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Advanced backcross QTL analysis of a *Lycopersicon esculentum* × *Lycopersicon parviflorum* cross

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Abstract *Lycopersicon parviflorum* is a sexually compatible, wild tomato species which has been largely unutilized in tomato breeding. The Advanced Backcross QTL (AB-QTL) strategy was used to explore this genome for QTLs affecting traits of agronomic importance in an interspecific cross between a tomato elite processing inbred, *Lycopersicon esculentum* E6203, and the wild species *L. parviflorum* (LA2133). A total of 170 BC2 plants were genotyped by means of 133 genetic markers (131 RFLPs; one PCR-based marker, *I-2*, and one morphological marker, *u*, uniform ripening). Approximately 170 BC3 families were grown in replicated field trials, in California, Spain and Israel, and were scored for 30 horticultural traits. Significant putative QTLs were identified for all traits, for a total of 199 QTLs, ranging from 1 to 19 QTLs detected for each trait. For 19 (70%) traits (excluding traits for which effects of either direction are not necessarily favourable or unfavourable) at least one QTL was identified for which the *L. parviflorum* allele was associated with an agronomically favourable effect, despite the overall inferior phenotype of the wild species.

Key words Molecular breeding · Germplasm utilization · *L. parviflorum* · Quantitative trait loci · Tomato · Introgression

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Introduction

The Advanced Backcross QTL mapping strategy was proposed several years ago as a new molecular breeding method, based on QTL mapping, that can integrate the process of QTL analysis and variety development while exploiting the full potential of genetic variation available in unadapted germplasm for the improvement of quantitative traits (Tanksley and Nelson 1996). This strategy uses molecular markers to identify beneficial alleles, from unadapted germplasm, that are potentially valuable for the improvement of the agronomic performance of elite cultivated lines. These QTL alleles are simultaneously transferred into near-isogenic lines (NILs) which are then field-tested in replicated trials.

The need for the development of the AB-QTL methodology was justified by several considerations. First, despite the fact that QTLs have been mapped in many different plant species and for many different traits, no systematic effort has been invested in the generation of improved varieties. Second, breeders have used unadapted germplasm almost exclusively as a source of major genes for disease and insect resistances, and have mostly relied on repeated intercrossing of adapted elite genotypes for the improvement of quantitative traits, like yield and quality. This has led to the narrow genetic-basis characteristic of many crops, particularly of self-pollinated crops including tomato and rice (Ladizinsky 1985; Miller and Tanksley 1990; Wang et al. 1992), which now represents a serious threat for future genetic improvements of modern varieties. The major reasons for such a limited use of wild germplasm are the undesir-

able effects often associated with introgressed segments, and the fact that much of the wild germplasm is phenotypically inferior to modern cultivars for many of the quantitative traits that breeders would like to improve.

The development of molecular technology and of the derived molecular maps have provided effective tools to overcome both limitations; in fact, using genetic markers, pleiotropy can often be distinguished from close linkage, and recombinants can be identified in which close linkages are broken, reducing the deleterious effects of genetic drag. Moreover, QTL mapping studies have shown that, despite their inferior phenotypes, wild species are likely to contain QTLs that can substantially increase the yield and the quality of elite cultivars (de Vicente and Tanksley 1993; Eshed and Zamir 1995).

The AB-QTL strategy has so far been tested in tomato (Tanksley et al. 1996; Fulton et al. 1997a, b; Bernacchi et al. 1998a, b), rice (Xiao et al. 1996, 1998) and maize (McCouch SR, personal communication). In each case, QTLs from the wild species have been identified which are capable of substantially increasing the quality or productivity of the cultivated species. The most extensive experiments have been conducted in tomato, where populations involving crosses with five wild *Lycopersicon* species (*L. pimpinellifolium* LA1589, *L. peruvianum* LA1708, *L. hirsutum* LA1777, *L. parviflorum* LA2133 and *L. pennellii* LA1657) have been field and laboratory tested in a number of locations around the world. The five wild accessions were chosen to represent a cross section of the genetic-distance ranges within the tomato genus based on both morpho/taxonomic data (Rick 1979) and DNA-marker based phylogenetic studies (Miller and Tanksley 1990). This was done with the purpose of increasing the probability of identifying a high proportion of new and useful QTLs in each separate study.

Results for the first three wild accessions have already been documented by Tanksley et al. (1996), Fulton et al. (1997b) and Bernacchi et al. (1998a, b), respectively. Here we report on the AB-QTL analysis conducted in tomato using the wild species *Lycopersicon parviflorum* (LA2133) as the donor parent.

L. parviflorum is a green-fruited wild species of tomato, characterised by small fruit (<1 cm in diameter), small flowers and small, relatively simple leaves carried on slender stems. Morphologically it is similar to *Lycopersicon chmielewskii*, though its flowers are much smaller. The species can be reciprocally hybridised with the cultivated tomato without having to overcome any major interspecific barriers. However, despite the relative ease of crossability with the cultivated tomato, *L. parviflorum* has not been extensively exploited by plant breeders, due in part to its comparatively recent discovery (Rick et al. 1976).

To our knowledge, this represents the first report of an extensive genetic study conducted on an interspecific tomato cross involving the wild species *L. parviflorum*.

Materials and methods

Population development

A backcross population was developed using the open-pollinated processing inbred *Lycopersicon esculentum* (E6203) (hereafter referred to as E) as the recurrent parent, and the wild species, *L. parviflorum* (LA2133) (hereafter referred to as PF), as the donor parent.

A total of 50 BC1 plants were genotyped with the RFLP marker TG279 to select for homozygous *esculentum* alleles at the *sp* locus on chromosome 6. This selects for a determinate growth habit, an essential requirement for field evaluations. One hundred and seventy selected BC2 plants, derived from eight fertile determinate BC1 plants, were grown in the greenhouse at Ithaca during the summer of 1995. These were backcrossed as females to E, and BC3 seed was collected for the later field testing of horticultural traits in the summer of 1996.

RFLP analysis

Procedures for DNA extraction, restriction enzyme digests and Southern blotting were as described in Bernatzky and Tanksley (1986). DNA from the two parents of the cross, E×PF, was surveyed for polymorphisms using the restriction enzymes *Eco*RI and *Hin*dIII. RFLP markers selected from a high-density tomato map (Tanksley et al. 1992) at 3-cM intervals were labeled by primer extension (Feinberg and Vogelstein 1983), hybridised, and washed to a stringency of 0.5×SSC at 65°C. Approximately 400 RFLP markers were surveyed, and 50% of them detected polymorphism between the two parental species. A subset of 131 polymorphic RFLPs covering the entire tomato genome was selected to genotype the 170 BC2 plants, along with one PCR-based marker, *I2*, and one morphological marker, *u*, uniform ripening.

Field evaluations

One hundred and seventy families of BC3 plants (derived from the 170 BC2 plants) were grown in the summer of 1996 in Woodland, California (CA), Badajoz, Spain (SP), and Akko, Israel (IS). Experiments were arranged in randomised plots of 30 plants each, along with six plots of *L. esculentum* cv E6203 as controls. In Israel, BC3S1 seed was bulk-harvested from each plot and saved for the future selection of QTL-NILs.

Trait evaluations

A total of 30 agronomic traits were evaluated for each plot in one or more locations; 18 of the traits were measured in three locations, CA, SP and IS; in addition, fruit weight was measured at Cornell University (CU) in the BC2 population. Details of trait evaluations are given below.

Yield. Yield was assessed in SP and IS, as the total weight (kg) of all the fruit taken from the plot and in CA as the total weight of the fruit from five plants only. *Total yield* (YLD) was then partitioned into *red yield* (RDY) (the weight of only the ripe red fruit), and green yield (only the green fruit). Total yield in all cases refers to all fruit (red and green), whereas red yield refers to red fruit only. Green yield was not analyzed due to the small number of data points.

Fruit weight (FW). Fruit weight is an average weight per fruit, and in CA, SP and IS it was determined from a random sample of 40 or more ripe fruits per plot. At CU this trait was measured as an average weight of ten or more ripe fruits per plant.

Fruit viscosity. *Viscosity* (BOS) was measured only in CA and SP. A modified Bostwick was utilized on pulped canned samples, with the viscosity measurement being expressed in cm of migration over a 30-s period at 25°C. A low value indicates high viscosity (desirable). In CA the Ostwald, *viscosity of the serum* (OST) was also measured.

Soluble-solids content (BRX). Total soluble-solids in tomato fruit are comprised mainly of sugars and, to a lesser extent, organic acids; this characteristic is an important parameter for the tomato processing industry. The soluble solids content was measured in all three locations by means of a refractometer (Brix°) as described in Tanksley et al. (1996).

*Brix*red yield* (BRY). This parameter was derived as the product of the brix reading multiplied by the red yield. In tomato there is often a negative relationship between total fruit yield and soluble-solids concentration (Stevens and Rudich 1978); therefore brix*red yield provides a better estimate of the amount of processed product (e.g., catsup, paste) that can be expected from a plot.

Yellow (YEL). Yellow was scored as a nominal trait, and only in CA. A plot showing no yellow fruit was scored as ”1” and a plot containing some plants producing yellow or yellow-orange fruit was scored as ”2”.

Fruit color. Fruit color was measured in several different ways. In all locations, *external fruit color* (EC) was determined visually at the time of harvest, on 10–40 ripe fruits from each plot (using a scale of one to five, 1=low color, 5=intense red color); the same fruits were then sliced open transversely and scored for *internal fruit color* (IC) in the same manner. In addition, spectrophotometer color measurements were made on raw de-aerated puree ”*fruit color, lab*” (FC) using an Agtron (LA/B) in California, and a Gardner Colorgard (A/B) in Spain. Lower Agtron (LA/B) readings indicate a more intense red color, whereas a higher A/B reading indicates less intense red color. In IS, the color of the gel inside the fruit, *internal gel color* (GEL), was also evaluated, and scored as 1, green gel, or 2, red gel (desirable).

Lycopene (LYC) and *b-carotene* (BC). These were measured in parts per million (ppm), only in CA, on the same fruits used for internal color measurements.

Stem scar (SCR). The size of the stem scar on the fruit was given a score of 1 (small scar, desirable) to 5 (large scar), and was evaluated in all three locations.

Epidermal reticulation (ER). Epidermal reticulation of the fruit was evaluated only in SP, and was scored as a nominal trait. Plots with normal skinned fruit were scored as 1 and plots containing fruit with reticulated, melon-like skin were scored as 2.

Shoulders (SHD). This trait was measured only in IS, on at least 40 ripe fruits, as the degree of uneven color in ripe fruit cut transversely near the stem end. A value of 1 indicates much mottled coloring (undesirable) and a value of 5 indicates little or no mottling (desirable).

Stem release (STR). The release of the flower peduncles from mature fruit is a desirable character in processing tomatoes since stems puncture other fruit during harvest and transport. This trait was measured only in SP and IS, as the proportion of harvested ripe fruit releasing the stem.

Fruit shape (FS). Fruit shape was evaluated visually, on at least 40 fruits per plot, as round (score=1), blocky (score=2), or long (score=3). Processing tomatoes are typically blocky shaped.

