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Introgressions from *Lycopersicon pennellii* can improve the soluble-solids yield of tomato hybrids

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Abstract RFLP-defined chromosome segments covering the entire tomato genome were introgressed from the wild green-fruited species *Lycopersicon pennellii* into the cultivated tomato (*L. esculentum* cv M82; Eshed et al. 1992). Six *L. pennellii* chromosome segments were selected for a detailed evaluation based on previous observations of their effects on the two yield components, fresh tomato yield and total soluble-solids content (Brix). Differences in the quantitative traits measured between M82 and the introgression lines, or their hybrids with different inbred parents, can be attributed to the alien chromosome segments. Replicated field trials, grown at wide and dense spacing, identified three quantitative trait loci (QTLs) for soluble-solids content on chromosomes 1, 5 and 7. In plants heterozygous for the chromosome-5 locus there was a 50% increase in soluble-solids yield in wide but not in dense spacing. Plants heterozygous for the chromosome-1 QTL/s were tested over a 2-year period, in three genetic backgrounds, and showed a significant 16% elevation in soluble-solids yield only in dense spacing. These results demonstrate that wild tomato germplasm can be used to improve the yield of the cultivated crop.

Key words Wild germplasm · RFLP mapping · Yield Soluble-solids content · Heterosis

Introduction

Analysis of the genetic basis of quantitative traits in plants has changed dramatically since it became possible to resolve them into discrete Mendelian factors using a saturated RFLP linkage map (Paterson et al. 1988). Recently, quantitative trait loci (QTL) mapping studies with markers that cover entire genomes have been conducted in maize (Edwards et al. 1992; Stuber et al. 1992) and soybean (Diers et al. 1992). The tomato is a model system for mapping quantitative trait loci; it is an economically-important crop with a genetic map of more than 1 000 molecular markers (Tanksley et al. 1992) and has a rich collection of exotic germplasm which can be used for tomato improvement (Rick 1982).

QTL mapping in tomato has concentrated on interspecific segregating populations because of their diversity at the molecular (RFLPs) and phenotypic levels (Paterson et al. 1990, 1991; De Vicente and Tanksley 1993). Analysis of economic yield is, however, not possible in early generations of interspecific crosses because the plants segregate for many agronomically-important traits, such as late flowering date, small fruit size, late maturity, and even partial sterility.

In the tomato QTL studies one of the measured traits was total soluble-solids content of the fruit (Brix). Total soluble-solids content (TSS) is one of the components of yield which shows an inverse relationship with fresh tomato yield. For example, water stress in the field results in substantial increases in TSS accompanied by a reduction in fruit yield. This is largely attributable to the limited physiological capacity of the plants to provide the raw materials needed for high fresh yield and TSS (Stevens and Rudich 1978). Therefore, in breeding programs, it is necessary to take into account both the fresh yield and TSS; the parameter which is often used to characterize economic yield is the product of the two yield components which represents the soluble-solids yield per plant or per unit area. An increase in soluble-solids yield is of importance for fresh market tomatoes where flavour is correlated with TSS content. In processing-tomatoes, high yields and TSS values enable an efficient manufacturing of concentrates.

In order to map QTLs associated with economic yield we developed an introgression-line (IL) population of 120 lines each containing a small RFLP-defined chromosome segment/s of the wild green-fruited species *Lycopersicon*

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pennellii in the background of *L. esculentum* cv M82 (Eshed et al. 1992). *L. pennellii* with its salt (Saranga et al. 1992), drought (Martin et al. 1989), and insect tolerance (Goffreda and Mutschler 1989) represents a widely-divergent gene pool which can be easily hybridized to the cultivated tomato. The ILs provide a set of nearly-isogenic lines (NILs) for segments of the wild-species genome and therefore their horticultural characteristics generally resemble those of the cultivated variety. Throughout the development of the ILs, which spanned over a 6-year period, we observed that certain genotypes out-performed the control variety with respect to yield, especially when heterozygous (Eshed, unpublished). These lines, which are the focus of this study, enabled us to conduct field trials and to associate yield increase with specific wild-species chromosome segments.

