and heterozygous (*EPn* and *EPp*) genotypes are reported for chromosome-2 markers which have the greatest $-\log P$ value associated with reduced fruit weight. *Error bars* indicate standard deviations

paring the homozygote (*EE*) to the heterozygous (*EPn* or *EPp*) genotypes, a significant ($P < 0.001$) reduction in mean fruit weight for the heterozygotes *EPn* (-18.8 g) and *EPp* (-11.1 g) is observed (Table 2). This represents a decrease of 36.6% and 28.1% respectively, for *EPn* and *EPp*.

The amount of phenotypic variance explained (PVE) by *fw2.2* was obtained by estimating the R^2 value for markers TG91 and TG167 (Table 2). For the Pp and Pn populations, the percentage of PVE attributable to *fw2.2* was 30% and 47% respectively, suggesting that *fw2.2* is a major QTL for fruit weight in both Pp and Pn.

Gene action of fw2.2

The gene action for *fw2.2* was determined in the Pn population (Table 2). The degree of dominance (d/a) of the *Pn* allele was found to be 0.44, which indicates that the *Pn* allele is partially dominant over the *L. esculentum* (*E*) allele. This is visually apparent in Figs. 3 and 4, in which the *PnPn* genotype is only 6.31 g less than the heterozygote *EPn* as compared to the 18.8 g reduction observed between the *EE* and *EPn* genotypic classes. In a previous study by Paterson et al. (1991), a fruit-mass QTL which mapped to a similar region on chromosome 2 of the wild tomato species *L. cheesmanii* also showed partial dominance in two different populations (d/a = 0.49 in F_2 and d/a = 0.69 in F_3). Together, these data support earlier findings in which partial dominance

Table 2 Fruit-weight differences between heterozygous and homozygous genotypes and gene action calculated for Pn population data

Genotype[a]	Marker[b]	Fruit weight Δ (gr.)[c]	Fruit weight Δ %[d]	R-square[e]	Gene action		
					a[f]	d[g]	d/a[h]
Pn	TG91	−18.8	−36.6	0.47	−0.143	−0.063	0.44
Pp	TG167	−11.1	−28.1	0.30			

[a] Pn = *L. pennellii* IL2–5 F_2 Population, Pp = *L. pimpinellifolium* BC_1 population
[b] The chromosome-2 marker which has the greatest $-\log P$ value associated with reduced fruit weight
[c] The mean fruit weight in grams (g) for the heterozygous (*E/Pn* or *E/Pp*) class subtracted by the mean fruit weight (g) of the homozygous (*E/E*) class for the marker indicated
[d] Fruit weight Δ (g) divided by the mean fruit weight (g) of the homozygous (*E/E*) class for the marker indicated
[e] R-square (R^2) = percent phenotypic variance explained by FW2
[f] a = additive effect (of a single allele) = $(Pn/Pn - E/E)/2$
[g] d = dominance deviation = E/Pn-$[(E/E + Pn/Pn)/2]$
[h] d/a = degree of dominance of the *Pn* allele

