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Effects of the *Lycopersicon chmielewskii* sucrose accumulator gene (*sucr*) on fruit yield and quality parameters following introgression into tomato

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Abstract A gene controlling fruit sucrose accumulation, *sucr*, was introgressed from the wild tomato species *Lycopersicon chmielewskii* into the genetic background of a hexose-accumulating cultivated tomato, *L. esculentum*. During introgression, the size of the *L. chmielewskii* chromosomal segment containing *sucr* was reduced by selection for recombination between RFLP markers for the *sucr* gene and flanking loci. The effects of *sucr* on soluble solids content, fruit size, yield and other fruit parameters were studied in the genetic background of the processing tomato cultivar 'Hunt100'. In a segregating BC_5F_2 generation, the smallest introgression containing *sucr*-associated markers was necessary and sufficient to confer high-level sucrose accumulation, the effects of which were completely recessive. Fruit of *sucr/sucr* genotypes were smaller than those of +/*sucr* or +/+ genotypes at all stages of development. The timing of sugar accumulation and total sugar concentration were unaffected by sugar composition. No differences in total fruit biomass (fresh weight of red and green fruit) at harvest were observed between the genotypes, and sucrose accumulators produced greater numbers of fruit than hexose accumulators in one family. However, the proportion of ripe fruit at harvest, and hence yield of ripe fruit, as well as average ripe fruit weight and seed set were reduced in *sucr/sucr* genotypes. Sucrose accumulation was also associated with increased soluble solids content, consistency, serum viscosity, predicted paste yield and acidity, and decreased color rating. In the first backcross to *L. chmielewskii*, hexose accumulators (+/*sucr*) had larger fruit than sucrose accumulators (*sucr/sucr*), while no difference in soluble solids was detected.

Key words Soluble solids · RFLPs · Breeding · Invertase · Marker-assisted selection

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Introduction

The composition and concentrations of soluble carbohydrates are important components of quality and yield in many crops. Despite the complex genetic and physiological controls underlying soluble carbohydrate accumulation, experiments have demonstrated the feasibility of making incremental changes by targeting specific enzymes in transgenic plants (Muller-Rober et al. 1992; Tieman et al. 1992). In tomato, *Lycopersicon esculentum* Mill., the concentration of soluble sugars is a major determinant of fruit quality for both processing and fresh market uses. Composed mostly of water, the typical tomato fruit contains approximately 5–7.5% dry matter (solids), roughly 50% of which is represented by soluble sugars, mainly glucose and fructose (Davies and Hobson 1981; Davies and Kempton 1975). Soluble sugars are important components of flavor in tomatoes consumed fresh (Bruyn et al. 1971; Stevens et al. 1977); they are also the major component of soluble solids content (SSC), a parameter that determines the yield of concentrated paste from processing tomatoes (Davies and Hobson 1981).

Efforts to breed tomato varieties with higher SSC are impeded by negative correlations with fruit size, yield, determinant habit and other factors that decrease the leaf: fruit ratio (Stevens 1986). Not surprisingly, the inheritance of SSC is complex, and expression is subject to environmental influence. Whereas modern tomato cultivars typically have a SSC of 5–6%, fruit of the wild species *L. chmielewskii* possess elevated SSC values in the vicinity of 10% (Rick 1974). Breeders have utilized this wild germ plasm to increase the SSC of *L. esculentum* without adversely affecting fruit size or plant yield (Poysa 1993; Rick

1974). Furthermore, specific quantitative trait loci (QTL) affecting SSC and other *L. chmielewskii* traits have been mapped with molecular markers (Osborn et al. 1987; Paterson et al. 1988, 1990; Tanksley and Hewitt 1988). The physiological effects of three of these QTL were studied following introgression into an *L. esculentum* background (Azanza et al. 1994).