Materials and methods

Plant material

The genetic constitution of the entire IL population, as defined using 175 RFLP markers covering the entire tomato genome, was described by Eshed et al. 1992. Since the original ILs were in the BC1S6 generation in crosses of *L. pennellii* (LA 716) to the processing tomato variety M82, most of the lines contained more than a single introgression. The six ILs analyzed in this study were derived from the original lines after an additional backcross to the cultivar M82; in the selfed generation, plants homozygous for the desired introgressions were selected for the crosses. The following ILs were analyzed in the 1991 experiment (see Fig. 1): IL10 – chromosome 5 from TG23 to TG185 (23.5 cM); IL82 – chromosome 5 from TG351 to TG413 (13.1 cM); IL47 – chromosome 2 from TG1B to TG165 (6.6 cM); IL121 – chromosome 2 from TG454 to TG131B (15.7 cM); IL32 – chromosome 1 from TG245 to TG259 (25.2 cM); IL 57 – contained two independent introgressions: chromosome 1 from TG245 to TG259 (25.2 cM) and chromosome 7 from Got2 to TG143 (5.9 cM). The 1992 experiment focused on further testing of IL47 and IL32. To reduce the possibility of undetected introgressions in these two ILs, an additional backcross generation was performed to the cultivar M82. In the selfed generation of each family, pollen from five plants homozygous for the introgressions of chromosome 2 or 1 was bulked and used for the crosses.

In the spring of 1991 the six derived ILs, their hybrids with M82, and hybrids with a different inbred processing line, A7, were transplanted in wide spacing to the field in Akko, Israel; the hybrids of the ILs with A7 were also transplanted in dense spacing. In the spring of 1992, the two ILs (IL47 and IL32), two inbreds (M82 and the processing inbred A8) and the hybrids between the ILs and the inbreds were grown in a dense stand at Akko. The inbreds A7, A8 and M82 are lines obtained after more than ten generations of selfing and originate from unrelated processing-tomato breeding projects.

The planting for the wide-spacing treatment (1991) was done in a randomized block design (12 replicated plants per genotype) in a drip-irrigated field with 50 cm between plants and 2 m between rows (1 m^2 per plant).

For the dense spacing in 1991 the tomato lines were planted in 12 replications of 10 m^2 plots using a randomized block design (35 plants per plot; 0.3 m^2 per plant). In 1992, the plots for each genotype were replicated six times in a randomized block design. Cultural practices in the field followed those recommended for processing-tomato (Saranga et al. 1991).

Phenotyping

Fruit were harvested when 90–100 percent of the tomatoes were red. For the wide-spacing experiment we measured total yield per plant (red and green fruit), TSS (assayed on a sample of 20 red fruits per plant), and mean fruit weight. The plots were harvested in bulk and the total fruit yield per plot was weighed. The mean fruit weight and total soluble-solids concentration (TSS) were measured from a random sample of 40 fruits per plot; TSS (Brix) was measured using the digital refractometer RFM-80 BS. The product of yield and TSS provided an estimate of the grams of soluble solids produced either per plant or per 10 m^2 plots. This parameter was calculated only for entries for which a complete data set was available.

Statistical analysis

Mean values for the parameters measured for the tested genotypes were compared to the appropriate control genotypes using the "contrast" function with a t test against the control line (using pooled error estimate). To compare the variability in the wide- and the dense-spacing experiments, the coefficient of variation (CV) was calculated by dividing the square root of MSE by the general mean for the measured traits. To evaluate the effect of the chromosome-1 introgression over a range of genetic backgrounds, a combined mean of the yield parameters of the hybrids between M82 and the inbreds A7, A8 and M82 was calculated for all the plots measured during the 2 years. The same was done for IL 32. Statistical analysis was made on a three-factor model without interactions. The factors were blocks (taking year into account), genetic background (inbreds involved in the hybrids) and presence or absence of the introgressed segment.