Fruit firmness (FIR). Fruit firmness was evaluated in all three locations subjectively by hand squeezing of at least ten fully ripe fruits per plot and given a numerical rating of 1 (soft) to 5 (very firm).

Total acids and pH. *Total acids* (TA) and *total organic acids* (TOA) were measured only in CA, whereas *fruit pH* (pH) was measured in all three locations. In all instances the measurements were made on the same samples used to determine the soluble-solids content (see above).

Maturity (MAT). Maturity was evaluated in CA, SP and IS, by a visual assessment of the percentage of fruit mature on the day of harvest using a visual scale of 1 to 5 (1=early, 5=late).

Horticultural acceptability (HA). The overall appearance of the plot as compared to a plot of the recurrent parent control (E6203) was evaluated as horticultural acceptability, only in CA. A score of 1 indicates very unacceptable, a score of 5 is highly acceptable.

Cover (CVR). Cover refers to the degree to which fruits are protected from the sun by the leaves, and was estimated visually in all three locations using a scale of 1 to 5 (1=poor cover, 5=good cover).

Internal core (COR). The size of the internal core of the fruit was evaluated only in CA and was scored on a rating of 1 (small, desirable) to 5 (large, undesirable).

Puffiness (PUF). Puffiness indicates the amount of free air space observed in the locules of transversely cut fresh fruit. The trait was evaluated in all three locations on at least ten fresh fruits, using a visual scale of 1–5 (1=no air/not puffy, 5=very puffy) in CA and SP, and using an inverse scale in IS (data taken by local collaborators).

Pericarp thickness (PCP). The thickness of the fruit wall (pericarp) was evaluated at all three locations, scored on a scale of 1 (thin wall) to 5 (thick wall).

Veins (VNS). This trait was evaluated only in CA and IS. It refers to the amount of white vascular veins visible in ripe fruit cut transversely. It was evaluated on ten ripe fruits, using a visual scale of 1–5: 1=much venation visible (undesirable) and 5=little or no venation visible (desirable) in Israel, and using an inverse scale in CA.

Data analysis

Trait correlations

Pearson correlation coefficients were calculated for each trait/location combination based on BC3 field data using the QGene software package (Nelson 1997).

Linkage analysis

The commands ”group” and ”ripple” (LOD 3.0) of Mapmaker (Lander et al. 1987) were used to establish a linear order of markers in each linkage group of the BC2. Recombination in Kosambi units was computed by QGene (Kosambi 1944; Nelson 1997).

QTL analysis

For traits scored as continuous variables, single-point regressions were employed to determine the effect of each marker on each trait measured on the BC3 plots using QGene, a program developed for QTL analysis (Nelson 1997). Traits scored as ordered categories (e.g., on a scale of 1 to 5), rather than as continuously distributed values, were analyzed using Kendall’s Tau, and traits scored as nominal (e.g., as 1 or 2 only) were analyzed by chi-square. Each trait/location combination was treated separately.

Regions of the genome were identified as putatively containing a QTL if the results met one or more of the following criteria: a significant effect was observed for a single marker/trait combination at a single location with $P<0.001$; significant effects were observed, in the same direction (i.e., either all positive effects or all negative effects) for a marker/trait combination at two or more locations with $P<0.01$; significant effects were observed, in the same direction, for a marker/trait combination at three or more locations with $P<0.1$.

The percent phenotypic variance (%PV) associated with each significant QTL was calculated from the regressions of each marker/phenotype combination. The percent phenotypic change (A%) of each significant QTL, associated with the presence of an *L. parviflorum* (PF) allele at a given marker locus, was estimated as 2×100 x (E/PF-EE)/EE, where E/PF is the phenotypic mean of individuals heterozygous (E/PF) for the marker locus and E/E is the phenotypic mean for individuals homozygous for *esculentum* alleles at the same locus. Since one-half of the individuals in each BC3 plot would be heterozygous for any one fragment that was heterozygous in the BC2 generation, a factor of 2 was included to obtain the final estimate of the percent phenotypic change or the additive effect of the PF allele. To gain an approximation of additivity and phenotypic variance values, traits scored as ordered or

nominal categories were also analyzed by single-point regression; caution should be exercised when evaluating the additivity and phenotypic variances for these traits as these numbers are only approximations.

Significance levels and %A of each QTL were given a +/– sign which indicates a positive or negative effect of the PF allele from an agronomic perspective. Therefore, an increase in yield is denoted by "+", but a *decrease* in Bostwick rating (indicating greater viscosity) is also denoted by "+", since that is the desirable effect. Three exceptions are total acids, total organic acids and pH where effects are not necessarily positive or negative; for these two traits, +/– simply indicates a measured increase or decrease.

Results and discussion

Marker segregation and genetic map

The BC2 population was genotyped with 131 RFLP markers; one PCR-based marker, *I2*, and one morphological marker, *u*, uniform ripening. The genetic constitution of the BC2 plants was visualised using QGene (Nelson 1997). The average number of heterozygotes per locus was 19%, close to that expected for a BC2 (25%). Of the 133 markers scored, 33 (25%) showed significant (P<0.001) deviation from the expected frequency of heterozygotes (Fig. 1). There was no clear genomic region skewed toward the wild allele; only three markers (CT216, CT68 and CT238) distributed on three different chromosomes (6, 8, and 10), displayed a higher-than-expected frequency of heterozygotes. In contrast, there were several regions significantly (P<0.001) skewed towards the E allele, including the tops of chromosomes 4 and 11, the pericentric region of chromosome 10, the bottom of chromosome 9, the middle of chromosome 12, and the top of chromosome 3. As expected, marker selection against the PF allele at the *sp* locus on chromosome 6 resulted in skewness towards the E allele. However, counter to what had been reported in previous AB-QTL studies conducted in tomato (Tanksley et al. 1996; Bernacchi and Tanksley 1997; Fulton et al. 1997a), the distortion reported in the PF study was minimal, involving only the marker CT109. In conclusion, for the PF population no area of the tomato map entirely unrepresented by the wild allele was identified.

Segregation distortion is a common phenomenon in interspecific crosses in plants, and it has been widely documented (as reviewed in Xu et al. 1997). Some of the regions showing aberrant deviations in this study have also been found to be similarly skewed in other studies. For example, the significant deviation towards E alleles found for the top of chromosome 11, the pericentric region of chromosome 10, and the middle of chromosome 12, were also reported in two other AB-QTL studies of *Lycopersicon peruvianum* and *Lycopersicon hirsutum*, both green-fruited species, as well (Bernacchi and Tanksley 1997; Fulton et al. 1997a).

The 133 markers spanned approximately 940 cM, 74% of the total cM on the high-density tomato map (Tanksley et al. 1992; Pillen et al. 1996), due to the reduced recombination which occurred on all chromosomes. The order of the markers that could be ordered with a LOD of 3 or higher corresponded to the order of markers on the high-density tomato map (Tanksley et al. 1992) with the exception of TG9, which mapped closer to the centromere in this population. This also occurred in two previous PV studies, suggesting that an intrachromosomal translocation may have occurred in these two species (van Ooijen et al. 1994; Fulton et al. 1997).

Correlations between traits

Figure 2 shows the correlation coefficients between most of the traits measured in this study on the BC3 families, and calculated separately for each location. Ten traits (YEL, GEL, ER, SHD, FS, FIR, TOA, COR, LYC and BC) were not included in the correlation matrix, either because they were measured in only one location, and/or the correlation results were not significant. Significant (P<0.05) correlations were observed between many traits; however, we will limit our discussion only to some of the strongest associations detected at P<0.001, and, when necessary, the values will be averaged across locations.

In agreement with previous studies, YLD showed a positive correlation with FW (r=0.33) and a negative correlation with BRX (r=–0.34) (Stevens and Rudich 1978; Stevens 1986; Tanksley et al. 1996; Fulton et al. 1997b; Bernacchi et al. 1998a). As expected, similar results were reported for RDY and BRX. This negative relationship between yield and brix represents the major factor limiting simultaneous improvements of the two traits (Stevens and Rudich 1978; Grandillo et al. 1999b). YLD and RDY were both positively correlated with HA (r=0.36 and r=0.52, respectively), and these results are consistent with those reported by Fulton et al. (1997b).

Also consistent with many other studies are the negative correlations between BRX and the two traits, FW

Fig. 1 Comparison of the BC2 molecular linkage map (the right chromosome of each pair) to the high-density tomato map (the left chromosome of each pair) (Tanksley et al 1992) and map locations of putative QTLs. The centimorgan scale is given on the far left. *Striped* sections of chromosomes and corresponding markers indicate regions not segregating for the PF alleles in the BC2. *White* and *gray* sections of chromosomes indicate markers with segregation significantly (P<0.0001) skewed towards the E and PF allele, respectively. Markers in "<>" were fixed for the E allele in the BC2. Markers at hash marks on the chromosome were ordered at a LOD 3 or greater; markers in "( )" could only be ordered at a lower significance. "o" denotes the position of the centromere. Known pigmentation genes are given in *italics*. "///" indicates markers linked at LOD 3 or greater but at a high cM distance. *Gaps* in the chromosome indicate no linkage at LOD 3. QTLs are designated by the *letter/number combinations* to the right of the chromosomes (also see Table 1). *Underlined* QTLs signify those for which the PF allele confers positive effects from a horticultural perspective. #QTLs possibly in common with those discovered in the *L. pimpinellifolium* population; ∧QTLs possibly in common with those discovered in the *L. hirsutum* population; @QTLs possibly in common with those discovered in the *L. peruvianum* population


cM
10
20
30
40
50
60
70
80
90
100
110
120
130
1
2
3
4
TG301
TG334
TG273
TG59
TG460
CT191
CT267
CT67
TG245
TG17
TG255
TG158
TG27
pcp1.1 fir1.1
yld1.1 cvr1.1
cor1.1 mat1.1
vns1.1
mat1.2 cvr1.2
fir1.2
fs1.1 # pcp1.2
ic1.1
ha1.1 ^@
cvr1.3 @
ec1.1 ^@
TG33
(TG276)
CT205
CT255
(TG290)
TG451
TG308
TG353
(TG337)
CT9
(TG34)
TG204
CT59
fs2.1 mat2.1 @
cvr2.1
fw2.1 mat2.2
rdy2.1
ic2.1 bc2.1
bos2.1 ^ pH2.1
cvr2.2
mat2.3 fw2.2 fs2.2 #
(CT9) ic2.2 ec2.1 # puf2.1
TG34 yld2.1 ^# str2.1 ^@ lyc2.1
scr2.1
TG479
(TG114)
TG517
TG132
CT141
CT82
TG251
TG42
TG359
TG377
TG411
TG214
TG501
TG479A cvr3.1 @
(TG114) mat3.1 @
TG517 fs3.1 ^
(TG132)
CT141 fir3.1 #
CT82 cvr3.2 ^
TG251 gel3.1 fs3.2 fw3.1 #
TG42 puf3.1 yld3.1 ^
TG377 pH3.1 # lyc3.1
TG411 scr3.1 ta3.1 mat3.2
TG214 cvr3.3
(TG501)
GP180
(TG123)
TG182
TG287
TG427
TG65
TG305
(TG50)
(TG22)
TG464
CT50
TG22
(TG305)
(GP180A) brx4.1 ta4.1
TG123
TG182 cvr4.1 bc4.1
CT145B puf4.1 pH4.1 ^
TG287
(TG427) fs4.1
TG65 pH4.2
TG305 cvr4.2
(CT50) puf4.2
(TG22) brx4.2 ic4.1 ec4.1 ^
TG464 er4.1

