Theor Appl Genet (2001) 103:1022–1027

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Evaluation of breeding utility of a chromosomal segment from *Lycopersicon chmielewskii* that enhances cultivated tomato soluble solids

Received: 15 April 2000 / Accepted: 13 January 2001

Abstract A chromosomal segment from the wild tomato species, *Lycopersicon chmielewskii*, when backcrossed into the tomato cultivar VF145B-7879, increases fruit soluble solids concentration. In the investigation reported here, the near-isoline (VF145B-7M) homozygous for the *chmielewskii* (*chm*) chromosomal segment was crossed to the cultivar to study allelic interactions and then hybridized to three commercial cultivars (UC204c, E6203, and ChicoIII) to investigate the effect of this segment when heterozygous in different genetic backgrounds. Parents, isogenic hybrids, and unmodified hybrid controls were evaluated in three consecutive years of field study. The *chm* segment, when either homozygous or heterozygous, significantly increased soluble solids concentration by 13% and 12%, respectively, over VF145B-7879 (*esc/esc*), suggesting dominant gene action. Averaged across the three isohybrids and one isoline, one dose of this segment significantly increased soluble solids concentration by 6.0% compared to the unmodified hybrids and VF145B-7879. Other than increasing fruit total and soluble solids in mature-green and ripe-red tomatoes, no consistent negative effects of the *chmielewskii* segment were observed in the various genetic backgrounds on plant yield, fruit weight, or fruit pH. These results favor the use of this segment in breeding programs to develop fresh market and processing tomato cultivars with enhanced quality and reduced processed product dehydration costs.

Keywords Soluble solids · Molecular markers · *L. chmielewskii* · Tomato quality

Communicated by A.L. Kahler

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Introduction

Soluble solids concentration (SSC) and total solids (TS) are the major determinants of tomato fruit quality for both processing and fresh market production (Rick 1974; Stevens et al. 1979). Increasing the SSC and TS concentration in processing tomatoes decreases the energy inputs for dehydration and the costs required for concentrating puree to sauce and paste. High SSC is highly desirable in fresh production due to the important contribution of sugars and acids to the overall flavor and nutritional value of tomatoes (Jones and Scott 1983). The typical tomato fruit contains approximately 5–7.5% TS, roughly 75% of which is reducing sugars (mainly glucose and fructose) with the remainder consisting of organic acids (citrate and malate) and minor amounts of minerals, lipids, pigments, vitamins, and volatiles (Davies and Hobson 1981). The levels of organic acids influence both fruit flavor and pH and are important factors in canned tomato products to control the growth of thermophilic microorganisms (Thompson et al. 1964). Even a small increase in tomato SSC can significantly enhance fruit dry matter, flavor, and quality (Rick 1974; Stevens et al. 1979; Wood 1992).

Genetic variability for SSC among cultivated tomato varieties is extremely limited (Lower and Thompson 1966). Therefore, related wild tomato species have been used as germplasm sources to introgress beneficial alleles associated with enhanced SSC (Young et al. 1993). In the past, efforts to develop tomato varieties with high SSC has been impeded by the negative correlation of this trait with fruit size, yield, determinant plant habit, and other factors (Stevens 1986).

Recent advances in DNA technology have helped in the identification of loci affecting tomato fruit quality (Tanksley et al. 1996). Several studies have identified alleles from wild tomato species that enhance SSC in cultivated backgrounds. Eshed and Zamir (1994) reported that marker-assisted introgression of chromosomal segments from the wild species *Lycopersicon pennellii* into *L. esculentum* improved the SSC of cultivated varieties

by as much as 16%. Tanksley et al. (1996) introgressed alleles from *L. pimpinellifolium* associated with high SSC into an elite processing cultivar. While most of the introgressed alleles enhanced SSC, they were also associated with negative effects on other fruit characteristics and yield. A gene controlling fruit sucrose accumulation, introgressed from *L. chmielewskii*, increased SSC but reduced fruit weight and yield (Chetelat et al. 1995). Goldman et al. (1995) indicated that there is an association between alleles increasing SSC from *L. cheesmanii* and smaller fruit and dry seed weight. Triano and St. Clair (1995) reported on the development of inbred backcrossed lines containing introgressions from *L. cheesmanii* with improved SSC and acceptable fruit size, pH, and color.

