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QTL analysis of an advanced backcross of *Lycopersicon peruvianum* to the cultivated tomato and comparisons with QTLs found in other wild species

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Abstract A BC_3 population previously developed from a backcross of *Lycopersicon peruvianum*, a wild relative of tomato, into the cultivated variety *L. esculentum* was analyzed for QTLs. Approximately 200 BC_4 families were scored for 35 traits in four locations worldwide. One hundred and sixty-six QTLs were detected for 29 of those traits. For more than half of those 29 traits at least 1 QTL was detected for which the presence of the wild allele was associated with an agronomically beneficial effect despite the inferior phenotype of the wild parent. Eight QTLs for fruit weight could be followed through the BC_2, BC_3, and BC_4, generations, supporting the authenticity of these QTLs. Comparisons were made between the QTLs found in this study and those found in studies involving two other wild species; the results showed that while some of these QTLs can be presumed to be allelic, most of the QTLs detected in this study are ones not previously discovered.

Key words Molecular markers · Quantitative trait loci · Molecular breeding · Germplasm

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Introduction

Due to reduced genetic variation in the cultivated varieties of many crops, it has become necessary to look beyond the elite varieties for novel genes to increase the potential for new improvements. The recently proposed advanced backcross method of quantitative trait locus analysis (AB-QTL) (Tanksley and Nelson 1996) has the potential to increase the efficiency of using wild, unadapted relatives of crops for the improvement of cultivated varieties and has been used to identify beneficial QTLs in wild tomatoes (Tanksley et al. 1996). The cultivated tomato, *Lycopersicon esculentum*, is an ideal candidate for QTL introgression as the elite germplasm contains very little genetic variation compared to landraces and wild species (Miller and Tanksley 1990). The great genetic diversity available in the wild relatives of tomato is for the most part unexploited due to the phenotypic inferiority and sterelity problems associated with the initial interspecific crosses. Recently, however, introgressions of DNA from wild species have been shown to improve the cultivated tomato, even for quantitatively inherited traits (Eshed and Zamir 1994).

Lycopersicon peruvianum is one of the most distant relatives of the cultivated tomato. It has been the source of many major resistance genes (Kalloo 1991), but no effort has been made to take advantage of the high level of genetic variation available in this species for the improvement of quantitative traits. In a companion paper a BC_3 population was developed by backcrossing *L. peruvianum* to the cultivated variety, *L. esculentum*. A molecular linkage map was constructed showing that 67% of the tomato genome was still represented by wild alleles and recombination

was suppressed only 25% compared to other published tomato maps, indicating the potential of this population for the introgression of DNA segments from the wild parent.

In this paper we describe QTL analysis of the BC_4 of this population. Thirty-five horticultural traits were evaluated at up to five locations. As several consecutive backcross generations had been genotyped with molecular markers (Fulton et al. 1997), QTLs affecting fruit weight could be followed through three generations. QTLs detected here were compared with those found in other wild species of tomato, and both possibly allelic and previously undiscovered QTLs are discussed. Our objectives were to determine if QTLs could be detected in such an advanced backcross population, and whether they would be new and useful in improving cultivated tomato varieties.

Materials and methods

Population development

The backcross populations were developed, as noted in Fulton et al. (1997), from an interspecific hybrid between *Lycopersicon peruvianum* (LA1706) (hereafter referred to as PV), the donor parent, and *L. esculentum* ('E6203') (E), the recurrent parent.

Field evaluations

Between 190–230 families of BC_4 plants were grown in the summer of 1995 in Spain (S), Israel (I) and two locations in California – Woodland (CA1) and Stockton (CA2). Experiments were arranged in randomized plots of 30 plants each with six plots of *Lycopersicon esculentum* cv 'E6203' as controls. In Israel, BC_4S1 seed was bulk harvested from each plot and saved for the future selection of QTL-NILs (near-isogenic lines).

Trait evaluations

A total of 35 traits were evaluated for each plot in one or more locations; 15 of the traits were measured in at least three locations. Details of trait evaluations are given below.

Yield and fruit weight

Yield was assessed in Spain and Israel as the total weight (kg) of all the fruit taken from the plot and in CA1 as the total weight of the fruit from 5 plants only. This was then partitioned into red yield (the weight of only the ripe red fruit), green yield (only the green fruit), and, in Spain only, the amount of fruit which was smaller or larger than average (40–60 mm). Two additional traits, brix*total yield and brix*red yield, were derived from Spain and Israel data. Fruit weight is an average weight per fruit determined from a random sample of 40 ripe fruit per plot in all locations except at Cornell University. At Cornell average fruit weight was evaluated in the BC_2 and BC_3 generations on plants grown in the greenhouse, for all fruit harvested, 10 fruit per plant on average.

Fruit composition and quality

The taste and processing qualities of the tomato are largely dependent on the pH, soluble solids content, and the amount and type of acids the fruit contains. Soluble solids were measured with refractometers in all locations as °Brix as described in Tanksley et al. (1996). Total acids and total organic acids were evaluated in CA1 only; pH was evaluated at all locations. Viscosity was evaluated at S and CA2, and firmness at S, CA1, and CA2, both as described in Tanksley et al. (1996).

Fruit color

Fruit color was measured in several ways. On site at the time of harvest, 10–40 ripe fruit from each plot were visually scored for external color (using a scale of 1–5, 1 = low color, 5 = intense red color), then sliced open transversely and scored for internal color in the same manner. In addition, spectrophotometer color measurements were made on raw de-aerated puree ("fruit color, lab") using an Agtron (L A/B) in California (CA1), and a Gardner Colorgard (A/B) in Spain and CA2. The color of the gel inside the fruit was evaluated only in Israel, and scored as 1, green gel, or 2, red gel (desirable).

Fruit appearance

The proportion of plants with sunscald (bleached fruit due to sun exposure), was evaluated only in Spain. The size of the stem scar on the fruit was given a score of 1 (small scar, desirable) to 5 (large scar) in Israel and of the two California locations. Evaluations of fruit shoulders, external uneven coloring near the stem, and internal white vascular veins, were made only in Israel, and the amount of puffiness, air space inside the fruit, was evaluated in Israel and Spain, all with a corresponding rating scale. The thickness of the fruit wall (pericarp) was evaluated at two locations; at one (CA1) it was measured quantitatively (in mm), while in Israel it was scored as either 1 (thin wall) or 3 (thick wall). Fruit shape was characterized simply as round (score = 1) or blocky (score = 2). A blocky shape is preferred for processing tomatoes.

Fruit ripening

The number of days from transplanting to first ripe fruit was assessed in Spain and CA1 only. A smaller number of days to ripening, indicating an earlier harvest, is desirable. Two related traits, maturity and overmaturity, were evaluated only in Spain by a visual assessment of the percentage of fruit mature or overmature on the day of harvest.

Stigma exsertion

The amount the stigma extends beyond the sepals of the flower was estimated visually and given a score of 1 (not exserted) to 5 (very exserted).

Stem release

The proportion of harvested ripe fruit releasing the stem (important for mechanical harvesting) was calculated in Spain, Israel, and at CA1.

Plot appearance

Cover, a visual estimate of the leaf cover of the plot, and growth, an estimate of the vegetative growth of the plot, were evaluated on

a scale of 1 (little cover or growth) to 5 (heavy cover or growth). The overall appearance of the plot in comparison to a plot of the recurrent parent control ('E6203') was assessed as "horticultural acceptibility" and given a score of 1, very unacceptable, to 5, highly acceptable. The proportion of unhealthy plants was estimated visually only in Spain.