Results

Single plants – wide spacing

Yield components were first analyzed on the basis of single-plant performance in crosses with M82. Since all the ILs were in the M82 genetic background, differences in the quantitative traits measured could be attributed to the *L. pennellii* introgressions. The introgressed segments were in a homozygous state in the ILs and heterozygous in the hybrids between M82 and the ILs.

The mean yield of M82 was 5.8 kg per plant, with a TSS of 4.4, and the mean soluble-solids yield per plant was

Table 1 Mean yield parameters of single plants (wide spacing) of the variety M82, the inbred introgression lines (ILs) and the hybrids between M82 and the ILs. The mean value of the tested genotypes was compared to the control variety M82; the numbers in brackets indicate Prob>(t)

Genotype	Yield kg per plant	Brix	Yield×Brix g per plant
M82	5.8	4.4	266
IL10	5.0	5.0 (0.007)	255
M82×IL10	8.1 (0.01)	5.2 (0.0002)	435 (0.002)
IL82	4.0	5.4 (5E-5)	226
M82×IL82	7.7 (0.03)	5.0 (0.005)	403 (0.02)
IL47	6.1	4.3	250
M82×IL47	7.1	4.2	301
IL121	8.5 (0.003)	4.7	411 (0.007)
M82×IL121	7.8 (0.03)	4.4	355
IL32	4.2	4.9 (0.04)	195
M82×IL32	6.0	4.2	262
IL57	2.8 (0.004)	5.4 (3E-5)	153
M82×IL57	7.4	5.2 (0.0004)	377 (0.05)