While fruit of *L. esculentum* accumulate primarily reducing sugars (glucose and fructose) and very little sucrose, fruit of *L. chmielewskii* accumulate high amounts of sucrose (Yelle et al. 1988). Genetic experiments have demonstrated that the trait of sucrose accumulation is controlled by a single recessive gene, *sucr*, which maps to the pericentromeric region of chromosome 3 (Chetelat et al. 1993). Biochemical and genetic data strongly suggest that *sucr* represents an allele of the acid invertase gene with little or no expression in fruit (Chetelat et al. 1993; Klann et al. 1993; Yelle et al. 1991).

On the basis of osmotic and respiratory considerations, Yelle et al. (1991) suggested that the accumulation of sucrose instead of hexoses might lead to higher SSC, and noted that many sugar storage organs accumulate sucrose. Although the aforementioned mapping studies did not detect a recessive QTL for high SSC in the vicinity of *sucr* from *L. chmielewskii*, this does not exclude the possibility that *sucr* contributes to SSC (for discussion, see Chetelat et al. 1993). Indeed, BC_1F_2 derivatives of *L. chmielewskii* which accumulated sucrose had higher total sugar concentrations than sibling hexose accumulators (Yelle et al. 1991).

In their model for fruit carbon metabolism, Walker et al. (1978) assigned a critical role to acid invertase in controlling the sucrose concentration gradient from source to sink, and thereby determining carbon import rates, via the hydrolysis of sucrose. In support of an apoplastic path for sucrose, Damon et al. (1988) established that imported sucrose is at least partially hydrolyzed by apoplastic invertases prior to uptake by fruit cells. Starch synthesis in the plastid also removes sucrose from the cytosol, thereby potentially contributing to sink strength. This is supported by the positive correlation among tomato cultivars between SSC and starch synthesis rates (Dinar and Stevens 1981). The effects on sink strength of abolishing vacuolar invertase activity, thereby leading to sucrose rather than hexose accumulation, are unknown. On the basis of osmotic considerations alone, the accumulation of dissacharides instead of monosaccharides should reduce water uptake, which would lead to higher SSC, although at the expense of fruit mass.

The gene *sucr* was introgressed from *L. chmielewskii* into tomato, as described in an accompanying paper (Chetelat et al. 1995). The objectives of the work reported in the present article were to evaluate the effects of sucrose accumulation on the pattern of soluble sugar accumulation during development, fruit biomass production and fruit quality characteristics, including SSC. These trends were studied in the genetic background of a processing tomato cultivar nearly-isogenic for introgressions containing *sucr* and in the first backcross to *L. chmielewskii*.

Materials and methods

Plant material

The wild species *L. chmielewskii* accession LA1028 was used as the donor parent for the sucrose accumulator gene, *sucr*. A backcrossing program was used to introgress *sucr* into *L. esculentum* cv 'Hunt100' as described in the accompanying paper by Chetelat et al. (1995). Cultivar 'Hunt100' was chosen as the recurrent parent since it is an open-pollinated processing cultivar that produces large fruit with good paste-making qualities. The first backcross of the F_1 to *L. chmielewskii* was made using the wild species as pollen parent; the resulting population being referred to herein as "RBC_1". In segregating populations, plants were genotyped at the *sucr* locus by Southern analysis using the tightly linked genomic clone TG102; in later generations an invertase cDNA, TIV1 (Klann et al. 1992), was used.

Experimental design

The effects of sucrose accumulation on fruit quality and yield parameters were tested in the BC_5F_2 and RBC_1 generations. The BC_5F_2 experiment, grown in Davis in 1992, was planted in a Completely Randomized Design (CRD) with 50 (family 92L6773) or 100 (family 92L6770) individuals segregating in a 1:2:1 fashion at the *sucr* locus. Following transplanting, young plants were genotyped for *sucr* using the TIV1 cDNA probe. Fruit were harvested from randomly chosen individuals in each genotypic category at weekly intervals starting 2 weeks after controlled self-pollinations. At harvest, fruit biomass (ripe and unripe) was determined for each plant. For fruit quality determinations, three pools of fruit from 3 plants (92L6773) or 4 pools from 4 plants (92L6770) were taken at harvest. Family 92L6773 was harvested a week later than 92L6770 and received one extra irrigation. The RBC_1 population was grown in 1990 at Sinaloa, Mexico, using a CRD consisting of 258 plants segregating in a 1:1 fashion for *sucr/sucr* or *+/sucr* genotypes. Following transplanting, seedlings were genotyped at *sucr* using TG102. Samples of ripe fruit were collected randomly from each plant for soluble solids and fruit weight determinations; 3 solids readings were taken per plant, and fruit weight was based on a sample of 10 fruit per plant. Statistical trends were determined by Analysis of Variance procedures, using the SAS software package (SAS, Cary, N.C.).