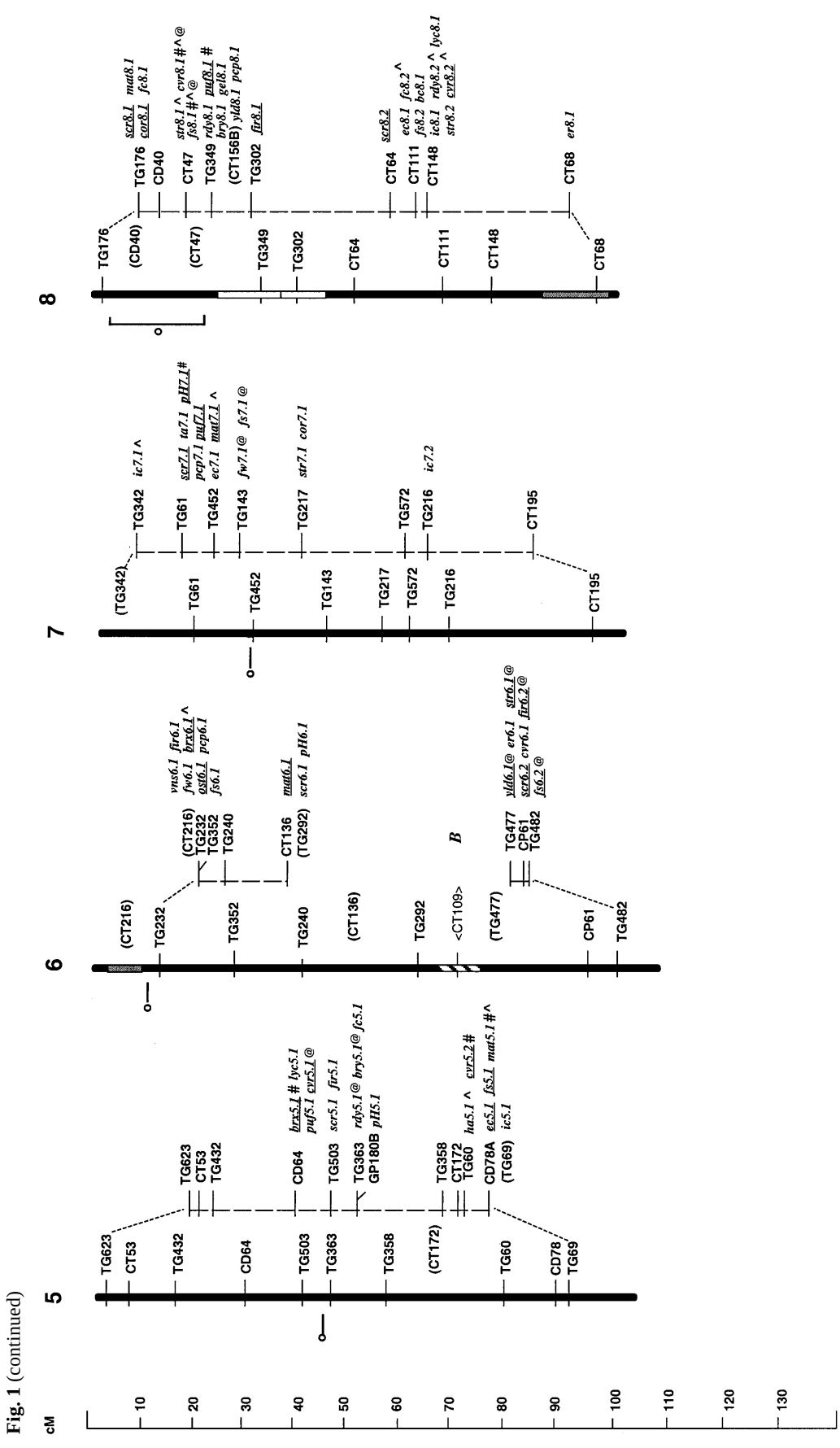
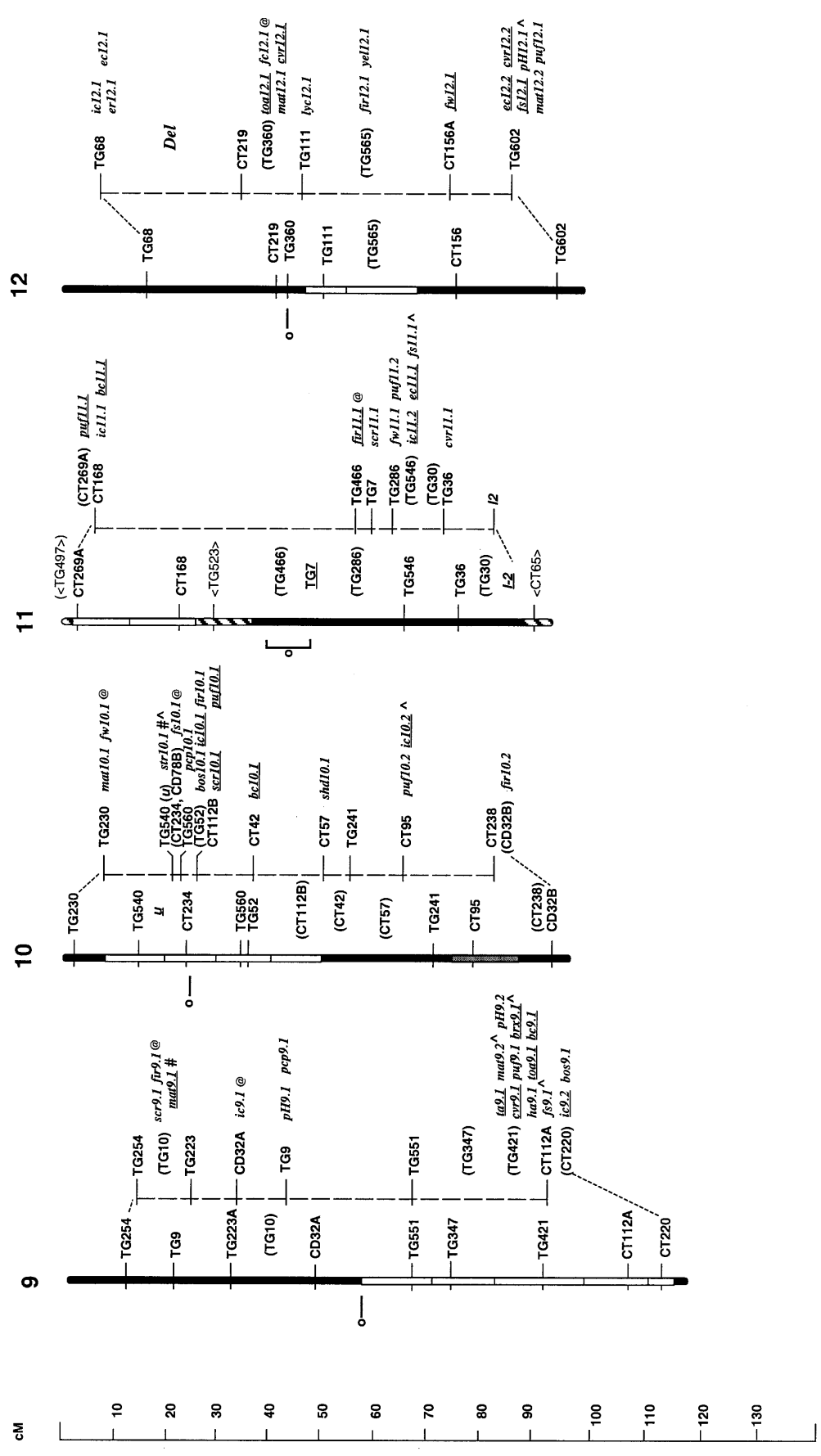
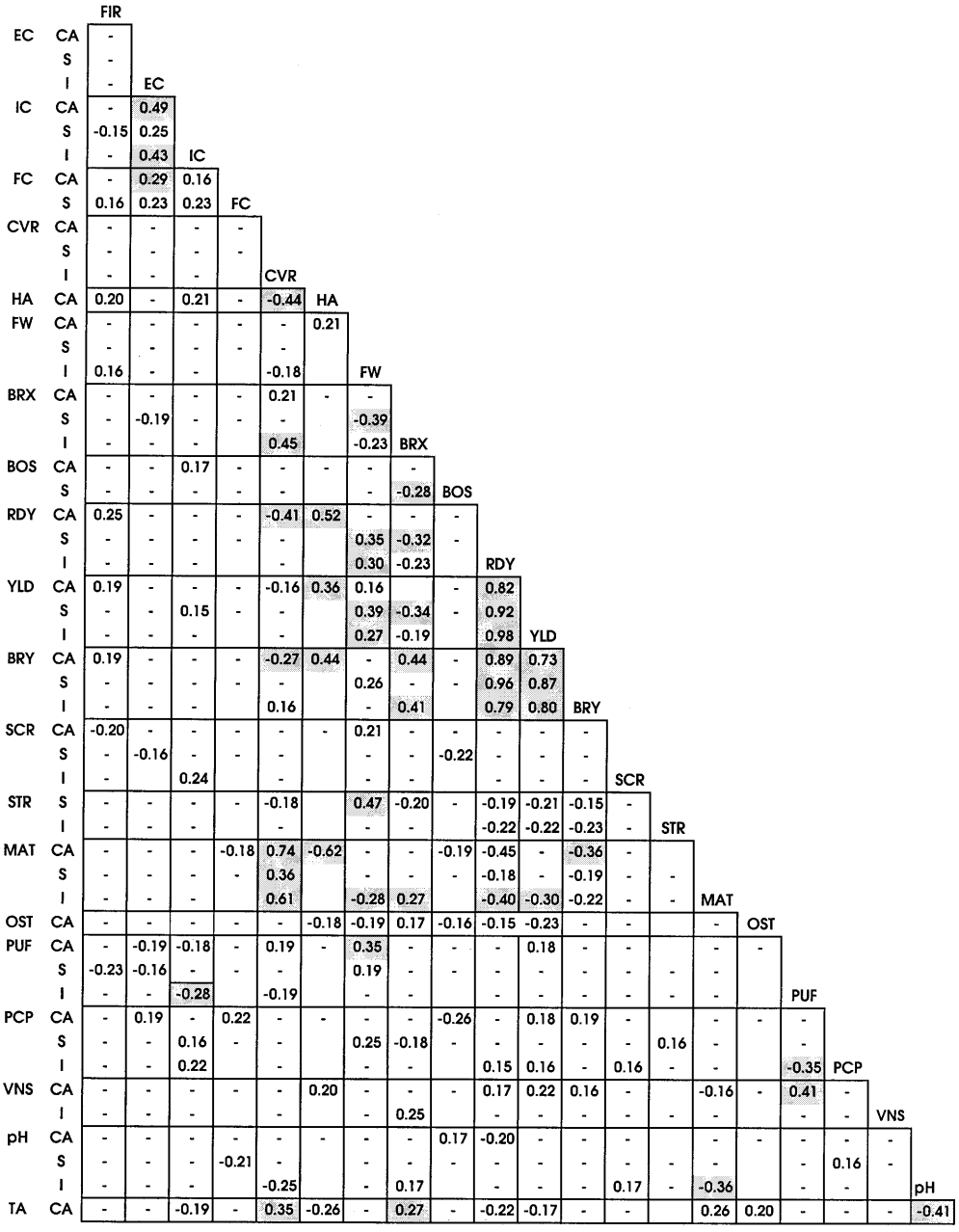


