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ORIGINAL PAPER

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Advanced backcross QTL analysis of a *Lycopersicon esculentum* × *L. pennellii* cross and identification of possible orthologs in the Solanaceae

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Abstract In this study, the advanced backcross QTL (AB-QTL) mapping strategy was used to identify loci for yield, processing and fruit quality traits in a population derived from the interspecific cross *Lycopersicon esculentum* E6203 × *Lycopersicon pennellii* accession LA1657. A total of 175 BC_2 plants were genotyped with 150 molecular markers and BC_2F_1 plots were grown and phenotyped for 25 traits in three locations in Israel and California, U.S.A. A total of 84 different QTLs were identified, 45% of which have been possibly identified in other wild-species-derived populations of tomato. Moreover, three fruit-weight/size and shape QTLs (*fsz2b.1*, *fw3.1*/*fsz3*.1 and *fs8.1*) appear to have putative orthologs in the related solanaceous species, pepper and eggplant. For the 23 traits for which allelic effects could be deemed as favorable or unfavorable, 26% of the identified loci had *L. pennellii* alleles that enhanced the performance of the elite parent. Alleles that could be targeted for further introgression into cultivated tomato were also identified.

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Introduction

Twenty years ago the first molecular genetic-linkage map of tomato was published (Tanksley et al. 1992). This map was based on an F_2 population derived from an interspecific cross between cultivated tomato, *Lycopersicon esculentum*, and its wild relative, *Lycopersicon pennellii*. Since this initial report, maps for other and more advanced *L. esculentum* × *L. pennellii* populations (for example, Eshed and Zamir 1995; Haanstra et al. 1999) and for populations from other wild species crosses (for example, Goldman et al. 1995; Tanksley et al. 1996; Fulton et al. 1997a; Bernacchi et al. 1998) have been published. Frequently these interspecific populations have also been used for the identification of quantitative trait loci (QTLs) for important agronomic and horticultural traits. As a result, comprehensive QTL information is now available for populations derived from several wild species of tomato: *Lycopersicon hirsutum* (Bernacchi and Tanksley 1997; Bernacchi et al. 1998), *Lycopersicon peruvianum* (Fulton et al. 1997b), *Lycopersicon parviflorum* (Fulton et al. 2000) and *Lycopersicon pimpinellifolium* (Grandillo and Tanksley 1996; Tanksley et al. 1996; Doganlar et al. 2002a). Most of this information was provided by analysis of advanced backcross (AB) populations. Although two studies examined some growth (de Vicente and Tanksley 1993) and yield-related (Eshed and Zamir 1995) parameters in *L. pennellii*-derived F_2 and introgression-line populations, there has been no report of QTLs identified in a *L. pennellii* AB population.

The AB-QTL mapping strategy integrates the processes of QTL discovery and introgression from wild germplasm into elite material (Tanksley and Nelson 1996). Instead of an F_2 population, this approach uses BC_2 or BC_3 populations derived from an interspecific cross for the identification and mapping of trait loci. Thus, both molecular-marker and phenotypic analyses occur at a more advanced generation when the cultivated parent's alleles are at a much higher frequency. Once favorable alleles for various loci are identified, only a few more crosses are required to develop near-isogenic lines

that can be field-tested and used for variety development. The AB-QTL method was first applied in tomato (Tanksley et al. 1996) and has since been adapted for use in rice (Xiao et al. 1996, 1998; Moncada et al. 2001), wheat (Huang et al. 2003), maize (Ho et al. 2003) and pepper (Rao et al. 2003).

The present paper describes the results from an AB-QTL study of a *L. esculentum* (cultivar E6203) × *L. pennellii* (accession LA1657) BC_2/BC_2F_1population. *L. pennellii* is found in some of the most-arid habitats of all tomato species, and accessions within the species can exhibit extreme genetic variability (Rick and Tanksley 1981). Like most other *L. pennellii* accessions, LA1657 is self-incompatible. Both of the previous *L. pennellii* QTL studies used the self-compatible accession, LA716 (de Vicente and Tanksley 1993; Eshed and Zamir 1995). Both LA1657 and LA716 are from the western regions of Peru; however, their distributions are not identical. LA1657 is usually found in northern regions of the geographic distribution while LA716 is found in southern regions. Moreover, LA1657 prefers higher elevations (about 700 m) than LA716 (20 m) (Rick and Tanksley 1981). Because LA1657 is from a different region of the geographical distribution of the species and is genetically divergent from LA716, it was chosen for this study. The AB-QTL population was grown in three locations in two important tomato-producing regions: Israel and California, U.S.A. Plots were assessed for 25 yield, processing and fruit-appearance traits. Thus, this work extends tomato AB-QTL analyses to a fifth wild species and allows more extensive cross-species comparisons of the control of agronomically important traits in tomato and other solanaceous crops.

Materials and methods

Population development and field evaluations

The population was developed using the processing inbred line *L. esculentum* cultivar E6203 (hereafter referred to as LE) as the recurrent parent and *L. pennellii* accession LA1657 (hereafter referred to as PN) as the donor parent. A total of 320 BC_1 plants were derived from a single F_1 individual and were genotyped with several RFLP markers to select against undesirable phenotypes. TG125 was used to select for homozygous LE alleles at the self-incompatibility locus, *S*, on chromosome 1 to increase the fertility of the plants. TG167 and TG36 were used to screen for LE alleles at fruit-weight QTLs on chromosomes 2 (*fw2.2*) and 11 (*fw11.3*), respectively, to select for larger fruit. In addition, TG279 was used to select for homozygous LE alleles at the *Sp* locus on chromosome 6, thus ensuring that the plants would have a determinate growth habit. This type of growth habit is essential for mechanical harvesting of processing tomatoes. After this marker-assisted selection, eight BC_1 plants were backcrossed to LE to obtain 175 BC_2 plants which were genotyped with RFLP markers for map development. BC_2F_1 families were derived from each of the BC_2 individuals by crossing with TA496 (E6203+*Tm2*^{a}) and were field-tested during the summer of 1998 in Akko, Israel (IS), Woodland, California, U.S.A. (CA1) and Acampo, California, U.S.A (CA2). Plants were grown in randomized plots of 30 plants each with six plots of LE as controls.

Marker and linkage analysis

Genomic DNA extraction, restriction enzyme digestion, Southern hybridization, washing and autoradiography were performed as described in Bernatzky and Tanksley (1986). Parental DNA was surveyed for polymorphism after digestion with *Eco*RI and *Hin*dIII using RFLP markers that were selected at 3-cM intervals from the high-density tomato map (Tanksley et al. 1992). From the surveys, 150 polymorphic markers spanning the entire genome at intervals of less than 20 cM were chosen to genotype the BC_2 individuals.

Marker segregation was tested for significant ($P<0.001$) deviation from the expected frequency of heterozygotes for a BC_2 population (25%) using the χ^2 goodness-of-fit analysis. The "group" and "ripple" commands of Mapmaker (Lander et al. 1987) were used to establish the most-likely order of markers in each linkage group at LODs 4.0 and 3.0, respectively. Recombination was computed in Kosambi units (Kosambi 1944) using the QGene computer program (Nelson 1997).