Several high SSC lines have been developed from repeated backcrossing of the wild green-fruited species, *L. chmielewskii* (LA1028), into the genome of *L. esculentum* cv. VF36 (BC_{1-2}) and cv. VF145B-22–8 (BC_{3-5}) (Rick 1974). One of these lines, LA1501, was used as a donor parent and crossed to the processing tomato cultivar VF145B-7879 where 64 backcross-inbred lines (BILs, BC_2S_5) were developed (Azanza et al. 1994). BILs homozygous for the chromosomal segment on the middle region of chromosome 7 (7 M) contained higher SSC, TS, and pH compared to the recurrent parent (Azanza et al. 1995). No adverse effects associated with this fragment on fruit yield was detected, suggesting the potential use of these lines as a germplasm source for improved fruit quality and yield. In the investigation reported here one of the above BILs homozygous only for the *chmielewskii* (*chm*) segment in the middle region of chromosome 7 was used to study the effects of this segment on tomato yield and fruit characteristics in an isogenic dosage series and when hybridized to three different tomato cultivars.

Materials and methods

Development of genetic material

LA1501, one of the high SSC lines released by Dr. C.M. Rick, was backcrossed twice to VF145B-7879 and selfed five generations to develop 64 BILs (Azanza et al. 1994). Hereafter in this paper, the VF145B-7879 cultivar will be referred to as VF145B. This BIL population was assayed for five restriction fragment length polymorphism (RFLP) markers within and flanking the 8.4-cM segment on chromosome 7 from *L. chmielewskii* (Fig. 1). It was observed that the 7 M fragment was inherited as a single block where no recombination was observed within the segment after two backcrosses and five generations of selfing (Azanza et al. 1995). One of the BILs, homozygous for the 7 M segment from *L. chmielewskii* (VF145B-7M, *chm/chm*), was crossed to its isogenic parent cultivar VF145B (*esc/esc*). This provided germplasm in a near-isogenic dosage series for the *L. chmielewskii* 7 M segment to evaluate allelic interactions.

The same BIL (*chm/chm*) was crossed to three commercial cultivars, UC204c (*chm/esc*), E6203 (*chm/esc*), and ChicoIII (*chm/esc*), to generate three F_1 hybrids heterozygous for the *chm* segment (*chm/esc*). VF145B (*esc/esc*) was also crossed to the same three cultivars to generate a set of three F_1 hybrid controls homozygous for the *esc* segment. These two sets of isohybrids were used to compare the effect of *chm* in different genetic backgrounds. The crossing direction is not stipulated since previous work indicated that the effects of this segment are not under maternal influence (Young et al. 1993).

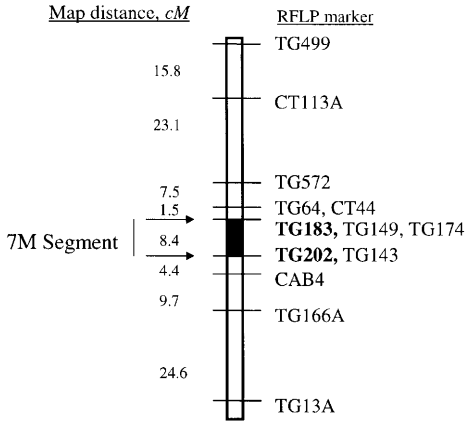

Fig. 1 Chromosome 7 on the tomato linkage map (Tanksley et al. 1992; Aranza et al. 1995. Probes in *bold* were used to genotype the parents for the presence of the *chm* segment

