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Characterization of the effect of introgressed segments of chromosome 7 and 10 from *Lycopersion chmielewskii* on tomato soluble solids, pH, and yield

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Abstract. Three chromosomal segments from the wild tomato *L. chmielewskii* have been introgressed into the *L. esculentum* genome. Using molecular markers they have been mapped to the middle and terminal regions of chromosome 7 (7M, 7T respectively), and to the terminal region of chromosome 10 (10T). This study was conducted to further clarify the physiological influence of the introgressed segments of chromosome 7 and 10 on tomato soluble solids (SS), and other fruit and yield parameters. The effect of the 10T segment was evaluated using five lines that differ for the presence of this segment. As previously reported this segment increased fruit pH with no significant effect on SS. Sixty-four BC2F5 backcross inbred lines (BILs) were developed from a cross using LA1501 (an *L. esculentum* line that contains the 7M and 7T fragments from *L. chmielewskii*) as the donor parent, and VF145B-7879 (a processing cultivar) as the recurrent parent. BILs were classified in four groups (+ +, inbreds without either of the *L. chmielewskii* segments; 7M +, lines with only the 7M segment; +7T, inbreds with only the 7T segment, and 7M7T, inbreds with both segments) based on RFLP information, and then compared to each other for all the parameters under study. Inbreds homoyzgous for the 7M fragment displayed greater SS (26%) and higher pH (0.10) than the control group (+ +). The 7L fragment did not influence either SS or pH, but was observed to significantly increase fruit yield by 12% when compared to the recurrent parent. A gene or genes that increase yield without affecting SS or pH may have potential in the development of commerical cultivars.

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Key words: Soluble solids – RFLPs – Backcross inbreds – Tomato quality – Vegetable breeding

Introduction

Higher fruit total- and soluble-solids concentration is positively correlated with processed product yield and negatively correlated with the energy cost of dehydration in processing tomato production. Therefore, high solids concentration is a major goal of many processing tomato breeding programs. Soluble solids (SS) are also of prime concern in fresh market tomato production due to the important contribution that sugars and acids make to the overall flavor of the fruit (Stevens et al. 1977; Jones and Scott 1983). An increase in SS would also improve the nutritional value of tomatoes.

Tomato dry matter concentration, among commercial lines, falls between 4 and 7.5%, with SS accounting for 75% of the total. SS are composed primarily of the reducing sugars, fructose and glucose, and the organic acids, citrate and malate. Fructose and glucose account for about 50% of the total solids (Davies and Hobson 1981), with sucrose a minor ($\geqq$ 1%) component (Davies 1966). A further 10–15% of the dry matter consists of citric and malic acid. In processed tomatoes, organic acid concentration is important because it enhances fruit flavor, and is associated with fruit pH. The pH of the processing tomato is an important factor determining grower, processor, and consumer preference (Thompson et al. 1964; Jones and Scott 1983). A pH of 4.5 is required in processed and canned tomato products to control growth of thermophilic microorganisms (Thompson et al. 1964).

Genetic variation for SS concentration is limited among the cultivated forms of *L. esculentum* (Lower and Thompson 1967). However, some wild relatives of the tomato have much higher concentrations (Rick 1974). Since most of the wild species of the tomato can be hybridized to cultivated forms, this variability provides he opportunity to breed for tomatoes with an enhanced SS concentration. In the cultivated species, additive, dominance, and epistatic gene action has been described for this trait, but their relative importance depends on the genetic material and on the mating design used (Stoner and Thompson 1966; Ibarbia and Lambeth 1969; Mittal and Singh 1979).

Rick (1974) reported on the introgression of genes for enhanced SS concentration from the wild tomato species *L. chmielewskii* into *L. esculentum*, resulting in lines with a 40% higher SS concentration. This was accomplished by repeated backcrossing of the *L. chmielewskii* accession LA 1028, a wild, green-fruited species (about 10% SS), to *L. esculentum* cv 'VF 36' (BC_{1-2}) and 'VF 145-22-8' (BC_{3-5}) (about 5% SS) to obtain a series of BC_5S_5 lines, including LA 1500, 1501, 1502, 1503 and LA 1563, which possess increased SS concentrations (about 7–8%) but a similar yield, fruit size and color to the recurrent parent (Rick 1974).