Trait evaluations

A total of 25 agronomic traits were evaluated for each plot. Six of the traits were measured at all three locations, seven at two locations and the remaining 12 at only one location. The criteria used for assessing each trait are described below.

Yield traits

Total yield (YLD), red yield (RDY) and percent green yield (PGY) were measured in both IS and CA1. YLD was measured in kilograms and pounds, respectively, and included both ripe (red) and unripe (green) fruit. RDY was the weight of the ripe-red fruit and the weight of the unripe fruit was used to calculate PGY. Plant fertility (FERT) was evaluated only in CA2 using a scale of 1 to 5. A low-fertility rating indicated that the plot had reduced fruit set while a high rating indicated heavy fruit set. The percentage of rotten fruit on the plants in a plot (ROT) at harvest time was assessed only in IS.

Processing traits

Soluble solids content (SSC) was measured in all three locations in Brix using a refractometer as described in Tanksley et al. (1996). Higher values indicated increased sugar content. Soluble solids content was multiplied by red yield to obtain Brix × red yield (BRY) in IS and CA1. This value gives an estimate of the amount of processed product that can be expected from a given line. Juice viscosity (VIS) was measured as Bostwick only in CA1, lower values indicated greater viscosity. Fruit pH (PH) was also measured only in CA1. Thickness of the fruit pericarp (PCP) was evaluated on transverse sections of the fruit on a scale of 1 to 5 (1, thin; 5, thick pericarp) in IS and CA2, and in millimeters in CA1. Fruit firmness (FIR) was assessed by hand-squeezing the fruit (1, soft; 5, very firm). Stem retention (STR) was evaluated only in IS as the percentage of fruit that retained their stems after harvest by shaking the fruit from the plants.

Fruit appearance

Fruit weight (FW) in grams was measured on a random sample of approximately 50 fruit from each plot in IS and CA1. In CA2, fruit size (FSZ) was rated visually (1, very small; 5, very large). Fruit shape (FS) was also measured visually in all three locations on a scale of 1 to 5 where 1 indicated round fruit and 5 indicated elongated fruit.

Fruit color was assessed in four ways. The external color (EC) of ripe fruit was measured using a scale of 1 to 5 (1, light-red; 5, dark-red) in all three locations. Internal color (IC) was also

measured on transverse sections of the fruit in all locations using the same scale as EC. The amount of orange coloration (OR) on the fruit exterior was measured only in CA2 using a scale of 1 to 5:1, very orange; 5, very red. Fruit color (FC) was also measured on raw, de-aerated puree using a spectrophotometer in CA1.

Puffiness (PUF), or the amount of intralocular air space in transversely cut fruit, was evaluated in IS and CA1 using a scale of 1 to 5 (1, very puffy; 5, not puffy). Epidermal reticulation (ER) was measured in IS and CA2, and described whether the fruit skin was smooth (scored as 1) or reticulated like a cantaloupe (scored as 5). The percentage of the fruit that were cracked (PCF) was evaluated only at CA1. Yellow eye (YE) assessed whether the stem-scar penetrated into the fruit. This was measured in CA1 by examining longitudinally cut fruit and estimating the percentage of fruit with YE. Grey wall (GW) was measured in CA1 on transversely cut fruit and was also assessed as a percentage of the fruit with GW. The color of the gel (GG) in the interior of the fruit was scored in CA2 using a scale of 1 (green-gel) to 2 (red-gel).

Data analysis

Pearson's correlation coefficients were calculated for each trait/location combination using the QGene program (Nelson 1997). QGene was also used to perform single-point regression analysis to identify molecular markers with significant linkage to each trait. A QTL is only reported here if it was observed in two or more locations at $P<0.01$ or in one location at $P<0.001$. The percent of the phenotypic variation explained (%PVE) by a given QTL was calculated from the regression of each marker/phenotype combination. The percent phenotypic change or additivity (%A) associated with the presence of a PN allele at a given locus was calculated as $2\times100[(AB-AA)/AA]$, where AA was the phenotypic mean for individuals homozygous for the LE allele at the most-significant marker for the locus and AB was the mean for heterozygous individuals. Because half of the individuals in each BC_2F_1 plot would be heterozygous for any fragment that was heterozygous in the BC_2 generation, the factor of 2 was included to obtain the estimate of %A. Multiple regression analysis was performed in StatView (SAS Institute Inc., Cary, N.C.).

Results

Marker segregation and the genetic map

A total of 152 RFLP markers were genotyped for the BC_2 population. Of these, 110 (72%) were segregating and could be mapped; the remaining 42 markers were fixed for LE alleles. Many of the markers fixed for LE alleles corresponded to the chromosomal regions for which marker-assisted selection was applied to remove the wild parent allele in the BC_1 population. Thus, the top half of chromosome 1 was fixed for LE alleles as a result of selection at the *S* locus (TG125). Marker-assisted selection at *fw2.2* and *fw11.3* resulted in fixation of the middle of chromosome 2 and the bottom half of chromosome 11. In addition, selection at the *Sp* locus on chromosome 6 resulted in fixation of the middle part of this chromosome for LE alleles. Three other regions of the genome encompassing more than one marker were also fixed for LE alleles: the bottom of chromosome 1, a bottom portion of chromosome 4 and the top of chromosome 7. Fixation of these regions cannot be explained by marker-assisted selection. Instead, it may be the result of genetic drift because the BC_1 population that gave rise to the BC_2 was very small.

The average number of heterozygotes per locus was 27% which was nearly identical to the expected value of 25% for a BC_2 population. A total of 31 markers (28%) showed significant ($P<0.001$) deviation from the expected frequency of heterozygotes. Most of these markers were concentrated on six chromosomes. Three regions showed severe skewing with fewer heterozygotes than expected: the bottom of chromosome 5 (TG 60 to CT138, three markers), the top of chromosome 6 (CT216 to TG178, two markers) and the top of chromosome 11 (TG497 to TG523, three markers). Three larger chromosomal regions exhibited segregation distortion with an excess of heterozygotes. The bottom half of chromosome 7 (TG217 to CT195, six markers) and the top half of chromosome 10 (TG230 to TG408, five markers) were moderately skewed while the top half of chromosome 12 (TG180C to CT211A, five markers) was very severely distorted. More than 90% of the population was heterozygous for three of the markers (TG180C, TG68, TG263) in this region.

The 110 mapped markers fell into 15 linkage groups, as markers from the tops and bottoms of chromosomes 2, 4 and 6 could not be linked at the LOD 3.0 threshold (Fig. 1). In all, 87 (79%) of the markers were considered to be framework markers as they were positioned with a ripple at $LOD\geq3.0$. All but one of the remaining markers mapped to the intervals between framework markers at $2.0\leq LOD<3.0$. TG587 on linkage group 4 did not link to the rest of the linkage group, therefore it was assigned to a separate linkage group. The map spanned approximately 703 cM, 55% of the genetic distance encompassed by the high-density tomato map (Tanksley et al. 1992). Coverage was primarily limited by the high percentage of non-segregating markers (28%) many of which (23 of 41 markers) corresponded to regions that were affected by marker-assisted selecton. With only one exception (TG581 on the bottom of chromosome 6), the marker order of the framework map agreed with the high-density map.