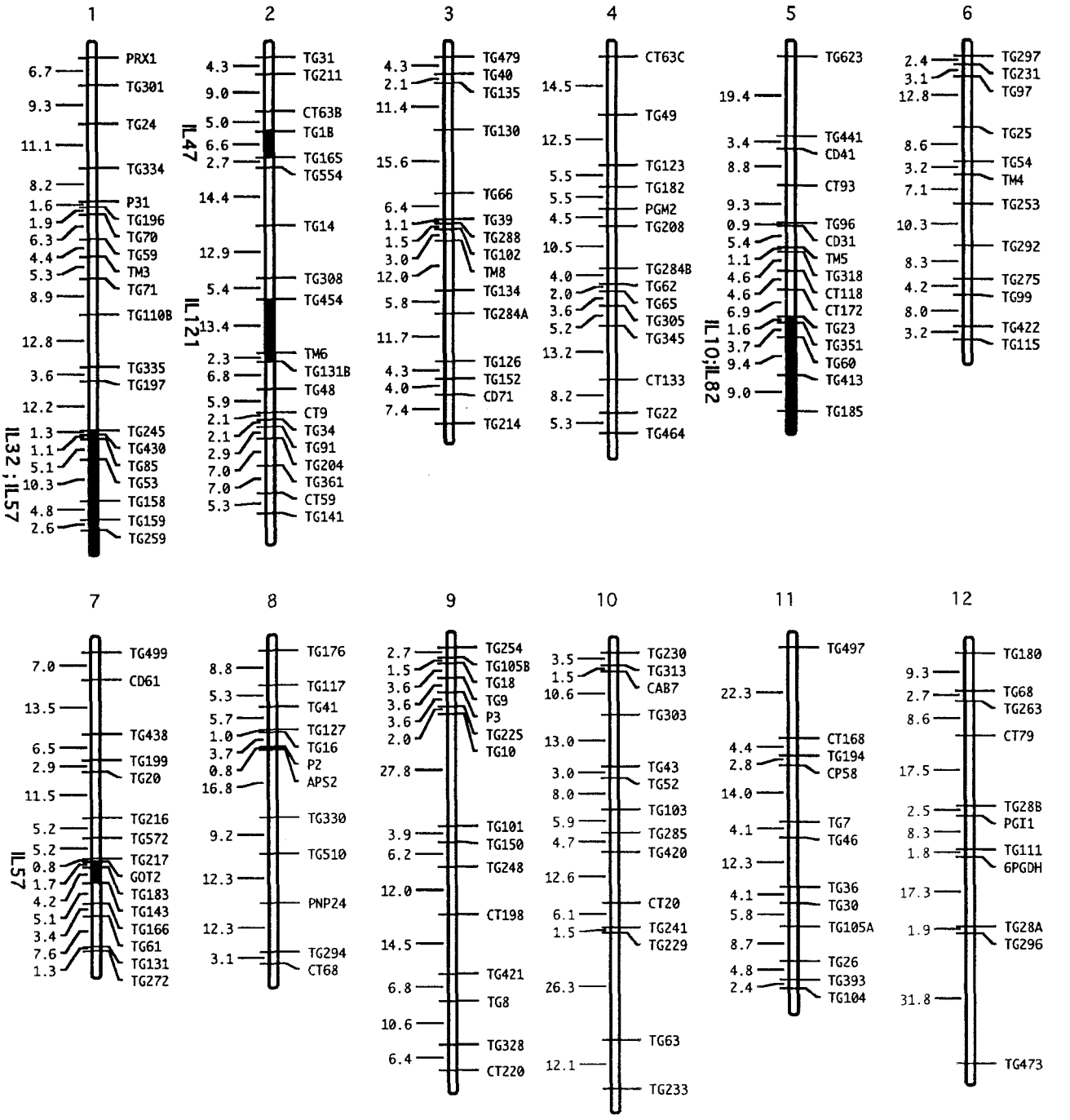

Fig. 1 RFLP linkage map of tomato derived from a backcross of 119 plants (Eshed et al. 1992). Scale in Kosambi cM is shown on the left of the chromosomes and loci names are listed to the right. *Dark chromosomal regions* mark the specific *Lycopersicon pennellii* introgressions

266 g (Table 1). The mean weight of a single fruit of M82 was 61 g, which did not differ from the fruit weight of the other genotypes presented in Table 1 (range: 51–66 g). IL10 and IL82 are lines from independent pedigrees having a 13.1-cM overlapping introgression in chromosome 5 (Fig. 1). Both lines had slightly lower yields than the control and their TSS was significantly higher. The hybrids of these ILs with M82 had 40 and 33% more yield than the highest parent, M82 (IL10 and IL82 respectively). TSS were similar to the IL parents; as a result the soluble-solids yield of the hybrid plants with the two lines was increased by 63 and 52% respectively.

The chromosome-2 introgression in IL47 and its hybrid did not have a significant effect on the parameters measured. IL121 and its hybrid, which cover a different segment of chromosome 2, both had a significantly-higher yield than M82. IL32 had a significant elevation in TSS while its hybrid did not differ significantly from M82. IL57 and IL32 contained an identical introgression in chromosome 1; IL57 had an additional introgression in chromo-

Table 2 Mean yield parameters of single plants (wide spacing) and plots (dense spacing) of the hybrid A7×M82 and the hybrids of the introgression lines (ILs) with A7. The mean value of the tested genotypes was compared to the control hybrid A7×M82 and the numbers in brackets indicate Prob>(t).The coefficient of variation (CV) was calculated for the general mean of each of the measured traits

