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QTL analysis of horticultural traits differentiating the cultivated tomato from the closely related species *Lycopersicon pimpinellifolium*

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Abstract Molecular markers were used to map and characterize quantitative trait loci (QTLs) for several characters of agronomic and biological importance in an interspecific backcross of tomato. The parents of the cross were an elite processing inbred *Lycopersicon esculentum* cv 'M82-1-7' and the closely related red-fruited wild species *L. pimpinellifolium* (LA1589). A total of 257 BC_1 plants were grown under field conditions in Ithaca, New York and scored for 19 quantitative traits. A genetic linkage map was constructed for the same population using 115 RFLP, 3 RAPD and 2 morphological markers that spanned 1,279 cM of the tomato genome with an average interval length of 10.7 cM. A minimum of 54 putatively significant QTLs ($P < 0.001$; LOD > 2.4) were detected for all characters with a range of 1–7 QTLs detected per character. Of the total 54 QTLs 11% had alleles with effects opposite to those predicted by the parental phenotypes. The percentage of phenotypic variation associated with single QTLs ranged from 4% to 47%. Multilocus analysis showed that the cumulative action of all QTLs detected for each trait accounted for 12–59% of the phenotypic variation. The difference in fruit weight was controlled largely by a single major QTL (*fw2.2*). Digenic epistasis was not evident. Several regions of the genome (including the region near *sp* on chromosome 6) showed effects on more than one trait. Implications for variety improvement and inferences about the domestication of the cultivated tomato are discussed.

Key words Molecular markers · Quantitative trait locus (QTL) · Plant breeding · *Lycopersicon pimpinellifolium* · Domestication

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Introduction

Phenotypes of most traits in nature and agriculture are continuous variables. This continuous distribution has been attribted to the collective action of many genes – termed quantitative trait loci, QTLs (Geldermann 1975) – interacting with the environment (Johanssen 1909; Nilsson-Ehle 1909; East 1915). Biometrical procedures, though useful, have only partially addressed many of the questions regarding quantitative genetics; indeed they are deficient in providing information about the inheritance, magnitude of effects and gene action of each specific locus that affects the quantitative character. Molecular markers and their derived saturated linkage maps have overcome many of these limitations, allowing the resolution of quantitatively inherited characters into discrete Mendelian factors (Paterson et al. 1988; Tanksley 1993).

To date, many agronomically and biologically important traits (e.g. resistance to biotic and abiotic stress, yield, nutritional quality) have been studied by means of molecular mapping in numerous crops including tomato, potato, maize, rice, barley and soybean (Edwards et al. 1987; Nienhuis et al. 1987; Stuber et al. 1987, 1992; Paterson et al. 1988, 1990, 1991; Weller et al. 1988; Martin et al. 1989; Keim et al. 1990; Doebley and Stec 1991; Hayes et al. 1993; Bonierbale et al. 1994; Leonards-Schippers et al. 1994; Schön et al. 1994; Wang et al. 1994). In most cases, the experiments have been conducted on balanced populations, backcrosses or F_2s derived from pure lines, and have generally been able to identify minimal numbers of putative QTLs responsible for the character of interest and to estimate the relative contributions of "major" and "minor" genes to the total phenotypic variation. Molecular markers have also allowed a partial insight into interlocus interactions (epistasis) and intralocus interactions (gene action) of loci controlling quantitative traits. Stuber et al. (1992) detected QTLs having an important role in heterosis, and several other QTL mapping studies have reported

direct evidence for the genetic basis of transgression (Tanksley et al. 1982; Paterson et al. 1988; de Vicente and Tanksley 1993).

While the marker-based QTL approach has been useful in describing the loci controlling quantitative traits, it has yet to be proven whether this approach offers an efficient alternative tool for the improvement of animal and plant species. Tomato (*Lycopersicon esculentum* Mill.) is an ideal system for testing the applications of molecular markers in plant breeding. A highly saturated molecular map is available (Tanksley et al. 1992), and a rich source of genetic variation is accessible in its wild forms (Rick 1982). Molecular markers made it possible to map and characterize specific favorable alleles provided by the unadapted germplasm, even when they were masked by unfavorable phenotypes (Tanksley et al. 1982; Paterson et al. 1988, 1991; Weller et al. 1988; Doebley and Stec 1991; de Vicente and Tanksley 1993). In the present study we have applied the procedures of QTL mapping to analyze the genetic basis of several quantitative traits of agronomic and biological interest in a backcross population derived from a cross between the cultivated tomato (*L. esculentum*) and its most closely allied wild relative (*L. pimpinellifolium*). Commercial tomato varieties are typically hybrids and thus a BC_1 population structure was chosen which allows the detection of additive, dominant and overdominant QTLs from the wild species which are valuable for hybrids while deliberately avoiding recessive QTLs that will not function in hybrid combinations.

L. pimpinellifolium is a red, small-fruited wild species originating in Peru and is closely related to the cultivated tomato (Luckwill 1943; Rick 1976; Miller and Tanksley 1990). It is the only wild species for which natural introgression with *L. esculentum* has been demonstrated, and it is very likely that genes derived from *L. pimpinellifolium* have been involved in the evolution of today's cultivated tomato (Rick 1958). Besides *L. esculentum* var 'cerasiforme', *L. pimpinellifolium* is the only other likely candidate as the direct ancestor of the modern cultivated tomato. Alternatively, it has been proposed that both species, *L. esculentum* and *L. pimpinellifolium*, have evolved independently from a common green-fruited ancestor (Rick 1976). Despite their close relationship, the two species differ in many morphological aspects, especially in fruit size and growth habit and several other economically interesting traits, many of which are polygeneically inherited (Luckwill 1943). For this reason *L. pimpinellifolium* has been frequently considered an attractive source of germplasm for the breeding of the cultivated tomato.

The objectives of this study were: (1) to map and characterize QTLs for quantitative traits of agronomic interest from *L. pimpinellifolium*; (2) to analyze the genetic basis of the key morphological traits distinguishing the cultivated tomato from one of its closest wild relatives; (3) to compare the map location and phenotypic effect of QTLs detected in the above-described interspecific cross with QTLs detected in other interspecific crosses previously described for tomato.

Materials and methods

Plant material

The BC_1 mapping population utilized in this study is described in Grandillo and Tanksley (1996). Briefly, the processing inbred *Lycopersicon esculentum* cv 'M82-1-7' (denoted Ea) was crossed as pistillate parent to the red-fruited wild species *L. pimpinellifolium* (LA1589) (denoted PM). A single interspecific F_1 plant was backcrossed to the related processing inbred *L. esculentum* cv 'E6203' (denoted Eb), the latter being used as male parent. The three parental lines (Ea, Eb and PM), along with the hybrids, Ea × PM (denoted F_1a) and Eb × PM (denoted F_1b), were also included in the experiment as controls. BC_1 and control plants were sown in flats in the greenhouse on April 18, 1992. At the end of May, 264 BC_1 progeny together with 100 control plants (20 of each type) were transplanted to the field in Ithaca, New York, in a completely randomized design, at a row and plant spacing of 6 feet.

Phenotyping

Individual BC_1 plants and controls were scored for 19 quantitative traits. Days to emergence (DE) was measured as the number of days from the sowing date to the day of complete opening of the cotyledons. Days to third leaf (DTL) indicates the number of days from the sowing date to the complete opening of the third true leaf. After transplanting to the field, the 364 plants were monitored for the appearance of the first opened flower, days to first flower (DFL). Days to first fruit (DFR) was taken as the number of days from sowing until the complete change of color (green to red) of the first fruit. Days to ripening (DR) indicates the number of days from the opening of a flower to the complete change of color of the fruit derived from that same flower. For all the plants, the third and fourth flowers of a randomly chosen truss were labeled on July 10 and their corresponding blooming and maturing dates recorded. If the first labeled flowers aborted, then the labeling was repeated on another truss. In a few instances this extended the range for the blooming date from the 10th of July until the 29th. Anther-tube with (ATW), in millimeters, was determined as the averaged maximum width taken on the anther tube of two to ten flowers per plant. On the same flowers the length of the anther tube (ATL), in millimeters, was also measured and averaged. The ratio of ATL over ATW was used to determine an anther-tube index (ATX). The number of flowers per truss (NFLT) was taken as an average of five randomly chosen trusses per plant.

At the end of the growing season ten representative ripened fruit were harvested from each plant for measurement of the average fruit weight and other fruit characters. Fruit weight (FW) was scored as the mean weight, in grams, of the ten fruits. A subset of five fruits of the ten harvested were cut transversely, and fruit color (FC) was subjectively evaluated on a visual scale from 1 to 3 (3 = more intense color). The mixed fresh juice of the same five fruits was used to determine the total soluble solids concentration (SSC), in degrees Brix (°Brix), by means of a hand refractometer. The same subset of five fruits was used to obtain the average number of seeds per fruit (NSF) and the thousand-seed weight (WTS), in grams. Fruit diameter (FD) (average of two perpendicular measurements taken per fruit, in mm), thickness of the pericarp (FP) (average of three measurements taken per fruit, in mm) and locule number (LOCN) were measured as the average of three fruits per plant taken from the second subset of five fruits of the ten harvested. Caliper measurements of polar (stem to blossom ends) and equatorial diameters were taken, from which a fruit shape index (FS) was derived by dividing the polar (height) by equatorial diameter. Two to three fruit were measured per plant, and the average value was used for the analyses. Plant vertical height (PVH), in centimeters, indicated the distance from the ground level to the height where the stem started becoming decumbent.

In addition to the above measurements, all plants were scored visually for determinacy and uniform ripening – two simply inherited morphological traits controlled by the *sp* and *u* genes, respectively. These two morphological markers were also included in the linkage map used for QTL mapping.

Genotyping

Molecular markers were analyzed on 257 BC_1 plants as reported in Grandillo and Tanksley (1996).

Statistical analysis

Means, standard deviations, contrasts and Pearson correlation coefficients were calculated for each trait, for the controls and for the BC_1 population using the JMP V 3.0 software package for Macintosh (SAS Institute 1989). Normality for each trait was tested with the Shapiro-Wilk W test available on the same program.

Segregation ratios for marker classes were summarized and checked for conformity with the expected 1:1 ratios with the chi-square test using the programs MAP MANAGER (Manly 1993) and qGENE (Nelson 1994).

Linkage analysis of the 257 BC_1 plants was performed with the software package MAPMAKER (Lander et al. 1987) as described in Grandillo and Tanksley (1996). The Kosambi mapping function (Kosambi 1944) was used to convert recombination frequencies to map distances in centiMorgans (cM).

Two analytical approaches were used to identify putative QTLs and estimate their phenotypic effects: single-point analysis and interval mapping (Lander and Botstein 1989). For the first procedure one-way ANOVAs were performed by the PROC GLM routine in SAS (SAS Institute 1988), in which marker-genotype groups were used as class variables. For single-point analysis the program qGENE (Nelson 1994) was also used which generates the same results as PROC GLM routine in SAS but in a convenient tabular form. Because of the high number of comparisons performed and in order to minimize the Type-I error of false positive QTLs, we chose a probability level of $P = 0.001$ as the threshold to define differences in marker class means as highly significant and thereby suggesting association of a QTL to the marker locus. The results were confirmed with interval mapping analysis using the computer program MAPMAKER-QTL version 1.1 (Lincoln et al. 1992). For consistency with the single-point analysis, a LOD score threshold of 2.4 was chosen as it is approximately equivalent to requiring a significance level of 0.001 for any single test. The program MAPMAKER-QTL was also used to obtain estimates of the percentage of the total phenotypic variation explained (PVE) by each QTL which is equivalent to R^2 values from regression analyses. The multilocus model from the same sorftware was used to estimate the percent of phenotypic variation accounted for by all significant QTLs for each trait. Tests for two-way interactions were evaluated betwen significant QTLs and all other marker loci using the qGENE program.