DNA analysis and probing

The BIL and the four commercial cultivars were grown in the greenhouse to screen for polymorphism at two RFLP markers within the 7 M region on chromosome 7. The selected markers (TG183 and TG202) are known to map within this segment (Tanksley and Hewitt 1988) and to be polymorphic between the BIL and its recurrent parent (Azanza et al. 1995). Twenty seeds of the BIL (*chm/chm*) and the four commercial cultivars (*esc/esc*) were sown in the greenhouse. Leaf tissue was harvested from seedlings (45 days old) and stored in a freezer –80°C prior to lyophilization. Total DNA was isolated from the powdered leaf samples according to the procedures described by Bernatzky and Tanksley (1986a). Ten micrograms of DNA was digested with 30 U *Eco*RI, loaded into 0.8% agarose gels, and subjected to Southern blotting analysis as described by Bernatzky and Tanksley (1986b). Membranes were wrapped in plastic and exposed to X-ray film at –80°C for 2–5 days depending on the intensity of the [P^{32}]-labeling and scored for probe bands. The two selected markers were found to be polymorphic between the BIL and all four commercial cultivars.

Experimental procedure and physiological analysis

Seeds of the five parents and seven F_1s were sown in flats containing a 1:1:1 soil mixture of soil: peat: perlite in the spring of 1994, 1995, and 1996. The parents included VF145B-7M (*chm/chm*), VF145B (*esc/esc*), E6203 (*esc/esc*), UC204c (*esc/esc*), and ChicoIII (*esc/esc*). The F_1s consisted of VF145B-7M×VF145B (*chm/esc*), VF145B-7M×E6203 (*chm/esc*), VF145B×E6203 (*esc/esc*), VF145B-7M×UC204c (*chm/esc*), VF145B×UC204c (*esc/esc*), VF145B-7M×ChicoIII (*chm/esc*), and VF145B×ChicoIII (*esc/esc*). Seedlings were hardened off and transplanted 35 days later into field plots of the University of Illinois at Urbana-Champaign. The experimental design was a randomized complete block design (RCBD) with ten replications each year. Each experimental unit consisted of one row with 15 plants, 30 cm apart, with 90 cm between rows. Standard commercial agricultural practices for tomato production were applied each year.

When 50% of the fruit in each plot were ripe-red, the central nine plants in each row were harvested and the fruits weighed to estimate plant yield (PLYD). For fruit composition evaluation, ten

fruits at two different maturity stages (mature-green and red-ripe) were randomly collected from each experimental unit, frozen and stored at –20°C for subsequent analysis.

The ten-fruit samples were weighed to estimate the fruit weight (FRWT) and ground into puree in a blender, from which two sub-samples were removed. A 25-gm puree sample was weighed, frozen at –80°C, then lyophilized using a Virtis Unitop 600L freeze-dryer to determine the fruit dry weight or total solids. Another sample of 40 gm was centrifuged at 12,000 *g* for 15 min at 20°C. The supernatant was poured off to measure the pH and Brix°. A bench refractometer (Model no. 33.45.58, Bausch and Lomb) was used to measure Brix° at 20°C for estimation of soluble solids concentration. The Brix° reading of red-ripe fruits was multiplied by the average plant fruit yield to estimate net plant yield of soluble solids (Brix°/plant).

Statistical analysis

The statistical analysis was performed on the combined data from the three years; therefore, replications were nested within years. The data were sorted into two separate sets: one contained the three VF145B isolines to be used for studying the *chm* segment allelic interaction; the second included nine genotypes (the cultivars E6203, UC204c, and ChicoIII and their crosses to VF145B and VF145B-7M) to study the effect of the *chm* segment in different genetic backgrounds. The normality of data was tested, and the statistical analysis was performed using SAS (1991). The experimental design was a randomized complete block design (RCBD) within each environment. The statistical model used to analyze the data sets $y_{ijk}=\mu+E_i+R(E)_{(ij)j}+\delta_{(ij)j}+G_k+GE_{ik}+\varepsilon_{(ijk)}$, where y=response from the experimental unit, μ=overall mean, E=environments, δ=restriction error, R=replications or blocks, G=genotype, and ε=residual error. The genotype means for all variables were compared using LSD at the $P<0.05$ probability level.