Self seed

The average number of self seed per fruit was evaluated only at Cornell in the BC_3 population and was determined by the average number of seed extracted from all the self fruit harvested (an average of 5 fruit per plant).

QTL analysis

Single-point regressions were used to determine the effect of each molecular marker on each trait using QGENE, a program newly developed for QTL analysis (Nelson 1997). Regions of the genome were identified as putatively containing a QTL if they 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 weights with $P < 0.01$; significant effects were observed in the same direction for a market/trait combination at three or more locations with $P < 0.1$.

Putative QTLs for all traits were determined using single-point regressions regardless of the methods used to score each trait. Many traits were scored as ordered categories (e.g., on a scale of 1–5) rather than as continuously distributed values. QTL analysis of such traits should strictly be based on nonparametric models. However, nonparametric significant tests of marker-trait or trait-trait correlation using chi-squared or Kendall's tau were found to be at least as sensitive as tests based on linear models. For ease of interpretation we chose to present only linear estimates of genetic effect, with the caution that they are only approximate.

The percent phenotypic variance associated with each significant QTL was calculated from the regressions of each marker/phenotype combination. The additivity percentage (A%) of each significant QTL was calculated as 100 times the additivity (AB-AA) divided by the observed mean of the recurrent parent homozygote (since the donor parent homozygote cannot be observed), where AA = pheno-typic mean for individuals homozygous for *esculentum* alleles at specified markers, and AB = phenotypic mean of heterozygotes (*esculentum*/*peruvianum*). Since one-half of the individuals in each BC_4 plot would be heterozygous for a given QTL locus, the resulting value was then multiplied by 2; therefore A% = 200 (AB-AA)/AA.

Significance levels and %A of each QTL were given a $+/-$ sign, which indicates a positive or negative effect of the PV 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. Two exceptions are stigma exsertion and pH where effects are not necessarily positive or negative; for these 2 traits, $+/-$ simply indicates a measured increase or decrease.

Results and discussion

Detection of QTLs

A total of 166 putative QTLs for 29 traits were identified from the BC_4 field data. Table 1 lists these putative QTLs and the direction of the effect (i.e., an increase or decrease), additivity percentage, and phenotypic variance associated with the PV allele at each QTL. Several traits had few and non-normal data points due to the method of measurement, i.e., small fruit (the amount of fruit smaller than 40 mm in diameter); for these traits, %A is not presented, only the phenotypic variance and the direction of the effect associated with the PV allele. Figure 1 displays significant ($P < 0.05$) correlations between traits. Map positions of each QTL are shown in Fig. 2. A brief summary of both the putative QTLs and their correlated effects follows. All effects discussed are those associated with the PV allele at each locus.

Yield

The PV allele was associated with decreased yield for 8 of the 10 significant QTL detected for total yield, but for 2 QTLs, on chromosomes 6 and 10 (*ydt6.1* and *ydt10.3*), the PV allele gave increased total yield of 22% and 34%, respectively. Twelve QTLs were detected for red yield; 7 of these were located at the same position as a yield QTL, and the correlation between these 2 traits was high ($r > 0.8$). For all but 2 red yield QTLs, the PV allele was associated with a decrease in the amount of red yield; but at *rdy3.1* (ch3) and *rdy10.3* (ch10) the PV allele gave increases in red yield. The PV allele increased green yield (indicating later maturity – a negative effect) at all of the 7 QTLs detected for this trait. Yield and red yield were inversely correlated with brix and leaf cover, concurring with previously reported findings (Stevens 1986; Tanksley et al. 1996).

Soluble solids (brix)

PV alleles were associated with an increase in soluble solids at all 8 QTLs identified for this trait. However, all but 1 were also associated with lower fruit weight and/or reduced yield. The exception, *brx1.1*, was linked only to a decrease in firmness (no other negative effects); however, the increase in brix, although highly significant ($P < 0.0001$), was detected at just one location, Israel. Correlated effects of increased brix with small fruit and deduced yield have been noted in other studies (Stevens 1986; Tanksley et al. 1996). In addition, all QTLs detected for the derived traits brix*red yield and brix*total yield showed the PV allele to be associated with a decrease in both types of yield.

Viscosity

Four QTLs were detected for which the PV allele caused increased viscosity (the desired effect for use in processing) by as much as 22%, but 3 were also associated with a reduction in fruit weight. One exception,

Table 1 List of putative QTLs detected from data collected from BC_4 field plots. [*Ca1* Woodland, Calif. · *CA2* Stockton, Calif. · *S* Spain · *I* Israel · *CU* Cornell University; BC_3 (fruit weight and self seed only) · *ns* not significant · *na* not available]

Trait		QTL[a]	Chromosome	Marker	CA1	CA2	S	I	CU	%A[b]	% PV[c]
Total yield		*ydt1.1*	1	TG158	** – [d]	na	*** –	**** –	na	– 44	15
	#	*ydt2.1*	2	TG507	**** –	na	**** –	**** –	na	– 38	18
		ydt6.1	6	CT206	* +	na	ns	*** +	na	22	6
		ydt7.1	7	TG143	* –	na	**** –	**** –	na	– 42	17
		ydt8.1	8	CT27	** –	na	**** –	**** –	na	– 35	20
		ydt9.1	9	CD32	* –	na	**** –	**** –	na	– 30	20
		ydt10.1	10	TG271	*** –	na	** –	**** –	na	– 38	11
		ydt10.2	10	TG420	** –	na	**** –	**** –	na	– 48	21
		ydt10.3	10	CD5	ns	na	*** +	ns	na	34	5
	#	*ydt12.1*	12	TG360	ns	na	ns	**** –	na	– 31	11
Red yield		*rdy1.1*	1	TG158	** –	na	** –	**** –	na	– 52	12
	^	*rdy2.1*	2	CT9	** –	na	*** –	**** –	na	– 56	24
		rdy3.1	3	TG324	*** + [e]	na	ns	** +	na	110	7
		rdy3.2	3	TG377	ns	na	*** –	ns	na	– 46	6
		rdy5.1	5	CT93	* –	na	**** –	ns	na	– 40	11
	^	*rdy7.1*	7	TG61	*** –	na	**** –	**** –	na	– 49	12
		rdy8.1	8	CT27	** –	na	**** –	**** –	na	– 46	21
		rdy9.1	9	CD32	* –	na	**** –	**** –	na	– 41	23
		rdy10.1	10	TG271	*** –	na	** –	**** –	na	– 48	10
		rdy10.2	10	TG420	* –	na	** –	**** –	na	– 60	20
	^	*rdy10.3*	10	CD5	ns	na	** +	** +	na	48	5
	^	*rdy12.1*	12	TG360	ns	na	ns	**** –	na	– 40	11
Fruit weight		*fw1.1*	1	TG158	** –	* –	* –	** –	* –	– 22	4
		fw2.1	2	TG507	**** –	** –	**** –	**** –	**** –	– 37	23
		fw3.1	3	TG324	* +	*** +	** +	*** +	*** +	– 30	5
		fw7.1	7	TG217	** –	ns	ns	**** –	**** –	– 31	8
		fw8.1	8	CT92	*** –	ns	** –	* –	*** –	– 20	7
		fw9.1	9	TG254	**** –	**** –	**** –	**** –	**** –	– 30	23
		fw10.1	10	TG230	*** –	ns	*** –	**** –	*** –	– 35	10
		fw10.2	10	CT112B	*** –	** –	**** –	**** –	*** –	– 44	11
		fw10.3	10	CD5	** +	ns	** +	**** +	* +	46	8
		fw12.1	12	TG360	** –	*** –	** –	**** –	**** –	– 40	12
Small fruit		*sm2.1*	2	CT59	na	na	**** –	na	na	NA	20
		sm5.1	5	CT53	na	na	*** –	na	na	NA	8
		sm9.1	9	TG254	na	na	**** –	na	na	NA	17
		sm11.1	11	I2	na	na	**** –	na	na	NA	13
		sm12.1	12	TG565	na	na	**** –	na	na	NA	9
Large fruit		*lg1.1*	1	TG255	na	na	*** +	na	na	NA	5
		lg9.1	9	GP39	na	na	*** –	na	na	NA	24
		lg10.1	10	CD5	na	na	**** +	na	na	NA	14
Green yield		*gny2.1*	2	TG48	** +	na	ns	**** –	na	NA	27
		gny5.1	5	CD64	ns	na	*** –	**** –	na	NA	12
		gny7.1	7	TG216	ns	na	*** –	ns	na	NA	6
	^	*gny8.1*	8	CT27	** +	na	ns	*** –	na	NA	6
		gny8.2	8	CT111	ns	na	ns	*** –	na	NA	6
		gny8.3	8	TG294	** –	na	*** –	* –	na	NA	7
		gny9.1	9	TG291	** +	na	** –	**** –	na	NA	16
Brix (soluble solids)		*brx1.1*	1	CT267	ns	ns	ns	**** +	na	22	8
		brx1.2	1	TG27	ns	** +	**** +	ns	na	16	8
		brx2.1	2	CT9	ns	** +	** +	ns	na	10	5
		brx2.2	2	TG507	* +	** +	*** +	ns	na	10	5
	#	*brx7.1*	7	TG61	ns	** +	*** +	* +	na	12	8
		brx8.1	8	CT92	* +	**** +	**** +	ns	na	16	18
		brx9.1	9	TG254	** +	*** +	**** +	na		17	15
		brx9.2	9	CD32	ns	**** +	**** +	**** +	na	16	21
		brx10.1	10	CT112B	** +	* +	**** +	** +	na	18	10