Results and discussion

Genetic map

For QTL analysis a total of 120 genetic markers (115 RFLP, 3 RAPD and 2 morphological loci, the *sp* and *u* genes) were scored for each of the 257 BC_1 plants. The linkage map spanned 1,279 cM with an average distance between markers of 10.7 cM (Fig. 1) (Grandillo and Tanksley 1996). Due to the low level of polymorphism, three gaps in the range of 30–40 cM were left, distributed on chromosomes 7, 9 and 12.

Quantitative trait analyses

Distributions of quantitative traits

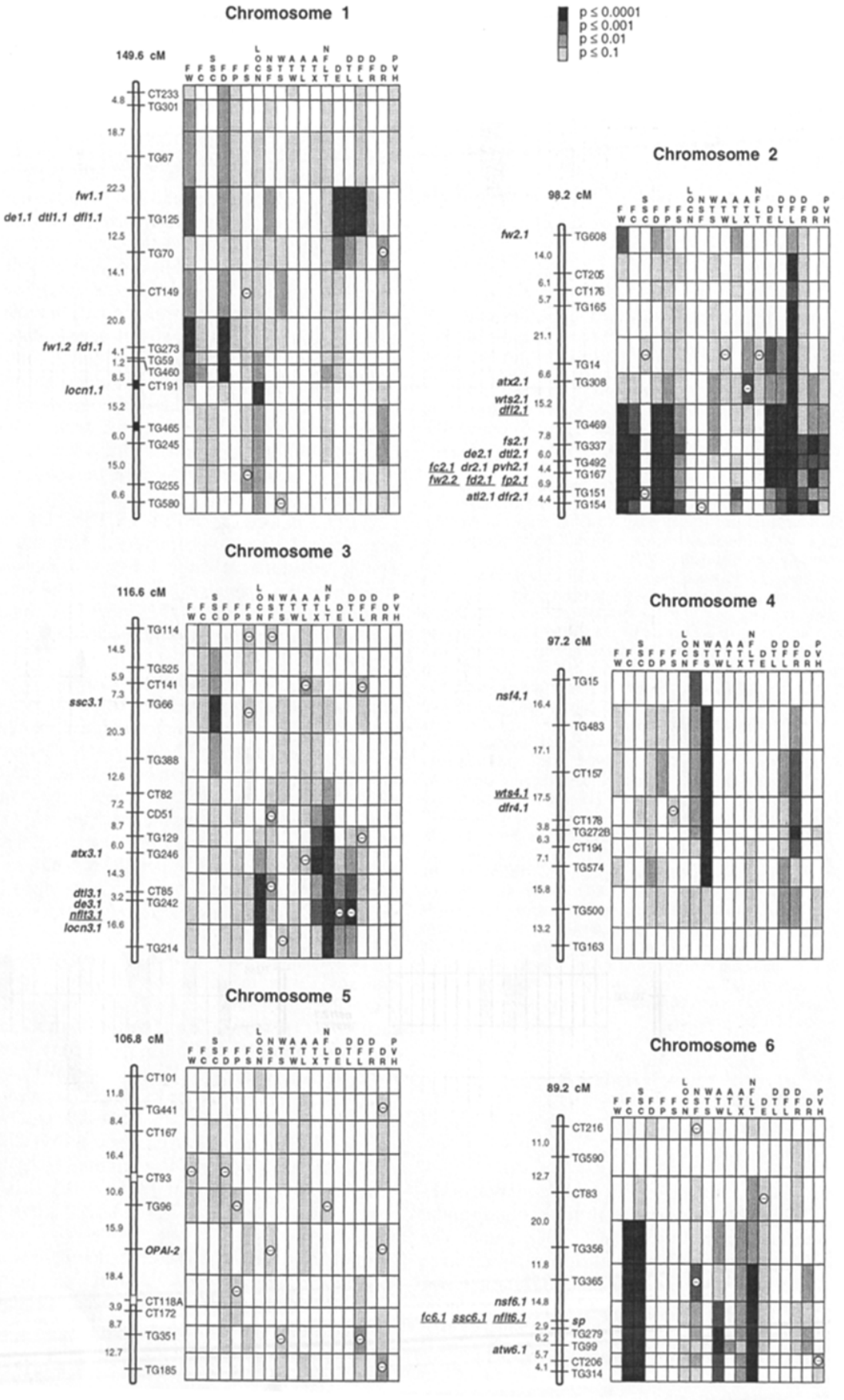
All 19 of the traits analyzed were characterized by continuous variation, which is typical of quantitative or polygenic inheritance (Fig. 2). Consistent with previous observations (Ibarbia and Lambeth 1969; Tanksley et al. 1982; Paterson et al. 1988) fruit weight (FW) showed a significant positively skewed distribution in the BC_1 population. Deviation from normality also characterized several other traits and in order to approach normality, we used $\log_{10}$ or square root transformations. Although the transformation reduced both skewness and kurtosis, the significance levels and magnitudes of the R^2 from regression analysis (and respectively the LOD and the PVE from interval analysis) for the transformed data did not differ substantially from those obtained from the raw data. For this reason, only results from non-transformed data have been reported.

The two *esculentum* lines used in the cross, Ea and Eb, differed significantly ($P < 0.05$) for 9 traits, including FW, FD, FP, LOCN, NSF, WTS, DFL, DR and PVH, while for the other 10 characters their means were not significantly different (Table 1; Fig. 2). *L. esculentum* (Ea and Eb) and *L. pimpinellifolium* (PM) differed significantly for all traits except DFL for which the means of cv 'M82-1-7' (Ea) and of the wild species (PM) were indistinguishable.

Fruit weight (FW) showed the most striking divergence between the two species (Table 1; Fig. 2). *L. pimpinellifolium* fruits were very small, averaging 1.5 g. In contrast, the fruits of the two *L. esculentum* parents averaged 77 g, approximately 48 times greater than those of *L. pimpinellifolium*. When large- and small-fruited cultivars are crossed, the fruit size of the F_1 hybrids typically resembles that of the smaller fruited parent (MacArthur and Butler 1938). Small fruit dominance was evident in the F_1s, which averaged 13 g FW, and the BC_1 was also skewed toward the small-fruited parent.

L. pimpinellifolium fruit were nearly spherical (as indicated by a mean FS of 1.03), intensely colored (FC = 2.5), biloculated (LOCN = 2), with a thin pericarp (FP = 1.49 mm) and a relatively high soluble solids concentration (SSC = 8.15 °Brix) and contained a lower number (NSF = 31.9) of small seeds (WTS = 1.27 g), whereas the fruit of the processing *L. esculentum* lines were blocky in shape (FS = 1.14), less intensely colored (FC = 1.02), had more than two locules (LO CN = 2.97), with a thicker pericarp (FP = 7.1 mm), lower total soluble solids concentration (SSC = 4.5 °Brix) and a greater number (NSF = 76) of larger seeds (WTS = 3.1 g).

For FS the high level of dominance of the wild parent was revealed in both the F_1 and BC_1 populations; the means of the F_1s and the BC_1 were all statistically identical to that of the wild parent (Table 1; Fig. 2). The same trend was detected in the F_1s for the traits FC and


Chromosome 1
p ≤ 0.0001
p ≤ 0.001
p ≤ 0.01
p ≤ 0.1
149.6 cM
CT233
TG301
TG67
fw1.1
de1.1 dtl1.1 dfl1.1
TG125
TG70
CT149
fw1.2 fd1.1
TG273
TG59
TG460
locn1.1
CT191
TG465
TG245
TG255
TG580
Chromosome 2
98.2 cM
fw2.1
TG608
CT205
CT176
TG165
TG14
atx2.1
TG308
wts2.1
dfl2.1
TG469
fs2.1
de2.1 dtl2.1
TG337
TG492
fc2.1 dr2.1 pvh2.1
fw2.2 fd2.1 fp2.1
TG167
TG151
atl2.1 dfr2.1
TG154
Chromosome 3
116.6 cM
TG114
TG525
CT141
ssc3.1
TG66
TG388
CT82
CD51
TG129
atx3.1
TG246
dtl3.1
de3.1
nflt3.1
locn3.1
CT85
TG242
TG214
Chromosome 4
97.2 cM
nsf4.1
TG15
TG483
CT157
wts4.1
dfr4.1
CT178
TG272B
CT194
TG574
TG500
TG163
Chromosome 5
106.8 cM
CT101
TG441
CT167
CT93
TG96
OPAI-2
CT118A
CT172
TG351
TG185
Chromosome 6
89.2 cM
CT216
TG590
CT83
TG356
TG365
nsf6.1
fc6.1 ssc6.1 nflt6.1
sp
TG279
TG99
atw6.1
CT206
TG314

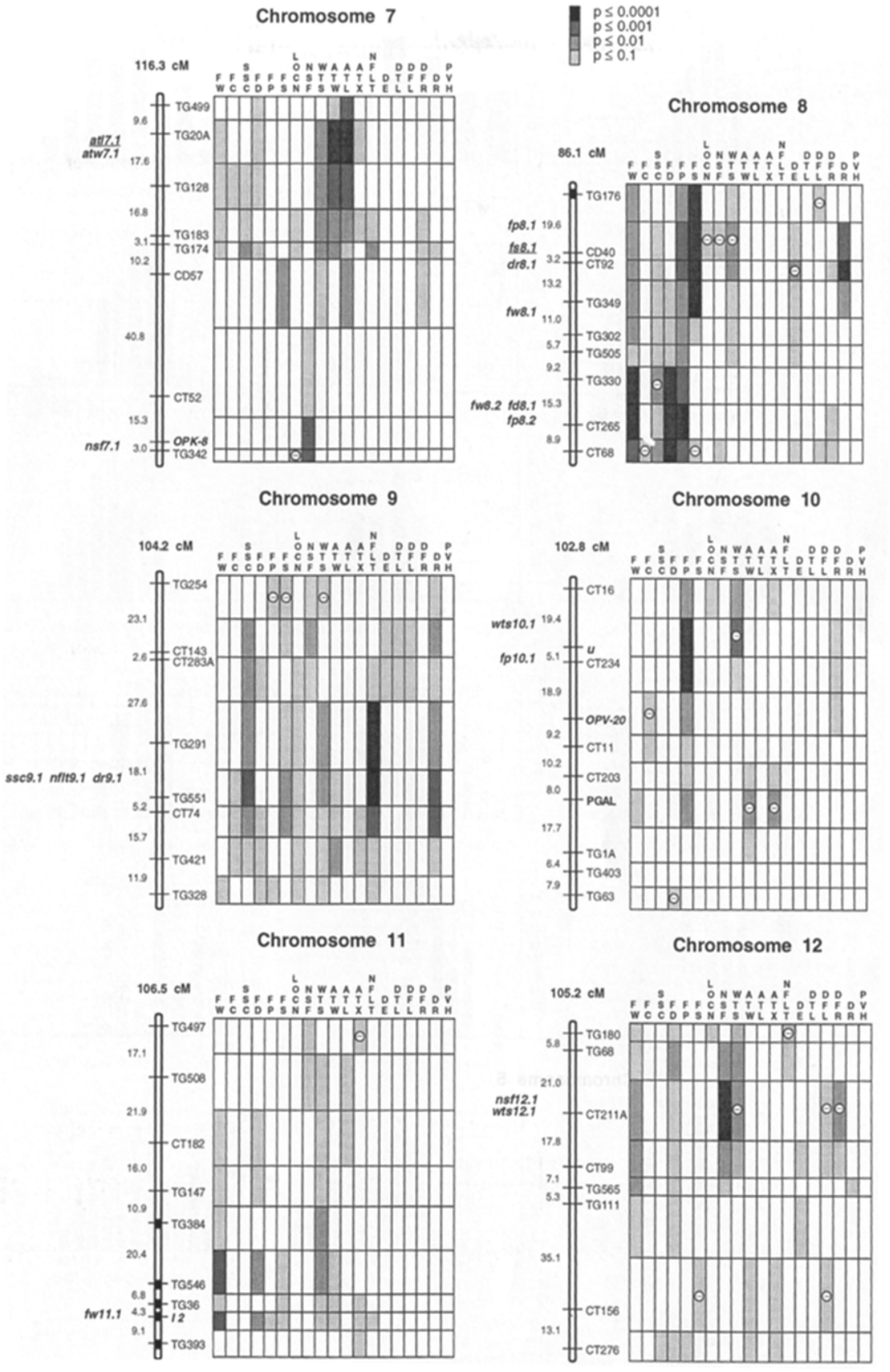


Fig. 1 Marker-trait associations ($P \leq 0.1$) detected in the *L. esculentum* × *L. pimpinellifolium* BC_1 population. Cells marked with a *minus sign* and all the *contiguous shaded* cells within a trait indicate that the PM allele at those loci have effects opposite to those expected based on parental means (see Table 2 for details). Symbols to *left* of chromosomes represent the most likely positions of significant QTLs ($P < 0.001$; LOD > 2.4) (see Table 2 and text for details) as determined using the interval mapping approach. *Underlined* QTLs had a phenotypic effect equal to or greater than 15% (PVE from interval mapping). *Black squares* on chromosomes 1, 8 and 11 indicate markers with a segregation significantly skewed in favor of the PM allele. *White squares* on chromosome 5 indicate markers with a segregation significantly skewed in favor of the E allele