Trait correlations

For traits measured in more than one location, the strongest correlations across locations were observed for YLD and RDY ($r=0.72$ and 0.71, respectively) in IS and CA1, and the yield-derived trait, BRY ($r=0.61$), at the same locations (data not shown). FW/FSZ also showed significant ($P<0.05$) positive correlations ($r=0.31$ to 0.53) across locations as did ER ($r=0.47$), SSC ($r=0.19$ to 0.33) and EC ($r=0.23$ to 0.27). None of the other traits that were measured in more than one location (FS, IC, PCP, FIR, PUF and PGY) showed significant correlations across locations.

Within each location, significant correlations were also detected between many traits. However, only those that were highly significant ($P<0.001$), or were observed in more than one location, are described here. For traits

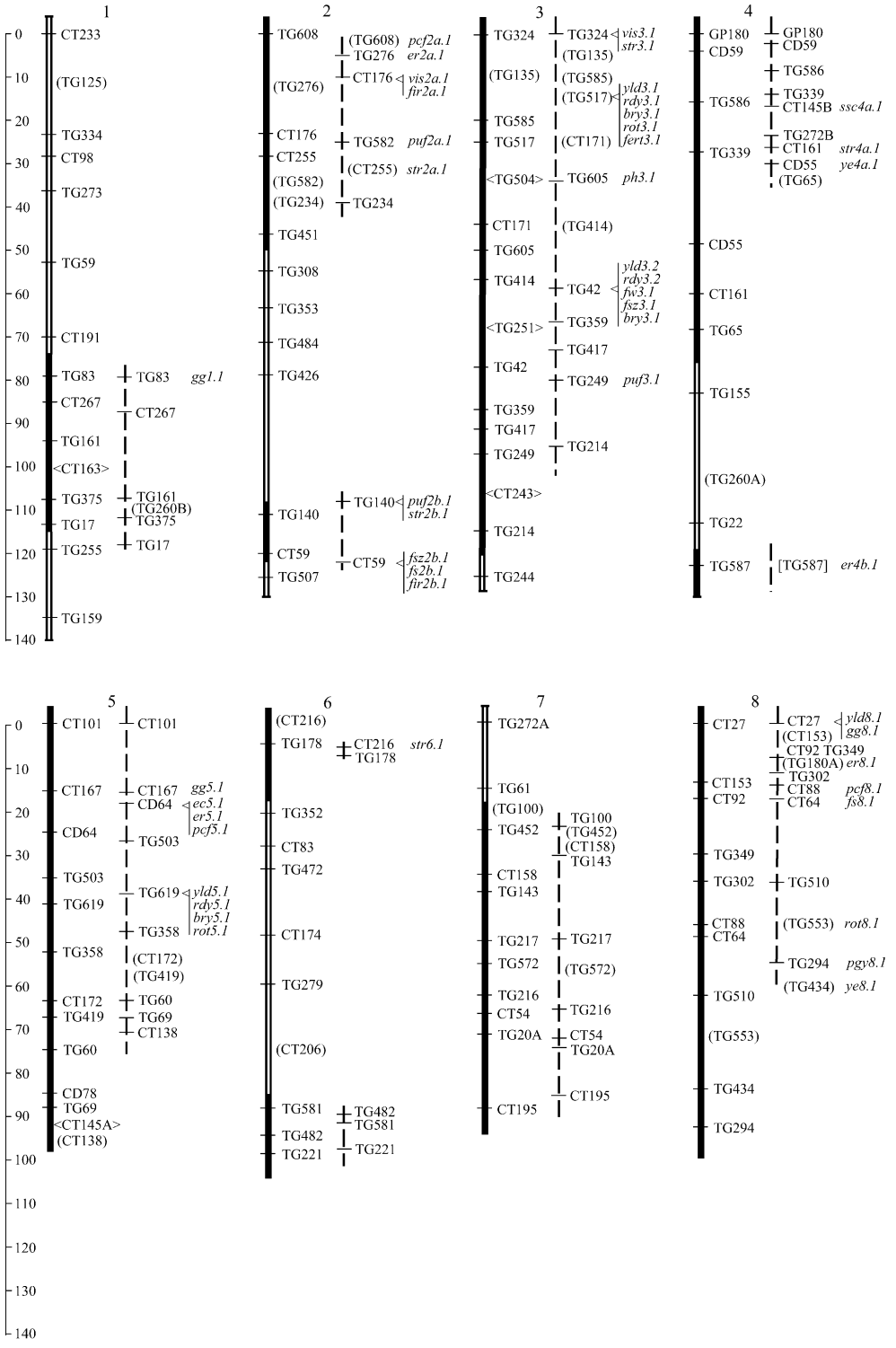
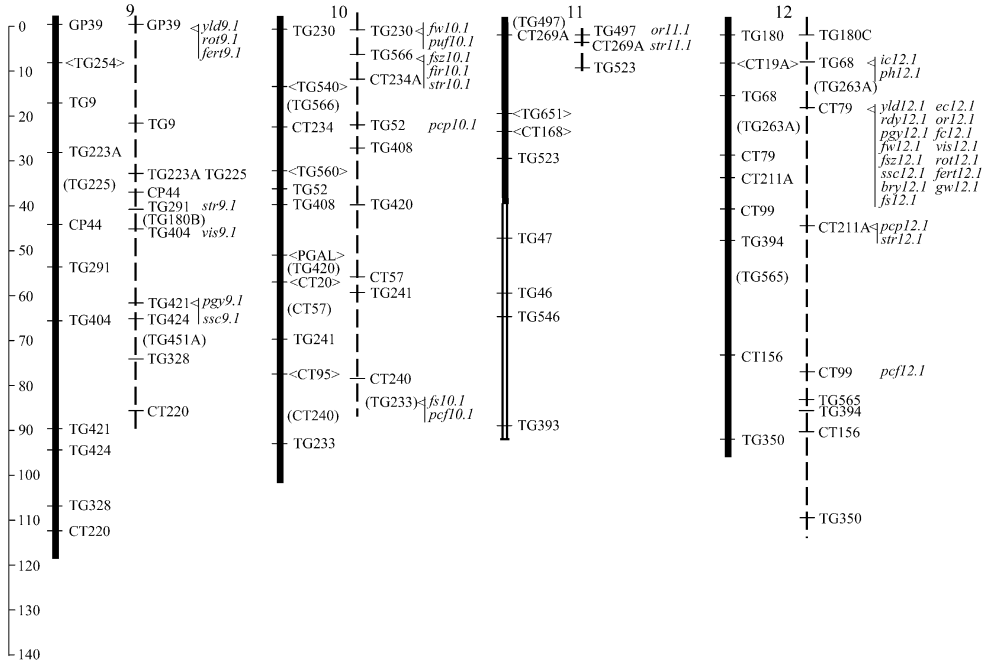