Sugar analysis by HPLC

Analysis of fruit sugars was performed by HPLC as described previously (Klann et al. 1993).

Fruit quality analysis

Fruit of the BC_5F_2 population were analyzed at the Department of Food Science, University of California, Davis, Calif.; fruit of the RBC_1 population were analyzed at Campbell Soup R & D, Davis, using similar protocols. Samples of ripe tomatoes were subjected to a microwave hot break to inactivate enzymes and then strained with a 0.033-inch screen. After pulping, samples were taken for pH, titratable acidity, serum viscosity, and Brix measurement. Brix readings were obtained from a digital refractometer and represent the concentration, as a percentage of total fresh weight, of soluble solids (SSC). Titratable acidity, a measure of fruit organic acid content, was determined by the titration of a known quantity of fruit pulp with 0.1 *N* NaOH to a pH 8.0 endpoint and is expressed as milliequivalents of NaOH per 100 g fruit. The remaining juice was deaerated, and the temperature of the sample was adjusted to 25°±0.2°C. Independent duplicate consistency (Bostwick) readings were obtained on each sample. Bostwick values represent the distance (cm) a volume of juice flowed in a trough of fixed dimension in 30 s. A smaller reading corresponds to less flow, or to a product with higher consistency. The same deaerated sample was used for color measurement

using a Gardner XL-23 tristimulus colorimeter; values are reported as the ratio of chromaticity indices "a" (redness) over "b" (yellowness) (Koskitalo and Ormrod 1972). For serum viscosity, samples of pulp were centrifuged, filtered and viscosity measured at 30°C using Cannon-Fenske size 100 viscometers. Flow time in seconds multiplied by the viscometer calibration constant gave viscosity in centistokes. The predicted paste yield was calculated from an empirical relationship: yield (g paste/kg fruit)=35.71×Brix.

Results

Pattern of sugar accumulation during fruit ripening

An analysis of the effects of *sucr* on fruit quality traits performed in an early backcross generation (BC_2F_3) was impeded by segregation for other SSC QTL and genes affecting related traits (e.g. fruit color modifiers, indeterminant habit, reduced fruit set, reduced fruit size). In order to minimize traits such as these that complicate interpretation of fruit yield and quality data, additional backcrosses were carried out. Simultaneously, the size of the *L. chmielewskii* chromosomal segment containing *sucr* was reduced by marker-facilitated selection. The markers TG102 and and TIV1 were used as probes for *sucr*, and recombinants were identified with the flanking markers *r*, TG288 and TG222. BC_5F_2 family 92L6770 had the smallest introgression, with crossovers between TIV1 and *r* on one side, and between TIV1 and TG288 on the other; BC_5F_2 family 92L6773 had a slightly larger introgression, with crossovers between *r* and TIV1, and between TG222 and TG288 (see Fig. 1 in accompanying paper by Chetelat et al. 1995).

Fruit from 92L6770 were harvested at weekly intervals starting at 2–3 weeks post-anthesis, weighed and sugars quantitated by HPLC. An analysis of variance revealed that differences among *sucr* genotypes for fruit mass, sucrose concentration and total hexose concentration were significant ($P<0.0001$). Throughout development, the fruit of *sucr/sucr* plants were smaller than fruit of +/+ or +/*sucr* genotypes (Fig. 1A). Fruit of *sucr/sucr* plants accumulated much higher levels of sucrose than those of the other genotypes, a trend becoming apparent at 4 weeks post anthesis (Fig. 1B). Conversely, hexose concentration was notably lower in the sucrose accumulators than in the other genotypes (Fig. 1C). There were no significant differences in the ratios of glucose to fructose (not shown) or in total sugar concentration (sum of sucrose and hexoses, Fig. 1D) amongst the three genotypes.