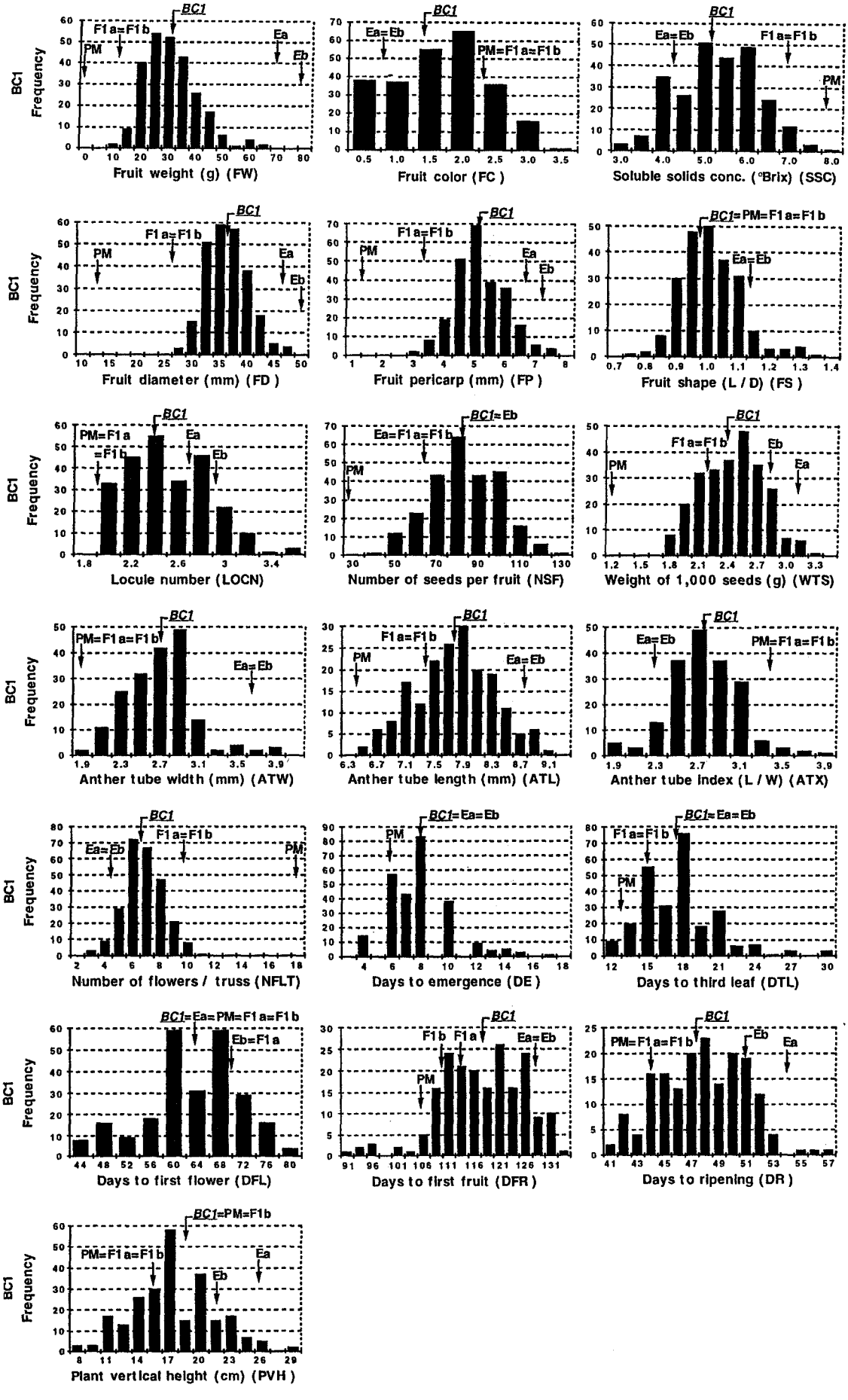

BC1
Frequency
Fruit weight (g) (FW)
F1a=F1b
PM
Ea
Eb
Fruit color (FC)
Ea=Eb
PM=F1a=F1b
Soluble solids conc. (°Brix) (SSC)
Fruit diameter (mm) (FD)
Fruit pericarp (mm) (FP)
Fruit shape (L / D) (FS)
BC1=PM=F1a=F1b
Locule number (LOCN)
PM=F1a
=F1b
Number of seeds per fruit (NSF)
Ea=F1a=F1b
BC1=Eb
Weight of 1,000 seeds (g) (WTS)
Anther tube width (mm) (ATW)
PM=F1a=F1b
Anther tube length (mm) (ATL)
Anther tube index (L / W) (ATX)
Number of flowers / truss (NFLT)
BC1=Ea=Eb
Days to emergence (DE)
Days to third leaf (DTL)
BC1=Ea=PM=F1a=F1b
Eb=F1a
Days to first flower (DFL)
F1b F1a
Days to first fruit (DFR)
Days to ripening (DR)
BC1=PM=F1b
PM=F1a=F1b
Plant vertical height (cm) (PVH)

Fig. 2 Frequency distributions for each character in the BC_1 progeny. Means for parental (Ea, Eb, PM) and F_1 (F_1a, F_1b) controls and for the BC_1 population are shown by *arrows*. *Equal sign* indicates that the means are statistically equal based on contrasts ($P < 0.05$)

LOCN, though in both cases a lower degree of dominance characterized the BC_1s, the means of these populations being closer to the midpoint between the *esculentum* strains and the F_1s. Dominance of *L. pimpinellifolium* was also the case for FD and FP as shown by the F_1 data, although a lesser degree of dominance was observed for both traits in the BC_1 populations. For SSC a partial dominance of the wild parent was detected in the F_1s, while the BC_1 mean, which was closer to the *esculentum* means, suggests partial dominance of the cultivated strains. For WTS the means of the F_1s and BC_1 fell between the parental means. For NSF the F_1 means were statistically equal to that of the processing inbred M82 (Ea), whereas the BC_1 mean was indistinguishable from that of the other variety (Eb) used in the cross, indicating a high degree of dominance exerted by the cultivated species for this trait.

L. pimpinellifolium had longer trusses that contained a greater number (NFLT = 18.4) of smaller flowers with thinner anther tubes (ATW = 1.9, ATL = 6.5, ATX = 3.4) than did the cultivated counterparts (NFLT = 5.0; ATW = 3.7; ATL = 8.9; ATX = 2.4). A high degree of dominance of the wild parent was deduced from the F_1 data for ATW and ATX. In both cases the means of the BC_1s were closer to the midpoint between the *esculentum* strain and the F_1s means, reflecting a lower degree of dominance in the BC_1 populations than in the F_1s. For ATL and NFLT the means of the F_1s and BC_1 fell very close to the midpoint between the two parental species.

Earliness of *L. pimpinellifolium* was expressed in all of the developmental traits analyzed except for DFL for which the Ea and PM means were statistically equal. For the very early stages (DE and DTL) the BC_1s were characterized by partial dominance of the recurrent parent, as shown by the means of these populations, which are indistinguishable from those of the cultivated strains. For DFR the means of the F_1s are closer to the early parent mean, whereas the BC_1 population has a mean closer to the midpoint between the cultivated species and the F_1s. For DR the F_1 means were statistically the same as those of *L. pimpinellifolium*, showing a high degree of dominance of this parent in he F_1s, whereas a lower level of dominance was observed in the BC_1 population, the BC_1 mean being closer to the midpoint between the cultivated parents and the F_1s. The data reported for DFR and DR indicate that dominance plays an important role in the expression of earliness, which is in agreement with previous studies (Banerjee and Kalloo 1989; Kemble and Gardner 1992).

Transgressive segregation was observed for NSF, DE, DTL, and to a lesser extent, for SSC and FS; several

Table 1 Mean phenotypic values, standard deviations and ranges for parents, F_1 hybrids and backcross population (*Ea L. esculentum* cv 'M82-1-7', *Eb L. esculentum* cv 'E6203', *PM L. pimpinellifolium* (LA1589), F_1a interspecific hybrid (Ea × PM), F_1b interspecific hybrid (Eb × PM), BC_1 = backcross progeny (F_1a × Eb), *nd* not determined)

Trait	Trait description	Ea	Eb	PM	F_1a	F_1b	BC_1	BC_1 range	
		Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Minimum	Maximum
FW	Fruit weight (gm)	72.3 ± 10.3	81.2 ± 11.7	1.63 ± 0.19	13.07 ± 1.14	13.46 ± 1.25	33.6 ± 10.3	13.4	68.3
FC	Fruit color (scale 1 to 3)	1.08 ± 0.47	0.96 ± 0.54	2.48 ± 0.47	2.73 ± 0.44	2.75 ± 0.41	1.65 ± 0.74	0.5	3.5
SSC	Soluble solids concentration (°Brix)	4.37 ± 0.32	4.71 ± 0.50	8.15 ± 0.60	7.36 ± 0.39	6.95 ± 0.58	5.48 ± 0.96	3.2	8.3
FD	Fruit diameter (mm)	48.2 ± 3.7	52.0 ± 2.2	13.37 ± 0.58	27.23 ± 1.12	27.30 ± 0.83	37.49 ± 3.91	27.83	49.0
FP	Fruit pericarp (mm)	6.76 ± 0.58	7.46 ± 0.91	1.49 ± 0.22	3.46 ± 0.37	3.68 ± 0.42	5.40 ± 0.86	3.36	7.97
FS	Fruit shape (height/diameter)	1.15 ± 0.03	1.13 ± 0.07	1.03 ± 0.03	1.01 ± 0.03	1.00 ± 0.04	1.03 ± 0.10	0.79	1.4
LOCN	Locule number	2.82 ± 0.35	3.11 ± 0.16	2.00 ± 0.0	2.00 ± 0.0	2.00 ± 0.0	2.52 ± 0.36	2.0	3.6
NSF	Number of seeds per fruit	64.2 ± 17.5	87.7 ± 24.4	31.9 ± 4.6	70.2 ± 4.4	75.1 ± 5.8	87.9 ± 16.7	48.4	135
WTS	Weight of 1,000 seeds (gm)	3.19 ± 0.24	2.91 ± 0.32	1.27 ± 0.09	2.26 ± 0.10	2.26 ± 0.14	2.46 ± 0.32	1.75	3.36
ATW	Anther-tube width (mm)	3.80 ± 0.27	3.67 ± 0.33	1.93 ± 0.11	2.13 ± 0.10	2.13 ± 0.08	2.79 ± 0.36	2.0	4.0
ATL	Anther-tube length (mm)	8.89 ± 0.69	8.81 ± 0.50	6.50 ± 0.46	7.59 ± 0.31	7.38 ± 0.39	7.87 ± 0.55	6.58	9.14
ATX	Anther-tube index (length/width)	2.37 ± 0.25	2.44 ± 0.28	3.37 ± 0.23	3.57 ± 0.15	3.48 ± 0.16	2.85 ± 0.34	1.93	4.0
NFLT	Number of flowers per truss	4.95 ± 0.66	4.95 ± 0.75	18.36 ± 1.37	10.3 ± 0.70	10.3 ± 0.84	7.17 ± 1.42	3.0	11.2
DE	Days to emergence	8.65 ± 1.68	8.68 ± 1.51	6.28 ± 1.32	nd	nd	8.15 ± 2.34	4.0	17.0
DTL	Days to third leaf	18.0 ± 1.8	19.0 ± 1.9	13.5 ± 0.95	15.8 ± 2.3	15.6 ± 1.8	18.06 ± 3.14	12.0	30.0
DFL	Days to first flower	63.3 ± 4.6	71.5 ± 3.2	60.3 ± 4.0	67.1 ± 7.0	65.8 ± 5.7	64.8 ± 8.1	44.0	82.0
DFR	Days to first fruit	128.8 ± 4.5	128.9 ± 4.4	107.5 ± 3.3	114.6 ± 4.9	111.0 ± 4.2	118.5 ± 8.2	91.0	134.0
DR	Days to ripening	54.7 ± 3.1	51.4 ± 1.6	45.2 ± 1.6	43.97 ± 1.36	44.3 ± 2.5	47.9 ± 3.1	41.0	57.0
PVH	Plant vertical height (cm)	26.5 ± 3.7	22.2 ± 3.6	16.4 ± 2.9	15.9 ± 3.0	16.8 ± 3.0	17.86 ± 3.98	8.0	30.0

individuals showed more extreme values than the means of the cultivated strains. For FS, many individuals more extreme than the wild parent were also observed in the BC_1 population (Table 1; Fig. 2).