Fig. 1 Comparison of the BC_2 molecular linkage groups (*dashed lines*) to the corresponding chromosomes from the high-density tomato map (*bars*). The centiMorgan scale is given on the far left. Sections of the chromosomes drawn as *open bars* were not segregating for PN alleles in the population. Markers in "<>" were also fixed for LE alleles. Markers in"()" were ordered at LOD<3.0. The marker in "[]" did not link to the rest of the linkage group. Identified QTLs are shown to the right of the BC_2 linkage groups. Co-segregating QTLs are connected by a *vertical line* with a "<" to indicate the most-significant marker

measured in multiple locations, correlation values are averaged across locations. YLD and RDY were both positively correlated with FW (r=0.55 and 0.53, respectively) but were negatively associated with SSC (r=–0.46 and –0.45, respectively). Negative correlations were also observed between SSC and the traits FW/FSZ (r=–0.46), VIS (r=–0.68), EC (r=–0.23) and FERT (r=–0.28). FW/FSZ was positively correlated with EC in two locations (r=0.31), FERT in CA2 (r=0.40) and YE in CA1 (r=0.46). The fruit-color traits, EC and IC, were positively associated in all three locations (r=0.53).

Fig. 1 (continued)



QTLs detected for each trait

A total of 48 QTLs were identified for the 15 traits measured in IS, 43 (90%) of these were significant at $P<0.001$ and the remaining five were significant at $P<0.01$ and identified in at least one other location. A total of 39 QTLs were detected for the 18 traits measured in CA1 with 28 (72%) of the loci detected at $P<0.001$. In addition, 25 QTLs were identified for the 11 traits measured in CA2 with 24 (96%) of the loci identified at the more-stringent significance threshold. For many traits, the QTLs detected in different locations mapped to the same chromosomal positions. When these overlapping QTLs are counted as single loci, it is found that 84 different loci were identified for the 25 traits measured in the study. QTLs were detected on all chromosomes except chromosome 7 with the most loci found on chromosome 12, 20 QTLs. The QTL identified for each trait are described below, listed in Table 1 and mapped in Fig. 1.

Yield traits

Six QTL were identified for total yield on five different chromosomes. All six of these loci were detected in both IS and CA1. The locus on chromosome 12, *yld12.1*, was the most-significant and explained 56% and 32% of the phenotypic variation for the trait in CA1 and IS, respectively. For the other QTL, the percent phenotypic-variance explained (%PVE) was 10% or less. As determined by multiple regression analysis, together the six loci explained 39 and 28% of the variation for yield in CA1 and IS, respectively. The PN allele of only *yld9.1*, which was a relatively minor QTL in terms of significance and magnitude of effect, was associated with increased yield. Four QTLs were detected for red yield on three different chromosomes and all four were identified in both locations where this trait was measured. All of the QTLs had small %PVEs except for *rdy12.1* which controlled as much as 61% of the variance for red yield (in CA1). Overall, the four RDY loci accounted for 34% of the red yield variation in CA1. None of the QTLs showed favorable effects from the wild-alleles.

Three QTLs were found for the percent green yield on chromosomes 8, 9 and 12. Although the loci were highly significant ($P<0.0001$), none of them was detected in both IS and CA1, the two locations where the trait was measured. The most-significant QTL, *pgy12.1*, accounted for up to 19% of variation for the trait. For all three loci, the LE alleles were associated with an increased percent green yield. Three loci were also identified for fertility. As with YLD, RDY and PGY, the locus on chromosome 12, *fert12.1*, had the greatest magnitude of effect, a PVE of 41%. The three FERT loci accounted for 24% of the variation for the trait at CA2. For one of the QTLs, *fert 9.1*, the PN allele was associated with increased fertility. Five QTLs were detected for the amount of rotten fruit on the plants. Similar to the other yield traits, the locus on chromosome 12, *rot12.1*, was the most-significant and explained 19% of the variation in the trait. The other QTLs each accounted for less than 10% of the PVE. Together, the five ROT loci explained 24% of the variation for the amount of rot in IS. For all but one locus, *rot9.1*, the wild-alleles were associated with an increase in the amount of rotten fruit.

Table 1 Putative QTLs identified for each trait. *P*-values for the most-significant marker for each locus are given for Israel (IS) and the two California locations (CA1 and CA2). *Nd* indicates that the trait was not determined at that location, *ns* indicates that the marker was not significant. The percent phenotypic variation explained (%PVE) and percent additivity (%A) are only given for the location for which the QTL was most-significant (indicated by *P*-value in bold). The favorable-allele column indicates whether the *L. esculentum* (LE) or *L. pennellii* (PN) allele was associated with an agronomically favorable effect on the trait. The relative significance of each QTL is coded such that the number of +s indicates the number of locations at which the QTL was detected at $0.001<P<0.01$ and the number of *s indicates the number of locations at which the QTL was identified at $P<0.001$. Populations with putative orthologs are abbreviated: CA = *Capsicum annuum*, pepper; CM = *Lycopersicon cheesmanii*; H = *L. hirsutum*; PF = *L. parviflorum*; PM = *L. pimpinellifolium*; PN = *L. pennellii*; PV = *L. peruvianum*; SM = *Solanum melongena*, eggplant. CA1 = intra-specific *C. annuum* F_2 population (Ben Chaim et al. 2001), CA2 = *C. annuum* x *C. frutescens* advanced backcross population (Rao et al. 2003), CM1 = *L. esculentum* x *L. cheesmanii* F_2 population (Paterson et al. 1991); CM2 = *L. esculentum* x *L. cheesmanii* recombinant inbred population (Goldman et al. 1995); CM3 = *L. esculentum* x *L. cheesmanii* F_2 population (Monforte et al. 1997); H1 = *L. esculentum* x *L. hirsutum* advanced backcross population (Bernacchi et al. 1998); H2 = *L. esculentum* x *L. hirsutum* near-isogenic lines (Monforte et al. 2001); PF = *L. esculentum* x *L. parviflorum* advanced backcross population (Fulton et al. 2000); PM1 = *L. esculentum* x *L. pimpinellifolium* advanced backcross population (Tanksley et al. 1996); PM2 = *L. esculentum* x *L. pimpinellifolium* backcross population (Grandillo and Tanksley 1996); PM3 = *L. esculentum* x *L. pimpinellifolium* F_2 population (Monforte et al. 1997), PM4 = *L. esculentum* x *L. pimpinellifolium* backcross population (Chen et al. 1999); PM5 = *L. esculentum* x *L. pimpinellifolium* F_2 population (Lippman and Tanksley 2001); PM6 = *L. esculentum* x *L. pimpinellifolium* advanced backcross population (Fulton et al. 2002); PM7 = *L. esculentum* x *L. pimpinellifolium* inbredbackcross lines (Doganlar et al. 2002a); PN = *L. esculentum* x *L. pennellii* introgression lines (Eshed and Zamir 1995); PV1 = *L. esculentum* x *L. peruvianum* advanced backcrosspopulation (Fulton et al. 1997b); PV2 = *L. esculentum* x *L. peruvianum* advanced backcrosspopulation (Fulton et al. 2002); PV3 = *L. esculentum* x *L. peruvianum* near-isogenic lines (unpublished data); SM = *Solanum linnaeanum* x *S. melongena* F_2 population (Doganlar et al. 2002b)