Yield and fruit quality in BC_5F_2

In terms of total fruit biomass (ripe plus unripe) per plant at harvest, there were no significant differences between genotypes in either family (Table 1). However, the yield of ripe fruit was lower in the *sucr/sucr* class than in either +/+ or +/*sucr* for family 92L6770 (Table 1). This was due to a decrease in the proportion of ripe fruit at harvest and average weight per fruit rather than to a decrease in the numbers of fruit produced (Table 1). In fact *sucr/sucr* plants produced greater numbers of fruit per plant, thereby compensating for the reduction in average fruit weight, although this trend was only significant in 92L6773 (Table 1). The average seed yield per fruit was lower in sucrose than in hexose accumulators (Table 1). No differences in seed size were detected among the genotypes (data not shown), hence the reduced seed yield indicates fewer seeds per fruit.

Soluble solids content (Brix) was higher in the sucrose accumulators than in hexose accumulators in both families (Table 2). SSC was inversely related to percent ripe fruit at harvest in both families, and to ripe fruit yield in 92L6770 (Tables 1, 2). Fruit of sucrose accumulators were more acidic, as measured by either fruit pH or titratable acidity, in both families (Table 2). Serum viscosity and juice consistency were also higher in the sucrose accumulators, though the trend was significant only in family 92L6770 (Table 2). Fruit color, as measured by the a/b ratio, was lower in the sucrose accumulators from both families (Table 2). The predicted paste yield per unit fruit weight, which is a function of SSC, was greater in sucrose than in hexose accumulators from both families (Table 2). Apparent differences between the two families (e.g. for absolute values of Brix and viscosity) could not be examined statistically since the families were planted separately in the field and samples were analyzed independently in the laboratory.

Table 1 Fruit yield data for BC_5F_2 hexose- (+/+, +/*sucr*) and sucrose- (*sucr/sucr*) accumulating individuals. Genotypes at the *sucr* locus were determined by RFLP analysis using the TIV1 probe. Values are the mean of 12 (92L6770) or 6 (92L6773) individuals in each genotypic class. Genotype means within families labelled with different letters are significantly different ($P<0.05$) based on the results of ANOVA *F*-tests and Least Significant Difference tests

	Family 92L6770			Family 92L6773		
Parameter	+/+	+/*sucr*	*sucr/sucr*	+/+	+/*sucr*	*sucr/sucr*
Total fruit yield (kg/plant)	7.51[a]	7.48[a]	6.37[a]	7.45[a]	9.45[a]	8.54[a]
Ripe fruit yield (kg/plant)	7.16[a]	6.38[a]	5.04[b]	7.36[a]	8.98[a]	6.97[a]
% Ripe fruit (by weight)	95.1[a]	87.3[b]	81.6[b]	98.8[a]	95.2[a]	82.0[b]
Total number fruit/plant	124[a]	129[a]	168[a]	97.5[a]	128[a]	177[b]
Ripe fruit weight (g F.W./fruit)	64.3[a]	66.8[a]	45.2[b]	77.4[a]	78.3[a]	56.3[b]
Seed yield (mg/fruit)	159[a]	137[a]	80.3[b]	168[a]	150[a]	79.1[b]