Identification, isolation, and incorporation of genes conferring higher SS into elite tomato germplasm would be of significant value to the tomato fresh market and processing industry. Osborn et al. (1987), studied RFLP variation among LA1028, VF-36, LA1563, and a low SS commercial cultivar (LA2038), using 60 random cDNA probes. The authors identified two cDNA clones that hybridized to chromosomal regions which had been introgressed into the backcross line LA1563 from the high SS LA1028 parent. Results from a segregating F_2 population generated from the cross of LA1563 with LA2038 suggested that one fragment had a significant effect on SS whereas the other no effect. The chromosomal positions of these fragments were not determined. Tanksley and Hewitt (1988) tested the association between mapped RFLP and isozyme markers and genes controlling SS and other characteristics in LA1563. Variation for 132 molecular markers of known chromosomal location were studied in LA1028, VF36 and LA1563. Only three introgressed chromosomal segments from *L. chmielewskii* were identified, mapping to the middle and the end of chromosome 7 and to the end of chromosome 10. LA1563 was crossed with three different tomato cultivars. Three F_2 and one F_3 populations were assayed for the effect of these segments. The fragment on the middle of chromosome 7, and the one at the end of chromosome 10 were both found to increase SS, although the effect depended on genetic background. The positive association found in one of the F_2 populations between the fragement on the middle of chromosome 7 and SS was lost when the F_3 population was assayed.

The current study was initiated to further clarify the physiological influence of the introgressed *L. chmielewskii* chromosomal segments on processing tomato soluble and insoluble solids, and other fruit and yield parameters. A replicated experiment using homozygous backcross inbred lines (BILs) (Wehrhahn and Allard 1965) that differ in the number of introgressed segments would minimize the environmental component of the total variability associated with the expression of trait, and therefore offer a better resolution of the genetic contribution that these fragments from *L. chmielewskii* exert on tomato SS, pH and yield.

Materials and methods

Plant material

Sixty-four BILs, the parents (LA1501 and VF145B-7879), and four high SS lines (LA1500, LA1502, LA1503, LA1563) were used in this study. VF145B-7879 is a cultivar used in the California tomato processing industry. The solids level of VF145B-7879 is among the highest of processing cultivars grown in California. LA1500-1563 are some of the high-solids breeding lines developed by Rick (1974) from repeated backcrossing of the wild green-fruited species *L. chmielewskii* to *L. esculentum* cv 'VF36' (BC_{1-2}) and cv 'VF145B-22-8' (BC_{3-5}). These two cultivars are similar in many respects but differ in some fruit characters (Rick 1974). The 64 BILs were developed using LA1501 as the donor, and VF145B-7879 as the recurrent, parent. VF145B-7879 is genetically identical to VF145B-22-8. The procedure involved two successive backcrosses to VF145B-7879. From the first backcross, 64 randomly-chosen plants were crossed back to VF145B-7879 to generate 64 BC2 plants. These plants were then selfed for five generations by single-seed descent (BC2F5), in the absence of selection, to produce 64 BC2F5 lines. Unless the number of genes which differentiate the donor parent from the recurrent parent is relatively large, most of the inbred-backcross lines will be either genetically identical to the recurrent parent or will deviate by a single gene. These lines were evaluated in the field at the University of Illinois South Farm in Champaign, Illinois, in the summer of 1990. Seeds of 64 inbred-backcross lines, the two parents, and LA1500, LA1502, LA1503 and LA1563 were sown in flats containing a 1:1:1:2 soil mixture of soil:peat:perlite:vermiculite in May of 1990. Seedlings were hardened off for 10 days and transplanted to the field in a randomized complete block design with eight replications. Yield and fruit weight were measured over the eight replicates, but only four were used for all the laboratory determinations. Plant spacing was 90 cm between plants within rows and 90 cm between rows. One experimental unit consisted of a single row containing nine tomato plants of a single BIL or parental line. The yield of all these was estimated by harvesting all the tomatoes from the five central plants of each nine plant row and weighing them. Ten randomly-sampled tomato fruits were harvested from each experimental unit at the red-ripe stage, weighed to obtain an averaged fruit weight and stored in freezer bags at −20 °C, for later analysis.