Results and discussion

Sources of variation

Analysis of variance was conducted to examine the sources of variation associated with each trait (Table 1). The statistical model described the effect of environments, replications nested within environments, genotypes, and genotype×environment interactions. Differences among environments were typically responsible for the greatest source of variation and significant for most variables. Differences among genotypes were significant for all variables except for Brix°/plant. Differences in the genotypes were the most important source of variation in Brix° in mature-green and ripe-red fruit and in TS in green fruit. The interaction between genotypes and environments was significant in about 50% of the data sets. Coefficients of variation (C.V.%) calculated as [(√MSE/grand mean)×100], which expresses the experimental error as a percentage of the mean, were low

Table 1 Mean squares from ANOVA of yield and fruit characteristics for the VF145B isolines (*chm/chm*, *chm/esc*, and *esc/esc*)

Source of variation[a]	*df*	PLYD[b]	Fruit characteristics								Brix°/ plant
			Brix°		TS[b]		pH		FRWT[b]		
			Green	Red	Green	Red	Green	Red	Green	Red	
E	2	344.5*	0.09	2.17*	1.24*	17.47*	0.29*	0.08*	29.0*	23.6*	818.4*
R(E)	27	0.7*	0.05	0.14	0.22	0.66	0.02*	0.04*	0.1	0.2	1.3
G	2	2.9*	0.96*	2.66*	1.92*	2.58*	0.02*	0.04*	0.2*	0.7*	1.8
G×E	4	1.5*	0.25*	0.07	0.36	0.80	0.05*	0.01	0.2*	0.3	1.0
Error	54	0.3	0.04	0.11	0.22	0.76	0.01	0.01	0.1	0.18	1.0
R^2		98%	65%	70%	54%	60%	76%	67%	93%	88%	97%
CV%[c]		14.1	4.9	7.1	7.9	14.8	2.0	2.5	10.1	11.2	16.1

* Significant at $P<0.05$

[a] E, environment, R, replication, G, genotype (VF145B-7M, *chm/chm*; VF145B-7M×VF145B, *chm/esc*; VF145B, *esc/esc*)

[b] PLYD, Plant yield; TS, total solids; FRWT, fruit weight

[c] Coefficient of variation

Table 2 Means of yield and fruit characteristics measured in the three VF145B isolines (*chm/chm*, *chm/esc*, and *esc/esc*) used for studying the *chm* segment allelic interaction

Genotype[a]	Dosage of *chm*	Fruit characteristics										Brix°/ plant (gm)
		PLYD[b] (kg)	Brix°		TS(%)[b]		Brix°/ TS ratio	pH		FRWT (gm)[b]		
			Green	Red	Green	Red		Green	Red	Green	Red	
VF145B	*esc/esc*	4.33a[c]	4.14b	4.25b	5.67b	5.53b	0.80a	4.23b	4.24b	95a	105a	188a
VF145B-7M×VF145B	*chm/esc*	4.10a	4.48a	4.74a	6.00a	6.08a	0.79a	4.24a,b	4.31a	91a	106a	197a
VF145B-7M	*chm/chm*	3.72b	4.38a	4.79a	6.16a	5.98a,b	0.82a	4.27a	4.28a,b	90a	97b	181a
LSD[d]		0.30	0.10	0.17	0.24	0.45	0.06	0.05	0.06	05	06	016

[a] Isolines of VF145B with either zero, one, or two doses of the *chm* segment from *L. chmielewskii*

[b] PLYD, Plant yield; TS, total solids; FRWT, fruit weight

[c] Means with different letters within columns are significantly different at $P<0.05$ probability level