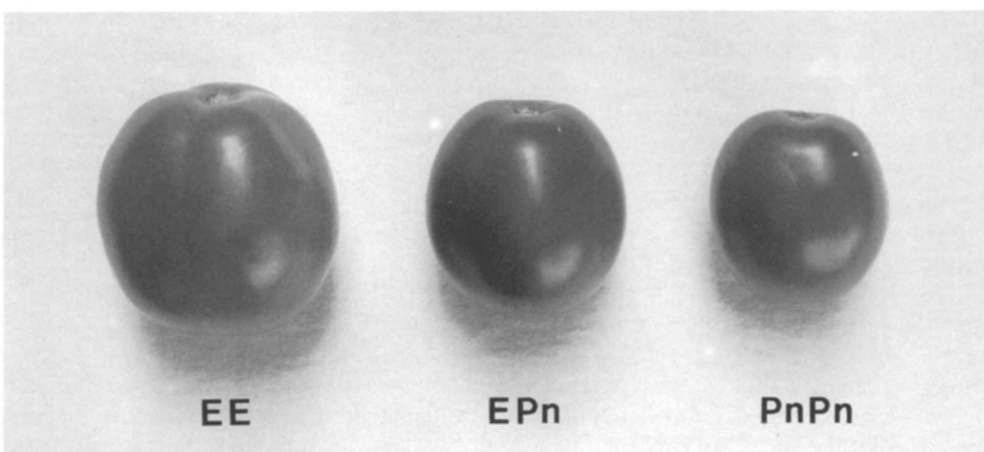


Fig. 4 Representative tomatoes from the *L. pennellii* (Pn) nearly-isogenic lines differ for only the 2.6-cM interval TG91–TG361 containing *fw 2.2* on chromosome 2 (see Fig. 1). Left, *L. esculentum* homozygote (*EE*), center heterozygote (*EPn*), and right *L. pennellii* homozygote (*PnPn*)

is associated with the small-fruited wild tomato species (MacArthur and Butler 1938; Khalf-Allah and Mousa 1972; Banerjee and Kalloo 1989).

Evolution from wild to cultivated tomato most likely involved a macromutation at fw2.2

The domestication of the cultivated tomato from its wild ancestors involved a major increase in fruit size. Since all wild tomato species are known to have small fruit, the presence of large-fruited modern-day cultivars are likely to have resulted, at least in part, by chance mutations occurring during the domestication process.

Results from the current study suggest that most, if not all, wild tomato species possess a small-fruited allele at the *fw2.2* locus. Moreover, variation at this locus accounts for a large portion of the phenotypic variation (for fruit weight) differentiating both green-fruited and red-fruited wild tomato species from the cultivated tomato. It seems likely, therefore, that domestication of the cultivated tomato involved a macromutation at the *fw2.2* locus. The effects of such a major mutation would have been readily observed and selected by humans. Also, the fact that *fw2.2* has such a major phenotypic effect suggests that evolution from small-fruited wild tomatoes to current large-fruited cultivated types may not have been gradual, but punctuated instead by major changes, such as that which is likely to have occurred at the *fw2.2* locus. Similar macromutations involving domestication of crop varieties from their wild ancestors has been proposed for maize (Doebley et al. 1994), cowpea and mungbean (Fatokun et al. 1992).

Implications and future work

The tomato (*L. esculentum* Mill.) and related wild species are members of the very large and diverse family Solanaceae. Among the 90 or so genera included in this family, *Lycopersicon* is one of the smallest and is closely related to the genus *Solanum* for which there are over 1500 species (Hunziker 1979). Recently, molecular studies have been conducted that relate tomato with other species of Solanaceae, (Olmstead and Sweere 1994; Tanksley et al. 1992; Bonierbale et al. 1988) including pepper (*Capsicum annum* L.) eggplant (*Solanum melongena* L.) and potato (*Solanum tuberosum*). The discovery of a major orthologous QTL for fruit size within one taxonomic group (e.g., *Lycopersicon*) may lead to the identification of the same orthologous QTL in additional species outside the tomato genus. The *fw2.2* locus controls a large portion of the fruit-weight difference between wild and cultivated tomatoes and may therefore also be a major controlling locus in other species such as pepper and eggplant. Because of conserved linkage within the Solanaceae, this hypothesis can be tested by conducting QTL studies of fruit size in these other species using conserved markers known to be linked to *fw2.2*. The fine mapping of major orthologous QTLs, such as *fw2.2*, may also aid in the understanding of the evolutionary relationship between QTLs in different species.

The size, shape, and appearance of fruit are key traits in many fruit and vegetable crops. Discovery of a major, conserved locus controlling fruit size may not only facilitate breeding for this character in tomato but may ultimately lead to the molecular cloning of this key locus. Such an event would open the door to understanding the molecular biology of fruit development and potentially to the genetic engineering of fruit size and shape characteristics.

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