Physiological analysis

Each sample of ten fruits was ground in a Waring blender for approximately 15 s. Two samples of 10 and 20 g of the resultant

puree were saved for later determination of color, and dry weight of puree (total solids), respectively. Forty grams of the puree was centrifuged in a JA-17 rotor with a Beckman J2-21M centrifuge at 10 000 rpm for 12 min at 59 °C. The supernatant or serum was saved in a vial and frozen at −20 °C for subsequent analysis of sugars, organic acids, pH, and dry weight of serum (SS). The dry weights of fruit-total and water-soluble solids were determined by lyophilization of puree and serum samples, respectively, on a Unitop 600L Virtis Freezemobile. Tared 20-ml vials, containing around 20 mg of the puree and serum, were placed in the freeze dryer for 7 days. After freeze drying, vials were reweighed to determine percent dry weight (dry weight × 100/wet weight). An Orion model SA520 pH meter was used to measure serum pH at room temperature. The color of the sample puree was measured with a Hunter Digital Color Difference Meter. The Hunter "a" value was used to measure the continuum between sample redness (when positive), grayness (when zero), or greenness (when negative). Color has been shown to provide a highly accurate estimation of fruit physiological age (Young et al. 1993). Color measurements were made to ascertain the uniformity of the samples for fruit physiological maturity.

The concentrations of fructose, glucose, malate and citric acid were determined by high pressure liquid chromatography (HPLC). About 4 ml of the centrifuged tomato serum from each sample was filtered through an 0.45-μm Gelman GN-6 Metracel membrane filter. Six standards were prepared, each containing different amounts of fructose, glucose, citrate, and malate, based on previous information about sugar concentrations in the fruit (Young et al. 1993). A set of standards was injected into the HPLC with every 40 tomato samples. Regression of known sample concentrations against compound peak areas generated equations that were used to determine the concentration of the individual sugars and organic acids present in the samples.

The HPLC system consisted of a Waters model 680 Automated Gradient Controller, a Waters model 510 HPLC pump, a Waters Intelligent Sample Processor (WISP) model 710B auto sampler, and a Waters series R-401 differential refractometer detector. A Hewlett Packard 3390A reporting integrator was used to record the detector signal. An Interaction model Ion-300 Organic Acid Column (0.95 cm) measuring 0.78 × 30 cm was employed for the separation of the sugars and organic acids. To protect the column an Interaction model Ion Guard GC-801 guard column was installed upstream of the column. Column temperature was maintained at 65–70 °C in a water jacket by a Forma Scientific bath and circulator. The mobile phase was 0.001 N H_2SO_4 (sulfuric acid). It was filtered through an 0.45-μm Alltech Nylon 66 membrane filter into a Kontes analytical HPLC mobile phase handling system. An ERMA ERC-3510 in-line degasser was used to remove gases from the solvent. The solvent flow rate was 0.4 ml/min, with sample and standard injection amounts set at 1 μl.

RFLP analysis

Harvested leaves of all the lines were collected and oven dried. Total DNA was isolated from the powdered leaf sample, using a procedure described by Bernatzky and Tanksley (1986 a). DNA was digested with four restriction enzymes (*Eco*RI, *Eco*RV, *BST*N1, and *Dra*I), and subjected to Southern analysis as described by Bernatzky and Tanksley (1986 b). Filters were probed using several genomic clones with chromosomal positions known to map within the three regions introgressed from *L. chmielewskii* (Tanksley and Hewitt 1988). Five probes inside the