Correlations among traits

Significant ($P < 0.01$) correlations were observed between many traits (Fig. 3). Among the fruit characters the strongest positive correlations were observed between FW, FD and FP with correlation coefficients ranging from $r = 0.77$ for FD and FP to $r = 0.88$ for FW and FD. These correlations might be expected as a consequence of pleiotropy (see QTL analyses section for further discussion). Another strong correlation coefficient was observed for FC and SSC ($r = 0.54$), which can be partly explained as a likely pleiotropic effect of the *sp* locus on both traits.

More unexpectedly, a significant, but low, positive correlation was found between FW and SSC ($r = 0.19$). Several studies have reported a negative relationship between FW and SSC (Goldenberg and von der Pahleen 1966; Rick 1974; Paterson et al. 1988, 1991). On the contrary Ibarbia and Lambeth (1971) concluded from their studies that the two traits are poorly correlated. The positive correlation between FW and SSC was obtained in both the indeterminate (*sp*/+) and determinate (*sp*/*sp*) subpopulations, which indicates that the correlation is not associated with differences in growth habit.

In agreement with previous observations, significant correlations were found between FW, FS and LOCN (Houghtaling 1935; Yeager 1937; Kemble and Gardner 1992). Both fruit shape and locule number can exert additional and independent effects on fruit size. A highly positive correlation was found between SSC and NFLT ($r = 0.4$) and a slightly lower between FC and NFLT ($r = 0.29$), both of which can likely be attributed to pleiotropic effects.

Most of the developmental traits (DE, DTL, DFL and DFR) were positively intercorrelated. The correlation between DE and DTL was the highest ($r = 0.85$); it was a little lower for DE and DFL ($r = 0.43$) and even lower between DE and DFR ($r = 0.21$). Consistent with previous observations (Banerjee and Kalloo 1989; Kemble and Gardner 1992) there was a moderately significant positive correlation between FW and DFR ($r = 0.30$) and between FW and DR ($r = 0.18$). These correlations can be explained as resulting from pleiotropic effects.

QTL analyses

Marker-trait associations are depicted in Fig. 1. Forty-nine highly significant QTLs were detected by both

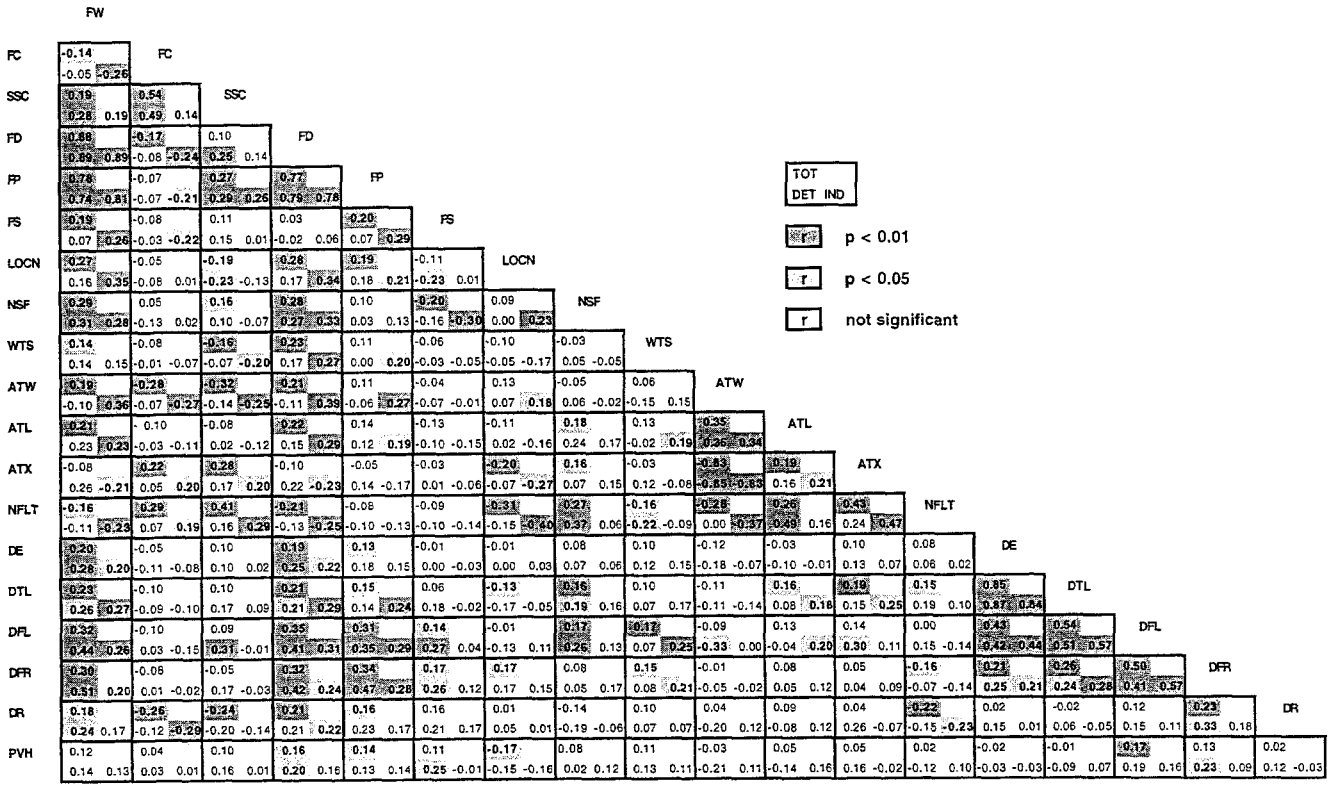


Fig. 3 Correlations among traits in the entire BC_1 population (*TOT*), and in the determinate (*DET*) and indeterminate (*IND*) subpopulations

single-point and interval mapping analyses (Table 2). In addition 3 QTLs, *fw8.1*, *wts2.1* and *wts12.1*, were detected only by interval mapping as they fell slightly below the threshold ($P = 0.001$) used for single point analysis. Two other QTLs, *fw11.1* and *de3.1*, were not detected by interval mapping because they fell slightly below the threshold of 2.4 LOD, but they were above the threshold based on single-point analysis.

Of the 54 significant QTLs, 6 (11%) showed allelic effects opposite to that predicted by the phenotype of the parent contributing them. Included in this list are QTLs for the number of seeds per fruit (*nsf6.1*), weight of 1,000 seeds (*wts10.1* and *wts12.1*), anther-tube index (*atx2.1*), days to emergence (*de3.1*) and days to third leaf (*dtl3.1*). The number of significant QTLs per character ranged from a maximum of 7 for FW to a minimum of 1 for PVH.

The proportion of phenotypic variation explained by individual marker loci associated with specific QTLs was determined both by R^2 from regression analysis and by the comparable statistic from interval mapping (percentage of phenotypic variance explained = PVE). In most of the cases when a QTL mapped close to a specific marker the R^2 and the PVE values were nearly equivalent. When the most likely position of the QTL (based on interval mapping) resided in the middle of an interval, the PVE estimates from interval mapping were usually higher than those from single-point analysis. The highest PVE value was 47.2 ($R^2 = 0.44$) for *ssc6.1*. This QTL corresponds to the *sp* locus on chromosome 6. The lowest PVE value was 4.0 ($R^2 = 0.047$) for *fw11.1*. Of the 54 significant QTLs, 17 (32%) were characterized by PVE values equal to or greater than 10%, 7 of which fell in the range of PVE values between 20% and 50%. A multilocus model was fitted to determine the percentage of phenotypic variance explained for each trait by all the mapped QTLs (Table 2). A maximum value of 58.6% was associated with the 7 QTLs mapped for FW. In contrast, a minimum value of 12.2% was explained by the 2 QTLs found for ATX.

QTLs detected for each trait

Fruit weight (FW) Seven QTLs were detected for FW on chromosomes 1 (*fw1.1* and *fw1.2*), 2 (*fw2.1* and *fw2.2*), 8 (*fw8.1* and *fw8.2*) and 11 (*fw11.1*). The most significant QTL was *fw2.2* on chromosome 2 and explained 32% of the phenotypic variation. When the 7 QTLs were fitted simultaneously with the multilocus model from Mapmaker-QTL, they explained 58.6% of the phenotypic variation. At all loci, the PM alleles had the expected effect, each reducing fruit weight (by 3.96 to 11.01 g) and all adding to a reduction of 41 g for a BC_1 plant carrying a PM allele at all 7 loci.

Fruit color (FC) Two highly significant QTLs were identified for fruit color: *fc6.1*, on chromosome 6, corresponding to the *sp* locus, and *fc2.1* at the lower end of chromosome 2. The two QTLs explained 27.6% and 14.3% of the total phenotypic variation, respectively. Their effects were in the direction expected, the PM allele always contributing a more intense color. A simultaneous fit of the 2 QTLs explained 38.9% of the phenotypic variation.

Total soluble solids concentration (SSC) Three QTLs were detected on chromosomes 3, 6 and 9. The most significant QTL was on chromosome 6, showing tight linkage to the *sp* gene, and accounting for 47.2% of the phenotypic variance. Simultaneous fit of the 3 QTLs explained 57.6% of the phenotypic variation. In each case, the effects of the PM alleles were in the direction expected, increasing soluble solids concentration (by 0.6 to 1.3 °Brix).

Fruit diameter (FD) Fruit diameter was affected by 3 QTLs distributed on chromosomes 1, 2 and 8. The most significant QTL was at the lower end of chromosome 2, *fd2.1*, and explained 29.6% of the phenotypic variance, while *fd1.1* and *fd8.1* had respective PVE values of 9% and 10%. When the 3 QTLs were fitted simultaneously they explained up to 41.4% of the phenotypic variation. All 3 QTLs had effects in the direction predicted by the parental means, with the PM allele always reducing fruit diameter (by 2.3 to 4.3 mm), adding to a total reduction of 9.1 mm. The 3 QTLs occupied similar positions as the QTLs mapped for FW. This coincidence of location of the QTLs detected for the 2 traits is in agreement with the high correlation coefficient ($r = 0.88$; $P < 0.01$) between FW and FD.