[d] Least significant differences

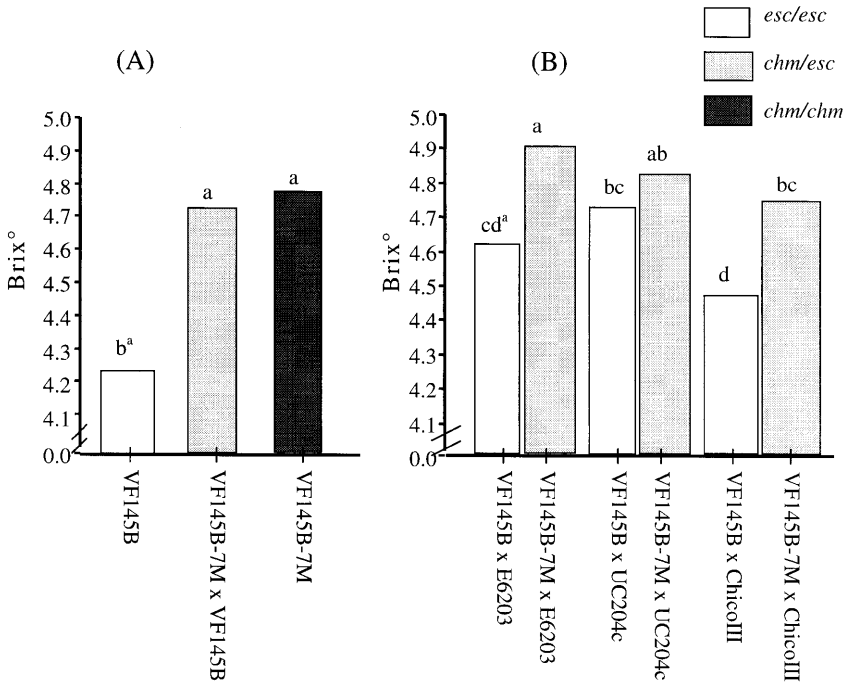

Fig. 2 SSC in ripe-red fruit of isolines of VF145B (*chm/chm, chm/esc, esc/esc*) (**A**) and isohybrids of the three commercial cultivars E6203, 4C204c, and ChicoIII (*chm/esc, esc/esc*) (**B**).

[a] Columns with *different letters* indicate significant differences in SSC in the isolines of 4F145B and isohybrids of the commercial cultivars at $P<5\%$

and ranged from 2.0 to 16.1. The R^2 values (% of variation explained by the statistical model) averaged 77% across traits and ranged from 54% to 98%, indicating that variation for most of the traits was fairly well described by the model.

Allelic interaction of the *chm* segment

As previously reported, the *chm* segment appears to exert substantial effects on fruit quality characteristics (Azanza et al. 1995). Fruit characteristics and yield of the isolines VF145B (*esc/esc*), VF145–7M (*chm/chm*), and VF145B-7M×VF145B (*chm/esc*) are presented in Table 2. Results from three years of replicated data indicated that there were significant changes in fruit characteristics associated with this segment. Soluble solids concentration, measured as Brix° in the ripe-red fruits, a key trait in tomato commercial production, was 4.79 and 4.74 in the *chm/chm* and *chm/esc* isolines, respectively, compared with 4.25 in the commercial parent (*esc/esc*) (Fig. 2). The Brix° in the *chm/chm* and *chm/esc* isolines was enhanced by 13% and 12%, respectively, over *esc/esc*. Ripe-red fruit TS in *chm/chm* and *chm/esc* was enhanced by 10% and 8%, respectively, over *esc/esc*. The allele(s) on the *chm* segment is dominant to the *esc* allele(s) present in the commercial parent, VF145B, supporting the feasibility of using this gene in producing high SSC hybrids containing only one dose of the *chm* segment.

The soluble solids concentration, measured as Brix°, in two fruit maturity stages (mature-green and red-ripe) in the F_1 genotype (*chm/esc*) was significantly higher than that of VF145B, indicating that the gene(s) on this segment exerts its physiological effects prior to fruit maturation and ripening. These results suggest that the *chm* segment will enhance fruit quality in both processing and long-distance fresh market cultivars harvested at the mature-green stage. The pH of the ripe-red fruit VF145B heterozygote (*chm/esc*) was also higher than that of the commercial parent. However, this increase did not exceed a pH of 4.5, the value required to control the growth of the thermophilic microorganisms in processed and canned tomato products (Thompson et al. 1964).

Comparisons between the heterozygous VF145B (*chm/esc*) and the commercial parent showed no significant reduction in plant yield or fruit weight. Hence, lines heterozygous for this segment can provide fruit yield comparable to lines homozygous for the esculentum segment on chromosome 7. The average ripe-red fruit weight of the *chm/esc* isoline was not significantly smaller than that of the commercial cultivar, suggesting that this segment exerts no adverse effect on the overall fruit development in a heterozygous state. The significant differences observed when SSC was based on fresh weight (Brix°) and the lack of significance when based on dry weight (Brix°/TS) suggest that the gene(s) on the *chm* segment may influence fruit water uptake during maturation and ripening.