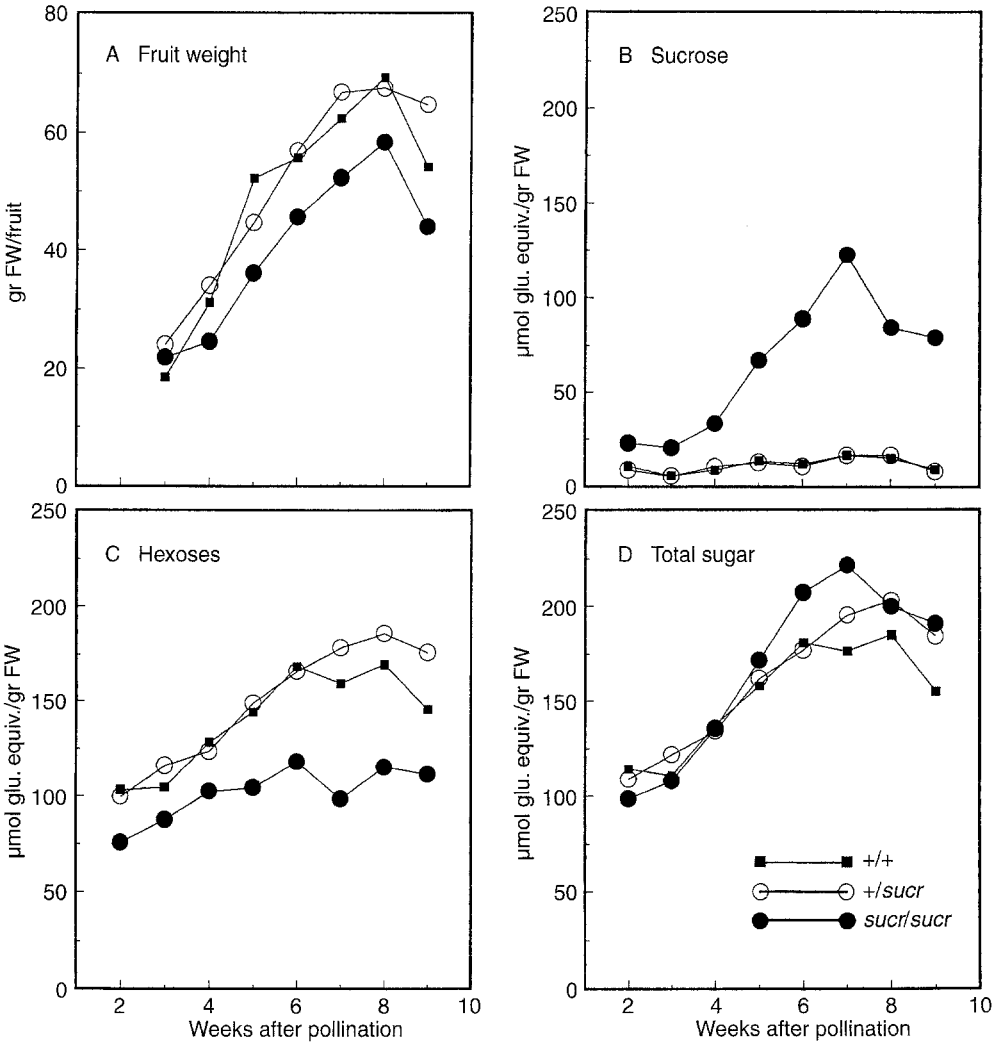

Fig. 1A–D Increase in fruit fresh weight and accumulation of soluble sugars by BC_5F_2 hexose (+/+, *+/sucr*) and sucrose (*sucr/sucr*) accumulators. **A** Fruit fresh weight, **B** sucrose concentration, **C** total hexose (fructose + glucose) concentration, and **D** total sugar (hexose + sucrose) concentration. Genotypes at the *sucr* locus were determined by RFLP analysis using the TIV1 probe. Values represent the mean of 5–17 samples per genotype by time-point combination. All sugar concentrations are expressed in glucose equivalent units

Table 2 Fruit quality data for BC_5F_2 hexose- (+/+, *+/sucr*) and sucrose- (*sucr/sucr*) accumulating individuals. Genotypes at the *sucr* locus were determined by RFLP analysis using the TIV1 probe. Values are the mean of 4 (92L6770) or 3 (92L6773) fruit pools in each genotypic class. Genotype means within families labelled with different letters are significantly different ($P<0.05$) based on the results of ANOVA F-tests and Least Significant Difference tests. Units are explained in Methods and materials