Genotype	Single plants				Plots			
	Yield kg per plant	Brix	Yield×Brix g per plant	Plant weight kg	Yield kg per 10 m^2	Brix	Yield×Brix g per 10 m^2	Canopy weight kg
A7×M82	6.6	4.3	297	0.68	76	5.2	395	17.2
A7×IL10	9.6 (0.02)	5.4 (2E-7)	465 (0.006)	1.10 (0.0005)	78	5.6 (0.02)	429	23.7 (1E-7)
A7×IL82	10.2 (0.0007)	5.1 (0.0003)	447 (0.02)	1.46 (1E-9)	65 (0.0002)	5.8 (0.001)	371	22.6 (2E-6)
A7×IL47	8.1	4.4	301	0.84	88 (0.0001)	5.0	434 (0.03)	17.9
A7×IL121	9.2 (0.01)	4.7 (0.04)	430 (0.02)	0.90	81	4.9	392	17.2
A7×IL32	8.4	4.9 (0.01)	388	0.95 (0.03)	87 (0.0007)	5.2	450 (0.003)	17.9
A7×IL57	8.1	5.0 (0.0005)	393	0.84	82	5.6 (0.02)	452 (0.002)	20.1 (0.07)
CV (percent)	33.4	10.2	36.1	32.7	9.4	6.9	10.9	13.5

some 7. IL57 produced a significantly-lower yield than the control accompanied with an increase in TSS. The hybrid with IL57 had higher TSS than both M82 and M82×IL32 suggesting that the chromosome-7 segment is associated with that increase.

The *L. pennellii* introgressions were evaluated in a different genetic background by comparing the performance of the experimental hybrid A7×M82 with that of A7×ILs (Table 2). A7×M82 is a nearly-isogenic hybrid to A7×IL and therefore any difference between such hybrid pairs would indicate the contribution of the specific heterozygous *L. pennellii* introgression.

Fruit size of the hybrid A7×M82 was 61 g and did not differ significantly from the other genotypes (range: 56–63 g). Overall, the effects of the introgressions on the yield components of plants of A7×IL were very similar to those described for M82×IL (Table 1). The major difference was that A7×IL57 (chromosomes 1 and 7) had a TSS similar to A7×IL32 (chromosome 1). All the ILs hybrids had a higher weight of the vegetative part relative to the control hybrid, while both introgressions of chromosome 5 were associated with the largest increase.

Plots – dense spacing

The next phase of the experiment was to compare the effects of the introgressions (A7×ILs) in a high population density, which is characteristic of the commercial production of processing-tomatoes, with that of the single plants (Table 2). It is important to note that yield in a 10 m^2 plot represents the total production of 35 plants. The experimental variability (CV) for fresh yield, Brix yield, and plant weight, was three-times higher for the single plants in wide spacing compared to the plots, whereas for Brix it was only 1.5-times higher. Therefore, only very-high differences between the genotypes in the wide spacing were statistically significant.

Inconsistency between the two densities with respect to yield was seen for the chromosome-5 ILs. Hybrids involving these two ILs had the highest yield among the genotypes tested under conditions of wide spacing (Tables 1, 2). The IL10 hybrid with A7 had a similar yield in plots as the control (A7×M82) while the IL82 hybrid had a significantly-lower yield. Both hybrids maintained their effects on TSS, while canopy weight was increased over the check hybrid by 35% compared to 88% in the wide-spacing trial. The hybrid involving IL57 had a significantly higher TSS than IL32, which is consistent with the postulated effect of chromosome 7; the soluble-solids yield of this line was significantly higher than the control. Hybrids involving IL47

Table 3 Mean yield parameters of 1992 replicated plots (10 m^2=35 plants) of the *L. esculentum* inbreds M82, A8, IL47 and IL32. The mean value of the hybrids of the ILs with M82 was compared to the M82 inbred and the mean value of the hybrids of the ILs with A8 were compared to the control hybrid A8×M82. The numbers in brackets indicate Prob>(t)

Genotype	Yield kg per 10 m^2	Brix	Yield×Brix g per 10 m^2
M82	127	4.4	560
A8	114	4.2	480
IL47	122	4.3	531
IL32	111	5.0 (0.02)	552
M82×IL47	127	4.1	516
M82×IL32	133	4.8 (0.04)	645 (0.07)
A8×M82	126	4.3	533
A8×IL47	125	4.4	547
A8×IL32	145 (0.03)	4.5	655 (0.01)