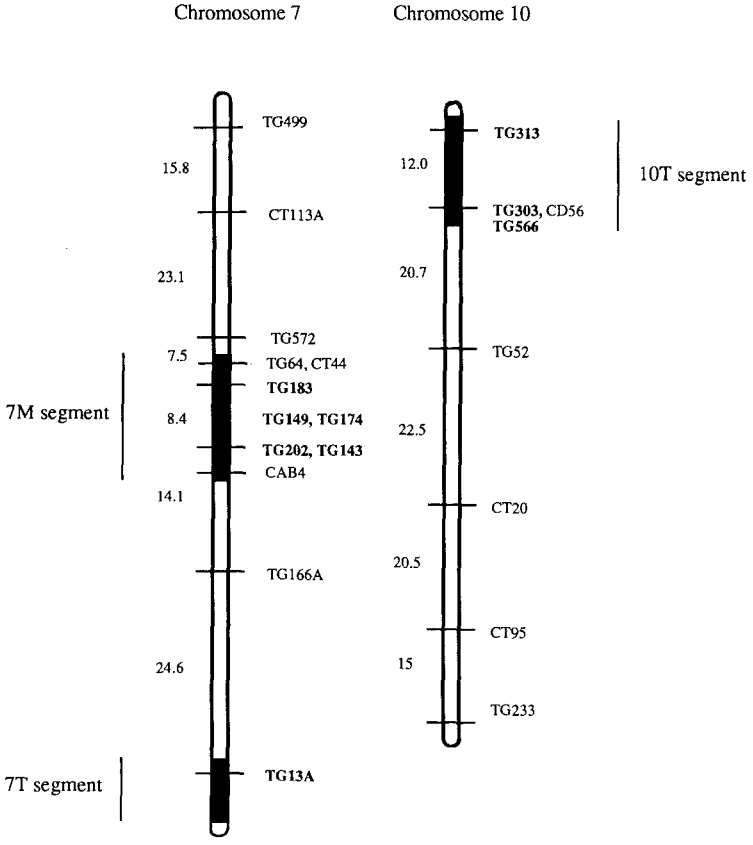

Fig. 1. Tomato RFLP map for chromosome 7 and 10 (Tanksley et al. 1992). Probes in bold were used to assay high SS lines, VF145B-7879 and RIs

7M segment were found to be polymorphic between the parents (LA1501 and VF145B-7879), but only one of six tested was found to be polymorphic in the 7T segment. Only these polymorphic probes were used to assay the BI population (Fig. 1).

Statistical analysis

Analysis of variance using SAS (SAS 1985) was conducted for all the variables to study the variation among replicates, BILs, parental lines, and LA1500, LA1502, LA1503 and LA1563 at the red-ripe stage. Linkage relationships between RFLPs and genes controlling the traits under study were determined by analysis of variance, using RFLP genotypic groups as class variables. Each genotype mean for all the physiological parameters is the average of four measurements (four replicates). Multiple comparisons using LSD tests were conducted to compare RFLP group means and ascertain the significance of the effect of the individual segments on all the variables. The number of lines in each group differed, with one group (7M7T) represented by only one line. This creates an unbalanced comparison with a low statistical power. To better control environmental variation that is typically associated with yield and to improve the statistical power or resolution of the effect of these fragments, data from all eight replicates of all these lines were evaluated for yield. For the same reason, the group having both segments (7M7T) was removed from the analysis of yield. By comparing the RFLP group means for weight, yield, pH and SS with parental means, the proportion of the difference between the parents accounted for by the two *L. chmielewskii* chromosomal fragments was estimated.

Results and discussion

Parental screening of VF145B-7879, LA1500, LA1501, LA1502, LA1503 and LA1563

Comparison of VF145B-7879 and the high-SS lines revealed significant differences among them for many of the yield and fruit chemical parameters (Table 1). Significant variation in these traits between the high-SS lines developed by Rick (1974) suggests that they differ in the number of *L. chmielewskii* introgressed segments, or in alleles contributed from their cultivated parents (VF145B-7879 or VF36). The interaction of the *L. chmielewskii* genes with allelic variation among the cultivars may also contribute to the observed variation among the lines. This could explain previous results (Tanksley and Hewitt 1988) where the *L. chmielewskii* segments were assayed in crosses with different cultivars and shown to vary in their effect on SS and pH.

Significant differences between VF145B-7879 and LA1501, the parental lines used to produce the BI population, were observed (Table 1). LA1501 was found to display a higher SS concentration, a higher pH, a lower citrate concentration and fewer but larger fruit per plant with a lower yield than VF145B-7879. Glucose and fructose concentrations were higher in LA1501 but only when expressed as a proportion of fresh weight.

Nine genomic probes, polymorphic for the three introgressed segments from *L. chmielewskii*, were tested in all the high soluble lines derived from C.M. Rick's breeding program. For the purpose of this discussion these segments will be identified as: 7M for the segment in the middle region of chromosome 7; 7T, a segment at the terminal position on the long arm of chromosome 7; and 10T, a segment at the terminal position on chromosome 10 (see Fig. 1). DNA was extracted from the parental lines and tested for RFLP variability. LA1500, LA1502 and LA1563 have the three introgressed segments previously reported (Tanksley and

Table 1. Means of all the physiological characteristics under study for the parental lines