Fig. 1 (continued)



Legend of figure 1 please see on page 1028



		FIR	EC	IC	FC	CVR	HA	FW	BRX	BOS	RDY	YLD	BRY	SCR	STR	MAT	OST	PUF	PCP	VNS	pH
EC	CA	-																			
	S	-																			
	I	-	EC																		
IC	CA	-	0.49																		
	S	-0.15	0.25																		
	I	-	0.43	IC																	
FC	CA	-	0.29	0.16																	
	S	0.16	0.23	0.23	FC																
CVR	CA	-	-	-	-																
	S	-	-	-	-																
	I	-	-	-		CVR															
HA	CA	0.20	-	0.21	-	-0.44	HA														
FW	CA	-	-	-	-	-	0.21														
	S	-	-	-	-	-															
	I	0.16	-	-		-0.18		FW													
BRX	CA	-	-	-	-	0.21	-	-													
	S	-	-0.19	-	-	-		-0.39													
	I	-	-	-		0.45		-0.23	BRX												
BOS	CA	-	-	0.17	-	-	-	-	-												
	S	-	-	-	-	-		-	-0.28	BOS											
RDY	CA	0.25	-	-	-	-0.41	0.52	-	-	-											
	S	-	-	-	-	-		0.35	-0.32	-											
	I	-	-	-		-		0.30	-0.23		RDY										
YLD	CA	0.19	-	-	-	-0.16	0.36	0.16		-	0.82										
	S	-	-	0.15	-	-		0.39	-0.34	-	0.92										
	I	-	-	-		-		0.27	-0.19		0.98	YLD									
BRY	CA	0.19	-	-	-	-0.27	0.44	-	0.44	-	0.89	0.73									
	S	-	-	-	-	-		0.26	-	-	0.96	0.87									
	I	-	-	-		0.16		-	0.41		0.79	0.80	BRY								
SCR	CA	-0.20	-	-	-	-	-	0.21	-	-	-	-	-								
	S	-	-0.16	-	-	-		-	-	-0.22	-	-	-								
	I	-		0.24		-		-	-		-	-	-	SCR							
STR	S	-	-	-	-	-0.18		0.47	-0.20	-	-0.19	-0.21	-0.15	-							
	I	-	-	-		-		-	-		-0.22	-0.22	-0.23	-	STR						
MAT	CA	-	-	-	-0.18	0.74	-0.62	-	-	-0.19	-0.45	-	-0.36	-							
	S	-	-	-	-	0.36		-	-	-	-0.18	-	-0.19	-	-						
	I	-	-	-		0.61		-0.28	0.27		-0.40	-0.30	-0.22	-	-	MAT					
OST	CA	-	-	-	-	-	-0.18	-0.19	0.17	-0.16	-0.15	-0.23	-	-		-	OST				
PUF	CA	-	-0.19	-0.18	-	0.19	-	0.35	-	-	-	0.18	-	-		-	-				
	S	-0.23	-0.16	-	-	-		0.19	-	-	-	-	-	-	-	-					
	I	-	-	-0.28		-0.19		-	-		-	-	-	-	-	-		PUF			
PCP	CA	-	0.19	-	0.22	-	-	-	-	-0.26	-	0.18	0.19	-		-	-	-			
	S	-	-	0.16	-	-		0.25	-0.18	-	-	-	-	-	0.16	-		-			
	I	-	-	0.22		-		-	-		0.15	0.16	-	0.16	-	-		-0.35	PCP		
VNS	CA	-	-	-	-	-	0.20	-	-	-	0.17	0.22	0.16	-		-0.16	-	0.41	-		
	I	-	-	-		-		-	0.25		-	-	-	-	-	-		-	-	VNS	
pH	CA	-	-	-	-	-	-	-	-	0.17	-0.20	-	-	-		-	-	-	-	-	
	S	-	-	-	-0.21	-		-	-	-	-	-	-	-	-	-		-	0.16	-	
	I	-	-	-		-0.25		-	0.17		-	-	-	0.17	-	-0.36		-	-		pH
TA	CA	-	-	-0.19	-	0.35	-0.26	-	0.27	-	-0.22	-0.17	-	-		0.26	0.20	-	-	-	-0.41

Fig. 2 Significant ($P<0.05$) correlations between traits in the *L. parviflorum* BC3 population. The sign of the correlation coefficient indicates the direction of correlation regardless of the scales used to measure the characters. *Shaded areas* indicate highly significant ($P<0.001$) correlations. "–"=not significant. *CA*=Woodland, CA; *SP*=Spain; *IS*=Israel. For trait abbreviations, see Table 1

(r=–0.39) (Ibarbia and Lambeth 1971; Stevens 1986; Paterson et al. 1991; Tanksley et al. 1996; Fulton et al. 1997b; Bernacchi et al. 1998a) and BOS (r=–0.28) (Stevens 1986). Increased BRX was associated with increased CVR (r=0.45); a result that could be explained by an increased sink/source ratio which favours a higher soluble-solids concentration in the fruit (Stevens and Rudich 1978). Although a certain degree of leaf coverage is desirable to reduce sun damage of the fruit, excessive vegetative growth is deleterious as it relates negatively with RDY (r=–0.40) and BRY (r=–0.27), and positively with delayed maturity (r=0.57).

For the fruit-color determinations, a moderate positive correlation was found between EC and IC (r=0.46), and a lower positive correlation between the lab measurement (FC) and EC (r=0.29). Similar results were reported in the PV study for the EC and IC data, although in that case a negative relationship was found in CA between the lab measurement and EC (Fulton et al. 1997b).

QTLs detected for each trait and comparison across species

Putative QTLs for each trait are listed and described in Table 1 and their map positions are shown in Fig. 1. Significant putative QTLs were identified for all 30 traits analyzed (ranging from 1 to 19 QTLs/trait), for a total of 199 QTLs.

Table 1 List of putative QTLs detected from data collected from BC3 field plots. CA=Woodland, CA; SP=Spain; IS=Israel; CU=Cornell University, BC2 (fruit weight only). "–1"=data taken by CU team, "–2"=data taken by local collaborators. * P=0.1, ** P<0.001, **** P<0.0001. ns=not significant, na=not available. "+/–" sign indicates positive or negative from an agronomic perspective (see Materials and methods) except for pH and acids, for which the sign indicates only an increase or decrease. Boxed area=location for which A (%) and PV (%) were calculated. A (%)=200(AB–AA)/AA where AA=phenotypic mean for individuals homozygous for *esculentum* alleles at specified markers, AB=phenotypic mean for heterozygotes *esculentum/peruvianum*). %PV=phenotypic variance estimated from regression of marker against phenotype. #=QTLs possibly in common with those discovered in *L. pimpinellifolium.* ∧=QTLs possibly in common with those discovered in *L. hirsutum.* @=QTLs possibly in common with those discovered in *L. peruvianum*

Trait		QTL	Chrm.	Marker	CA-1	CA-2	SP-1	SP-2	IS-1	IS-2	CU	%A	%PV
Total yield		*yld1.1*	1	TG301	na	***–	na	*–	na	ns	na	–31	8
	#∧	*yld2.1*	2	TG34	na	**–	na	****–	na	ns	na	–30	5
	∧	*yld3.1*	3	TG42	na	ns	na	*+	na	***–	na	–15	7
	@	*yld6.1*	6	TG477	na	***+	na	ns	na	ns	na	27	7
		yld8.1	8	TG349	na	**–	na	***–	na	*–	na	–37	7
Red yield		*rdy2.1*	2	TG920	na	*–	na	*–	na	*–	na	–19	2
	@	*rdy5.1*	5	TG363	na	****–	na	*–	na	**–	na	–54	13
		rdy8.1	8	TG349	na	*–	na	***–	na	*–	na	–39	6
	∧	*rdy8.2*	8	CT148	na	*–	na	*–	na	*–	na	–23	4
Fruit weight		*fw2.1*	2	TG290	na	ns	na	*–	na	***–	***–	–27	9
		fw2.2	2	CT9	na	***–	na	****–	na	**–	****–	–33	15
	#	*fw3.1*	3	TG251	na	*–	na	*–	na	*–	**–	–25	7
		fw6.1	6	CT216	na	ns	na	**–	na	ns	**–	–17	5
	@	*fw7.1*	7	TG143	na	***–	na	**–	na	*–	***–	–23	8
	@	*fw10.1*	10	TG230	na	***–	na	***–	na	*-	***–	–34	9
		fw11.1	11	TG286	na	***–	na	**–	na	ns	****–	–27	11
		fw12.1	12	CT156A	na	*+	na	ns	na	*+	***+	30	8
Ostwald		*ost6.1*	6	TG232	na	****+	na	na	na	na	na	59	17
Bostwick	∧	*bos2.1*	2	TG353	na	**–	na	****–	na	na	na	–31	11
		bos9.1	9	CT220	na	***–	na	ns	na	na	na	–45	7
		bos10.1	10	TG52	na	***–	na	****–	na	na	na	–47	16
Soluble solids		*brx4.1*	4	GP180A	na	***+	na	ns	na	ns	na	28	8
(Brix)		*brx4.2*	4	TG22	na	ns	na	****+	na	**+	na	15	12
	#	*brx5.1*	5	CD64	na	ns	na	ns	na	****+	na	17	11
	∧	*brx6.1*	6	CT216	na	**+	na	**+	na	**+	na	11	5
	∧	*brx9.1*	9	TG421	na	ns	na	ns	na	***+	na	20	8
Brix*red yield	@	*bry5.1*	5	TG363	na	****–	na	ns	na	ns	na	–55	11
		brx8.1	8	CT156B	na	*–	na	***–	na	*–	na	–42	8
Yellow		*yel12.1*	12	TG565	****–	na	na	na	na	na	na	–84	21
Internal fruit color		*ic1.1*	1	TG255	**+	na	*+	na	*+	ns	na	23	4
		ic2.1	2	TG308	***+	na	**+	na	****+	ns	na	38	7
		ic2.2	2	CT9	***+	na	*+	na	**+	ns	na	30	5
		ic4.1	4	TG22	**–	na	ns	na	**–	**–	na	–28	4
		ic5.1	5	TG69	***–	na	*–	na	ns	ns	na	–23	6
	∧	*ic7.1*	7	TG342	ns	na	ns	na	****–	ns	na	–31	7
		ic7.2	7	TG216	***–	na	ns	na	*–	ns	na	–24	4
		ic8.1	8	CT148	***–	na	**–	na	ns	****–	na	–56	8
	@	*ic9.1*	9	CD32A	***–	na	ns	na	*–	**–	na	–24	5
		ic9.2	9	CT220	***+	na	*+	na	ns	*–	na	49	4
		ic10.1	10	TG52	***+	na	****+	na	+*	ns	na	38	7
	∧	*ic10.2*	10	CT95	ns	na	ns	na	ns	***+	na	43	4
		ic11.1	11	CT168	ns	na	ns	na	ns	***–	na	–89	3
		ic11.2	11	TG546	*+	na	ns	na	ns	***+	na	39	4
		ic12.1	12	TG68	****–	na	**–	na	**–	ns	na	–30	9
External fruit color	∧@	*ec1.1*	1	TG27	ns	na	ns	na	***–	na	na	–33	6
	#	*ec2.1*	2	CT9	***+	na	ns	na	ns	na	na	34	6
	∧	*ec4.1*	4	TG22	***–	na	****–	na	**–	na	na	–24	8
		ec5.1	5	CD78A	*–	na	ns	na	****+	na	na	34	6
		ec7.1	7	TG452	*–	na	*+	na	****–	na	na	–31	7
		ec8.1	8	CT111	****–	na	ns	na	*–	na	na	–26	8
		ec11.1	11	TG546	***+	na	ns	na	ns	na	na	23	6
		ec12.1	12	TG68	****–	na	*–	na	ns	na	na	–27	7
		ec12.2	12	TG602	*+	na	ns	na	****+	na	na	36	6
Fruit color, lab		*fc5.1*	5	TG363	na	***–	na	ns	na	na	na	–5	7
		fc8.1	8	CD40	na	***–	na	*–	na	na	na	–5	9
	∧	*fc8.2*	8	CT111	na	****–	na	**–	na	na	na	–5	11
	@	*fc12.1*	12	TG360	na	ns	na	***–	na	na	na	–7	8