Table 4 Combined mean yield parameters of 1991 and 1992 replicated plots (10 m^2=35 plants) of the hybrids between M82 and the inbreds A7, A8 and M82, compared to the hybrids with IL32. The numbers in brackets indicate Prob>(t)

Genotype	Yield kg per 10 m^2	Brix	Yield×Brix g per 10 m^2
Inbreds×M82	99.1	4.80	465
Inbreds×IL32	110.6 (0.0001)	4.98 (0.17)	541 (0.0001)

and IL32, which were associated with a non-significant increase in yield in the single plants, had a highly-significant contribution (14%) to both yield and soluble-solids yield in the plots; this fruit yield effect was not associated with a change in canopy weight compared to the control.

The experiment conducted in 1992 (Table 3) was designed to test the effect of the introgressions in chromosome 1 (IL32) and chromosome 2 (IL47) in an additional season and with different inbred parents. The two ILs had slightly-lower yields than M82 while TSS for IL32 was significantly higher than M82; this is consistent with the results presented in Table 1. The yield of the hybrids of IL47 with M82 and the inbred A8 did not differ from the control; this is in contrast to the results obtained in 1991 with the inbred A7 (Table 2). The hybrid of IL32 with M82 showed a yield similar to M82 and a significant increase in TSS compared to M82. The yield of the hybrid A8×IL32 was significantly higher than the isogenic control hybrid A8×M82 and both parents; these results are consistent with the 1991 trial (Table 2).

The combined yield parameters of the 1991 and 1992 trials demonstrate that the chromosome-1 introgression is responsible for an 11% increase in fresh yield and a 16% increase in the soluble solids produced per unit area (Table 4).

Discussion

The objective of this study was to determine the effects of selected *L. pennellii* chromosome segments on yield as measured on single plants under conditions of wide spacing and in replicated plots of a dense stand. Single plants in wide spacing represent the agricultural practice used in growing tomatoes for the fresh market where the important yield parameter is fruit yield. Closer spacing is used for processing-tomatoes where the important measure of yield is the soluble-solids output per unit area.

The association between yield and the *L. pennellii* chromosome segments which were assayed in an identical genetic background (hybrids with A7) differed between the single plants and the plots (Table 3). Chromosome 5 (IL10, IL82) and chromosome 2 (IL121) made the highest contribution to yield in the single plants whereas chromosome 1 (IL32) and a different segment of chromosome 2 (IL47) were most effective in the plots. In the wide-spacing treatment each plant had a growth area of 1 m^2 while in the dense stand each plant had an area of 0.3 m^2. Therefore, in the wide spacing, plants with vigorous growth rates produced the highest yield whereas in the dense stand other factors appear to regulate yield.

The introgressions on chromosomes 1, 5 and 7 were associated with an increase in the TSS in both densities. Similar effects of these chromosome segments were previously reported for a different interspecific tomato population involving *L. chmielewskii* (Paterson et al. 1990). The resemblance between the results of both studies demonstrates the possibility of using QTL data assessed in one species for identifying similar QTLs in a related species (Fatokun et al. 1992).

The single-plants experiment in the M82 background (Table 1) provided a system to detect heterotic QTLs since both inbred parents (M82 and M82 homozygous for a specific introgression) and their hybrid were examined. For five of the six ILs, the fresh yield of the hybrid was higher than the highest parent. A significant advantage of the hybrid over its highest parent (M82) was found for the two independently-bred chromosome-5 ILs; this heterotic effect was manifested in soluble-solids yield. The chromosome-1 and -7 IL showed heterosis for soluble-solids yield.

Hybrid vigor was also observed in the 2-year plot experiment: in 1991, the hybrid A7×IL32 had 15% higher fresh yield than the control hybrid A7×M82 with no increase in total soluble solids. In 1992, the hybrid M82×IL32 had a slight increase in fresh yield and a significant increase in TSS compared to M82. The third hybrid, A8×IL32, produced a 15% higher fresh yield than both parents and the isogenic hybrid A8×M82 with only a small increase in TSS. Yield and TSS in tomato have a negative relationship (Stevens and Rick 1986). Our results argue that the chromosome-1 introgression had a significant effect on the soluble-solids yield per unit area either through an effect on fresh yield, TSS, or both. The results presented demonstrate the importance of using TSS output per unit area as the yield parameter in selection programs since an increase in soluble solids alone can be associated with a reduction in fresh yield (IL82; Table 2).