Variable		Lines						
		VF145B	LA1500	LA1501	LA1502	LA1503	LA1563	LSD[a]
Fruit weight	g/fruit	104	125	133	96	105	103	21
No. of fruit/plant		28	20	19	24	23	22	3
pH		4.35	4.58	4.51	4.62	4.39	4.62	0.15
Total solids (TS)	g/100g	5.34	5.65	5.50	6.35	5.29	5.51	0.68
Soluble solids (SS)	g/100g	3.32	3.86	4.39	4.70	4.40	4.23	0.53
Ratio SS/TS	%	62.3	68.5	80.3	73.9	83.6	77.0	9.0
Yield	Kg/plant	2.96	2.52	2.54	2.30	2.44	2.26	0.30
Yield × TS	g/plant	158	143	140	146	129	124	23
Yield × SS	g/plant	99	97	112	108	109	95	21
Citrate (fresh)	g/100g	0.39	0.36	0.34	0.30	0.39	0.29	0.07
(dry matter)	g/100g	11.8	9.58	7.73	6.41	9.09	6.89	2.31
Glucose (fresh)	g/100g	0.71	1.00	1.07	1.15	0.87	0.97	0.14
(dry matter)	g/100g	21.5	26.0	24.2	24.3	21.9	22.9	4.28
Fructose (fresh)	g/100g	1.02	1.30	1.33	1.49	1.14	1.28	0.15
(dry matter)	g/100g	30.6	34.0	30.4	31.9	27.6	30.1	5.26
Total sugar (fresh)	g/100g	1.73	2.31	2.40	2.64	2.01	2.25	0.28
(dry matter)	g/100g	53.2	60.0	54.7	56.2	49.5	53.0	9.48

[a] Least significant difference at $P = 0.05$

Table 2. Mean values and LSDs for fruit weight, fruit pH, total and soluble solids (TS and SS), ratio soluble vs total solids (SS/TS), yield, and yield of soluble solids, for the different genotypic classes at the terminal fragment on chromosome 10

Variable	7M7T+[a]	7M7T10T[b]	LSD[c]
Fruit weight (g/fruit)	119	108	20
pH	4.45	4.61	0.15
Total solids (g/100g)	5.40	5.84	1.09
Soluble solids (g/100g)	4.40	4.26	1.00
Ratio SS/TS (%)	81.7	73.1	10.6
Citrate (g/100g)	0.36	0.32	0.10
Yield (kg/plant)	2.52	2.36	0.39
Yield × SS (g/plant)	112	101	18

[a] Lines (LA1501 and LA1503) that have only the two *L. chmielewskii* segments on chromosome 7
[b] Lines (LA1500, LA1502, and LA1563) that have all three introgressed fragments from *L. chmielewskii*
[c] Least significant difference at $P = 0.05$

Hewitt 1988), but LA1501 and LA1503 were found to lack the *L. chmielewskii* segment at the terminal position of chromosome 10. The fact that LA1501 has only two of the introgressed segments simplifies studies of the effect of the 7M and 7T fragments in a BI population derived from the cross between this line and VF145B-7879. The high concentration of SS and the high pH displayed by LA1501 also recommends its use for further experimentation. In preliminary studies using the backcross inbred population described in Materials and methods, cluster analysis based on fruit soluble solids and pH had indicated that the backcross inbred lines grouped into four clusters for SS and pH, as would be anticipated if it had independently segregated for the two *L. chmielewskii* segments on chromosome 7 from LA1501 (Kim 1990). Results of the cluster analysis based on both physiological parameters suggested that allelic variation at two loci was primarily responsible for the differences between the groups in SS and pH. This suggests that there are only two segments introgressed from *L. chmielewskii* that significantly influence tomato soluble solids and pH in LA1501.

The effect of the fragment on chromosome 10 was compared among LA1500, LA1501, LA1502, LA1503, LA1563, since this fragment was not segregating in the backcross inbred popualtion. A potential association of the 10T segment with the physiological characteristics was tested by analysis of variance procedures using RFLP genotypic groups as class variables (Table 2). Genotypes were classified into two groups. The 7M7T+ class consists of LA1501 and LA1503, both having the *L. chmielewskii* segment on chromosome 7 but not the terminal segment on 10. The 7M7T10T class has all three introgressed segments, and included lines LA1500, LA1502, and LA1563. The 10T segment in combination with the two introgressed segments on chromosome 7 was found to exert a significant effect only on fruit pH (Table 2), as was previously observed by Tanksley and Hewitt (1988). This increase in pH was not associated with a decrease in citrate concentration. Both parameters seem to be independently controlled in these lines. No significant differences in either SS concentration or yield were associated with the 10T segment. A small reduction in fruit weight was compensated by an increase in the number of fruits per plant. Our data suggest that the genes on the *L. chmielewskii* 10T segment do not exert a beneficial influence on cultivated tomato quality and production.