Table 1 (continued)

Trait		QTL	Chrm.	Marker	CA-1	CA-2	SP-1	SP-2	IS-1	IS-2	CU	%A	%PV
Internal gel color		*gel3.1*	3	TG251	na	na	na	na	na	***–	na	–8	7
		gel8.1	8	TG349	na	na	na	na	na	****–	na	–17	16
Lycopene		*lyc2.1*	2	CT9	na	**+	na	na	na	na	na	24	5
		lyc3.1	3	TG214	na	**+	na	na	na	na	na	19	5
		lyc5.1	5	CD64	na	****–	na	na	na	na	na	–31	10
		lyc8.1	8	CT148	na	**–	na	na	na	na	na	–19	5
		lyc12.1	12	TG111	na	**–	na	na	na	na	na	–27	6
Beta-carotene		*bc2.1*	2	TG308	na	**+	na	na	na	na	na	51	6
		bc4.1	4	CT145B	na	****+	na	na	na	na	na	171	21
		bc8.1	8	CT111	na	**–	na	na	na	na	na	–39	6
		bc9.1	9	TG421	na	**+	na	na	na	na	na	69	5
		bc10.1	10	CT42	na	****+	na	na	na	na	na	91	17
		bc11.1	11	CT168	na	***+	na	na	na	na	na	115	8
Stem scar		*scr2.1*	2	CT59	ns	na	ns	na	ns	****+	na	91	4
		scr3.1	3	TG214	*+	na	*+	na	ns	*+	na	24	1
		scr5.1	5	TG503	****–	na	ns	na	ns	ns	na	–24	7
		scr6.1	6	TG292	***–	na	**–	na	ns	*–	na	–22	5
		scr6.2	6	CP61	***+	na	ns	na	ns	ns	na	16	5
		scr7.1	7	TG61	***+	na	ns	na	ns	****+	na	52	5
		scr8.1	8	TG176	*+	na	**+	na	ns	*+	na	19	3
		scr8.2	8	CT64	ns	na	ns	na	****+	**+	na	35	6
		scr9.1	9	TG10	***–	na	**–	na	ns	ns	na	–15	3
		scr10.1	10	CT112B	*+	na	***+	na	ns	ns	na	30	5
		scr11.1	11	TG7	ns	na	ns	na	***–	ns	na	–35	5
Epidermal reticulation		*er4.1*	4	TG464	na	na	****–	na	na	na	na	–140	67
		er6.1	6	TG477	na	na	***–	na	na	na	na	–38	8
		er8.1	8	CT68	na	na	***–	na	na	na	na	–33	8
		er12.1	12	TG68	na	na	***–	na	na	na	na	–38	8
Shoulders		*shd10.1*	10	CT57	na	na	na	na	na	****–	na	–27	5
Stem release	∧@	*str2.1*	2	TG34	na	na	na	****–	na	*–	na	–104	11
	@	*str6.1*	6	TG477	na	na	na	**+	na	***+	na	33	9
		str7.1	7	TG217	na	na	na	***–	na	ns	na	–75	11
	∧	*str8.1*	8	CT47	na	na	na	****–	na	**–	na	–102	12
		str8.2	8	CT148	na	na	na	****–	na	*–	na	–91	14
	#∧	*str10.1*	10	TG540	na	na	na	**–	na	***–	na	–43	7
Fruit shape	#	*fs1.1*	1	CT67	ns	ns	***+	na	*+	na	na	14	4
		fs2.1	2	TG33	****–	ns	ns	na	ns	na	na	–15	5
	#	*fs2.2*	2	CT9	****–	****–	****–	na	***–	na	na	–34	19
	∧	*fs3.1*	3	TG517	*+	*+	ns	na	*+	na	na	15	2
		fs3.2	3	TG251	ns	ns	****–	na	**–	na	na	–22	14
		fs4.1	4	TG427	ns	**+	**+	na	ns	na	na	12	3
		fs5.1	5	CD78A	*+	****+	**+	na	*+	na	na	14	5
		fs6.1	6	TG352	****–	*–	**–	na	*–	na	na	–22	9
	@	*fs6.2*	6	TG482	****+	**+	*+	na	*+	na	na	16	5
	@	*fs7.1*	7	TG143	****–	*–	****–	na	***–	na	na	–15	8
	#∧@	*fs8.1*	8	CT47	****–	****–	****–	na	****–	na	na	–39	28
		fs8.2	8	CT111	ns	ns	***–	na	**–	na	na	–11	4
	∧	*f9.1*	9	CT112A	*–	****–	ns	na	ns	na	na	–37	9
	@	*fs10.1*	10	CT234	****–	****–	****–	na	****–	na	na	–35	16
	∧	*fs11.1*	11	TG546	***–	*–	*–	na	ns	na	na	–12	4
		fs12.1	12	TG602	*+	*+	**+	na	**+	na	na	22	3
Firmness		*fir1.1*	1	TG301	****+	*+	*+	***+	*+	na	na	16	8
		fir1.2	1	TG460	*+	ns	***+	***+	*+	na	na	12	8
	#	*fir3.1*	3	CT141	ns	***+	ns	ns	ns	na	na	29	6
		fir5.1	5	TG503	****–	****–	**–	ns	ns	na	na	–15	7
		fir6.1	6	CT216	****–	ns	ns	***–	*–	na	na	–13	9
	@	*fir6.2*	6	CP61	*+	*+	ns	***+	ns	na	na	12	9
		fir8.1	8	TG301	***+	*+	ns	ns	ns	na	na	15	4
	@	*fir9.1*	9	TG10	*–	****–	*–	**–	ns	na	na	–34	7
		fir10.1	10	TG52	***–	ns	ns	*–	ns	na	na	–14	5
		fir10.2	10	CD32B	ns	***–	ns	ns	ns	na	na	–26	6
	@	*fir11.1*	11	TG466	****+	****+	***+	*+	ns	na	na	15	9
		fir12.1	12	TG565	ns	***–	*–	**–	*+	na	na	–35	5
Total acids		*ta3.1*	3	TG214	na	****–	na	na	na	na	na	–11	11
		ta4.1	4	GP180A	na	****+	na	na	na	na	na	22	12
		ta7.1	7	TG61	na	***–	na	na	na	na	na	–8	7
		ta9.1	9	TG421	na	****+	na	na	na	na	na	20	11

Table 1 (continued)