Table 1 Continued

Trait	QTL[a]	Chromosome	Marker	CA1	CA2	S	I	CU	%A[b]	% PV[c]
Brix*red yield	*bry1.1*	1	TG158	na	na	ns	**** –	na	– 46	11
∧ #	*bry2.1*	2	TG48	na	na	*** –	**** –	na	– 51	20
	bry5.1	5	CT93	na	na	**** –	ns	na	– 38	11
	bry7.1	7	TG143	na	na	**** –	**** –	na	– 45	11
	bry8.1	8	CT27	na	na	*** –	**** –	na	– 40	16
	bry9.1	9	CD32	na	na	ns	**** –	na	– 28	11
	bry10.1	10	TG271	na	na	* –	**** –	na	– 42	9
	bry10.2	10	TG420	na	na	* –	**** –	na	– 54	18
	bry12.1	12	TG360	na	na	ns	**** –	na	– 31	7
Brix* total yield	*bty1.1*	1	TG158	na	na	* –	**** –	na	– 28	11
	bty2.1	2	CT59	na	na	**** –	**** –	na	– 40	16
	bty3.1	3	TG377	na	na	*** –	ns	na	– 31	6
	bty7.1	7	TG143	na	na	**** –	**** –	na	– 34	12
	bty8.1	8	CT153	na	na	* –	**** –	na	– 38	16
	bty9.1	9	TG551	na	na	**** –	* –	na	– 27	9
	bty10.1	10	TG271	na	na	* –	**** –	na	– 34	8
	bty10.2	10	TG420	na	na	** –	**** –	na	– 42	16
	bty12.1	12	TG360	na	na	ns	*** –	na	– 22	5
Viscosity	*vis1.1*	1	TG158	*** +	** +	* +	na	na	22	7
	vis2.1	2	TG507	** +	** +	ns	na	na	16	4
	vis8.1	8	CT27	ns	**** +	* +	na	na	21	10
	vis9.1	9	TG223	**** +	ns	** +	na	na	21	19
Fruit color, lab ∧	*fc1.1*	1	TG570	*** –	ns	** –	na	na	– 10	6
∧	*fc1.2*	1	TG375	** –	ns	*** –	na	na	– 11	6
	fc6.1	6	TG482	*** +	ns	**** +	na	na	9	8
∧ #	*fc7.1*	7	TG61	**** –	ns	** –	na	na	– 7	11
#	*fc8.1*	8	CT92	**** –	ns	** –	na	na	– 5	11
∧	*fc9.1*	9	CD32	ns	ns	*** –	na	na	– 7	7
	fc10.1	10	TG52	**** –	ns	** –	na	na	– 12	11
	fc12.1	12	CT211	**** –	* –	**** –	na	na	– 8	17
Fruit color, external ∧	*ec1.1*	1	TG27	* –	* –	* –	na	na	– 21	3
#	*ec3.1*	3	TG324	* +	ns	** +	na	na	26	4
∧	*ec8.1*	8	TG349	ns	*** –	ns	na	na	– 38	6
	ec9.1	9	CT143	**** –	ns	ns	na	na	– 20	9
	ec12.1	12	CT219	ns	ns	**** –	na	na	– 28	10
Fruit, color, internal	*ic6.1*	6	TG482	* +	ns	*** +	na	na	25	7
	ic9.1	9	CD32	ns	na	* –	**** –	na	– 44	9
Fruit shape	*fs1.1*	1	TG580	**** –	** –	* –	**** –	na	– 62	14
#	*fs2.1*	2	TG507	**** –	** –	*** –	**** –	na	– 49	16
	fs6.1	6	TG482	ns	* +	* +	*** +	na	26	5
	fs7.1	7	TG61	*** –	** –	*** –	**** –	na	– 29	16
∧	*fs7.2*	7	TG143	**** –	* –	**** –	*** –	na	– 28	16
∧ #	*fs8.1*	8	CT92	**** –	** –	**** –	**** –	na	– 71	45
	fs8.2	8	TG294	* +	* +	* +	*** +	na	24	6
	fs9.1	9	CD32	** –	**** –	*** –	**** –	na	– 28	10
	fs10.1	10	TG540	**** –	ns	* –	ns	na	– 53	15
	fs10.2	10	TG420	**** –	*** –	** –	**** –	na	– 32	11
	fs12.1	12	TG180	ns	*** –	**** –	ns	na	– 21	12
	fs12.2	12	TG360	*** –	** –	** –	ns	na	– 31	13
Firmness	*fir1.1*	1	CT267	ns	ns	*** –	na	na	– 32	6
#	*fir3.1*	3	TG324	ns	*** +	* +	na	na	22	5
#	*fir4.1*	4	TG287	* –	* –	* –	na	na	– 24	2
	fir6.1	6	TG482	ns	* +	*** +	na	na	20	7
	fir9.1	9	CD32	* –	** –	**** –	na	na	– 22	11
∧	*fir11.1*	11	TG466	* +	* +	** +	na	na	25	2
First ripe	*fr2.1*	2	TG507	ns	na	**** –	na	na	– 4	13
	fr3.1	3	TG324	*** +	na	** +	na	na	11	8
	fr8.1	8	CT27	*** –	na	**** –	na	na	– 3	9
	fr9.1	9	GP39	*** –	na	**** –	na	na	– 4	12