Fruit pericarp thickness (FP) Four QTLs for FP were detected on chromosomes 2, 8 (2 QTLs) and 10. The most significant QTL was on chromosome 2 and explained 24.7% of the phenotypic variance. The PVE values for the other 3 QTLs were all lower than 10%, with a minimum value of 6.8% detected for *fp8.1*. Simultaneous fit of all 4 QTLs explained up to 42.3% of the total phenotypic variance. In each case the PM allele had the expected effect, reducing the thickness of the pericarp (by 0.45 to 0.85 mm), adding to a total reduction of 2.24 mm. Three (*fp2.1*, *fp8.1* and *fp8.2*) of the 4 QTLs showed similar positions to QTLs mapped for FW and FD. This clustering of QTLs influencing the 3 traits is in agreement with the high positive correlation found between FP and FW ($r = 0.78$; $P < 0.01$) and between FP and FD ($r = 0.77$; $P < 0.01$). The QTL detected on chromosome 10, *fp10.1*, did not have any counterpart for FW and FD, giving a partial explanation for the lower values of the correlation coefficients found between FP and either FW or FD compared to the one calculated between FW and FD ($r = 0.88$; $P < 0.01$).

Fruit shape (FS) Two QTLs were detected for FS on chromosomes 2 (*fs2.1*) and 8 (*fs8.1*). The QTL on chromosome 8 explained 27.4% of the phenotypic variation and *fs2.1* explained 5.7%. The simultaneous fit of

Table 2 QTLs ($P < 0.001$; LOD > 2.4) detected for each trait. QTLs are named according to trait abbreviations and followed by chromosome number. A second number is used to distinguish QTLs mapping to the same chromosome and affecting the same trait (e.g. *fw2.2*). For each QTL: MML = most closely associated molecular marker loci. In cases where a trait was significantly associated with two adjacent MMLs, both are listed. For regression analyses the MML with the most significant association is indicated by *. If the trait showed approximately equal associations with both MMLs, then neither are indicated by the *. For interval mapping the most likely QTL position is indicated in the column following the interval length (in cM). PVE = percent phenotypic variation; LOD = log-likelihood; phenotypic effect = E/PM−E/E; multilocus PVE = percentage of phenotypic variation accounted for by all significant QTLs for each trait. Parentheses (in the QTL column) indicate QTLs with effects opposite to those expected from the parental means

Trait	Description	QTL	MML	Interval length (cM)	QTL position (cM)	Regression						Interval mapping			
						Number of plants	R^2 %	*P* value	E/E means	E/PM means	E/PM−E/E	PVE	LOD	Phenotypic effect	Multilocus PVE
FW	Fruit weight (gm)	*fw1.1*	TG67-TG125*	22.3	14.0	255	4.4	0.0008	35.61	31.51	−4.10	6.8	2.88	−5.10	
		fw1.2	TG273			250	8.1	<0.0001	36.55	30.67	−5.88	7.7	4.31	−5.36	
		fw2.1	TG608			247	5.5	0.0002	36.12	31.28	−4.84	5.5	3.06	−4.53	
		fw2.2	TG167*-TG151	6.9	4.0	255	30.0	<0.0001	39.32	28.21	−11.11	32.1	20.50	−11.01	
		fw8.1	TG349*-TG302	11.0	4.0	252	5.0	0.003	35.42	31.08	−4.34	6.4	3.25	−4.92	
		fw8.2	TG330*-CT265	15.3	8.0	256	7.6	<0.0001	35.90	30.52	−3.58	9.8	4.93	−6.08	
		fw11.1	*12*			250	4.7	0.0007	36.95	31.66	−5.29	4.0	2.30	−3.96	58.6
FC	Fruit color (scale 1 to 3)	*fc2.1*	TG167			246	14.1	<0.0001	1.35	1.91	0.56	14.3	8.30	0.56	
		fc6.1	TG365-*sp**	14.8	14.0	238	26.2	<0.0001	1.25	2.00	0.75	27.6	16.69	0.75	38.9
SSC	Soluble solids concentration (° Brix)	*ssc3.1*	TG66			251	8.1	<0.0001	5.20	5.74	0.54	8.1	4.61	0.55	
		ssc6.1	TG365-*sp**	14.8	14.0	245	44.1	<0.0001	4.79	6.07	1.28	47.2	33.68	1.32	
		ssc9.1	TG291-TG551*	18.1	10.0	251	4.3	0.0009	5.29	5.69	0.40	6.5	2.94	0.49	57.6
FD	Fruit diameter (mm)	*fd1.1*	TG273			243	9.4	<0.0001	38.68	36.29	−2.39	9.0	5.04	−2.34	
		fd2.1	TG167-TG151*	6.9	4.0	242	26.8	<0.0001	39.71	35.63	−4.08	29.6	17.91	−4.26	
		fd8.1	TG330-CT265*	15.3	10.0	234	6.7	0.0001	38.51	36.50	−2.01	10.1	4.95	−2.48	41.4
PP	Fruit pericarp thickness (mm)	*fp2.1*	TG167-TG151*	6.9	4.0	242	23.5	<0.0001	5.85	5.01	−0.84	24.7	14.63	−0.85	
		fp8.1	TG176-CD40*	19.6	10.0	239	5.5	0.0002	5.62	5.21	−0.41	6.8	3.10	−0.45	
		fp8.2	TG330-CT265*	15.3	14.0	234	6.5	0.0001	5.62	5.19	−0.43	7.8	4.13	−0.48	
		fp10.1	u-CT234*	5.1	4.0	240	6.2	0.0001	5.60	5.19	−0.41	7.2	3.74	−0.46	42.3
FS	Fruit shape index (height/diameter)	*fs2.1*	TG377			221	5.5	0.0004	1.06	1.01	−0.05	5.7	2.92	−0.05	
		fs8.1	TG176-CD40*	19.6	18.0	217	26.8	<0.0001	1.09	0.99	−0.10	27.4	14.93	−0.10	33.4
LOCN	Locule number	*locn1.1*	CT191*-TG465	15.2	2.0	234	6.4	0.0001	2.61	2.43	−0.18	6.9	3.54	−0.19	
		locn3.1	TG242-TG214*	18.6	8.0	244	6.9	<0.0001	2.61	2.42	−0.19	9.8	4.70	−0.23	16.6
NSF	Number of seeds per fruit	*nsf4.1*	TG15A*-TG483	16.4	6.0	243	4.5	0.0008	91.57	84.39	−7.18	5.7	2.75	−7.95	
		(*nsf6.1*)	TG365*-*sp*	14.8	8.0	252	4.3	0.0009	84.52	91.47	6.95	5.7	2.78	7.96	
		nsf7.1	OPK8-TG342	3.0	2.0	244	5.0	0.0004	91.34	84.03	−7.31	5.2	2.83	−7.60	
		nsf12.1	TG68-CT211A*	21.0	18.0	237	6.0	0.0001	91.61	83.31	−8.30	7.4	3.61	−9.08	24.0
WTS	Weight of 1,000 seeds (gm)	*wts2.1*	TG308*-TG469	15.2	6.0	245	4.2	0.0013	2.52	2.39	−0.13	5.9	2.78	−0.16	
		wts4.1	CT157-CT178	17.5	8.0	245	15.1	<0.0001	2.59	2.34	−0.25	24.5	11.88	−0.32	
		(*wts10.1*)	CT16*-*u*	19.4	12.0	251	5.2	0.0003	2.38	2.53	0.15	6.8	3.12	0.17	
		(*wts12.1*)	TG68-CT211A*	21.0	18.0	236	3.9	0.002	2.40	2.53	0.13	5.2	2.63	0.15	37.2
ATW	Anther-tube width (mm)	*atw6.1*	TG99*-CT206	5.7	2.0	170	8.6	0.0001	2.95	2.72	−0.23	8.4	3.38	−0.22	
		atw7.1	TG20A*-TG128	17.6	6.0	183	10.0	<0.0001	2.90	2.67	−0.23	11.6	4.30	−0.25	15.9
ATL	Anther-tube length (mm)	*atl2.1*	TG151			177	7.6	0.0002	8.02	7.72	−0.30	6.5	2.69	−0.28	
		atl7.1	TG20A*-TG128	17.6	4.0	182	13.6	<0.0001	8.05	7.64	−0.41	17.5	6.22	−0.46	24.1
ATX	Anther-tube index (length/width)	(*atx2.1*)	TG308			180	6.9	0.0004	2.94	2.76	−0.18	6.6	2.72	−0.17	
		atx3.1	TG246			184	7.9	0.0001	2.76	2.95	0.19	8.0	3.34	0.19	12.2

Table 2 (Continued)

Trait	Description	QTL	MML	Interval length (cM)	QTL position (cM)	Regression						Interval mapping			
						Number of plants	R^2 %	*P* value	E/E means	E/PM means	E/PM − E/E	PVE	LOD	Phenotypic effect	Multilocus PVE
NFLT	Number of flowers per truss	*nflt3.1*	TG242*-TG124	16.6	6.0	252	14.3	<0.0001	6.63	7.70	1.07	17.7	9.35	1.19	
		nflt6.1	TG365-*sp**	14.8	14.0	247	16.6	<0.0001	6.53	7.70	1.17	15.1	8.89	1.11	
		nflt9.1	TG291-TG551*	18.1	10.0	253	6.4	<0.0001	6.84	7.55	0.71	9.5	4.42	0.88	45.0
DE	Days to emergence	*de1.1*	TG125*-TG70	12.5	2.0	255	8.0	<0.0001	8.84	7.52	−1.32	9.1	4.86	−1.41	
		de2.1	TG337*-TG492	6.0	4.0	250	8.2	<0.0001	8.84	7.49	−1.35	9.1	4.91	−1.41	
		(*de3.1*)	TG242*-TG214	16.6	4.0	252	4.4	0.0008	7.62	8.60	0.98	4.6	2.32	1.00	20.3
DTL	Days to third leaf	*dtl1.1*	TG125			255	7.6	<0.0001	18.95	17.18	−1.77	7.9	4.58	−1.79	
		dtl2.1	TG337*-TG492	6.0	2.0	250	8.3	<0.0001	18.99	17.15	−1.84	8.2	4.57	−1.83	
		(*dtl3.1*)	TG242*-TG214	16.6	2.0	252	6.1	0.0001	17.19	18.78	1.59	6.6	3.47	1.64	20.0
DFL	Days to first flower	*dfl1.1*	TG125			247	6.1	0.0001	66.91	62.88	−4.03	6.3	3.50	−4.05	
		dfl2.1	TG308-TG469*	15.2	8.0	242	12.4	<0.0001	67.67	61.94	−5.73	15.3	7.64	−6.30	20.7
DFR	Days to first fruit	*dfr2.1*	TG151*-TG154	4.4	2.0	192	6.6	0.0003	121.47	116.29	−5.18	7.2	3.08	−4.39	
		dfr4.1	CT157-CT178*	17.5	12.0	192	8.9	<0.0001	121.20	116.29	−4.91	11.9	4.25	−5.67	19.6
DR	Days to ripening	*dr2.1*	TG167	6.1	2.0	172	9.3	0.0001	48.98	47.04	−1.94	9.3	3.69	−1.93	
		dr8.1	CT92			174	10.3	<0.0001	48.88	46.87	−2.01	10.3	4.12	−2.02	
		dr9.1	TG291-TG551*	18.1	10.0	171	7.8	0.0002	48.68	46.91	−1.77	10.8	3.35	−2.07	27.9
PVH	Plant vertical height (cm)	*pvh2.1*	TG337-TG492*	6.0	4.0	241	5.4	0.0003	18.83	16.96	−1.87	6.2	3.25	−1.99	

the 2 QTLs explained 33.4% of the phenotypic variance. Both QTLs had effects in the direction expected based on the parental means, with the PM allele always giving smaller values for the fruit shape index, thereby indicating more spherical fruits.

Locule number (LOCN) LOCN was affected by 2 QTLs on chromosomes 1 (*locn1.1*) and 3 (*locn3.1*). Respective PVE values were 6.9% and 9.8%. When the 2 QTLs were fitted simultaneously they explained 16.6% of the phenotypic variation. Both QTLs had effects in the direction expected, the PM allele reducing the number of locules per fruit.