Physiological and genetic analysis of the backcross inbred population

Analysis of variance was conducted to estimate the proportion of the total variation that is accounted for by genetic differences between the BILs. For this purpose F values, coefficients of variation, and a ratio of the sums of squares contributed by the variation between genotypes out of the total sum of squares for the experiment, were computed (Table 3) for each of the variables. Significant differences (F values) were found for all the characteristics except for fruit color and malate concentration. Differences among genotypes was the factor that described the greatest percentage of the total variation. This justifies the use of a segregating BI population as an appropriate methodological approach to isolate the genotypic variation from the environmental variation that significantly influences the expression of these traits. This technique appears to be promising in studying any traits that are controlled

Table 3. Analysis of variance among the BILs for fruit weight, number of fruits per plant, pH, color, total and soluble solids, glucose, fructose, and yield

Variable	F Value[a]	Variation due[b] to genotype	Means	C.V.[c]
Fruit weight (g/fruit)	3.09*	50%	104	14.5
No. of fruits/ plant	1.22ns	29%	29	36.9
pH	2.90*	38%	4.38	1.6
Fruit color	0.74ns	21%	13.1	16.1
Total solids (g/100g)	3.94*	43%	5.15	9.0
Soluble solids (g/100g)	4.67*	57%	3.65	12.4
Citrate (g/100g)	1.52*	33%	0.35	16.0
Glucose (g/100g)	2.97*	44%	0.79	21.4
Fructose (g/100g)	2.34*	41%	1.11	15.5
Total sugar (g/100g)	2.67*	43%	1.90	17.8
Yield (kg/plant)	4.73*	50%	2.92	10.0

[a] F value testing the significance of the genotypic effect in the analysis for each of the variables, where * indicates significance at $P = 0.01$ and ns, non significance with $P > 0.05$ ($df = 63, 185$)
[b] Ratio between the sum of squares for the genotypic effect and the total sum of squares
[c] Coefficient of variation

by genes with measurable effects (Beckmann and Soller 1983). These genetic differences among the BILs in the population can be attributed to the presence of the introgressed segments from *L. chmielewskii*. Malate concentration was very low in all the genotypes, accounting for less than 2% of the soluble fraction, and was not included in the discussion of the results.

The 64 BILs were classified into four RFLP groups, based on probe polymorphisms at 7M and 7T regions. The + + group consisted of all the lines which were genetically identical to the recurrent parent (VF145B-7879) at 7M and 7T. The 7M+ group was made up of BILs that have the *L. chmielewskii* introgressed segment in the medial region of chromosome 7, but not the terminal segment. The +7T group consisted of BILs that are lacking the medial segment but are homozygous for the 7T *L. chmielewskii* segment. 7M7T genotypes have both *L. chmielewskii* segments. None of the BILs were found to be heterozygous for either 7M or 7T.

The observed and expected numbers of BILs in the population which segregated into the four genotypic classes were calculated. Fifty-one BILs displayed an RFLP pattern identical to VF145B-7879 (+ +), six fell into the 7M+ class, six into the +7T group, and one line possessed both segments (7M7T). Assuming that these two fragments are inherited independently, the expected number of lines per group according to genetic theory would be 49 (+ +), seven (7M+), seven (+7T), and one (7M7T), respectively. Therefore, the observed segregation conforms to the expected ratio, suggesting that no selection during the backcrossing or selfing generations took place and that the loci segregated independently.

In the tomato genetic map constructed from a cross between *L. esculentum* and a wild accession of *L. pennellii* the 7M segment from *L. chmielewskii* was found to be 8.4 cM long (Tanksley et al. 1992). According to more recent evidence from additional RFLP probes, this region may be larger. In our study, after two backcrosses and five generations of selfing, no recombinants within the 7M region were recovered. During the generation of the BILs the size of the introgressed chromosomal fragments was expected to decrease. The probability of not finding any recombinant in a population this size after two generations of selfing is below 0.001. It appears, therefore, that this segment is inherited in a block in the population under study. One hypothesis that could explain these results is that all, or portions, of the 7M segment from *L. chmielewskii* may be non-homologous to this region in *L. esculentum*, interfering with synapsis and eliminating the possibility of crossing-over. This non-homology could be due to the presence of chromosomal deletions, insertions, or an inversion. If this is the case, it may not be possible using classical genetic procedures to break the association between increased SS and increased pH as was suggested by Tanksley and Hewitt (1988). Since only one polymorphic probe for the 7T region was found between the parents, no conclusions can be made regarding recombination in this region.