Parameter	Family 92L6770			Family 92L6773		
	+/+	*+/sucr*	*sucr/sucr*	+/+	*+/sucr*	*sucr/sucr*
Soluble solids (°Brix)	5.35^a	5.65^b	6.25^c	4.93^a	4.83^a	5.40^b
Fruit pH	4.50^a	4.49^a	4.38^b	4.52^a	4.49^a	4.36^b
Titratable acidity (meq OH^-/100 g fruit)	3.68^a	4.25^a	5.18^b	3.73^a	3.89^a	5.45^b
Serum viscosity (centistokes)	6.03^a	7.32^a	11.48^b	4.21^a	4.81^a	5.84^a
Juice consistency (Bostwick cm)	12.41^a	9.81^b	8.48^b	10.85^a	10.25^a	8.87^a
Fruit color (a:b ratio)	2.12^a	2.18^a	1.86^b	2.31^a	2.31^a	2.12^b
Predicted paste yield (g/kg fruit)	191^a	202^b	223^c	176^a	173^a	193^b

Effect of *sucr* on fruit size and SSC in the RBC_1

To study the effects of sucrose versus hexose accumulation in the genetic background of *L. chmielewskii*, the F_1 hybrid was backcrossed to the wild parent to produce the RBC_1. Out of 264 plants, 139 were hexose accumulators and 125 were sucrose accumulators. No differences in fruit set or overall plant habit (all were indeterminate) were noticed between the two groups. Average fruit weight was greater in hexose (3.71 g/fruit, SE=0.10) than in sucrose accumulators (2.90 g/fruit, SE=0.08), a difference significant at the $P<0.0001$ level. No difference in SSC was noted, with both groups averaging 7.9°Brix (SE=0.09 for both groups).

Discussion

Experiments have demonstrated the feasibility of utilizing *L. chmielewskii* to increase soluble solids concentration through conventional (Rick 1974; Poysa 1993) or restriction fragment length polymorphism (RFLP)-assisted breeding (Paterson et al. 1990). In order to better understand the genetic and physiological basis of a quantitative trait, SSC, the present study analyzed the effects of a single gene, *sucr*, which leads to the accumulation of high sucrose concentrations in fruit.

Results from previous studies supported a correlation between sucrose accumulation and elevated total sugar concentration (reducing sugars plus sucrose) in the first backcross to cv 'UC204C', a processing cultivar (Yelle et al. 1991). However, this previous study did not address the effects of *sucr* on SSC directly, nor did it look at other quality parameters. Since the earlier study was conducted in the greenhouse under conditions of manual self-pollination, a realistic evaluation of fruit set, size and yield potential could not be obtained.

Following introgression, the effects of *sucr* on sugar composition and concentration during fruit development were studied by HPLC analysis. The finding that the smallest introgression containing the *L. chmielewskii* TIV1/TG102 alleles is both necessary and sufficient for high-level sucrose accumulation is consistent with biochemical data that point to invertase as the controlling enzyme (Klann et al. 1993; Yelle et al. 1991). Dali et al. (1992) reported that a rise in sucrose phosphate synthase activity late in development was important for attaining high sucrose concentrations. In contrast, the genetic data presented here do not support involvement of a second gene, nor were differences in sucrose phosphate synthase activity between hexose and sucrose accumulators confirmed by biochemical tests in an earlier backcross generation (Klann et al. 1993).

Yelle et al. (1988) demonstrated that *L. chmielewskii* differed from *L. esculentum* not only by its high sucrose levels but also by a developmental delay in sugar accumulation and a greater final total sugar concentration on a fruit fresh weight basis. In contrast to *L. chmielewskii*, no differences between sucrose- and hexose-accumulating BC_5F_2 introgression lines were detected in terms of developmental timing or final sugar concentration. Thus, the effect of *sucr* is primarily to alter the partitioning of sugars between the hexose and sucrose pools.