Number of seeds per fruit (NSF) A total of 4 highly significant QTLs of nearly equal effect were identified on chromosomes 4, 6, 7 and 12. The PVE values ranged from 5.2%, for *nsf7.1*, to 7.4%, for *nsf12.1*. Simultaneous fit of the 4 QTLs explained 24.0% of the phenotypic variation. One of the 4 QTLs, *nsf6.1*, had an allelic effect opposite of that predicted from the parental means. In this case, the PM allele increased the number of seeds per fruit.

Weight of one thousand seeds (WTS) Four QTLs for WTS were detected distributed on chromosomes 2,4,10 and 12. The most significant QTL, on chromosome 4, explained 24.5% of the phenotypic variance. When the 4 QTLs were fitted simultaneously they explained 37.2% of the phenotypic variation. Two QTLs, *wts10.1* and *wts12.1*, had effects opposite to that expected based on the parental means as the PM allele increased the weight of the seeds. The QTLs for seed weight appear to be independent of those controlling fruit weight.

Anther-tube width (ATW) Anther-tube width was affected by 2 QTLs on chromosomes 6 and 7 with PVE values of 8.4% and 11.6%, respectively. When the 2 QTLs were fitted simultaneously they explained 15.9% of the phenotypic variance. These QTLs had allelic effects in the direction expected, and the PM allele reduced the width of the anther tube by 0.22 and 0.25 mm, respectively.

Anther tube length (ATL) Two QTLs were found to influence ATL, *atl2.1*, on chromosome 2, and *atl7.1*, on chromosome 7, with respective PVE values of 6.5% and 17.5%. Simultaneous fit of the 2 QTLs explained 24.1% of the phenotypic variance. At both loci the PM allele reduced the length of the anther tube by 0.28 and 0.46 mm, respectively. The QTL *atl7.1* mapped at the same position as *atw7.1*, thereby, explaining part of the positive correlation coefficient calculated between ATW and ATL ($r = 0.35$; $P < 0.01$).

Anther-tube index (ATX) Two QTLs were detected for ATX distributed on chromosomes 2 and 3. For both QTLs the PVE values were lower than 10% and when fitted simultaneously they explained only 12.2% of the

total phenotypic variation. The QTL mapped to chromosome 2, *atx2.1*, had an allelic effect opposite of that predicted by the parental phenotypes.

Number of flowers per truss (NFLT) Three QTLs for NFLT were detected on chromosomes 3, 6 and 9. All 3 QTLs had moderate to large effects, with respective PVE values of 17.7%, 15.1% and 9.5%. Simultaneous fit of the 3 QTLs explained up to 45% of the total phenotypic variation. All QTLs had effects in the direction expected, with the PM allele always increasing the number of flowers per truss (by 0.9 to 1.2), adding to a total increase of 3.2 flowers per truss.

Days to emergence (DE) Three significant QTLs influencing DE were distributed on chromosomes 1, 2 and 3. None of the 3 QTLs had a PVE value greater than 10%, and when they were fitted simultaneously they explained 20.3% of the phenotypic variation. The QTL maped on chromosome 3, *de3.1*, had an effect opposite to that expected as the PM allele increased the number of days to emergence. For the other 2 QTLs the PM allele reduced the number of days to emergence by 1.4 days in both cases.

Days to third leaf (DTL) Three QTLs for DTL were detected on chromosomes 1, 2 and 3. The PVE values ranged from 6.6% for *dtl3.1* to 8.2% for *dtl2.1*. Simultaneous fit of the 3 QTLs explained 20% of the total phenotypic variation. All 3 QTLs shared very similar positions with the correspondent QTLs mapped for DE. This was in agreement with the high correlation coefficient ($r = 0.85$; $P < 0.01$) calculated between these two traits. The QTL mapped on chromosome 3 had an effect in the opposite direction, with the PM allele increasing the number of days to third leaf by 1.6 days; at the other 2 QTLs the PM allele reduced the number of days to third leaf by approximately 1.8 days.

Days to first flower (DFL) Two QTLs for DFL were detected on chromosomes 1 and 2, with respective PVE values of 6.3% and 15.3%. When fitted simultaneously, the 2 QTLs explained 20.7% of the phenotypic variance. Both QTLs exerted an effect in the direction expected, with the PM allele reducing the number of days to first flower by 4.1 and 6.3 days, respectively.

Days to first fruit (DFR) Two QTLs influencing DFR were mapped: *dfr2.1*, on chromosome 2, with a PVE value of 7.2%, and *dfr4.1*, on chromosome 4, with a PVE value of 11.9%. When the 2 QTLs were fitted simultaneously, they explained 19.6% of the phenotypic variation. Both QTLs had positive effects, the PM allele reducing the number of days to first fruit by 4.4 and 5.7 days, respectively.

Days to ripening (DR) Days to ripening was affected by 3 QTLs distributed on chromosomes 2, 8 and 9. The percentage of phenotypic variation explained ranged from 9.3% for *dr2.1* to 10.8% for *dr9.1*. Simultaneous fit of the 3 QTLs explained 27.9% of the phenotypic variation. For all these QTLs the PM allele had the expected effect, always reducing the number of days to ripening by 1.9 to 2.1 days, adding to a total reduction of 6 days.

Plant vertical height (PVH) One QTL was detected for PVH at the lower end of chromosome 2 that explained 6.2% of the phenotypic variance. The PM allele had positive effect, reducing the plant vertical height by 2 cm.

Number of QTLs

The number of QTLs detected for each trait in this study should be considered to be a minimum estimate for several reasons. (1) QTLs for which the recurrent parent has completely dominant alleles will not be detected in a BC_1 population. This may be especially relevant for traits like NSF, DE, DTL and DFL for which the F_1 and/or BC_1 data indicate a degree of dominance of the *L. esculentum* parent (Table 1; Fig. 2). (2) The experiment was conducted in a single environment. As previous results have demonstrated in tomato, QTLs are often only expressed under particular environmental conditions (Paterson et al. 1991). (3) The population size (257 plants) is insufficient to detect QTLs of small effect. For example, no QTL with a PVE value smaller than 4.0% was detected. (4) Because of the lack of polymorphism, a few regions of large gaps were left (e.g. CD57-CT52 on chromosome 7, CT283A-TG291 on chromosome 9 and TG111-CT156 on chromosome 12). Thus, QTLs affecting the traits under study, and located in those regions of the genome, may have gone undetected. (5) The stringent threshold chosen ($P = 0.001$; LOD = 2.4), while reducing the chance of Type-I errors (false positive), would lead to higher frequency of Type-II errors (not detecting valid QTLs).

Possible pleiotropic effects of major QTLs

Several regions of the genome clearly had effects on more than 1 trait (Fig. 1; Table 2). Such results may be due to the chance linkage of 2 or more QTLs or pleiotropic effects of a single gene on multiple traits. High-resolution linkage maps or the cloning of QTLs is required to definitively distinguish these two possibilities. However, based on the types of traits affected, one can infer whether linkage or pleiotropy is a more likely explanation.

Fruit traits The region characterized by the largest cluster of QTLs affecting fruit traits was found at the lower end of chromosome 2. These QTL exerted strong effects on FW, FC, FD, FP and somewhat lesser effects on other characters, including FS, DE, DTL, DFR, DR, ATL and PVH. Three of these traits, FW (fruit weight), FD (fruit diameter) and FP (pericarp thickness), have to

do with fruit morphology and were strongly correlated in general in the BC_1 population (Fig. 3). It seems likely that a single gene at the lower end of chromosome 2 is affecting all of these traits. For example, a gene reducing fruit size would also be likely to decrease fruit diameter and the thickness of the pericarp. The same logic can be applied to the cluster of QTLs affecting these same 3 traits at the lower end of chromosome 8. Likewise, *fw1.2* and *fd1.1*, near TG273 on chromosome 1, may be pleiotropic effects of a single gene. The *o* (*pr*) gene, which gives ovate- or pear-shaped fruit, has been mapped to the same region of chromosome 2 (Lindstrom 1927; MacArthur 1928; Tanksley et al. 1992). Several studies have shown that qualitative recessive mutant factors can further influence fruit size by modifying fruit shape or locule number or both (Lindstrom 1935; Yeager 1937). The *ovate* (*o*) gene that elongates the fruit tends to decrease the size, whereas the genes for *fasciation* (*f*) and *tangerine* (*t*) and those increasing locule number can increase fruit size (MacArthur and Butler 1938).

sp and growth habit The *sp* locus on chromosome 6 is a major gene affecting the growth habit of tomato (+/+ and +/*sp* = indeterminate; and *sp*/*sp* = determinate). Paterson et al. (1988, 1991) have shown that *sp* influences many traits. The interval containing *sp* in the E × PM cross was also found to contain major QTLs for FC, SSC and NFLT having a relatively lower effect on ATW and NSF. In the previous studies (Paterson et al. 1988, 1991), indeterminacy was associated with reduced fruit mass and high soluble solids. In contrast, in *L. esculentum* it has been found that indeterminacy can increase both traits (Emery and Munger 1970). It has been proposed that these divergent results could be explained by either a second, tightly linked locus or by unlinked modifier genes (Paterson et al. 1988). The fact that in the E × PM cross a major QTL for FW was not associated with the *sp* locus while a strong effect was still exerted on SSC could be considered as evidence that FW and SSC are controlled by two tightly linked genes, as opposed to the pleiotrpic effect of a single gene. In contrast, a pleiotropic effect of the indeterminate habit of growth on SSC and NFLT seems plausible. Indeterminacy implies prolonged vegetative growth, which increases the sources of carbohydrates available for the sinks (e.g. fruit). Consequently, fruits with increased SSC can be expected (Emergy and Munger 1970; Stevens and Rudich 1978). Also, prolonged growth potential applied to a reproductive bud can be expected to increase the number of flowers per truss (NFLT). Less clear is how the wild *sp* allele could have a pleiotropic effect on the color of the fruit, favoring a more intense coloration.

Positive and negative effects of QTLs

Since the first reports, QTL mapping studies have shown the power of marker linkage analysis to unmask hidden genetic variation (Tanksley et al. 1982; Paterson et al. 1988, 1991; Weller et al. 1988; Doebley and Stec 1991). Complementary QTLs with allelic effects opposite to that predicted by the parental phenotypes can explain the occurrence of transgressive phenotypes and provide a resource of new alleles for plant breeding (de Vicente and Tanksley 1993).

In the present study 11% of the detected QTLs had allelic effects opposite to those expected based on the parental phenotypes. This value may be compared with the 36% reported in another interspecific cross of tomato in which botanical traits were measured (de Vicente and Tanksley 1993). The current study, in contrast, was oriented toward horticultural traits which are likely to have been subjected to disruptive selection by breeders who fixed a higher proportion of favorable alleles in the cultivated counterpart. For horticultural traits, such as fruit weight, other studies have also reported that most of the QTLs were in the expected direction (Paterson et al. 1988, 1991). However, a number of QTLs with allelic effects opposite to those expected from the parental phenotypes were detected in this study. For example the *pimpinellifolium* allele increased the WTS for 2 of the 5 QTLs mapped for this trait (*wts10.1* and *wts12.1*). A higher number of seeds per fruit (NSF) was determined by the wild allele for 1 of the 4 QTLs mapped (*nsf6.1*). Alleles of opposite effect were also found for anther-tube index (*atx2.1*), days to emergence (*de3.1*) and days to third leaf (*dtl3.1*).

Epistasis between QTLs

Tests for two-loci interactions were performed between the markers associated with each of the 54 significant QTLs and all of the other segregating markers, for a total of 6,426 two-way tests. Consistent with previous QTL mapping studies conducted in other tomato crosses (Paterson et al. 1988, 1991; de Vicente and Tanksley 1993), only minimal evidence of epistasis was found: 5.9%, 1.12% and 0.11% of the pairwise tests were significant at $P \leqslant 0.05$, $P \leqslant 0.01$ and $P \leqslant 0.001$, respectively, which is close to the frequencies that would be expected by chance.