Trait		QTL	Chrm.	Marker	CA-1	CA-2	SP-1	SP-2	IS-1	IS-2	CU	%A	%PV
Total organic acids		*toa9.1*	9	TG421	na	***+	na	na	na	na	na	18	7
		toa12.1	12	TG360	na	***+	na	na	na	na	na	14	9
pH		*pH 2.1*	2	TG353	na	*+	na	ns	na	****–	na	–4	13
	#	*pH 3.1*	3	TG411	na	**+	na	****+	na	ns	na	2	10
	^	*ph 4.1*	4	CT145B	na	**–	na	****–	na	***–	na	–6	19
		ph 4.2	4	TG65	na	****–	na	**–	na	ns	na	–3	17
		ph 5.1	5	GP180B	na	ns	na	****–	na	**–	na	–3	13
		pH 6.1	6	TG292	na	**–	na	***–	na	*–	na	–3	9
	#	*pH 7.1*	7	TG61	na	*+	na	**+	na	*+	na	1	6
		pH 9.1	9	TG9	na	****–	na	****–	na	ns	na	–4	22
		pH 9.2	9	TG421	na	*–	na	****–	na	****–	na	–5	17
	^	*pH 12.1*	12	TG602	na	ns	na	**–	na	***–	na	–3	10
Maturity		*mat1.1*	1	TG301	***–	**–	**–	**–	ns	na	na	–14	4
		mat1.2	1	TG273	***–	**–	***–	ns	ns	na	na	–24	5
	@	*mat2.1*	2	TG33	***–	ns	ns	ns	****–	na	na	–38	3
		mat2.2	2	TG290	***–	*–	**–	*–	****–	na	na	–38	3
		mat2.3	2	TG337	***–	*–	*–	*–	***–	na	na	–16	4
	@	*mat3.1*	3	TG114	*+	ns	ns	ns	***+	na	na	37	1
		mat3.2	3	TG214	ns	ns	****+	ns	*–	na	na	21	6
	#^	*mat5.1*	5	CD78A	****–	ns	***–	ns	**–	na	na	–28	18
		mat6.1	6	CT136	ns	ns	ns	***+	*+	na	na	27	4
	^	*mat7.1*	7	TG452	ns	*+	***+	**+	ns	na	na	18	5
		mat8.1	8	TG176	ns	ns	ns	***–	ns	na	na	–23	3
	#	*mat9.1*	9	TG10	ns	ns	****+	ns	ns	na	na	28	9
	^	*mat9.2*	9	TG421	***–	ns	ns	ns	ns	na	na	–25	5
		mat10.1	10	TG230	ns	ns	ns	*–	****–	na	na	–56	4
		mat12.1	12	TG360	***–	ns	ns	*–	*–	na	na	–18	6
		mat12.2	121	TG602	*–	*–	**–	ns	*–	na	na	–18	3
Horticultural acceptibility	@^	*ha1.1*	1	TG27	***+	na	na	na	na	na	na	16	3
	^	*ha5.1*	5	TG60	****–	na	na	na	na	na	na	–31	15
		ha9.1	9	TG421	***–	na	na	na	na	na	na	–34	6
Cover		*cvr1.1*	1	TG301	**+	na	**+	***+	ns	na	na	29	3
		cvr1.2	1	TG273	****+	na	***+	**+	*+	na	na	25	8
	@	*cvr1.3*	1	TG27	ns	na	ns	****+	**–	na	na	44	7
		cvr2.1	2	TG33	***+	na	ns	ns	*+	na	na	14	4
		cvr2.2	2	TG353	****+	na	ns	**+	*+	na	na	21	6
	@	*cvr3.1*	3	TG479A	ns	na	ns	****+	*–	na	na	48	7
	^	*cvr3.2*	3	CT82	***–	na	ns	*–	ns	na	na	–19	5
		cvr3.3	3	TG215	***–	na	*–	**–	*–	na	na	–15	4
		cvr4.1	4	CT145B	***+	na	*+	ns	ns	na	na	44	8
		cvr4.2	4	TG305	*+	na	*+	ns	*+	na	na	13	3
	@	*cvr5.1*	5	CD64	****+	na	**+	ns	****+	na	na	28	9
	#	*cvr5.2*	5	TG60	****+	na	**+	**–	***+	na	na	37	20
		cvr6.1	6	CP61	*–	na	*–	ns	**–	na	na	–16	3
	#^@	*cvr8.1*	8	CT47	****–	na	ns	ns	*–	na	na	–23	6
	^	*cvr8.2*	8	CT148	ns	na	*+	ns	***+	na	na	20	4
		cvr9.1	9	TG421	***+	na	ns	ns	**+	na	na	32	5
		cvr11.1	11	TG36	ns	na	ns	*+	***–	na	na	–19	5
		cvr12.1	12	TG360	***+	na	ns	ns	ns	na	na	18	4
		cvr12.2	12	TG602	**+	na	*+	ns	**+	na	na	21	4
Internal core		*cor1.1*	1	TG301	****+	na	na	na	na	na	na	<1	7
		cor7.1	7	TG217	***–	na	na	na	na	na	na	–<1	2
		cor8.1	8	TG176	***+	na	na	na	na	na	na	<1	2
Puffiness		*puf2.1*	2	CT9	****+	na	***+	na	ns	*+	na	28	8
		puf3.1	3	TG42	***+	na	*+	na	ns	ns	na	19	6
		puf4.1	4	CT145B	***–	na	*–	na	**–	n*–	na	–25	3
		puf4.2	4	CT50	*–	na	**–	na	ns	**–	na	–24	2
		puf5.1	5	CD64	****–	na	**–	na	ns	*–	na	–29	9
		puf7.1	7	TG61	ns	na	****+	na	ns	*+	na	41	10
	#	*puf8.1*	8	TG349	**+	na	*+	na	ns	***+	na	–49	4
		puf9.1	9	TG421	***–	na	*–	na	ns	*–	na	–23	3
		puf10.1	10	TG52	ns	na	***+	na	ns	**+	na	38	3
		puf10.2	10	CT95	****–	na	ns	na	**–	ns	na	–16	5
		puf11.1	11	CT269A	***+	na	ns	na	**+	ns	na	36	4
		puf11.2	11	TG286	****–	na	**–	na	ns	ns	na	–23	12
		puf12.1	12	TG602	**–	na	***–	na	ns	ns	na	–36	5

Table 1 (continued)

Trait	QTL	Chrm.	Marker	CA-1	CA-2	SP-1	SP-2	IS-1	IS-2	CU	%A	%PV
Pericarp thickness	*pcp1.1*	1	TG301	**+	na	ns	na	**+	na	na	28	3
	pcp1.2	1	CT67	ns	na	****+	na	ns	na	na	24	8
	pcp6.1	6	TG232	*-	na	****–	na	ns	na	na	–15	6
	pcp7.1	7	TG61	****–	na	**–	na	ns	na	na	–11	5
	pcp8.1	8	CT156B	***–	na	ns	na	ns	na	na	–15	4
	pcp9.1	9	TG9	ns	na	**–	na	**–	na	na	–11	3
	pcp10.1	10	TG560	*–	na	***–	na	ns	na	na	–16	4
Veins	*vns1.1*	1	TG334	****+	na	na	na	na	*+	na	27	4
	vns6.1	6	CT216	ns	na	na	na	na	***–	na	–41	5

Most traits reported in this study for *L. parviflorum* (PF) have also been analysed in three other AB-QTL studies conducted in tomato using the same recurrent parent *L. esculentum* (E6203) and as donors the wild species *Lycopersicon pimpinellifolium* (PM) (Tanksley et al. 1996), *L. peruvianum* (PV) (Fulton et al. 1997b) and *L. hirsutum* (H) (Bernacchi et al. 1998a). Therefore, for these common traits it was possible to directly compare the results obtained for the four wild species, and to identify those QTLs more likely to be conserved across species. Since different subsets of RFLP markers were used to develop the specific linkage maps, QTLs for two or more wild species were inferred to be potentially orthologous if they mapped to the same 15-cM region, with distances determined on the basis of the high-density tomato map (Tanksley et al. 1992; Pillen et al. 1996). For the two traits FW and FS the comparison was extended to a wider range of QTL studies conducted in tomato (as reviewed in Grandillo et al. 1999a).

Traits measured also in other studies

Total yield. Five QTLs were significantly associated with total yield. For all these QTLs the percent phenotypic variance (PV) explained was lower than 10%. For four QTLs the PF allele decreased total yield. However, for *yld6.1*, on chromosome 6, the wild PF allele had an effect opposite to the one expected based on the parental phenotype, increasing total yield by 27% (Table 1). This QTL may be conserved with a QTL identified in the same chromosomal region for the *L. peruvianum* (PV) study (Fulton et al. 1997b), and similarly the PV allele at this QTL increased the trait. Two other QTLs showing conservation across species are *yld2.1* and *yld3.1*. The QTL mapping to chromosome 2 could be orthologous to the H and PM QTLs and in all cases the wild allele decreased total yield; *yld3.1* shares a similar chromosomal location with the H QTL *ydt3.1*, and the H allele also decreased total yield.

Red yield. Red yield was affected by four significant QTLs, with PV values ranging from 2% to 13%. In all instances the PF allele decreased the trait. *rdy5.1* and *rdy8.2* was conserved with the corresponding red yield QTLs detected in the PV and H studies, respectively, and in all cases the wild allele decreased red yield.

Fruit weight. Eight QTLs were detected which significantly affected fruit weight, with PV values ranging from 5% to 15%. For only one QTL, *fw12.1*, the PF allele was associated with an increase in fruit weight (30% increase). Of the eight QTLs detected for this trait, *fw2.2* was the one explaining the largest portion of the total phenotypic variation (PV=15%) and decreased the fruit weight by 33%. This FW QTL has been found to be conserved across both red-and green-fruited species of tomato (Alpert et al. 1995; Grandillo et al. 1999a), and high-resolution physical and genetic maps have also been established (Alpert and Tanksley 1996). The QTL on chromosome 3, *fw3.1*, is potentially orthologous to the FW QTL found at the same chromosomal location in at least three other wild species of tomato including PM (Grandillo et al. 1999a), and in all instances the wild alleles at this QTL reduced fruit weight. *fw7.1* and *fw10.1* seem to be conserved with the corresponding QTL detected in the PV study and again all the wild alleles at this QTL caused a reduction in fruit weight.

Bostwick. Paste viscosity was significantly associated with three QTLs, *bos2.1*, *bos9.1* and *bos10.1*, each explaining 11%, 7% and 16% of the total phenotypic variance, respectively. At all these QTLs, the PF allele reduced the viscosity. *bos2.1* is possibly orthologous to the H QTL *bos2.1*, which also exerted a negative effect.

Soluble-solids content. Five QTLs were identified for soluble-solids with PV values ranging from 5% (*brx6.1*) to 12% (*brx4.2*). In all cases the PF allele increased the trait, with the highest effect of 28% observed for *brx4.1*. *brx5.1* is potentially orthologous to the PM QTL *ssc5.2*, and also the PM allele at this QTL had a positive effect. *brx6.1* has a similar map position to H QTL *ssc6.1*; however, the H allele decreased the trait. Finally, *brx9.1*, is potentially in common with the H QTL *ssc9.1*, and similarly, the H allele is associated with an increase in the soluble-solids content.

*Brix*red yield.* Two QTLs were significantly associated with BRY, *bry5.1* and *bry8.1*, and the wild PF allele reduced the trait in both cases. *bry5.1* mapped to the same chromosomal location as the red yield QTL *rdy5.1*, while *bry8.1* had the same map position as *yld8.1* and *rdy8.1*. Neither of the two BRY QTLs detected for

L. parviflorum share a similar map position with the BRY QTLs identified in other tomato AB-QTL studies.

Fruit color. Fifteen QTLs were identified for *internal fruit color* (IC), each explaining less than 10% of the total phenotypic variation. For seven (47%) of these the PF allele had a favourable effect on the trait, increasing the intensity of the red color. Two IC QTLs, *ic7.1* and *ic10.2*, are potentially in common with the fruit color QTLs detected in the H study by means of a visual determination. For *ic10.2*, however, the direction of the H allele was opposite to the PF one, decreasing the trait. *ic9.1* had a similar map position to the PV QTLs *fc9.1* (lab measurement) and *ic9.1* (visual measurement). In all instances the wild alleles decreased the trait.

External fruit color (EC) was significantly associated with nine regions of the genome. Similar to the IC QTLs, none of the QTLs for this trait explained more than 8% of the total phenotypic variance. For four QTLs (*ec2.1*, *ec5.1*, *ec11.1* and *ec12.2*) the PF had a positive effect. Consistent with the significant positive correlation coefficient found between IC and EC (r=0.46), six of the nine EC QTLs (*ec2.1*, *ec4.1*, *ec5.1*, *ec8.1*, *ec11.1* and *ec12.1*) shared the same, or very similar, map positions as the corresponding QTLs detected for IC. Only for the two QTLs mapping on chromosome 5, *ec5.1* and *ic5.1*, was the effect of the PF allele different, increasing EC while decreasing IC. *ec1.1* is potentially in common with the H QTL *fc1.3* (visual measurement) and the PV QTL *ec1.1*. In all cases the wild alleles had a detrimental effect on the trait. *ec2.1* shares a similar chromosomal position with the PM QTL *fc2.1* (visual determination), and the PM allele also had a positive effect on the trait. *ec4.1* is potentially in common with the H QTL *fc4.2* (visual measurement); however, the H allele improved the trait.

For the lab measurement, FC, taken only in CA and SP, four significant QTLs were detected, with PV values ranging from 7% to 11%. In all instances the PF allele had a negative effect. Only one QTL, *fc8.1*, had the same map position as *ec8.1* and was very close to *ic8.1*, and in all instances the wild allele caused a reduction in fruit color. *fc8.2* is potentially orthologous to the H QTL *fc8.1* (lab measurement) and the H allele also decreased the trait. *fc12.1* is potentially in common with the PV QTLs *fc12.1* (lab measurement) and *ec12.1* (visual measurement), and in all instances the wild alleles decreased the trait.