Association of the physiological variables with both chromosomal segments was tested with analysis of variance procedures. Significant differences in the physiological characteristics of RFLP genotypes were interpreted as an indication of linkage between RFLPs and genes controlling these characteristics. By grouping all the genotypes into RFLP classes, it is possible to estimate the single and combined effect of these segments color, fruit weight, number of fruits per plant, pH, total and soluble solids, citrate, glucose and fructose concentration, yield, yield of total solids and yield of soluble solids (Table 4). The last two variables are calculated from the product of the yield times total soluble solids, and have been used in the past as a measure of the relative value of tomato varieties for commerical processing.

The *L. chmielewskii* segment in the middle of chromosome 7 (7M) showed a very significant effect on SS. This fragment was also associated with greater total solids, but the increase in the soluble fraction was larger (Table 4). The 7M segment was also associated with an increase in pH. This increase could partially be attributed to a significant decrease in citric acid concentration on a dry weight basis. The 7M fragment reduced yield but not significantly (Table 4). Neither fruit weight nor the number of fruits per plant were altered by this fragment.

The terminal fragment on chromosome 7 (7T) did not modify either fruit SS, total solids, pH, or the concentrations of glucose, fructose and citric acid (Table 4). However, lines with the 7T segment averaged a 12% greater yield than lines with the *L. esculentum* segment (+ +) (Table 4). The observation that average fruit weight was 10% greater in these lines suggests that the increased yield may be primarily associated with larger fruits and not from greater numbers of fruits per plant.

Comparing the RFLP group means with the differences in SS, pH, fruit weight and yield, it is possible to estimate the proportion of the difference between the two parents (VF145B-7879 and LA1501) can be accounted for by the two fragments (Fig. 2). The 7M segment accounted for all the difference between the parents in SS, and 80% of the difference in pH, while the 7T segment accounted for 35% of the difference in fruit weight and all the difference in yield between the parents. These data suggest that, while other genes may have been introgressed from *L. chmielewskii* into the BILs, the gene(s) in the 7M and 7T fragments are primarily responsible for the differences between LA1501 and VF145B-7879 for the measured characteristics.

Table 4. Mean values and LSDs for the fruit variables calculated on a fresh and dry weight basis for the four different genotypic classes

Variable		++	7M+	+7T	7M7T	LSD[a]
Fruit color		13.0 a	14.0 a	13.3 a	14.0 a	1.4
Fruit weight	(g/fruit)	104 ab	98 b	114 ab	122 a	21
No. of fruits/plant		29 a	28 a	29 a	20 b	5
pH		4.37 b	4.47 a	4.37 b	4.52 a	0.08
Total solids (TS)	(g/100g)	5.15 b	5.83 a	4.94 b	6.33 a	0.65
Soluble solids (SS)	(g/100g)	3.52 c	4.45 b	3.68 c	5.17 a	0.61
Ratio SS/TS	(%)	68.7 c	76.1 ab	74.2 bc	81.9 a	7.2
Yield	(kg/plant)	2.90 b	2.75 b	3.27 a	2.50	0.24[b]
Yield × SS	(g/plant)	103 b	121 a	119 a	130	14[b]
Citrate (fresh)	(g/100g)	0.36 a	0.34 a	0.34 a	0.37 a	0.06
(dry matter)	(g/100g)	10.3 a	7.96 bc	9.62 ab	7.15 c	2.20
Glucose (fresh)	(g/100g)	0.77 b	0.93 b	0.74 b	1.28 a	0.21
(dry matter)	(g/100g)	21.9 ab	20.3 b	20.3 b	24.5 a	3.71
Fructose (fresh)	(g/100g)	1.09 b	1.23 b	1.05 b	1.49 a	0.19
(dry matter)	(g/100g)	31.3 ab	27.6 b	29.2 ab	31.4 a	3.72
Total sugar (fresh)	(g/100g)	1.86 b	2.16 b	1.79 b	2.77 a	0.40
(dry matter)	(g/100g)	53.3 a	48.0 a	49.4 a	53.1 a	7.11

[a] Least significant difference at $P = 0.05$

[b] To calculate the LSD for yield, eight replicates were used instead of four and the 7M7T group removed from the analysis