Trait	QTL	Chr	Marker	*P*-value			%PVE	%A[a]	Favorable allele[b]	Relative significance	Populations with putative orthologs
				IS	CA1	CA2					
Total yield	*yld3.1*	3	TG517	**0.0003**	0.002	nd	8	−71	LE	*+	
	yld3.2	3	TG42	**0.0003**	0.002	nd	8	−77	LE	*+	H1;PF;PN
	yld5.1	5	TG619	**<0.0001**	0.0003	nd	10	−84	LE	**	
	yld8.1	8	CT27	**0.002**	0.004	nd	6	−78	LE	++	PF;PV1
	yld9.1	9	GP39	**0.005**	0.004	nd	5	86	PN	++	
	yld12.1	12	CT79	<0.0001	**<0.0001**	nd	56	−128	LE	**	H1;PV1
Red yield	*rdy3.1*	3	TG517	**0.0009**	0.005	nd	7	−70	LE	*+	
	rdy3.2	3	TG42	**0.0003**	0.005	nd	8	−80	LE	*+	
	rdy5.1	5	TG619	**0.0001**	0.001	nd	9	−84	LE	*+	PF;PV1
	rdy12.1	12	CT79	<0.0001	**<0.0001**	nd	61	−114	LE	**	H1
Percent green yield	*pgy8.1*	8	TG294	**0.0001**	ns	nd	9	271	LE	*	PV1
	pgy9.1	9	TG421	**<0.0001**	ns	nd	12	313	LE	*	H1
	pgy12.1	12	CT79	ns	**<0.0001**	nd	19	509	LE	*	
Fertility	*fert3.1*	3	TG517	nd	nd	**0.0002**	9	−53	LE	*	
	fert9.1	9	GP39	nd	nd	**0.0007**	7	72	PN	*	
	fert12.1	12	CT79	nd	nd	**<0.0001**	41	−97	LE	*	
Rotten	*rot3.1*	3	TG517	**0.0003**	nd	nd	8	−81	PN	*	
	rot5.1	5	TG619	**0.0003**	nd	nd	7	−81	PN	*	
	rot8.1	8	TG553	**0.0002**	nd	nd	9	−80	PN	*	PM7
	rot9.1	9	GP39	**0.0008**	nd	nd	7	121	LE	*	
	rot12.1	12	CT79	**<0.0001**	nd	nd	19	−106	PN	*	
Soluble solids content	*ssc4a.1*	4a	CT145b	ns	**0.0006**	ns	8	−15	LE	*	PF;PM1,6
	ssc9.1	9	TG421	ns	**0.0006**	ns	8	15	PN	*	H1;PF;PM7;PN
	ssc12.1	12	CT79	**<0.0001**	<0.0001	0.0005	30	48	PN	***	PM1,4;PN;PV2
Brix × red yield	*bry3.1*	3	TG517	**0.0003**	ns	nd	8	−65	LE	*	
	bry3.2	3	TG42	**0.0003**	0.006	nd	8	−68	LE	*+	H1;PN
	bry5.1	5	TG619	**<0.0001**	0.002	nd	11	−79	LE	*+	PF;PV1
	bry12.1	12	CT79	<0.0001	**<0.0001**	nd	53	−126	LE	**	H1;PN;PV1
Viscosity	*vis2a.1*	2a	CT176	nd	**0.0009**	nd	7	19	LE	*	
	vis3.1	3	TG324	nd	**0.0004**	nd	8	−20	PN	*	
	vis9.1	9	TG404	nd	**<0.0001**	nd	18	−24	PN	*	PM1;PV1
	vis12.1	12	CT79	nd	**<0.0001**	nd	18	−30	PN	*	
pH	*ph3.1*	3	TG605	nd	**0.0007**	nd	8	4	PN	*	
	ph12.1	12	TG68	nd	**<0.0001**	nd	18	7	PN	*	PM4;PV1
Pericarp thickness	*pcp10.1*	10	TG52	ns	ns	**<0.0001**	17	−24	LE	*	PF;PM2
	pcp12.1	12	CT211	**0.001**	ns	0.007	6	16	PN	++	
Fruit firmness	*fir2a.1*	2a	CT176	**<0.0001**	ns	ns	16	−50	LE	*	
	fir2b.1	2b	CT59	ns	ns	**<0.0001**	13	−44	LE	*	PM1
	fir10.1	10	TG566	ns	ns	**0.0006**	9	−31	LE	*	PF;PM7

Table 1 (continued)