Table 1 Continued

Trait		QTL[a]	Chromosome	Marker	CA1	CA2	S	I	CU	%A[b]	% PV[c]
Maturity		*mat3.1*	3	TG324	na	na	*** +	na	na	26	6
		mat5.1	5	CT93	na	na	**** –	na	na	– 18	9
		mat7.1	7	TG216	na	na	*** –	na	na	– 18	6
		mat8.1	8	TG294	na	na	*** –	na	na	– 14	7
		mat9.1	9	GP39	na	na	**** –	na	na	– 26	17
Overmaturity		*ovm2.1*	2	CT251	na	na	**** –	na	na	– 116	12
		ovm5.1	5	TG363	na	na	**** –	na	na	– 96	10
		ovm10.1	10	CT240	na	na	*** –	na	na	– 75	6
Stem release	∧	*str2.1*	2	TG361	* +	na	ns	**** +	na	21	6
		str6.1	6	CP61	* +	na	ns	**** –	na	– 30	9
		str9.1	9	GP39	**** +	na	ns	* –	na	56	15
		str9.2	9	TG429	ns	na	* –	**** +	na	34	9
		str12.1	12	TG68	ns	na	*** –	**** +	na	26	8
Sunscald		*sca2.1*	2	CT9	na	na	**** +	na	na	86	8
		sca3.1	3	TG324	na	na	**** –	na	na	– 174	11
	#	*sca8.1*	8	TG72	na	na	*** +	na	na	77	7
		sca9.1	9	TG254	na	na	**** +	na	na	89	23
Stigma exsertion		*stg2.1*	2	TG48	na	na	**** +	na	na	137	48
		stg9.1	9	TG10	na	na	*** +	na	na	38	9
Puffiness		*puf9.1*	9	CT143	na	na	**** –	ns	na	– 20	8
Cover		*cvr1.1*	1	TG580	ns	** +	ns	**** +	na	53	8
	∧	*cvr2.1*	2	CT9	**** +	**** +	**** +	**** +	na	52	19
		cvr3.1	3	TG324	* –	**** –	**** –	ns	na	– 58	13
		cvr5.1	5	CD64	** +	** +	**** +	**** +	na	31	13
	∧ #	*cvr8.1*	8	CT27	* +	** +	* +	**** +	na	38	9
	#	*cvr9.1*	9	CT143	**** +	**** +	**** +	* +	na	54	36
		cvr10.1	10	TG271	** +	* +	ns	** +	na	36	6
		cvr10.2	10	TG420	* +	ns	ns	**** +	na	46	8
Growth		*grw1.1*	1	TG158	** +	** +	na	na	na	34	5
		grw2.1	2	CT9	**** +	**** +	na	na	na	56	19
		grw3.1	3	TG324	** –	**** –	na	na	na	– 58	11
	#	*grw7.1*	7	TG61	** +	*** +	na	na	na	27	6
		grw8.1	8	CT92	**** +	**** +	na	na	na	36	10
		grw9.1	9	CD32	**** +	**** +	na	na	na	46	22
Horticultural acceptibility		*ha1.1*	1	TG158	*** –	*** –	na	na	na	– 88	7
		ha2.1	2	CT9	**** –	**** –	na	na	na	– 98	15
		ha3.1	3	TG324	**** +	**** +	na	na	na	138	10
		ha5.1	5	CD64	**** –	** –	na	na	na	– 80	15
		ha7.1	7	TG61	** –	** –	na	na	na	– 60	5
		ha8.1	8	CT27	*** –	**** –	na	na	na	– 72	9
		ha9.1	9	CT143	**** –	**** –	na	na	na	– 83	34
Unhealthy		*unh3.1*	3	TG324	na	na	**** –	na	na	*	7
		unh4.1	4	TG22	na	na	**** –	na	na	*	9
pH		*pH2.1*	2	TG48	* –	** –	ns	**** –	na	– 5	10
	#	*pH3.1*	3	TG244	* +	ns	ns	**** +	na	4	7
		pH5.1	5	TG432	**** +	ns	ns	** +	na	2	10
		pH9.1	9	TG254	ns	ns	ns	**** +	na	4	8
	∧	*pH10.1*	10	CT16	** +	* +	* +	**** +	na	8	14
		pH12.1	12	TG180	** +	ns	* +	**** +	na	3	5
Gel		*gel2.1*	2	TG507	na	na	na	**** –	na	– 13	12
		gel10.1	10	TG420	na	na	na	**** –	na	– 13	7

Table 1 Continued

Trait	QTL[a]	Chromosome	Marker	CA1	CA2	S	I	CU	%A[b]	% PV[c]
Self seed	*ssd1.1*	1	TG507	na	na	na	na	**** +	146	7
	ssd3.1	3	TG324	na	na	na	na	**** +	308	16
	ssd9.1	9	GP39	na	na	na	na	**** −	− 117	24

$^{*}P < 0.1$, $^{**}P < 0.01$, $^{***}P < 0.001$, $^{****}P < 0.0001$

[a] # denotes QTLs possibly in common with those discovered in *L. pimpinellifolium*; ∧ denotes QTLs possibly in common with those discovered in *L. hirsutum*

[b] A(%) = 200(AB − AA)/AA where AA is the phenotypic mean for individuals homozygous for *esculentum* alleles at specified markers and AB is the phenotypic mean for heterozygotes *esculentum*/*peruvianum*. NA denotes where %A was not calculated (see Results and discussion)

[c] %PV = Phenotypic variance estimated from regression of marker against phenotype

[d] + / − Sign indicates positive or negative from an agronomic perspective (see Materials and methods) except for pH and stigma, for which the sign indicates only an increase or decrease