Effect of the *chm* segment in different genetic backgrounds

Tomato yield and fruit characteristics of the hybrids lacking or heterozygous for the *chm* segment are listed in Table 3. Incorporating *chm* in the three genetic backgrounds (*chm/esc*) showed significant improvements in fruit quality compared to their respective *esc/esc* isohybrids in two of the three genetic backgrounds. The solu-

Table 3 Means of yield and fruit characteristics measured in the three cultivars (E6203, UC204c, and ChicoIII) and the isohybrids from crosses to VF145B-7M (*chm/chm*) and VF145B (*esc/esc*)

Genotype[a]	Dosage of *chm*	Fruit characteristics										Brix°/ plant (gm)
		PLYD[b] (kg)	Brix°		TS (%)[b]		Brix/ TS ratio	pH		FRWT (gm)[b]		
			Green	Red	Green	Red		Green	Red	Green	Red	
E6203	*esc/esc*	4.45ab[c]	4.34 cd	4.61 cd	5.89c	6.23ab	0.76a	4.28a	4.26bc	81bc	091c	203bc
VF145B-7M×E6203	*chm/esc*	4.52a	4.56a	4.91a	6.27a	6.40a	0.78a	4.23b	4.36a	84b	101ab	223a
VF145B×E6203	*esc/esc*	4.73a	4.38bc	4.62 cd	6.00bc	5.95bcd	0.79a	4.19bcd	4.25bc	85ab	102ab	216ab
UC204c	*esc/esc*	3.78d	4.32 cd	4.73bcd	6.14ab	6.13abc	0.78a	4.15d	4.23c	77c	085d	179d
VF145B-7M×UC204c	*chm/esc*	4.41abc	4.46ab	4.83ab	6.25a	6.16abc	0.80a	4.17 cd	4.29bc	89a	104a	216ab
VF145B×UC204c	*esc/esc*	4.05 cd	4.26d	4.73bc	6.02bc	6.06abc	0.80a	4.20bc	4.23c	84ab	097b	191cd
ChicoIII	*esc/esc*	4.13bcd	4.12e	4.42e	5.82c	5.61d	0.80a	4.17 cd	4.24bc	706d	083d	183d
VF145B-7M×ChicoIII	*chm/esc*	3.97d	4.49ab	4.75bc	6.22ab	6.13abc	0.79a	4.19bcd	4.30b	76c	091c	19 cd
VF145B×ChicoIII	*esc/esc*	4.50a	4.30 cd	4.57d	5.85c	5.81 cd	0.80a	4.18bcd	4.27bc	81bc	100ab	205bc
LSD [d]		0.37	0.12	0.15	0.23	0.38	0.05	0.05	0.06	06	005	018

[a] Three tomato commercial cultivars (E6203, UC204c, and Chico-III) and their isohybrids resulted from the crosses to VF145B-7M or VF145B. The isohybrids contain either zero or one dosage of the *chm* segment from *L. chmielewskii*

[b] PLYD, Plant yield; TS, total solids; FRWT, fruit weight

[c] Means with different letters within columns are significantly different at $P<0.05$

[d] Least significant differences

ble solids concentration (Brix°) measured in ripe-red fruit was significantly enhanced with one dose of the *chm* allele in E6203 (6.3%) and ChicoIII (4.0%) compared to their isohybrids without the *chm* segment (*esc/esc*) (Fig. 2). In the UC204c background, the increase in SSC (2.1%) was not significant in the ripe-red fruit. TS followed the same pattern as SSC, where hybrids with one dose of *chm* segment contained higher TS compared to hybrids without the *chm* gene and their commercial parents in two of the three genetic backgrounds. The data suggest that the *chm* segment influences water uptake during fruit maturation but does not change the amount of fruit sugar accumulation.