Internal gel color (GEL) was evaluated only in IS, and two significant QTLs were found, *gel3.1* and *gel8.1*, explaining 7% and 16% of the total phenotypic variance, respectively. For both QTL the PF allele reduced the intensity of the internal gel color. None of the GEL QTLs shared a similar map position to other fruit color QTLs. This trait was measured also in the PV study, but no significant QTL was found.

Pooling together the results obtained from the four different fruit color determinations, IC, EC, FC and GEL, we could infer that a minimum of 23 putative QTLs influence fruit color in the PF population.

Stem scar. Eleven QTLs were detected for stem scar, none of which explained more than 6% of the total phenotypic variance. For seven of these the PF allele had a favourable effect, reducing the size of the scar. This trait was measured also in the PV study, but no significant association was found.

Shoulders. The shoulders trait was measured only in IS, and a single QTL was detected on chromosome 10 at which the PF allele increased the mottled coloring (undesirable). This trait was studied also in the PM study, but no significant QTL was found in that case.

Percent stem release. The percentage of stem release was evaluated only in SP and IS. Six QTLs were detected for this trait, with PV values ranging from 7% to 14%. For one QTL, str6.1, the PF allele had a positive effect, increasing the percentage of fruit with detached stems by 33%. This QTL may be conserved with the QTL, str6.1, detected in the PV study; however, the PV allele at this QTL had a deleterious effect. For str2.1, similar QTLs were reported in the PV study (the PV allele had a favourable effect), and in the H study (the H allele had a negative effect). str8.1 could be in common with the H QTL, str8.1, also characterised by a negative effect of the H allele. Finally, str10.1 is potentially common to the QTLs detected in the PM and H studies, with the PM allele exerting a favourable effect on the trait, and the H allele a negative one.

Fruit shape. Sixteen QTLs, distributed on all 12 chromosomes, were significantly associated with fruit shape. This represents the largest number of fruit-shape QTLs detected so far in a single mapping population (Grandillo et al. 1999a). For four of these QTLs the percent of the phenotypic variance explained was higher than 10%; these include *fs2.2*, *fs3.2*, *fs8.1* and *fs10.1*, with PV values of 19%, 14%, 28% and 16%, respectively. At these four QTLs and six others, the PF allele exerted the expected effect, making the fruit rounder. In contrast, for six QTLs (38%) the PF allele elongated the shape of the fruit, which is desirable for processing tomatoes; however the percent phenotypic variance explained by these transgressive QTLs was lower than 5%.

Several QTLs associated with fruit shape in the current study may be conserved with the QTLs identified in previous studies (Grandillo et al. 1999a). For example, *fs8.1*, mapping at the centromeric region of chromosome 8, was detected in all four AB-QTL studies conducted so far in tomato, as well as in a PM BC1 population (Grandillo and Tanksley 1996). At this QTL all the wild alleles caused the fruit to be rounder. With the exception of the H population, this QTL explained a large portion of the total phenotypic variance, with PV values of 45%, 37% and 28% for the PM, PV and PF populations, respectively.

Firmness. The firmness of the fruit was associated with 12 QTLs and none of them explained more than 9% of

the total phenotypic variance. For six (50%) of these QTLs, PF alleles were associated with increased firmness. Two of these positive QTLs, *fir6.2* and *fir11.1*, were detected in the PV study, and also the PV allele at the corresponding QTL increased fruit firmness. In the PM study a QTL in common with *fir3.1* was found, and in that case too the wild allele increased the firmness of the fruit.

Total acids. The total acids content was measured only in CA and four genomic regions were significantly associated with the trait, with PV values ranging from 7% to 12%. For two of these QTLs, *ta4.1* and *ta9.1*, the PF allele determined an increase in total acids. This trait was measured also in the PV study; however in that population no region of the genome was significantly associated with total acids.

Total organic acids. The total organic acids content was measured only in CA. Two significant QTLs were identified, *toa9.1* and *toa12.1*; in both cases the PF allele increased the trait. TOA was evaluated also in the PV study, and no significant QTL was identified.

pH. Ten significant QTLs were found for pH, and for two of them, *ph3.1* and *pH7.1*, the PF allele increased the trait. For six QTLs the percent of the phenotypic variance explained was higher than 10%, with the highest value of 22% reported for *pH9.1*. Several of these QTLs may be in common with the pH QTL detected in previous studies. *pH4.1* and *pH12.1* share similar positions with the H QTL, and in both cases the wild allele decreased pH. In the PM study two QTLs *pH3.1* and *pH7.1*, were found which could be in common with the PF QTL; at *pH3.1* the PM allele increased the pH, whereas at *pH7.1* the PM allele caused a decrease of the trait. *pH9.1* is potentially in common with the PV QTL *pH9.1*; however, the PV allele increased the pH.

Maturity. Sixteen significant QTLs were identified for maturity. *mat5.1* was the QTL explaining the largest portion of the total phenotypic variation (18%), whereas all the other QTLs explained less than 10%; *mat5.1* was also found in the PM and H studies. In all instances the wild alleles had an undesirable effect, delaying maturity. Five (30%) QTLs detected in this study, *mat3.1*, *mat3.2*, *mat6.1*, *mat 7.1* and *mat9.1*, had a favourable effect on maturity. Two of these, *mat3.2* and *mat6.1*, were not detected in other tomato QTL studies. *mat 7.1*, on the other hand, was also found in the H study, but the H allele had a negative effect on the trait. *mat 3.1* and *mat 9.1* were in common with QTLs in the PV and PM studies, respectively, and in both cases the wild allele reduced the time to maturity. Other potentially orthologous QTLs are *mat2.1* and *mat9.2*, detected also in the PV and H studies, respectively; in all instances the wild alleles delayed maturity.

Horticultural acceptability. This trait was measured only in CA, and three significant QTLs were identified, *ha1.1*, *ha5.1* and *ha9.1*, with PV values of 3%, 15% and 6%, respectively. For *ha1.1*, the PF allele increased the horticultural acceptability. This QTL is potentially orthologous to the PV QTL *ha1.1*, and the H QTL *vu1.1*; however, both the PV and H alleles at these QTLs decreased the horticultural acceptability. *ha5.1* is potentially in common with the H QTL *vu5.1*, and the H allele also decreased the trait.

Cover. Nineteen QTLs, distributed over ten chromosomes, were significantly associated with cover. The largest portion of the total phenotypic variation was explained by *cvr5.2* (PV=20%); all the other QTLs were characterized by PV values lower than 10%. For 14 QTLs (74%), including *cvr5.2*, the PF allele improved the trait. Three of these favourable QTLs (*cvr1.3*, *cvr3.1* and *cvr5.1*) were detected also in the PV study, while *cvr 8.2* was in common with the QTL in the H study and *cvr5.2* to a QTL in the PM study. Although for *cvr1.3*, *cvr 5.1* and *cvr 5.2* the effects of the different wild species were consistent, contrasting effects were found in the case of *cvr3.1* and *cvr8.2*. A QTL, detected in all four AB-QTL studies conducted in tomato so far, was *cvr8.1*. At this locus only the PV allele had a favourable effect, whereas all the other three wild species (PF, PM and H) determined a reduction in cover. *cvr3.2* was detected also in the H study, and the H allele increased the trait.

Puffiness. Thirteen QTLs significantly influenced puffiness, with PV values ranging from 2% to 12%. For five (39%) of these the PF allele reduced the puffiness of the fruit. *puf8.1* mapped to the same chromosomal position as the PM QTL *puf8.1*, and both wild alleles at this region improved the trait.

Pericarp thickness. Seven QTLs were identified for this trait, all explaining less than 9% of the total phenotypic variance. At two QTLs, *pcp1.1* and *pcp1.2*, the PF allele increased the thickness of the pericarp (which is desirable) by 28% and 24%, respectively. This trait has been measured also in the PV study where no significant QTLs were detected, and in a PM BC1 population (Grandillo and Tanksley 1996) where four QTLs were detected. Only *pcp10.1* shares a similar chromosomal location with the PM QTL *fp10.1*, and in both cases the wild alleles decreased the thickness of the pericarp.

Veins. This trait was measured only in CA and IS. Two significant QTLs were found, *vns1.1* and *vns6.1*, explaining 4% and 5% of the total phenotypic variance, respectively. For *vns1.1*, the PF allele exerted a positive effect on the trait. No common QTLs were detected for VNS between this and the other AB-QTL studies.

Traits measured only in this study

Ostwald. The serum viscosity, evaluated only in CA, was associated with a single QTL on chromosome 6, *ost6.1*,

which explained 17% of the total phenotypic variation and increased the serum viscosity by 59%.

Yellow. The internal yellow color was evaluated only in CA, and a single QTL of major effect was identified on chromosome 12, which explained 21% of the total phenotypic variance. At this QTL the PF allele had a negative effect, increasing the trait by 84% (Tanksley et al. 1998).

Lycopene and b-carotene. *Lycopene* (LYC) and *b-carotene* (BC) were measured only in CA. For LYC, five significant QTL were found. The largest portion of the total phenotypic variance was explained by *lyc5.1* (PV=10%). For two QTLs, *lyc2.1* and *lyc3.1*, the PF allele increased lycopene levels.

BC was significantly associated with six QTLs, two of which, *bc4.1* and *bc10.1*, explained a large portion of the total phenotypic variance (PV values of 21% and 17%, respectively). For five (83%) of these QTLs the PF allele increased the b-carotene content in the fruit.

Two regions of the genome contain both a LYC and a BC QTL. On chromosome 2, *lyc2.1* and *bc2.1* are less than 20 cM apart, and on chromosome 8, *lyc8.1* and *bc8.1* are less than 5 cM apart. In both cases, the effect of the wild allele is in the same direction (the region on chromosome 2 increasing both beta-carotene and lycopene, and the region on chromosome 8 decreasing both). Therefore, these QTLs appear to affect some step in the pigmentation pathway prior to the conversion of beta-carotene to lycopene. However, none of the QTLs identified here (see Fig. 1) are located near the known pigmentation genes (with the possible exception of *lyc12.1* which is 20–25 cM away from Delta), so further inferences are not possible.

Some of the LYC and BC QTLs shared similar chromosomal locations with fruit color QTLs. For example, *bc2.1* is most probably the same QTL as *ic2.1*; for both QTLs the PF allele improved the color. *lyc2.1*, on the other hand, maps to the same position as *ic2.2* and *ec2.1*. In all instances the PF allele increased the intensity of the red color. It is likely that these three QTLs identify the same locus. Another region characterized by the clustering of different fruit color QTL is the interval between CT111 and CT148 on chromosome 8 (*ec8.1*, *ic8.1*, *fc8.2*, *lyc8.1* and *bc8.1*). For all these QTLs the PF allele exerted a negative effect on the color of the fruit. Although beta-carotene is generally associated with an orange (rather than a red) color, the close proximity and unidirectional effects of the wild allele for all these color-related traits implies that they are in some way involved in the same pigmentation pathway.

Epidermal reticulation. Epidermal reticulation of the fruit, evaluated only in SP, was associated with four QTLs. One of these, *er4.1*, explained a very large portion of the total phenotypic variance (PV=67%), whereas the other three, *er6.1*, *er8.1* and *er12.1*, had PV values of 8%. In all instances the PF allele had a negative effect from an agronomic point of view, increasing the reticulation of the fruit.