Trait	QTL	Chr	Marker	*P*-value			%PVE	%A[a]	Favorable allele[b]	Relative significance	Populations with putative orthologs
				IS	CA1	CA2					
Stem retention	*str2a.1*	2a	CT255	**0.0001**	nd	nd	10	55	LE	*	
	str2b.1	2b	TG140	**<0.0001**	nd	nd	17	102	LE	*	H1;PV1
	str3.1	3	TG324	**<0.0001**	nd	nd	11	65	LE	*	
	str4a.1	4a	CT161	**<0.0001**	nd	nd	15	73	LE	*	
	str6a.1	6a	CT216	**0.0001**	nd	nd	9	69	LE	*	
	str9.1	9	TG291	**0.0002**	nd	nd	8	44	LE	*	H1;PV1
	str10.1	10	TG566	**0.0003**	nd	nd	8	42	LE	*	H1;PF;PM2
	str11.1	11	CT269	**<0.0001**	nd	nd	25	139	LE	*	
	str12.1	12	CT211	**0.0002**	nd	nd	8	−35	PN	*	
Fruit-weight	*fw3.1*	3	TG42	**0.0002**	0.004	nd	8	−26	LE	*+	CM1,2;PF;PM1,4,5;PN;CA1,2;SM
	fw10.1	10	TG230	**0.0002**	0.004	nd	8	−20	LE	*+	PF;PN;PV1
	fw12.1	12	CT79	**<0.0001**	<0.0001	nd	20	−30	LE	**	PM4;PV1
Fruit size	*fsz2b.1*	2b	CT59	nd	nd	**0.0006**	8	−24	LE	*	CM1,3;H1;PF;PM1,3,5;PN;PV;CA1,2
	fsz3.1	3	TG42	nd	nd	**0.0008**	8	−23	LE	*	CM1,2;PF;PM1,4,5;PN;CA1,2
	fsz10.1	10	TG566	nd	nd	**<0.0001**	18	−29	LE	*	PF;PN;PV1
	fsz12.1	12	CT79	nd	nd	**<0.0001**	16	−32	LE	*	PM4;PV1
Fruit shape	*fs2b.1*	2b	CT59	ns	0.001	**0.0006**	8	−16	LE	*+	PF;PM4;PV1
	fs8.1	8	CT64	**<0.0001**	0.0001	ns	12	−26	LE	**	H1;PF;PM2;PV1;CA1
	fs10.1	10	TG233	0.007	ns	**<0.0001**	17	−21	LE	*+	
	fs12.1	12	CT79	ns	ns	**0.0002**	10	−19	LE	*	PM4;PV1
Fruit external color	*ec5.1*	5	CD64	ns	ns	**0.0001**	12	−48	LE	*	H1
	ec12.1	12	CT79	<0.0001	0.0001	**<0.0001**	16	−44	LE	***	PF;PV1
Fruit internal color	*ic12.1*	12	TG68	**0.0002**	ns	ns	8	−48	LE	*	PF
Fruit orange color	*or11.1*	11	TG497	nd	nd	**0.0004**	10	86	LE	*	
	or12.1	12	CT79	nd	nd	**<0.0001**	20	142	LE	*	
Fruit color (lab)	*fc12.1*	12	CT79	nd	**<0.0001**	nd	18	−45	LE	*	PV1
Puffiness	*puf2a.1*	2a	TG582	0.009	**0.003**	nd	6	90	PN	++	
	puf2b.1	2b	TG140	**<0.0001**	ns	nd	10	47	PN	*	
	puf3.1	3	TG249	**0.0009**	ns	nd	7	25	PN	*	
	puf10.1	10	TG230	**0.0002**	ns	nd	8	24	PN	*	
Epidermal reticulation	*er2a.1*	2a	TG276	**0.0001**	nd	ns	9	87	LE	*	
	er4b.1	4b	TG587	**<0.0001**	nd	<0.0001	43	222	LE	**	H2;PF;PV3
	er5.1	5	CD64	0.002	nd	**0.0007**	9	47	LE	*+	
	er8.1	8	TG180a	**<0.0001**	nd	<0.0001	12	108	LE	**	
Percent cracked fruit	*pcf2a.1*	2a	TG608	nd	**<0.0001**	nd	10	133	LE	*	
	pcf5.1	5	CD64	nd	**0.0003**	nd	8	137	LE	*	
	pcf8.1	8	CT88	nd	**0.0009**	nd	7	118	LE	*	
	pcf10.1	10	TG233	nd	**<0.0001**	nd	13	144	LE	*	
	pcf12.1	12	CT99	nd	**0.0001**	nd	10	−84	PN	*	
Yellow eye	*ye4a.1*	4a	CD55	nd	**0.0006**	nd	11	87	LE	*	
	ye8.1	8	TG434	nd	**0.0001**	nd	13	−80	PN	*	
Grey wall	*gw12.1*	12	CT79	nd	**0.0004**	nd	10	−77	PN	*	
Green gel	*gg1.1*	1	TG83	nd	nd	**0.0003**	10	64	LE	*	
	gg5.1	5	CT167	nd	nd	**0.0001**	11	66	LE	*	
	gg8.1	8	CT27	nd	nd	**0.0001**	12	64	LE	*	PF

[a] %A=200(AB−AA)/AA where AA is the phenotypic mean for individuals homozygous for the *L. esculentum* allele at the most-significant marker and AB is the mean for heterozygous individuals

[b] For pH and fruit shape, this column indicates which allele was associated with an increase in the trait mean

Processing traits

The soluble-solids content of the fruit was determined in all three locations and three different loci were identified. Two relatively minor QTLs mapped to chromosomes 4 and 9, and the most-significant locus, *ssc12.1*, mapped to chromosome 12. This QTL accounted for up to 30% of the variation in soluble solids (in IS). Overall, the three loci accounted for 24% of the variation in the trait in CA1. The PN alleles for both *ssc9.1* and *ssc12.1* were associated with increased soluble solids. Four QTLs were detected for the derived-trait soluble solids (Brix) × red yield and were distibuted on three chromosomes: 3, 5 and 12. By far, the most-significant was *bry12.1* on chromosome 12 which explained 19% of the phenotypic variation in CA1 and 53% in IS. Together, the four BRY loci explained 23% of the Brix × red yield variation in IS. For all four loci, the LE alleles were associated with increased BRY.

The viscosity of juice from the tomatoes was measured only in CA1 where four QTLs were identified. Two of these loci, *vis9.1* and *vis12.1*, each explained 18% of the variation in juice viscosity and all together, the four QTLs accounted for 21% of the phenotypic variation. For all but *vis2a.1*, the wild-alleles had favorable effects and were associated with a more-viscous product. The pH of the fruit was also only determined in CA1. Two loci were detected, *ph3.1* and *ph12.1*, which accounted for 8 and 18% of the PVE for the trait, respectively. For both QTLs, the PN alleles were associated with increased acidity of the fruit.

Pericarp thickness was measured in all three locations and two different QTLs were identified. The more-significant locus was located on chromosome 10 and accounted for 17% of the variation for the trait. The combined effects of both loci explained 14% of the variation for pericarp thickness. The wild alleles for the two loci had opposite effects. The PN allele increased pericarp thickness for *pcp12.1* and decreased it for *pcp10.1*. Fruit firmness was also determined in all three locations and three loci were identified: *fir2a.1*, *fir2b.*1 and *fir10.1*. *Fir2a.1* had the greatest %PVE, 16%. Together, the two loci identified in CA2 accounted for 15% of the variation in firmness. The LE alleles for all three QTLs were associated with firmer fruit. Stem retention was measured only in IS where nine QTLs were detected, the most for any trait in this study. These loci were distributed on eight different chromosomes with two QTLs on the separate linkage groups representing chromosome 2. Most of the loci had magnitudes of effect of 8 to 15%; however, the most-significant QTL, *str11.1*, explained 25% of the variation for stem retention. Overall, the nine loci explained 25% of the variation in the trait. With only one exception, *str12.1*, the LE alleles were associated with decreased stem retention.

Fruit appearance traits

Fruit size was assessed by weighing the fruit in IS and CA1 (FW), and with a visual scale in CA2 (FSZ). Three loci were detected for FW on chromosomes 3, 10 and 12. The QTL on chromosome 12, *fw12.1*, was the most-significant and explained as much as 20% of the PVE. Together, the three FW loci accounted for 12% of the variation for the trait in IS. Four QTLs were identified for FSZ, three of which corresponded closely to the FW loci. The fourth locus was identified on the lower portion of chromosome 2. The FSZ loci on chromosomes 10 and 12 were both highly significant and had similar magnitudes of effect, 18 and 16%, respectively. The combined effects of these four loci explained 15% of the phenotypic variation. It should be noted that marker-assisted selection was deliberately applied to remove three regions containing some of the most-significant fruit-weight QTLs previously identified in tomato: *fw1.1* near the *S* locus on chromosome 1, *fw2.2* on chromosome 2 and *fw11.3* on chromosome 11. Thus, the analysis for fruit-weight loci probably does not reflect the entire potential of this accession of *L. pennellii* as a source of the fruit-weight QTL. For all of the FW and FSZ loci, the PN alleles were associated with reduced fruit size as expected.