The yield effect in plots of the chromosome-2 introgression (IL47) was significant in 1991 in a hybrid with A7, but not in 1992 in a hybrid with A8 and M82. This inconsistency can be due to an interaction of the introgression line with the different inbreds or the environments in the 2 years. Another possibility is a shift in the constitution of the line during its development: the parent for the 1991 experiment could have contained an additional introgression (linked or unlinked to chromosome 2) which was not detected by the RFLP analysis and was sorted out during the backcross generation which gave rise to the parents for the 1992 trial.

Heterosis is a phenomenon which underlies much of the improvement in crop yields over the past century. In spite of the extensive use of hybrid varieties in modern agriculture the genetic and physiological basis for heterosis is still unclear. Heterosis can result from dominant factors from one parent which mask deleterious recessive mutations from the other parent (the dominance theory; Bruce 1910; Keeble and Pellew 1910). Alternatively, hybrids carrying two different alleles at a locus can be superior to either parental type (the overdominance theory; East 1908; Shull 1908). In this study, heterotic effects were mapped to chromosomal regions which may either carry a number of interacting loci or a single overdominant locus. Only fine mapping of the heterotic loci, followed by their cloning, will provide an insight into the mechanism of heterosis in the tomato lines.

ILs for QTL mapping and breeding

Several genetic populations were developed for QTL mapping by providing a permanent set of fixed genotypes which can be evaluated in replicated measurements in various environments and seasons. Using such populations it is possible to obtain accurate measurements of the components of the phenotypic variability. Wehrhahn and Allard (1965) have demonstrated that effects of individual QTLs in wheat can be measured using inbred backcross lines. Such lines are produced by repeated backcrossing followed by self fertilization. In wheat, QTLs derived from *Aegilops longissima* were associated with yield components through the study of addition lines in which a pair of chromosomes from the wild donor was added to the full complement of common wheat (Levy et al. 1988). Recombinant inbred populations constitute a permanent population in which segregation is fixed; such populations were used for QTL mapping in maize (Burr and Burr 1991). However, fine mapping of a QTL is difficult to perform using recombinant inbreds since the closer the marker is to the QTL, the fewer genotypes remain informative and therefore the assumption of a random distribution of other QTLs affecting the trait is not fulfilled.

The tomato ILs also constitute a permanent mapping resource of fixed genotypes which can be evaluated in various environments and seasons. The original IL population (Eshed et al. 1992) was further refined by three additional backcrosses to M82. We developed a set of 60 lines which give a complete coverage of the genome, where each line contained a single *L. pennellii* introgression. The identity of the introgressions in the new population was defined using 350 RFLP markers (Eshed and Zamir, in preparation). By using such a population, quantitative differences between M82 and the ILs, or their hybrids, can be mapped to short chromosome segments. Since the tomato RFLP map is covered by more than 1 000 markers (Tanksley et al. 1992), the *L. pennellii* introgressions can be further recombined into smaller segments to allow finer mapping of QTLs.

Domesticated plants carry only a small fraction of the variability present in their wild relatives. Comparisons of genetic variation of many crop plants with their wild progenitors suggest that plant domestication was initiated from a limited number of individuals (Ladizinsky 1985). Gene flow between wild and domesticated populations was limited due to selection against wild-species traits in the cultivated crops. Modern plant breeders value the potential of wild germplasm for the improvement of their crops. Disease resistance genes were the first to be introgressed into modern cultivars. We demonstrate in this study that it is possible to utilize the potential of wild species for improving the yield of crop plants.

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