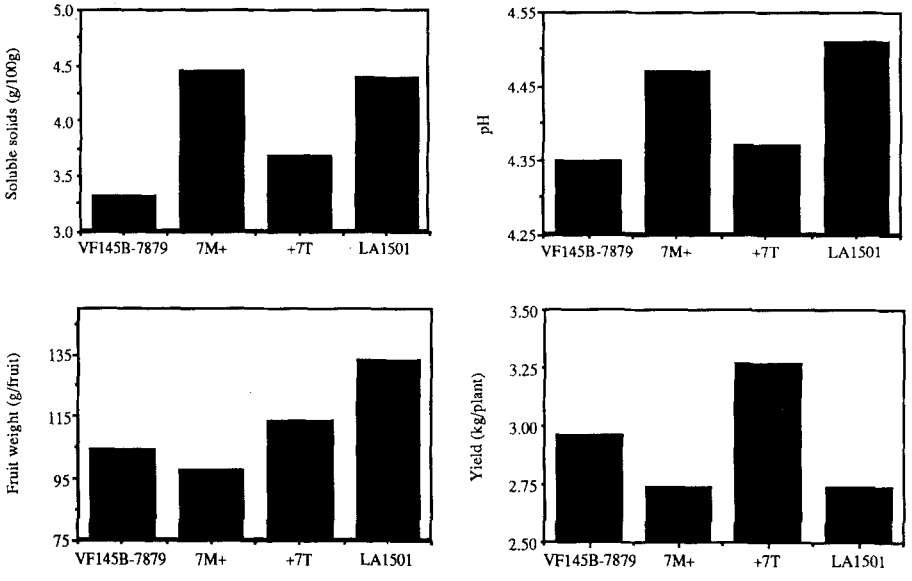

Fig. 2. Comparisons between parents and the recombinant inbreds with either of the chromosomal segments from *L. chmielewskii* for soluble solids, pH, fruit weight and yield

The effect of the combination of both segments into the genome of one of the BILs on pH and total and soluble solids was very significant (Table 4). This effect was found to be non-additive, suggesting the operation of epistasis between genes in these regions. The line that possessed both introgressed fragments displayed reduced yield with bigger fruits but much fewer fruits per plant (Table 4). This effect was also observed in the LA1501 parent which possesses the *L. chmielewskii* 7M segment but displays a significantly-lower yield than VF145B-7879.

The yield of soluble solids, a parameter commonly used in the processing industry to determine the commercial value of a cultivar, was also measured in this study. Both segments were associated with a significant increase in this parameter (Table 4) suggesting that lines that have either of these introgressed segments may possess a higher commercial value. When compared with VF145B-7879, lines with the 7T fragment have larger tomatoes with a greater yield and comparable SS. In contrast, lines with the 7M segment displayed yield values comparable to VF145B-7879 with increased SS concentration. When both segments are combined in the same line, SS was significantly improved but with a concomitant reduction in yield. While the 7M fragment increased SS, the incorporation of this *L. chmielewskii* segment into tomato cultivars was associated with an increased pH, which

could interfere with its commercial utillization. However, 7T may be of use for increasing the value of varieties for the processing industry by increasing yield while maintaining a low pH and SS concentration comparable to that of VF145B-7879.

Higher SS in LA1563 was thought to result from an increase in sugar concentrations (Tanksley and Hewitt 1988). In this experiment the high-SS lines displayed greater concentrations of SS only on a fresh weight basis, and not when SS was measured as a proportion of dry matter, indicating that fruits from these lines had lower concentrations of water. This suggests that the 7M segment is associated with a physiological mechanism that influences fruit water uptake and not by changing the total amount of sugars. This has application to the processing industry since tomatoes with lower water content would cost less to dehydrate into sauce and paste. Tanksley and Hewitt (1988) observed that the 7T fragment had no significant influence on yield, pH, or soluble solids in their study, and suggested that its introgression into the *L. esculentum* genome by Rick was due to random chance. In this study, while the 7L fragment did not affect either SS or pH, it was associated with increased yield. It is probable that the 7T fragment was introgressed into the high-SS lines developed by Rick (1974), since selection for both SS and yield were applied during the course of the backcross program.

Research to study the effect of these segments in total and soluble solids, fruit weight and pH at different stages during the development of the tomato fruit is currently underway. This will allow us to further investigate the physiological mechanisms controlled by these segments, and their regulation during fruit maturation. Future research to study the effect of the fragments in different genetic backgrounds will clarify the utility of these segments for the commercial tomato industry.

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