Fruit shape was controlled by four QTLs all of which were detected in two of the three locations where the trait was measured. *Fs8.1* had the highest significance levels; however, *fs10.1* had a larger effect on variation for fruit shape, maximums of 12 and 17%, respectively. The three loci detected in CA2 had a combined magnitude of effect of 18%. As expected based on the parental phenotypes, the PN alleles were associated with rounder fruit.

Fruit color was measured in four ways: external color (EC), internal color (IC), the amount of external orange color (OR) and a laboratory measurement on juice (FC). Two QTLs were identified for EC, *ec5.1* and *ec12.1*, accounting for 12 and 16% of the variation for the trait, respectively. Loci for IC were not identified in either CA location; however, one QTL was detected in IS, *ic12.1*. This locus only explained 8% of the phenotypic variation in internal fruit color. Two loci for OR were found in CA2. The more significant QTL, *or12.1*, had a magnitude of effect of 20%. Together, the two loci accounted for 16% of the variation for OR. Only one QTL was identified for FC, *fc12.1*, which explained 18% of the variation in the trait. For all of the fruit-color loci, the LE alleles were associated with improved, that is, redder color.

Puffiness or the amount of air space in the fruit locules was measured in two locations (IS and CA1) where four different QTLs were identified. Two of these QTLs mapped to the different linkage groups of chromosome 2 and the other two loci were located on chromsomes 3 and 10. All of the loci had relatively minor %PVEs of 10% or less and a combined magnitude of effect of 15%. The PN alleles were always associated with decreased puffiness. Epidermal reticulation describes the cantaloupe-like veining that is observed on the skin of some fruit. Four QTLs

controlling this trait were identified in IS and CA2 on chromosomes 2, 4, 5 and 8. The locus on chromsome 4, *er4b.1*, was the most-significant and accounted for as much as 43% of the phenotypic variation in IS. In combination, the four loci had a PVE of 41%. For all four QTLs, the PN alleles were linked to increased reticulation. The percent of cracked fruit was only measured in CA1 where five QTLs were found. The most-significant of these was *pcf10.1* with a %PVE of 13% and, together, the loci accounted for 22% of the phenotypic variation for the trait. For only one QTL, *pcf12.1*, the wild alleles were associated with reduced cracking.

Yellow eye measured the penetration of the stem scar in the fruit. Two QTLs were identified for this trait, *ye4a.1* and *ye8.*1, controlling 11 and 13% of the phenotypic variation, respectively. The PN alleles for these loci had opposite effects increasing the percentage of fruit with yellow eye at *ye4.1* and decreasing it at *ye8.1*. Grey wall was measured only in CA1 where only one QTL was detected. This QTL, *gw12.1*, explained only 10% of the variation for the trait and its PN alleles were associated with improved fruit appearance. The color of the gel in cut fruit was assessed only in CA2. At this location, three QTLs were identified on chromosomes 1, 5 and 8, all of which had similar significances and magnitudes of effect ranging between 10 and 12%. None of the loci showed favorable effects from the wild parent-allele.

Discussion

Segregation distortion

A common feature of many interspecific plant populations is distorted segregation. This has been attributed to structural differences or loci that affect gamete transmission in the affected chromosomal regions (Zamir and Tadmor 1986). Six segments of the genome showed significant skewing of marker segregation ratios in the *L. esculentum* × *L. pennellii* BC_2 population. Regions on chromosomes 5, 6 and 11 had excesses of LE alleles while portions of chromosomes 7, 10 and 12 had higher than expected frequencies of PN alleles. The segregation distortion toward the LE genotype seen on chromosomes 6 and 11 was probably the result of the marker-assisted selection in these regions. Deviant segregation for some of these chromosomal regions has been reported in other tomato populations. For example, segregation distortion toward PN alleles of the top of chromosome 10 was observed in two *L. esculentum* × *L. pennellii* F_2 populations (deVicente and Tanksley 1993; Haanstra et al. 1999). Skewing was also detected in *L. hirsutum*, *L. peruvianum* and *L. parviflorum* interspecific populations for an overlapping region; however, in these populations excesses of LE alleles were observed (Bernacchi and Tanksley 1997; Fulton et al. 1997a, 2000). Similar to the current study, deviation from expected segregation ratios with an excess of LE alleles on chromosome 11 was reported in the *L. hirsutum*, *L. peruvianum* and *L. parviflorum* populations (Bernacchi and Tanksley 1997; Fulton et al. 1997a, 2000). It is interesting to note that none of these studies performed marker-assisted selection for this region. In contrast, deVicente and Tanksley (1993) observed that all of the markers on chromosome 11 were skewed toward the PN alleles in the *L. pennellii* F_2 population. The most-dramatic distortion observed in the BC_2 population occurred on a 45 cM portion of chromosome 12. Approximately 90% of the individuals in the population were heterozygous for this region. Zamir and Tadmor (1986) also saw a very marked preference for PN alleles in this region in an F_2 population.

The reasons for such dramatic segregation distortion are largely unknown. The BC_2 population was derived from a very small BC_1 population and therefore was very susceptible to genetic drift. Such drift might account for both fixation and segregation distortion in the population. Pelham (1968) attributed skewing on chromosome 9 of *L. peruvianum* to a gamete promoter gene. Preferential inheritance of the *L. peruvianum* allele in this region was also observed by Fulton et al. (1997a); however, conclusive evidence of a gamete promoter gene on the chromosome has not been reported. Analysis of the mechanism(s) responsible for distorted segregation is difficult as skewed regions vary greatly among species and even among populations derived from the same parent. Preferable inheritance of certain alleles in a given region has practical ramifications as it may necessitate additional backcross generations to achieve a desired level of homozygosity in breeding programs.

Correlations across locations and between traits

Correlations across locations were not significant for six of the 13 traits, measured in more than one location. However, there were strong associations across locations for the yield and yield-derived traits, and moderate correlations for fruit-weight, soluble solids and external color. From an agronomic perspective, these are the most-important traits for processing tomato cultivars. Similar to many previous studies, YLD/RYD and FW were found to be positively correlated (Stevens and Rudich 1978; Stevens 1986; Tanksley et al. 1996; Fulton et al. 1997b; Bernacchi et al. 1998; Fulton et al. 2000). However, both the yield and fruit-weight/size traits were negatively correlated with SSC. This is a well-documented phenomenon that suggests that attempted improvement in soluble solids will be at the expense of yield (Ibarbia and Lambeth 1971; Stevens 1986; Paterson et al. 1991; Tanksley et al. 1996; Fulton et al. 1997b; Bernacchi et al. 1998; Chen et al. 1999; Fulton et al. 2000; Doganlar et al. 2002a). A negative correlation was also identified between SSC and VIS, a result that was expected based on previous work (Stevens 1986, Fulton et al. 2000) and the fact that juice with higher soluble solids is, by its nature, more viscous. The significant positive correlation between FSZ and FERT suggests that an increased

number of fruit is not necessarily associated with a reduction in fruit size. External and internal fruit colors were also positively correlated as has been observed in *L. peruvianum*, *L. parviflorum* and *L. pimpinellifolium* mapping populations (Fulton et al. 1997b, 2000; Doganlar et al. 2002a).