Comparison across species

QTL studies for fruit weight and soluble solids have been reported for several interspecific populations of tomato (Tanksley et al. 1982; Paterson et al. 1988, 1991; Eshed and Zamir 1995). Of the 11 QTLs detected for fruit weight in the *L. esculentum* × *L. cheesmanii* (CM) F_2 population, 3 shared similar positions with QTLs for the same trait mapped in the *L. esculentum* × *L. chmielewskii* (CL) BC_1 (Paterson et al. 1988, 1991). The current study of a *L. esculentum* × *L. pimpinellifolium* BC_1 confirms 2 of the 3 common QTLs for fruit mass (chromosome 1, *fw1.1*, and chromosome 11, *fw11.1*). However, in this case the QTL on chromosome 1 was resolved into 2

distinct QTLs, *fw1.1* and *fw1.2*, with the most likely positions being close to TG125 and TG273, respectively. This result might be attributed to higher recombination in this region for the E × PM BC_1 population than for those populations used by Paterson et al. (1988, 1991). The most significant fruit weight QTL (*fw2.2*) detected in our population was not detected in the E × CL BC_1 study (Paterson et al. 1988) but was detected in the E × CM F_2F_3 study (Paterson et al. 1991). However, it should be noted that in the CL study the map was not extended to the very end of chromosome 2, and the LOD scores showed an increase in association with the last marker for this chromosome (CD66). Analysis with additional markers at the end of chromosome 2 might have revealed the *fw2.2* QTL. In both previous studies a major QTL for fruit weight was detected near the *sp* locus on chromosome 6 (Paterson et al. 1988, 1991), yet this QTL was not detected in the E × PM population.

For soluble solids (SSC) 2 QTLs were considered to match between the CL BC_1 and the CM F_2/F_3 studies: 1 mapped to the centromeric region of chromosome 3 and the other near the *sp* locus at the lower end of chromosome 6. Both QTLs were also detected in the E × PM BC_1 population.

Fruit mass and seed weight have also been studied in the *L. pennellii* background by means of isozymes (Tanksley et al. 1982). At the time of that study only 12 markers were available that sparsely covered 9 of the 12 tomato chromosomes; nevertheless, some significant associations were found. *Pgm-2*, which maps close to CT157 on chromosome 4 (Tanksley et al. 1992), showed a significant effect on both fruit and seed weight. In the current study a significant QTL was detected in the same region for WTS. Similarly, on chromosome 8, *Aps-2* showed a highly significant association with seed weight and a weaker one with fruit weight. A QTL for FW, *fw8.1*, was mapped to this same region in the E × PM cross. Recently, a complete restriction fragment length polymorphism (RFLP) map has been used to localize yield-associated QTLs in an introgression line population of *L. pennellii* in the cultivated tomato (Eshed and Zamir 1995), and the results confirm at least 5 (*fw1.1*, *fw2.1*, *fw2.2*, *fw8.2* and *fw11.1*) of the 7 highly significant QTLs detected for fruit weight in the current study. Also for this population, the indeterminate growth habit, due to the presence of the wild allele at the *sp* locus on chromosome 6, was significantly associated with increased soluble solids. Interestingly, of the two overlapping introgression lines carrying the wild allele at the *sp* locus only one, (IL 6-2), showed a significant effect on fruit weight. These data clearly exclude the possibility of a pleiotropic effect of the indeterminate growth habit on fruit weight. However, IL 6-2 spanned a long interval of the chromosome and therefore it did not allow us to differentiate whether the gene affecting fruit weight is closely linked to the *sp* locus or is more distantly located.

Days to first flower (DFL) has also been studied in a *L. esculentum* × *L. pennellii* F_2 population (de Vicente and Tanksley 1993). Seven significant QTLs were reported, and only the one mapping to the lower end of chromosome 2 shares a similar position with *dfl2.1* mapped in the current study.

Major QTLs

For several traits a mode of inheritance was discerned in which 1 or more QTLs with relatively major effects (PVE > 15%) acted in concert with a variable number of smaller effect QTLs. Similar results have been reported in other QTL mapping studies (Paterson et al. 1988, 1991; Doebley and Stec 1991; de Vicente and Tanksley 1993). For example, in the present study a single region of chromosome 6 (overlapping *sp* locus), *ssc6.1*, accounted for 44% of the total phenotypic variation for SSC, while the other 2 significant QTLs explained no more than 8%. Likewise, fruit weight was affected by a minimum of 7 putative QTLs with only 1 (*fw2.2*) exerting a major effect (30% of the phenotypic variation); the other 6 loci all explained less than 10%.

Cumulatively, these results weaken the theory that quantitative traits are determined by numerous loci with small individual phenotypic effect (Lande 1983). From an evolutionary point of view, both the number of genes determining a character and the relative magnitude of their effects are important factors since the time required for selection to fix a new phenotype can vary greatly depending on the combination of the two factors. In the case of many genes with small effects, one would expect continuous and gradual gene mutations followed by recombination events to be responsible for the overall changes occurring between wild and cultivated forms. If major genes can act together with a variable number of minor genes, then mutations with a large effect might have played an important role in the evolutionary process, likely causing periods of rapid changes to be alternated with periods of more gradual changes.

The derivation of the cultivated tomato from its wild relatives was undoubtedly accompanied by changes in a number of morphological traits, the most notable of which being an increase in the size of the fruit, the organ utilized by humans. The immediate wild ancestor of the cultivated tomato is not known with certainty. However, *L. pimpinellifolium* is the most closely related wild species and is considered to be a possible progenitor of the cultivated tomato by some (Luckwill 1943; Rick 1976). This wild species can be easily crossed with tomato to produce highly fertile F_1 hybrids (Humphrey 1937).

Several studies have shown that the inheritance of size differences in tomato fruit is complex (Fogle and Currence 1950; Powers et al. 1950; Powers 1955). Breeding experiments suggest that a relatively small number of loci affect this traits. The large fruit size of *L. esculentum* cultivars was restored after a cross with *L. pimpinellifolium* followed by only three generations of backcrossing and selection (Rick 1976). Stubbe (1971) dem-

onstrated that it is possible, by only five successive steps of induced mutations and selection, to increase fruit size in *L. pimpinellifolium* to a level comparable with that of small-fruited cultivars. He also observed stepwise changes of the vegetative organs toward the anatomy of *L. esculentum*, and similar progress was reported in the reverse direction, in reducing the fruit size of *L. esculentum* cultivars toward that of *L. pimpinellifolium*. QTL studies support the oligogenic model for the differentiation of fruit size from that of the wild to that of the cultivated tomato. The current study shows that 1 of those loci, *fw2.2*, is a major determinate of fruit size, controlling approximately 30% of the phenotypic variation in a BC_1 generation. Rare large-fruited alleles at the *fw2.2* locus are likely to have been visually detectable by early humans and to have been fixed by strong selective pressure. Similar major QTL variation is thought to have been involved in the domestication of maize (Doebley et al. 1994), cowpea and mung bean (Fatokun et al. 1992).

The small-fruited wild species *L. pimpinellifolium* is also characterized by smaller flower size than the cultivated tomato. Interestingly, only one of the significant QTLs mapped in the current study for ATW and ATL shared similar positions with those found for fruit size. This suggests that independent evolutionary paths might have been involved in the increased sizes of the two interrelated plant organs.

Implications for crop improvement

Domestication of crop species from their wild relatives and the intense breeding of crop varieties by modern science has resulted in very limited genetic variation among modern cultivars (Simmonds 1976; Ladizinsky 1985). This problem is especially acute in self-pollinated crops where the level of genetic variation in cultivated varieties often drops below 5% of that available in nature (Miller and Tanksley 1990; Wang et al. 1992).

Wild and unadapted germplasm represent a rich source of variation that could be efficiently exploited by means of the newly available molecular techniques. Molecular markers can counter the negative consequences of linkage drag and can detect valuable alleles contributed by wild and unadapted species, even when hidden in unfavorable phenotypes (Paterson et al. 1988, 1991; Weller et al. 1988; Tanksley et al. 1989; de Vicente and Tanksley 1993). In the current study QTL alleles from *L. pimpinellifolium* were detected that might be valuable in breeding for both the processing industry and the fresh market tomato industry. A few examples are given below.

The quality of tomatoes for processing is determined mainly by total solids content, color, pH and firmness. Soluble solids directly influence flavor and the degree of concentration required to manufacture products (e.g. pulp and paste) whose standards of quality are determined by solids content. Thus, one of the main goals of tomato breeders is to develop cultivars with a higher fruit solids contents. Considerable genotypic variation in solids exists within *L. esculentum* and its wild relatives. Lambeth et al. (1966) surveyed the soluble solids content of 175 *L. esculentum* lines and 25 *L. pimpinellifolium* lines and found soluble solids ranging from 4.1% to 8.9% and 4.9% to 9.2% respectively. Even higher values can be found among certain green-fruited species, though these tend to be avoided in tomato breeding programs because of sterility problems and other undesirable genes. Rick (1974) developed high-sugars lines from an interspecific cross between a commercial cultivar and *L. chmielewskii*. The *L. pimpinellifolium* accession (LA1589) used in the current study had a mean value of 8.2 °Brix, significantly higher than the average 4.5 °Brix of the cultivated counterparts. The major QTL, *ssc6.1*, found for this trait is unlikely to be useful in breeding since it is probably a pleiotropic effect of the gene for the indeterminate growth habit (*sp*/+). Indeterminate growth is an undesirable character in processing tomatoes. However, the other 2 significant QTLs for this trait, *ssc3.1* and *ssc9.1*, are both of potential breeding interest since the PM allele apparently increases soluble solids content with little or no effect on fruit size. In order to define the real value of these QTLs to improve solids content of modern cultivars, they need to be tested in different genetic backgrounds and environments as well as in combination with yield and other fruit quality characters (Tanksley and Hewitt 1988).

Among other quality requirements, the fresh market demands large, round fruits. The current study revealed a major QTL affecting fruit shape, *fs8.1* (PVE = 27.4%). The *L. pimpinellifolium* alle for *fs8.1* is able to convert a blocky-shaped fruit (FS = 1.12) to a round fruit (FS = 1.0) without any major undesirable effect on fruit size. This QTL could thus be used to convert blocky-shaped processing tomato types to round fresh market types.

Earliness in tomato cultivars is very desirable especially in order to extend the production period in short-season area. However, a negative correlation between earliness and fruit weight is generally found (Pierce and Currence 1959; Khalf-Allah and Pierce 1963, 1964; Banerjee and Kalloo 1989). Recently, Lindhout et al. (1994) found markers for 3 loci associated with earliness in tomato; 2 of them, however, resulted also in a reduction in fruit weight. The authors explained these data as likely being due to pleiotropic effects. The earliness QTL associated with fruit ripening time mapped at the lower end of chromosome 2. Interestingly, this region was introgressed from *L. pimpinellifolium* and explained 4% of the earliness variation and 21% of the fruit weight variation. These data are in agreement with the results obtained in the current study since *dr2.1* explained 9% of the variation in days to fruit ripening and was associated with the fruit weight QTL, *fw2.2*, which explained 32% of the fruit weight variation of the BC_1. The clustering of these 2 QTLs is likely due to the

pleiotropic effects of a single gene on both traits, and thus *dr2.1* may be of little breeding value. Three QTLs were detected which affect different stages of earliness but which had no detectable effect on fruit size. The *L. pimpinellifolium* allele for *de1.1* caused a significant reduction in days to emergence and appears also to have favorable pleiotropic effects on DTL and DFL, with only a minor effect on fruit size. The *L. pimpinellifolium* allele for *dfr4.1* resulted in a significant reduction in the days to first fruit with no detectable effect on fruit weight. Finally, *dr9.1* explained 11% of the variation for days to ripening, with no significant effect on fruit weight and with significant favorable effect on soluble solids.