[e] Boxed area indicates location for which A(%) and %PV were calculated

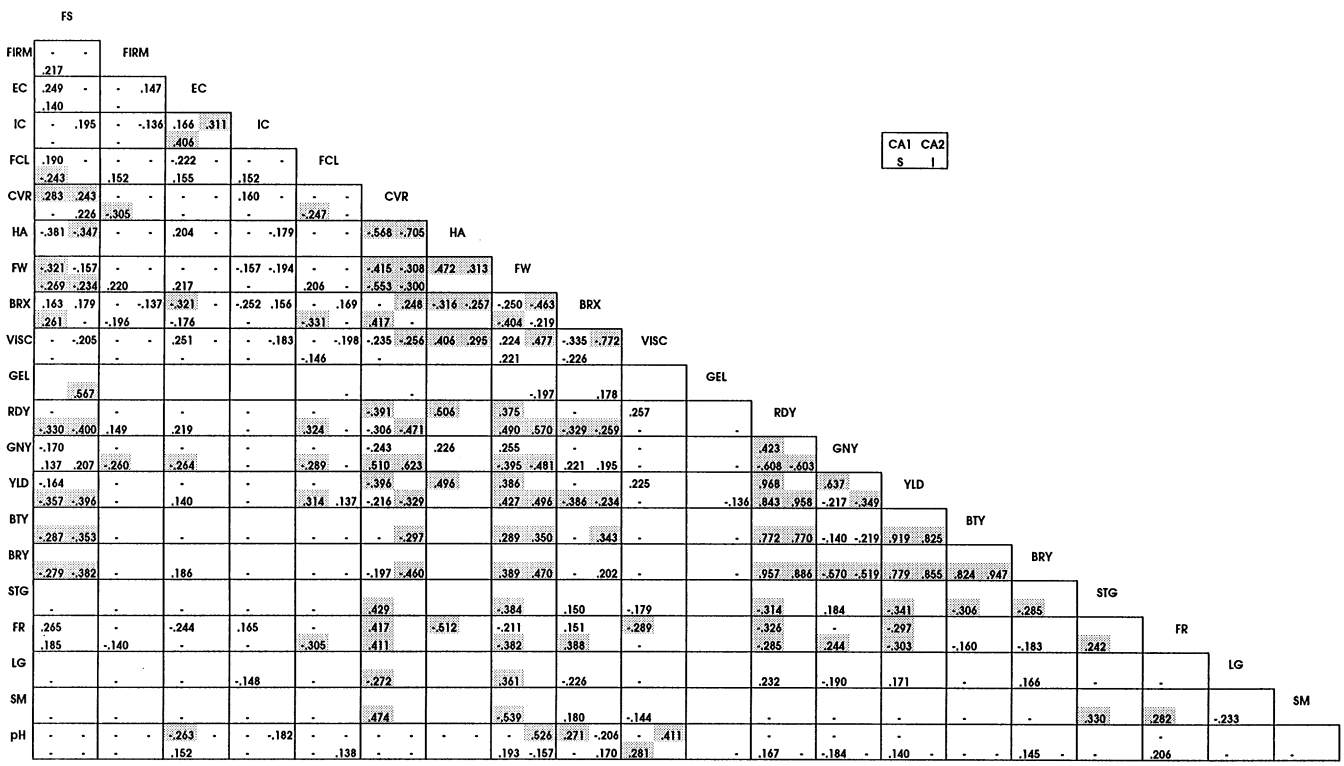

Fig. 1 Significant ($P < 0.05$) correlations between traits in the *L. peruvianum* BC_4 population. The *sign* of the correlation coefficient indicates the direction of correlation regardless of the scales used to measure the characters. *Shaded areas* indicate highly significant ($P < 0.0001$) correlations (— not significant). *CA1* Woodland, Calif., *CA2* Stockton Calif., *S* Spain, *I* Israel. For trait abbreviations, see Table 1

vis9.1, was not linked to (within 15 cM) QTLs for decreased fruit weight.

Fruit color

Fruit color showed the most significant effects when measured quantitatively in the laboratory, as opposed to the more subjective visual measurements. For most QTLs found, the PV allele gave a less intense red color as would be predicted from the green-fruited phenotype of the PV parent. A region on chromosome 6, however, showed the opposite effect for both the lab measurements and the internal color evaluations done visually. A 9% increase in red color was measured in the lab (*fc6.1*) and a 25% (*ic6.1*) increase noted visually. PV alleles in this region were also associated with increased firmness and yield. One additional positive QTL was noted for external fruit color only, on chromosome 3 (*ec3.1*) which was likewise associated with increased firmness and yield. Firmness and yield were positively correlated with color (but not to each other), with the strongest correlation found

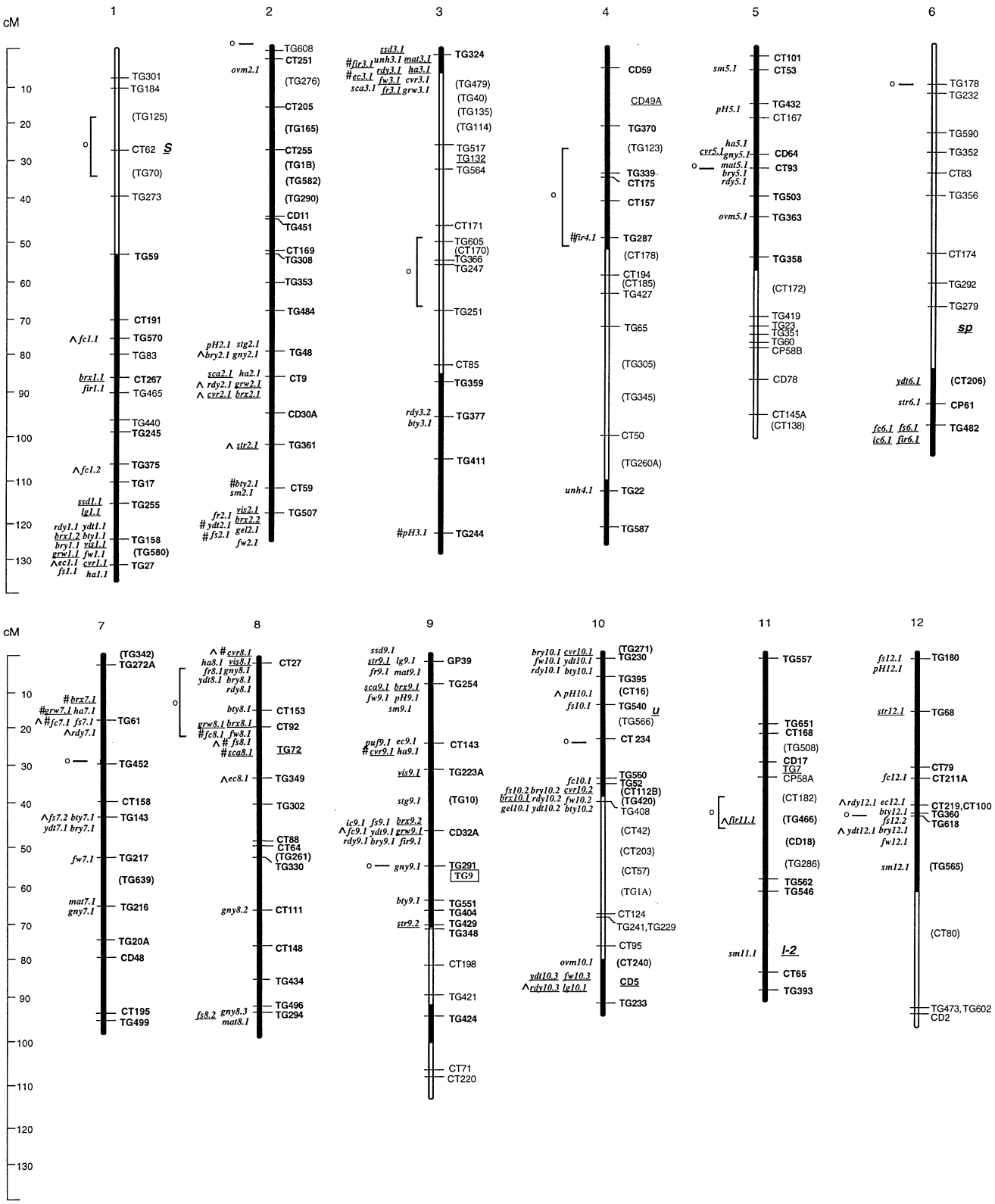

Fig. 2 Map locations of putative QTLs. CentiMorgan distances are based on the molecular linkage mp of tomato (Tanksley et al. 1992); the centimorgan scale is given on the *left*. *Shaded sections* of chromosomes and corresponding *bold markers* indicate regions still showing segregation of PV alleles in the BC_3. Map position of TG9 (ch9) and CT112B and TG420 (ch10) have been modified according to Fulton et al. (1997). "*o*" denotes the position of the centromere. QTLs are designated by the *letter/number* combinations to the *left* of the chromosomes (also see Table 1). *Underlined* QTLs signify those for which the PV allele confers positive effects from a horticultural perspective. *#QTLs* indicate those possibly in common with those discovered in the *L. pimpinellifolium* population; *∧ QTLs* possibly in common with those discovered in the *L. hirsutum* population

between yield and fruit color measured in the lab ($r = 0.314$).