Internal core. The internal core, evaluated only in CA, was significantly associated with three QTLs, all explaining less than 8% of the total phenotypic variance. For two QTLs, *cor1.1* and *cor8.1*, the PF allele had a desirable effect, reducing the amount of the internal core.

Conservation of QTLs across environments (locations)

Of the 30 traits analyzed in this study, 11 were evaluated at only one location, four traits at two locations, 14 traits at three locations and one trait at four locations. A total of 167 QTLs were detected for the 19 traits that were assessed at more than one location. Of these 167 QTLs, 19% were significant (at the parameters indicated above) at only one location, 44% were detected at two locations and 37% were detected at three or four locations. These results indicate that a large portion (81%) of the QTLs detected in this study are conserved across locations, suggesting very little environment by QTL interaction. This is in agreement with other QTL studies conducted in tomato (Tanksley et al. 1996; Fulton et al. 1997b; Bernacchi et al. 1998a), as well as in maize (Ragot et al. 1995).

Among the 19 traits evaluated at more than one location, seven gave inconsistent results among locations, for a total of 11 QTLs. For example, 4 of the 19 CVR QTLs (*cvr1.3*, *cvr3.1*, *cvr5.2* and *cvr11.1*) showed opposite effects at different locations. This could be due to different growing conditions and horticultural practices among locations. However, for 9 of the 11 QTLs, the difference in the direction of the effect associated with the PF allele was detected only at the lowest level of significance ($P<0.1$), suggesting that overall the direction of the effect associated with the PF allele was conserved across locations.

Favourable QTL alleles of wild origin

In the following section only 27 traits, out of the total 30 evaluated, will be considered. The three traits pH, TA and TOA will not be included because changes in these characters are not necessarily positive or negative as long as the traits are kept within an acceptable range for processing purposes. Of the 183 QTLs identified for the 27 traits considered, 76 (42%) corresponding to 19 (70%) traits, had trait-improving alleles derived from *L. parviflorum* (Table 1). Desirable PF alleles were identified not only for traits for which *L. parviflorum* showed a superior phenotype (e.g., BRX and CVR) but also for those traits for which the PF phenotype was agronomically inferior (e.g., YLD, FW, IC, EC and HA). However, no favourable PF alleles were found for eight traits (RDY, BOS, BRY, YEL, FC, GEL, ER and SHD). The highest percentages of trait-improving PF alleles, 100%, 83% and 74%, were detected for the traits BRX, BC and

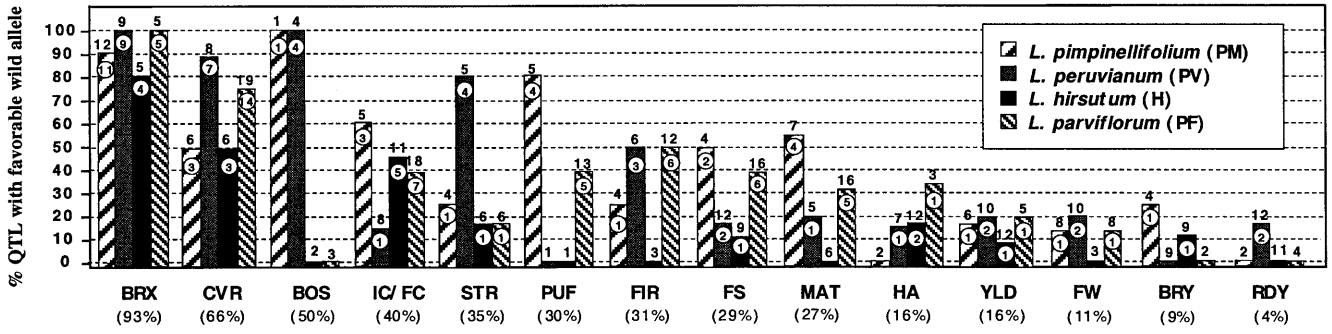


Fig. 3 Percentages of QTLs with favourable alleles (from an horticultural perspective) detected for *L. pimpinellifolium* (*wide striped bars*) (Tanksley et al. 1996), *L. peruvianum* (*gray bars*) (Fulton et al. 1997b), *L. hirsutum* (*black bars*) (Bernacchi et al. 1998) and *L. parviflorum* (*narrow striped bars*). The total numbers of QTLs detected for each trait are indicated above the bars. The number of QTLs with favorable wild alleles are indicated in *white circles*. The average percent of favourable QTL alleles estimated across the four wild species are indicated in *parenthesis* below each trait acronym. For trait abbreviations, see Table 1

CVR, respectively. Relatively high percentages of desirable PF alleles were also found for COR (67%), FIR (50%) and IC (47%).

Of the 27 traits considered, 15 (YLD, RDY, BRX, BRY, FW, FS, IC, FC, BOS, CVR, STR, PUF, FIR, MAT and HA) were also measured in all three previous AB-QTL studies, PM, PV and H, for a total of 130 QTL. However, it is worth pointing out that for a few traits, e.g., fruit color and horticultural acceptability, the evaluations were performed in slightly different ways in each study. In order to be consistent across the different studies, the two traits IC (internal fruit color determined visually on fresh fruits) and FC (analytical measurements taken on processed products) were combined into one trait (referred to as IC/FC) for the purpose of comparison. When the QTLs of the original traits, IC and FC, mapped to the same marker, they were assumed to be the same and a single QTL was then considered.

For the resulting 14 traits it was possible to compare the different rates of positive QTLs detected in all four wild tomato accessions (Fig. 3). Similarly to the results reported for the PF study, high rates of wild QTL alleles were found in all AB-QTL populations considered for BRX and, to a lower extent, for CVR. More specifically, for 100%, 90% and 80% of the QTLs detected, the wild allele exerted a positive effect in the PV, PM and H studies, respectively. These results were expected, since all four wild species had a superior phenotype with respect to BRX and CVR. In contrast, more unexpected were the frequencies of positive QTLs found for IC/FC, FS, YLD, FW and BRY, traits for which almost all wild species are characterized by an inferior phenotype.

The average percent of favourable QTL alleles estimated across the four wild species ranged between a minimum of 4% for the trait RDY to a maximum of 93% for BRX. Over all 14 traits, the highest percentage of positive QTL was identified in the PM study (42%), followed by 39%, 32% and 17% found for the PV, PF and H studies, respectively. No favourable QTLs were found for three (out of these 14) traits in the PF study, as compared to two traits in the PM and PV studies and six traits in the H study (Fig. 3).

The breeding value of trait-improving wild QTL alleles depends on their possible association with negative effects on other traits. In the present study a large number of traits were measured, which increased the chance of detecting QTLs for a specific trait associated with QTLs affecting other traits. There are, in fact, several regions of the genome that appear to influence clusters of traits. For example, a 22-cM region at the bottom of chromosome 9 is significantly associated with 12 (40%) of the 30 traits measured in this study. Although for some of the QTLs falling in this region the PF alleles caused desirable effects (e.g., *cvr9.1*, *brx4.1*, *bc9.1* and *ic9.2*), for other traits the wild alleles exerted negative effects (e.g., *mat9.2*, *puf9.1*, *fs9.1*, *bos9.1* and *ha9.1*). The mapping resolution achieved in this study is not sufficient to determine whether pleiotropy (where a single gene affects multiple characters) or tight linkage is the genetic cause of the association of the multiple QTLs. In order to be able to rule out either one of these possibilities, fine mapping and a more detailed study of the regions containing these QTLs would be needed. For those instances in which the association is due to linkage, molecular-assisted breakage of the unfavourable linkage would make it possible to utilize those potentially positive wild-QTL alleles for breeding purposes.

Despite the tendency of negative and positive QTL to cluster together, at least 12 of the trait-improving PF QTLs had no detectable deleterious effects on any other measured trait (Fig. 1, Table 1); this is the case, for example, for several of the QTLs mapping on chromosome 1 (*vns1.1*, *fs1.1*, *pcp1.2* and *ic1.1*) and on chromosome 3 (*cvr3.1*, *mat3.1* and *fs3.1*). Although further evaluation is required to determine whether new, previously undetected, secondary effects would be observed in near-isogenic lines containing single-QTL introgressions, it is possible that these agronomically favourable PF QTL alleles would be immediately useful for improving processing tomatoes.

Conservation of QTLs across species

Of the total 30 traits evaluated in this study, 16 (including pH), were also measured in all previous AB-QTL

studies. For these traits a total of 140 QTLs were identified, and 56 (39%) of them were potentially orthologous between PF and at least one of the three wild species, PM, H and PV (Table 1, Fig. 1). The largest number of 26 (19%) potentially common QTLs was found with the H wild species followed by the 23 (16%) and 15 (11%) found for PV and PM, respectively. This concurs with previous information regarding the genetic distance between these species (Miller and Tanksley 1990). Seven (13%) QTLs were in common with at least two other populations, and two of them, *fs8.1* and *cvr8.1*, were detected in all four AB-QTL studies conducted so far.

For 42 (75%) of the apparently orthologous QTLs, the QTL alleles from different species had similar allelic effects. These include for example *yld2.1*, *fw3.1*, *fw7.1* and *pH4.1*, for which the different wild alleles were all associated with an inferior performance or a decrease in the trait in the case of pH; and *brx5.1*, *fs1.1* or *pH3.1*, for which the wild alleles were all associated with a superior performance or an increase in the trait in the case of pH. For the remaining 14 (25%) QTLs the different wild-species QTL-alleles had opposite effects. More specifically, for nine (16%) potentially common QTLs the PF allele had a positive effect on the trait, whereas the PM, H or PV allele had a negative effect.

For the 15 traits measured in all AB-QTL studies (not including pH), a total of 130 QTLs were detected, and for 52 (42%) of them the PF allele exerted a favourable effect. Of these 52 positive PF QTLs, 60% (31) are potentially unique for the PF genome. This is the case, for example, for *fw12.1* in which the PF allele caused a 30% increase in fruit weight; or for *ic1.1* and *ic2.1*, characterised by PF alleles improving the intensity of the internal color by 23% and 38%, respectively. For the two traits, CVR and PUF, a large number of QTLs potentially unique for *L. parviflorum*, were found (nine and five QTLs, respectively).

The estimate of 31 favourable PF QTLs potentially unique for *L. parviflorum*, however, has to be considered as only an approximate estimate. In fact, there are probably more PF QTL that were not detected in the present study; moreover, only a subset of the seven wild species of the cultivated tomato has been screened so far for many of the traits reported in the present study. In addition, in the PV and H studies several regions of the genome showed partial or complete skewness towards the recurrent parent allele, not allowing the identification of any QTL.

Since these QTLs are linked to molecular markers, marker-assisted selection can be readily applied and the different QTL-NILs produced by AB QTL breeding can be easily intercrossed to pyramid different QTL alleles for the same traits or different traits in order to obtain can even greater potential improvement. The fact that sometimes the direction of the allelic effect of the different species (relative to the E parent) varies for a given QTL is encouraging, and justifies a wider marker-assisted exploitation of exotic accessions for the identification of trait-improving wild-QTL alleles.

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