The effects of the *sucr* introgression on fruit quality traits in the BC_5F_2 generation included increases in soluble solids, consistency and acidity, and reduced color. Within tomato cultivars, a negative correlation exists between SSC and factors that decrease the source to sink ratio, such as yield, fruit size and determinant habit (Stevens 1986). Since *sucr/sucr* genotypes had reduced ripe fruit yield, smaller fruit, and a less uniform fruit set, a direct effect of sugar composition on SSC cannot be readily distinguished from the indirect consequences of these other changes. The observed increases in consistency and acidity suggest a generalized concentrating of fruit constituents (soluble and insoluble carbohydrates, organic acids, etc.), which is consistent with a restriction of fruit water uptake resulting from an osmotic effect of sucrose versus hexose accumulation. The results could also be explained by an increased source:sink ratio of *sucr/sucr* genotypes, since under source-limiting conditions, one would predict that a direct increase in soluble sugars should, if anything, decrease the proportion of acids and insoluble carbohydrate. The decreased color values can be tentatively attributed to other genes on the *sucr* introgression segment, since a change in sugar composition seems unlikely to directly affect pigment accumulation. Alternatively, the smaller fruit size of sucrose accumulators could increase sun damage by virtue of the increased surface area to volume ratio.

To evaluate sucrose accumulation without the compounding effects on fruit size and yield, one could perform thinning experiments to maintain a constant number of fruit per cluster. However, since fruit size is positively correlated with seed numbers (Dempsey and Boynton 1965), the reduced seed set of *sucr/sucr* genotypes would complicate interpretation of such experiments. The alternative pursued in the present investigation was to examine the effects of sucrose accumulation in a backcross to the donor parent, *L. chmielewskii*, in which source:sink ratios did not appear to be greatly altered by *sucr*. The results verified one prediction from osmotic considerations, that sucrose accumulation would reduce fruit size. Surprisingly, no correlated increase in SSC was observed. In this population, an effect of *sucr* may have been masked by the segregation of other SSC genes, and the factors limiting sugar uptake might be quite different in such small-fruited indeterminate genotypes.

Complete or partial sterility is a common feature of interspecific hybrids and their derivatives (Stebbins 1958). In attempts to transfer high SSC from *L. chmielewskii* to *L. esculentum*, Rick (1974) encountered reduced fecundity that persisted through BC_5 and that was correlated with elevated SSC. However, this association was eventually broken, and Azanza et al. (1994) found one of the introgressed segments on chromosome 7 actually increased fruit yield. The basis of the impaired seed set of sucrose accumulators seen here is unknown. Hybrid sterility can be classified according to the type of underlying genetic disharmony: "genic sterility", caused by the action of specific genes, and "chromosomal sterility", caused by structural differences at a chromosomal level (Stebbins 1958). The sterility of *sucr/sucr* genotypes is almost certainly of the genic type, since it is most pronounced in the homozygote. The roughly equal transmission of *sucr* and $sucr^+$ alleles (Chetelat et al. 1993) suggests that the sterility acts at the sporophytic rather than the gametophytic level.

The question of whether the sterility is caused by linked gene(s) or pleiotropic effects of *sucr* cannot be answered in the absence of recombination between sucrose accumulation and the partial sterility phenotypes. Taking into account the average relationship between physical and genetic distances in tomato [750 kb per map unit according

to Tanksley et al. (1992)], the smallest *sucr* introgression [0.8–7.1 cM, see Chetelat et al. (1995)] represents 600 –5,350 kb of DNA. This is probably an underestimate, given the clustering of genes and suppressed recombination in the vicinity of *sucr*. Therefore, even a genetically small introgressed segment could contain many other genes.

In support of the linkage hypothesis, the effects of *sucr* on sugar composition appear to be completely recessive (Fig. 1B) while the sterility is at least partially evident in heterozygotes (Table 1, family 92L6770). While the distribution of acid invertase mRNA in different organs suggests that expression is greatest in fruit (Elliott et al. 1993; Klann et al. 1993), reproductive tissues were not examined. Invertases have been detected in both pollen (Bryce and Nelson 1979) and ovaries (Estruch and Beltran 1991), and have been implicated in the chemotropic response of pollen tubes to stigma tissue (Reger et al. 1992). Therefore, the current data on invertase expression are consistent with both the linkage and pleiotropy hypotheses, and neither can be ruled out at the present time.

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