Fruit shape

Twelve QTLs on eight chromosomes were detected for fruit shape. All but 2 caused the fruit to be rounder, as would be predicted from the PV phenotype. However, 2 QTLs (*fs6.1* and *fs8.2*) were found to give the opposite effect, the blocky, elongated shape which is preferred by processors (and therefore given a " + " sign in Table 1).

Firmness

Of the 6 QTLs detected for firmness, half caused an increase in firmness. Despite the subjectiveness of the evaluation for this trait (rating firmness by manually squeezing the fruit), the QTL on chromosome 3, *fir3.1*, mapped to the same position as a similar QTL detected in a *L. pimpinellifolium* backcross (Tanksley et al. 1996), not only supporting the authenticity of these QTLs but suggesting that the 2 are allelic (see later discussion). The QTL found on chromosome 11 (*fir11.1*) is the only significant QTL detected for any trait in that region of the genome.

First ripe

Days to first fruit ripening was measured in only two locations, and 4 QTLs were identified. For 3, the PV allele increased the number of days to ripening (an undesirable effect, thus denoted by a " − " sign, Table 1); one of these, *fr2.1,* coincides with the location of a fruit-weight QTL *fw2.1.* The opposite effect, earlier fruit ripening, was observed in the *L. pimpinellifolium* population but at a position approximately 15 cM closer to the centromere (Tanksley et al. 1996). One QTL was detected for which the PV allele was associated with a decrease in the days to first ripening, *fr3.1.* This region on chromosome 23 also showed significant QTLs for 11 other traits and will be discussed in more detail later.

A related trait, maturity, was evaluated only in Spain where 5 QTLs were detected. Two of these *mat3.1* (ch3) and *mat9.1* (ch9), map to the same regions as QTLs for first ripening, which is not surprising since plants with fruit ripening earlier would have a greater percentage of mature fruit at harvest. *mat3.1* caused earlier ripening and earlier maturity, while the other QTLs detected showed the opposite effects. Three QTLs detected for overmaturity all gave an increase in the amount of overripe fruit.

Stem release

Stem release was measured in three locations. Five highly significant ($P < 0.0001$) QTLs were detected, 4 of which were associated with an increase in the percentage of stems released. The PV allele for *str2.1* was associated with an increase in released stems and mapped to the same region of chromosome 2 as the *fw2.1* QTL for fruit-weight reduction. This same correlation was also noted in the *pimpinellifolium* population (Tanksley et al. 1996). For 3 other QTLs for this trait, *str9.1* (ch9), *str9.2* (ch9), and *str12.1* (ch12), the PV allele caused an increase in stems released in Israel ($P < 0.0001$). For 1 QTL on chromosome 6, *str6.1*, the PV allele caused a decrease in stems released in Israel. However, all QTLs but 1 (*str2.1*) showed an opposite effect at one other location (at lower significance levels). This may be due to differences in harvesting methods or environmental conditions.

Sunscald

This trait was evaluated only in Spain, and 4 QTLs were detected. Three of those, *sca2.1*, *sca8.1*, and *sca9.1*, showed decreased levels of sunscald and were also associated with increased cover, while *sca3.1* showed increased sunscald damage and a decrease in cover. It is reasonable to infer that having more leaf cover protects the fruit from sun damage.

Stigma exsertion

Stigma exsertion was estimated only in Spain, where 2 QTLs (*stg2.1* and *stg9.1*) were detected. The PV allele increased stigma exsertion in both cases, an effect predicted by the exserted stigma of the self-incompatible wild parent.

Puffiness

Only 1 QTL (*puf9.1*) was detected for this trait for which the PV allele was associated with puffier fruit (an undesirable effect).

Cover and growth

These traits were highly correlated ($r > 0.8$, $P < 0.0001$, data not shown), and all but 1 of the 6 QTLs detected for growth were near QTLs detected for cover. For both traits, the PV allele increased the amount of cover/growth in all but 1 QTL. On chromosome 3, the PV allele was associated with a decrease in both cover and growth (*cvr3.1* and *grw 3.1*).

Horticultural acceptibility

This trait was measured only at the two California locations. Of the 7 QTLs detected 6 were associated

with a decrease in horticultural acceptibility. The QTL for which PV allele increased horticultural acceptibility (*ha3.1*, ch3) was also associated with a decrease in growth and cover, and there was a high inverse correlation between these 2 traits ($r = -0.705, -0.568$); it may be that an increase in growth and cover leads to a less cultivated appearance.

Unhealthy

The plants were scored for an unhealthy appearance only in Spain. Two QTLs were detected, *unh3.1* and *unh4.1*, both of which increased the number of unhealthy-looking plants.

pH

Six QTLs were detected, 5 increasing the pH and 1 decreasing the pH. Changes in pH are not necessarily positive or negative as long as the pH is in an acceptable range for processing purposes; therefore the "+/−" sign for the pH QTLs listed in Table 2 signifies only a decrease or increase. The changes in pH were of only 2–8%, keeping the pH within a range of 4.4–4.7.

Gel

Only 2 QTLs were detected for the interior gel color of the fruit, and both caused the gel to be green rather than the more desirable red. This is consistent with the green fruit color seen in the PV parent.

Self seed

The number of seed produced by the fruit is an important aspect of commercial seed production. Three QTLs were found which affected this trait. For 2 QTLs (*ssd1.1* and *ssd3.1*) the PV allele was associated with an increase of up to 16% in the number of self seed per fruit, for 1 (*ssd9.1*) it was associated with a decrease.