Conservation of loci across environments

Of the 25 traits evaluated in this work, six were measured in all three locations, seven were assessed in two locations and 12 were determined at only one location. For the 13 traits that were evaluated in more than one environment, 43 QTLs were detected. Of these, two loci (5%) were identified at all three locations and 24 loci (56%) were identified at two locations. The only two QTLs identified in all three locations were *ssc12.1* and *ec12.1*. Notably, all of the YLD and RDY loci (six and four QTLs, respectively) were detected in both locations where these traits were measured. Moreover, all three FW loci and three of the four FS, BRY and ER QTLs were identified at two locations. This conservation across locations suggests that locus by environment interactions for these traits are relatively low. Strong conservation of QTLs across locations has been reported previously for several different interspecific AB-QTL tomato populations (Tanksley et al. 1996; Fulton et al. 1997b; Bernacchi et al. 1998; Fulton et al. 2000).

Co-localization of QTLs

The largest cluster of QTLs was on chromosome 12 where CT79 was a significant marker for 15 different loci. Smaller clusters of loci (three or more QTLs) were also present on chromosomes 2, 3, 5, 9 and 10. As expected, similar or related traits tended to be co-localized in the genome. For example, the four RDY QTLs always mapped with the YLD QTL. In addition, YLD loci mapped to the same regions as FERT QTLs on chromosomes 3, 9 and 12, and FW/FSZ QTLs on chromosomes 3 and 12. FW/FSZ loci also were co-localized with FS QTLs on chromosomes 2 and 12. Many of these clusters of related traits may reflect the pleiotropic effects of single loci. However, linkage of genes cannot be ruled out as a possible cause unless additional mapping is performed. For example, many studies have localized both fruit-weight and shape QTLs to the bottom half of chromosome 2 (reviewed in Grandillo et al. 1999). However, recent isolation of *fw2.2* (Frary et al. 2000) and *ovate* (Liu et al. 2002) have demonstrated that there are indeed distinct fruit-weight and shape-loci in this region of the genome.

QTLs with potential for breeding improved tomatoes

Many previous studies in tomato have demonstrated that phenotypically inferior wild species can be a source of agronomically favorable alleles (deVicente and Tanksley 1993; Eshed and Zamir 1995; Grandillo and Tanksley 1996; Tanksley et al. 1996; Fulton et al. 1997b; Bernacchi et al. 1998; Chen et al. 1999; Fulton et al. 2000; Doganlar et al. 2002a). In the present work, 11 (48%) of 23 traits had at least one QTL for which the *L. pennellii* allele had a positive agronomic effect. Traits for which effects were neither favorable nor unfavorable were excluded from this analysis. For example, pH was not included because increases or decreases in this character are not necessarily positive or negative but must be kept within an acceptable range for processing. Overall, 26% of the identified loci (20/78) had wild-alleles that enhanced the agronomic performance of the advanced backcross lines. Even higher percentages of traits with favorable wild-alleles were obtained with *L. peruvianum* (more than 50%, Fulton et al. 1997b), *L. hirsutum* (60%, Bernacchi et al. 1998) and *L. parviflorum* (70%, Fulton et al. 2000).

Some of the loci identified in this study may be targeted for breeding purposes. The *L. pennellii* allele(s) for the overlapping soluble solids and viscosity QTLs on chromosome 9 improved these two traits by 8 and 18%, respectively. Because of the related nature of these traits, it is probable that these effects are due to pleiotropy. The wild-alleles for several loci, centered around CT79 on chromosome 12, also had beneficial effects. The *L. pennellii* allele(s) at this location was (were) associated with a 48% increase in soluble solids content, an 18% improvement in viscosity, 19% and 10% reductions in fruit rot and cracking, respectively, a 16% increase in pericarp thickness and slight decreases in stem retention and grey wall. Unfortunately, cultivated alleles from the same region were also significantly linked to great improvements in total and red yields (56% and 61%, respectively), fertility (41%) and fruit-weight (20%), and lesser increases in external and internal fruit color.

Although it is possible that the multiple effects of this region of chromosome 12 are the result of pleiotropy, the diversity of phenotypes for the QTLs suggests that more than one locus does indeed exist in the neighborhood of CT79. Given the breeding potential of this region, it may be worthwhile to break the linkage between the sugar- and yield-traits so that the *L. pennellii* allele for improved soluble solids can be introgressed into cultivated tomato. This will require additional mapping to verify that the loci are indeed distinct and the screening of large populations for individuals that contain recombinations that break the linkages between the various traits. Such an approach has been used to break linkages between poor yield, low fruit-weight and high soluble solids in a *L. hirsutum* introgression (Monforte and Tanksley 2000), and between orange fruit color and high sugars in a *Lycopersicon chmielewskii* introgression (Frary et al. 2003a).

Loci shared among populations and species

With the addition of the present study, comprehensive QTL analyses are now available for AB populations derived from crosses with five different wild-species of tomato. In addition, the first QTL studies for pepper (Ben Chaim et al. 2001; Rao et al. 2003) and eggplant (Doganlar et al. 2002b; Frary et al. 2003b) have recently been published. This availability allows the identification of loci that are putatively conserved across tomato and its related wild- and crop-species. Of the 84 QTLs identified in this study, 38 (45%) are possibly the same as loci detected in other populations and species (Table 1). QTLs were considered to be potentially orthologous if they mapped to the same 20-cM region of the high-density tomato map (Tanksley et al. 1992). The majority (76%) of the putatively conserved loci were identified in three or more populations derived from different tomato species. In general, the yield-related, soluble solids and fruit size, shape and color traits had the highest proportions of QTLs that had been previously identified. This is probably because these traits have been examined in many studies whereas traits such as the amount of rotten and cracked fruit, puffiness and yellow eye have been examined in very few or no previous studies. The most-frequently identified loci were: *fsz2b.1*, detected in nine tomato populations representing six different species; *fw3.1/ fsz3.1*, identified in seven tomato populations encompassing four different species and *fs8.1*, detected in four tomato populations representing four different species. In addition, three loci appear to have orthologous counterparts outside of tomato. The fruit-weight/size QTL on chromosome 3 and the fruit-shape locus on chromosome 8 have been identified in pepper, *Capsicum annuum* (Ben Chaim et al. 2001; Rao et al. 2003). Moreover, *fsz2b.1* has been identified in both pepper and eggplant, *Solanum melongena* (Ben Chaim et al. 2001; Doganlar et al. 2002b; Rao et al. 2003). Such putative conservation of loci within the genus *Lycopersicon* and across other solanaceous species re-inforces the validity of the shared QTLs and supports the hypothesis that evolution and domestication in the Solanaceae has proceeded via mutations in loci that have been functionally conserved since divergence from a common ancestor (Doganlar et al. 2002b; Frary et al. 2003b).

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