QTL mapping studies extended to a wider range of tomato wild relatives are allowing the detection of common key QTLs affecting quantitative traits of agronomic importance. For some characters, such as fruit weight, the analysis has already been conducted on several wild relatives. To date at least two regions of the genome, corresponding to *fw1.1* and *fw11.1*, seem to affect the same trait in a minimum of four wild species: *L. pennellii*, *L. cheesmanii*, *L. chmielewskii* and *L. pimpinellifolium*. The major QTL mapped in the present study, *fw2.2*, has potential orthologous counterparts in at least other two wild relatives: *L. pennellii* and *L. cheesmanii*. Common QTLs from different species that affect the same character and that have been tested in different localities and diffeent population structures represent ideal targets for molecular marker-assisted selection as well as for the establishment of QTL-NILs (near-isogenic lines) that could be utilized in the characterization, fine mapping and ultimate map-based cloning.

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References

Banerjee MK, Kalloo (1989) The inheritance of earliness and fruit weight in crosses between cultivated tomatoes and two wild species of *Lycopersicon*. Plant Breed 102:148–152

Bonierbale MW, Plaisted RL, Pineda O, Tanksley SD (1994) QTL analysis of trichome-mediated insect resistance in potato. Theor Appl Genet 87:973–987

de Vicente MC, Tanksley SD (1993) QTL analysis of transgressive segregation in an interspecific tomato cross. Genetics 134: 585–596

Doebley J, Stec A (1991) Genetic analysis of the morphological differences between maize and teosinte. Genetics 129:285–295

Doebley J, Bacigalupo A, Stec A (1994) Inheritance of kernel weight in two maize-teosinte hybrid populations: implications for crop evolution. J Hered 85:191–195

East EM (1915) Studies on size inheritance in Nicotiana. Genetics 1:164–176

Edwards MD, Stuber CW, Wendel JF (1987) Molecular-marker-facilitated investigations of quantitative-trait loci in maize. I. Numbers, genomic distribution and types of gene action. Genetics 116:113–125

Emery GC, Munger HM (1970) Effect of inherited differences in growth habit on fruit size and soluble solids in tomato. J Am Soc Hortic Sci 95:410–412

Eshed Y, Zamir D (1995) An introgression line population of *Lycopersicon pennellii* in the cultivated tomato enables the identification and fine mapping of yield associated QTLs. Genetics 141:1147–1162

Fatokun CA, Menancio-Hautea DI, Danesh D, Young ND (1992) Evidence for orthologous seed weight genes in cowpea and mung bean based on RFLP mapping. Genetics 132:841–846

Fogle HW, Currence TM (1950) Inheritance of fruit weight and earliness in a tomato cross. Genetics 35:363–380

Geldermann H (1975) Investigations on inheritance of quantitative characters in animals by gene markers. I. Methods. Theor Appl Genet 46:319–330

Goldenberg JB, von der Pahleen A (1966) Genetic and phenotypic correlation between weight and dry matter content of tomato fruits and their heritabilities. Bol Genet 2:1–15

Grandillo S, Tanksley SD (1996) Genetic analysis of RFLPs, GATA microsatellites and RAPDs in a cross between *L. esculentum* and *L. pimpinellifolium*. Theor Appl Genet 92:957–965

Hayes PM, Blake TK, Chen THH, Tragoonrung S, Chen F, Pan A, Liu B (1993) Quantitative trait loci on barley (*Hordeum vulgare*) chromosome 7 associated with components of winter hardiness. Genome 36:66–71

Houghtaling HB (1935) A developmental analysis of size and shape in tomato fruits. Bull Torrey Bot Club 62:243–252

Humphrey LM (1937) A cytological and morphological analysis of tomato species. Cytologia 8:306–318

Ibarbia EA, Lambeth VN (1969) Inheritance of soluble solids in a large/small-fruited tomato cross. J Am Soc Hortic Sci 94:496–498

Ibarbia EA, Lambeth VN (1971) Tomato fruit size and quality interrelationships. J Am Soc Hortic Sci 96:199–201

Johanssen W (1909) Elemente der exakten Erblichkeitslehre. Fisher, Jena

Khalf-Allah AM, Pierce LC (1963) A comparison of selection methods for improving earliness, fruit size and yield in the tomato. Proc Am Soc Hortic Sci 82:414–419

Khalf-Allah AM, Pierce LC (1964) The effect of sib-mating on variation and selection of quantitative characters in the tomato. Proc Am Soc Hortic Sci 85:471–477

Keim P, Diers BW, Olson TC, Shoemaker RC (1990) RFLP mapping in soybean: association between marker loci and variation in quantitative traits. Genetics 126:735–742

Kemble JM, Gardner RG (1992) Inheritance of shortened fruit maturation in the cherry tomato Cornell 871213-1 and its relation to fruit size and other components of earliness. J Am Soc Hortic Sci 117:646–650

Kosambi DD (1944) The estimation of map distances from recombination values. Ann Eugen 12:172–175

Ladizinsky G (1985) Founder effect in crop-plant evolution. Econ Bot 39:191–199

Lambeth VN, Straten EF, Fields ML (1966) Fruit quality attributes of 250 foreign and domestic tomato accessions. Mo Res Bull 908

Lande R (1983) The response to selection on major and minor mutations affecting a metrical trait. Heredity 50:47–65

Lander ES, Botstein D (1989) Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121: 185–199

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Leonards-Schippers C, Gieffers W, Schäfer-Pregl R, Ritter E, Knapp SJ, Salamini F, Gebhardt C (1994) Quantitative resistance to *Phytophtora infestans* in potato: a case study for QTL mapping in an allogamous plant species. Genetics 137:67–77

Lincoln S, Daly M, Lander E (1992) Mapping genes controlling quantitative traits with MAPMAKER/QTL 1.1 Whitehead Institute Technical Report, 2nd edn

Lindhout P, Van Heusden S, Pet G, Van Ooijen JW, Sandbrink H, Verkerk R, Vrielink R, Zabel P (1994) Perspectives of molecular marker assisted breeding for earliness in tomato. Euphytica 79: 279–286

Lindstrom EW (1927) The inheritance of ovate and related shapes of tomato fruits. J Agric Res 34: 961–985

Lindstrom EW (1935) Segregation of quantitative genes in tetraploid tomato hybrids as evidence for dominance relations of size characters. Genetics 20: 1–11

Luckwill LC (1943) The genus *Lycopersicon*, an historical, biological, and taxonomic survey of the wild and cultivated tomatoes. Aberdeen University Studies, Scotland, No. 120

MacArthur JW (1928) Linkage studies with the tomato II. Three linkage groups. Genetics 13:410–420

MacArthur JW, L Butler (1938) Size inheritance and geometric growth processes in the tomato fruit. Genetics 23:253–268

Manly KF (1993) A Macintosh program for storage and analysis of experimental genetic mapping data. Mamm Genome 4: 303–313

Martin B, Nienhuis J, King G, Schaefer A (1989) Restriction fragment length polymorphism associated with water use efficiency in tomato. Science 243:1725–1728

Miller JC, Tanksley SD (1990) RFLP analysis of phylogenetic relationships and genetic variation in the genus *Lycopersicon*. Theor Appl Genet 80:437–448

Nelson CJ (1994) Molecular mapping in bread wheat. PhD thesis. Cornell University. Ithaca, N.Y.

Nienhuis J, Helentjaris T, Slocum M, Ruggero B, Schaefer A (1987) Restriction fragment length polymorphism analysis of loci associated with insect resistance in tomato. Crop Sci 27:797–803

Nilsson-Ehle H (1909) Kreuzunguntersuchungen an Hafer und Weizen. Lunds. Univ Aarskz NF 5:1–122

Paterson AH, Lander ES, Hewitt JD, Peterson S, Lincoln SE, Tanksley SD (1988) Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. Nature 335:721–726

Paterson AH, DeVerna JW, Lanini B, Tanksley SD (1990) Fine mapping of quantitative trait loci using selected overlapping recombinant chromosomes, in an interspecies cross of tomato. Genetics 124:735–742

Paterson AH, Damon S, Hewitt JD, Zamir D, Rabinovitch HD, Lincoln SE, Lander ES, Tanksley SD (1991) Mendelian factors underlying quantitative traits in tomato: comparison across species, generations, and environments. Genetics 127:181–197

Pierce LC, Currence TM (1959) The efficiency of selecting for earliness, yield, and fruit size in a tomato cross. Proc Am Soc Hortic Sci 73:294–304

Powers L (1955) Components of variance method and partitioning method of genetic analysis applied to weight per fruit of tomato hybrid and parental populations. US Dep Agric Tech Bull 1131:1–64

Powers L, Locke LF, Garret JC (1950) Partitioning method of genetic analysis applied to quantitative characters of tomato crosses. US Dep Agric Tech Bull 998:1–56

Rick CM (1958) The role of natural hybridization in the derivation of cultivated tomatoes in western South America. Econ Bot 12: 346–367

Rick CM (1974) High soluble-solids content in large-fruited tomato lines derived from a wild green-fruited species. Higardia 42:493–510

Rick CM (1976) Tomato *Lycopersicon esculentum* (Solanaceae). In: Simmonds NW (ed) Evolution of crop plants. Longman, London, pp 268–273

Rick CM (1982) The Potential of exotic germplasm for tomato improvement. In: Vasil IK, Scowcroft WR, Frey KJ (eds) Plant improvement and somatic cell genetics. Academic Press, New York, pp 478–495

SAS Institute (1988) SAS users guide: statistics. SAS Institute, Cary, N.C.

SAS Institute (1989) JMP users guide: Version 3.0 of JMP. SAS Institute, Cary, N.C.

Schön CC, Melchinger AE, Boppenmaier J, Brunklaus-Jung E, Herrmann RG, Seitzer JF (1994) RFLP mapping in maize: quantitative trait loci affecting testcross performance of elite European flint lines. Crop Sci 34:378–389

Simmonds NW (1976) Evolution of crop plants. Longman, London New York

Stevens MA, Rudich J (1978) Genetic potential for overcoming physiological limitations on adaptability, yield, and quality in the tomato. Hortic Sci 13:673–678

Stubbe H (1971) Weitere evolutionsgenetische Unterschungen in der Gattung *Lycopersicon*. Biol Zbl 90:545–559

Stuber CW, Edwards MD, Wendel JF (1987) Molecular marker-facilitated investigations of quantitative trait loci in maize. II. Factors influencing yield and its component traits. Crop Sci 27:639–648

Stuber CW, Lincoln SE, Wolff DW, Helentjaris T, Lander ES (1992) Identification of genetic factors contributing to heterosis in a hybrid from two elite maize inbred lines using molecular markers. Genetics 132:823–839

Tanksley SD (1993) Mapping polygenes. Annu Rev Genet 27: 205–233

Tanksley SD, Hewitt J (1988) Use of molecular markers in breeding for soluble solids in tomato–a re-examination. Theor Appl Genet (1988) 75:811–823

Tanksley SD, Medina-Filho H, Rick CM (1982) Use of naturally-occurring enzyme variation to detect and map genes controlling quantitative traits in an interspecific backcross of tomato. Heredity 49:11–25

Tanksley SD, Ganal MW, Prince JP, de Vicente MC, Bonierbale MW, Broun P, Fulton TM, Giovannoni JJ, Grandillo S, Martin GB, Messeguer R, Miller JC, Miller L, Paterson AH, Pineda O, Röder MS, Wing RA, Wu W, Young ND (1992) High-density molecular linkage maps of the tomato and potato genomes. Genetics 132:1141–1160

Wang G, Mackill DJ, Bonman JM, McCouch SR, Champoux MC, Nelson RJ (1994) RFLP mapping of genes conferring complete and partial resistance to blast in a durably resistant rice cultivar. Genetics 136:1421–1434

Wang ZY, Second G, Tanksley SD (1992) Polymorphism and phylogenetic relationships among species in the genus *Oryzae* as determined by analysis of nuclear RFLPs. Theor Appl Genet 83:565–581

Weller JI, Soller M, Brody T (1988). Linkage analysis of quantitative traits in an interspecific cross of tomato (*Lycopersicon esculentum* × *Lycopersicon pimpinellifolium*) by means of genetic markers. Genetics 118:329–339

Yeager AF (1937) Studies on the inheritance and development of fruit size and shape in the tomato. J Agric Res 55:141–152