Fruit weight

Ten QTLs were detected for average fruit weight. In most instances the PV allele decreased fruit weight; however, for 2 QTLs (*fw3.1* and *fw10.3*) the PV allele was associated with an increase in fruit weight. *fw3.1*, chromosome 3, was also associated with firmer, redder, and earlier ripening of fruit, and *fw10.3*, chromosome 10, showed increased yield and a higher amount of larger (> 60 mm) fruit. All 10 QTLs detected in these field trials also showed significant effects at all locations in the same direction as was observed in the previous generation (BC_3) in the greenhouse at Cornell (see later discussion of fruit-weight QTLs). Like yield, fruit weight was inversely correlated with brix and cover.

fw2.1 (chromosome 2) had the strongest effect on fruit weight with the PV allele decreasing fruit weight by 23%. In fact, the PV allele was significantly associated with decreased fruit weight at most markers throughout the entire length of this chromosome (e.g., $P = 0.1$ even at CT251, the top of the chromosome), with the most significant effect at the very bottom of the chromosome at TG507. This chromosome has been identified as containing a major fruit-weight QTL in several other tomato species as well (Alpert et al. 1995). In those species, however, the highest effects (lowest fruit weight) were localized to a region approximately 15 cM higher than was noted in this study, and they were associated with earlier fruit ripening, the opposite of the effect seen here. Fine mapping of fruit-weight QTLs in a *L. pennellii* population suggested that there are actually at least 3 fruit-weight QTLs on chromosome 2 (Eshed and Zamir 1995). One of these, *FW-3*, is located near the bottom of chromosome 2 and most likely corresponds to the major fruit-weight QTL

Table 2 QTLs associated with changes in fruit weight, followed through three generations. The marker most associated with the QTL, significance level (*P* value), and % phenotypic variance (%PV) are given for the BC_2, BC_3, and BC_4 generations

QTL		Marker (*P* value/PV)						fw inc/dec[a]
	Chromosome	BC_2		BC_3		BC_4		
fw1.1	1	TG245	(0.033/16%)	TG158	(0.034/2%)	TG158	(0.008/4%)	−
fw2.1	2	CT9	(0.015/15%)	TG507	(0.000/23%)	TG507	(0.000/16%)	−
fw7.1	7	TG61	(0.056/11%)	TG217	(0.000/8%)	TG217	(0.000/8%)	−
fw7.1	8	TG330	(0.046/12%)	CT92	(0.001/5%)	CT92	(0.001/7%)	−
fw10.1	10	TG540	(0.048/10%)	TG230	(0.000/6%)	TG230	(0.000/10%)	−
fw10.2	10	CT234	(0.022/16%)	CT112B	(0.001/6%)	CT112B	(0.000/11%)	−
fw10.3	10	CT240	(0.034/11%)	CD5	(0.017/3%)	CD5	(0.000/8%)	+
fw12.1	12	TG565	(0.149/5%)	TG360	(0.000/11%)	TG360	(0.000/12%)	−

[a] fw inc/dec = fruit weight (g) — increase (+)/decrease (−) in all generations

found in PV. However, due to the large region of chromosome 2 that showed decreased fruit-weight effects, we cannot rule out the possibility that more than 1 QTL for fruit weight was segregating in this population.

Transmission of fruit-weight QTLs

Of the 10 putative QTLs detected in the BC_4 population for fruit weight, 8 (80%) could be traced back to both the BC_2 and BC_3 generations (Table 2). While different (and fewer) markers were used to analyze the BC_2 population (Fulton et al. 1997), a marker within 25 cM of the marker associated with the QTL in the BC_4 showed significance in the BC_2 and BC_3 as well. The PV allele was associated with the same direction of change (increase or decrease) in fruit weight in all 8 cases; 7 of these QTLs were associated with decreases in fruit weight 1 (on chromosome 10) caused an increase in fruit weight. *fw2.1* accounted for the largest (or nearly the largest) effect on fruit weight in each generation. These findings support the reproducibility of these QTLs and suggest minimal epistasis, as such effects would have diminished with each generation of backcrossing.

Comparisons among species

Two other recent introgression studies in tomato have used a similar advanced backcross method to detect QTLs. *L. pimpinellifolium* (PM) and *L. hirsutum* (HS) were each studied in advanced backcross populations using the same recurrent *L. esculentum* parent as this study (Tanksley et al. 1996; D. Bernacchi, unpublished data). Comparisons can thus be made between the QTLs detected in these wild species and those reported in this study of *L. peruvianum* (Fig. 2). QTLs of the same effect that map to the same chromosomal regions across different species support the hypothesis that these QTLs are allelic and also boister the likelihood that these QTLs are genuine and not some spurious effect of analytical methods. Nevertheless, the hope in using wild relatives of the cultivated tomato is that new genetic variation will be found that can be used to improve the elite varieties. Both new (previously unreported) QTLs and QTLs possibily allelic with those found in previous work were found in this study.

QTLs shared among species

Different sets of markers were used to genotype each population, making it possible for QTLs of the same location and trait association to be associated with different markers in each population. Therefore, QTLs were considered to be in common if they mapped to the same 15-cM region of the high-density tomato map (Tanksley et al. 1992); it was not necessary that they be associated with the same marker. Of the total 166 QTLs found in the PV study, 31 (19%) were in common with either one or both the HS and PM populations (Table 1, Fig. 2). Those of particular interest are discussed below.

Since PM is a red-fruited tomato and HS and PV are green-fruited, it was not surprising that the QTLs detected for color showed variable results among the species. Five QTLs, (*fc1.1*, *fc1.2*, *ec1.1*, *ec8.1*, *fc9.1*), were consistent between the PV and HS populations, all causing a decrease in red color. *fc8.1* on chromosome 8 gave decreased color in both the PV and PM populations. The only QTL for fruit color found in all three populations (*fc7.1*, chromosome 7) had opposite allelic effects. At *fc7.1* the wild allele was associated with a decrease in color in the PV and HS studies but with an increase in color in the PM population. This QTL can be hypothesized to be involved in the differentiation of the species as it distinguishes the green-fruited from the red-fruited species. One QTL, however, had an effect unpredictable on the basis of the parental phenotype. *ec3.1* on chromosome 3 was associated with an increase in color in both the PM and PV populations, even though the PM parent is red-fruited and the PV parent is green-fruited. It showed no significant effect in the HS population.

Only 3 other QTLs detected in PV were also found in both the other populations. Located near the major fruit-weight QTLs, *bry2.1* decreased brix*red yield in all populations. However, at *cvr8.1* the wild allele was associated with rounder fruit in all three populations. However, at *cvr8.1* on chromosome 8, the PV allele was associated with an increase in vegetative cover while the other two alleles were associated with a decrease in cover. Of the QTLs in common with either PM or HS, but not both, most were associated with effects in the same direction, but many showed opposite allelic effects between populations. For example, *rdy2.1*, *rdy7.1*, and *rdy12.1* all showed decreased red yield associated with the wild allele, but at *rdy10.3* on chromosome 10 the PV allele gave an increase in red yield while the HS allele gave a decrease in the red yield. For fruit shape, both the PV and PM allele were associated with rounder fruit at *fs2.1*, but at *fs7.2* the PV allele gave rounder fruit while the HS allele was associated with blockier fruit.

QTLs found only in L. peruvianum

As a slightly different set of traits were evaluated in each population, it is difficult to give an exact number of QTLs detected from this population that are definitely newly discovered ones. However, since 166 QTLs were detected in this study and only 31 of these are also noted in the two other studies, it does seem likely that

most of the QTL alleles detected here are unique to the PV genome. Three regions of particular interest in this population showed an association of the PV allele with improvements of agronomically important traits that were not detected in the other populations. At the bottom of chromosome 6, QTLs were detected for which the PV allele increased total yield, firmness, and fruit color intensity and were all localized to the same marker, TG482. Four QTLs were localized to CD5 on chromosome 10 that caused increases in total yield, red yield, fruit weight, and fruit size. These two regions were not associated with similar QTLs for any of the traits studied in the HS or PM populations. PV alleles on the top of chromosome 3 near TG324 were associated with several favorable characters, including increases in fruit color, firmness, fruit weight, red weight, and horticultural acceptibility and a decrease in days to ripening. Two of these QTLs, for firmness and color, can also be found in the PM study, but otherwise this region has been unremarkable until now. In fact, for 20 (69%) of the 29 traits for which QTLs were detected, at least 1 QTL was found for which the PV allele was associated with an horticulturally favorable effect.

Figure 3 shows the distribution of red yield data obtained from the plants harvested from the BC_4 field plots. While the mean red yield of most of the plots was below the mean of the cultivated variety used as a control ('E6203'), at each location there were plots which outperformed the control for this trait. The AB-QTL method of analysis makes it possible to search for the favorable wild alleles that may account for such transgressive phenotypes, alleles which otherwise might have been masked by the phenotypic inferiority of the wild parent.

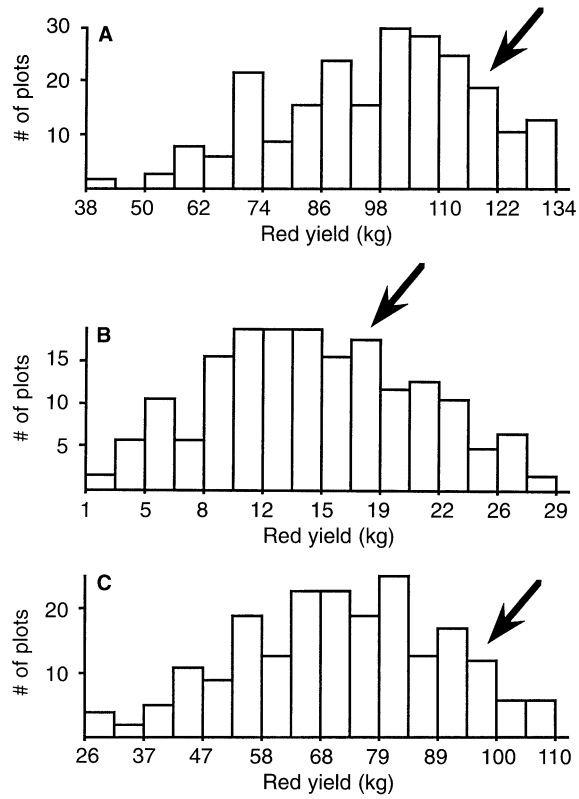

Fig. 3A–C Distribution of red yield data for BC_4 field plots in **A** Israel (kilograms of red fruit harvested from entire plot), **B** CA1 (kilograms of red fruit harvested from 5 plants), and **C** Spain (kilograms of red fruit harvested from entire plot). *Arrow* indicates the mean red yield of the control plots ('E6203')

Clusters of QTLs

Previous QTL studies in maize noted some regions of the genome that seemed to influence clusters of traits (Edwards et al. 1987). This phenomenon was observed in this study as well. For example, alleles from a 25-cM region on the bottom of chromosome 1 affect 15 of the 35 traits measured. As mentioned in the previous section, areas of chromosomes 3, 6, and 10 have clusters of agronomically beneficial QTLs that have remained undiscovered until now. Further genetic studies, such as fine mapping of these regions, could differentiate closely linked multiple QTLs from the effects of pleiotropy.

Consistency of QTLs between locations

Of the 166 total QTLs (for 29 traits) detected in this study, 139 were detected for traits that were assessed at more than one location (20 traits at up to five locations). Of these 139 QTLs, only 19 (14%) showed significance (at the previously indicated parameters) at only one location; the rest (86%) were significant at two or more locations. Among the 20 traits evaluated at more than one location, only 2 gave inconsistent results between locations. Of the 7 QTLs detected for green yield 3 *gny2.1*, *gny8.1*, and *gny9.1*, gave a decrease in green yield at CA1 (a desirable effect) while showing an increase in green yield for at least one of the two other locations where it was evaluated (Spain and Israel). For stem release, 4 out of the 5 QTLs detected also showed opposite effects at different locations. These inconsistencies may be due to the different dates and methods of harvest between the locations. However, for 18 of the 20 traits evaluated at more than one location, the direction of the effect associated with the PV allele was consistent among locations.

Evaluation of field traits used in this study

The comprehensive list of traits evaluated in this study includes agronomic traits important for tomato cultivation such as days to first ripening, key processing characters including soluble solids, horticultural traits such as leaf cover, and important commercial aspects

such as yield and color. Several traits were evaluated for which no significant QTLs were detected: fruit wall thickness, stem scar size, total and organic acids, shoulders, and veins. This may be because there are in reality no significant genetic differences between the parents with respect to these characters. Several of these traits were evaluated at only one location, in which case a higher significance level was required to qualify as a QTL. It may also be related to the manner in which these traits were scored. Scoring an extremely quantitative trait like veins on a categorical scale of 1–5 may be too subjective to pick up any significant QTLs; however, it would be difficult to find a better method of measurement without making the evaluation more labor intensive. Furthermore, significant QTLs were indeed found for many other traits that were also scored in this manner, such as firmness.

As mentioned previously, 2 traits related to the vegetative growth of the plants, cover and growth, were highly correlated. These 2 traits could be more efficiently evaluated as one combined trait. In addition, the 4 QTLs identified for sunscalded fruit were always inversely associated with cover; that is, less vegetative cover led to more sunscald, as would be predicted. Thus, evaluating sunscald could probably be eliminated if cover were scored.

Conclusions

This study marks the first attempt at detecting QTLs in the BC_3/BC_4 generation of a cross between a cultivated and wild species. Previous studies have used BC_2/BC_4 populations (Tanksley et al. 1996; D. Bernacchi unpublished data). The advantages of using BC_3/BC_4 populations to analyze interspecific crosses include reducing linkage drag and epistatic effects and decreasing the amount of time later needed to turn an introgressed segment into a near-isogenic line. Due to the extreme skewing of alleles toward the recurrent parent, however, simulations had suggested that it might be statistically more difficult to detect QTLs in more advanced populations (Tanksley and Nelson 1996). However, results from this study suggest that a backcross population can be advanced as least as far as the BC_4 without a decrease in the number of genuine QTLs detected. Despite the additional backcross used in the *peruvianum* study, for 13 of the 16 traits evaluated in common between this and the *pimpinellifolium* study (Tanksley et al. 1996), an equal number or more QTLs were detected from the *peruvianum* population. In fact, as several regions of the genome were no longer represented by PV alleles by the BC_3 generation, possibly due to sterility in the early crosses or the genetic bottleneck suffered by the BC_1, there are probably additional QTLs from PV that were undetected.

What is the feasibility of actually using QTLs detected in the wild species for the improvement of cultivated varieties? Are there actually QTLs found in the wild germplasm that will improve cultivated varieties for traits not predicted by looking at the phenotype of the wild plant? While *L. peruvianum* has been used to introgress single genes into the cultivated tomato (mainly disease resistance genes), this is the first time an accession of this species has been screened for genes controlling quantitative traits. It was known from Miller and Tanksley (1990) that this species contained high amounts of genetic variation, but not whether any of this variation would be useful to the tomato breeder. The QTLs detected in this study indicate that, as suggested by deVicente and Tanksley (1993), genes for improving agronomical traits can be found in species even when positive effects would not be predicted by the parental phenotype. For more than half of the traits evaluated, at least 1 QTL was found in which the *peruvianum* allele was superior to the *esculentum* allele for that trait. In addition, most of the QTLs found were new QTLs, not allelic to those found in previous studies, thereby increasing the potential for combining these alleles with QTLs detected in other species. This could greatly increase the rate of improvement of the cultivated varieties of tomato.

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