In the E6203 background, one dose of *chm* significantly increased fruit pH compared to the hybrid without the *chm* segment, but the increase was not significant in the UC204c and ChicoIII backgrounds. The pH was below the 4.5 level suitable for bacterial reproduction. No adverse effects of a single dose of *chm* was observed in mature-green and ripe-red fruit weight. Net plant yield of soluble solids, which is a primary concern in the processing tomato industry, was enhanced significantly in the *chm* heterozygotes for the crosses with UC204c and ChicoIII compared to their *esc/esc* isohybrids. Incorporating the *chm* segment did not significantly reduce total plant yield in any of the three genetic backgrounds. In contrast to previous studies reporting negative effects of introgressed wild tomato germplasm, this segment was not observed to dramatically or consistently reduce yield or average fruit size. In the ripe-red fruit, averaged across all four genetic backgrounds, one dose of the *chm* segment increased Brix°, TS, pH, and Brix°/plant by 6.0%, 6.2%, 1.6%, and 3.8%, respectively, while decreasing plant yield and fruit size by 3.2% and 0.5%, respectively.

Specific genes influencing quantitative traits in a particular genotype are commonly assumed to be background-specific due to the interaction (epistasis) among alleles at different loci in the genome (Zehr et al. 1992; Danzmann et al. 1999). Experimental results of beneficial genes identified in one background are equivocal when tested in different genetic backgrounds (McKendry et al. 1996; Wang 1997; Toojinda et al. 1998). This study clarified the gene effects of an introgressed allele(s) from the wild tomato species *L. chmielewskii* with the aid of DNA markers on economically important tomato traits. Dominant expression of this gene(s) is of value in hybrid production. Indirectly enhancing SSC in tomato ripe fruit by decreasing the water content would have value to the processing tomato industry due to a reduction in dehydration and transportation costs. The introgressed segment (*chm*) was tested for the ability to exert comparable effects when incorporated into three different genetic backgrounds and evaluated for associated effects on the characters of agronomic importance. This *chm* segment was observed to exert a similar effect on tomato fruit quality in different genetic backgrounds. This study offers a more optimistic view that beneficial genes in one background can exert similar effects in a wider range of germplasm and also indicates that the use of DNA markers can be an effective means to select for beneficial alleles influencing quantitative traits in breeding programs. Marker-assisted selection is particularly effective when introgressing genes from the wild germplasm that cannot be readily identified by phenotypic performance (Bernacchi et al. 1998).

Acknowledgments The authors wish to acknowledge funding from Hatch Project 65–0348 of the University of Illinois Agricultural Experimental Station, Minia University of Egypt, and the Egyptian Cultural and Educational Bureau in Washington, D.C. for support to the senior author during his graduate study in the University of Illinois, USA. The experiments described in this manuscript complies with the United States' government.

References

Azanza F, Young TE, Kim D, Tanksley SD, Juvik JA (1994) Characterization of the effect of introgressed segments of chromosome 7 and 10 from *Lycopersicon chmielewskii* on tomato soluble solids, pH, and yield. Theor Appl Genet 87:965–972

Azanza F, Tanksley SD, Juvik JA (1995) Genes from *Lycopersicon chmielewskii* affecting tomato quality during fruit ripening. Theor Appl Genet 91:945–504

Bernacchi D, Beck-Bunn T, Eshed Y, Lopez J, Petiard V, Uhlig J, Zamir D, Tanksley SD (1998) Advanced backcross QTL analysis in tomato. I. Identification of QTLs for traits of agronomic importance from *Lycopersicon hirsutum*. Theor Appl Genet 97:381–397

Bernatzky R, Tanksley SD (1986a) Genetics of actin-related sequences in tomato. Theor Appl Genet 72:314–321

Bernatzky R, Tanksley SD (1986b) Methods for detection of single- or low-copy sequences in tomato on Southern blots. Plant Mol Biol Rep 4:37–41

Chetelat RT, DeVerna JW, Bennett AB (1995) Effects of the *Lycopersicon chmielewskii* sucrose accumulator gene (sucr) on fruit yield and quality parameters following introgression into tomato. Theor Appl Genet 91:334–339

Danzman RG, Jackson TR, Ferguson MM (1999) Epistasis in allelic at upper temperature tolerance QTL in rainbow trout. Aquacult 173:45–58

Davies JN, Hobson GE (1981) The constituents of tomato fruit – the influence of environment, nutrition, and genotype. CRC Crit Rev Food Sci Nutr 15:205–280

Eshed Y, Zamir D (1994) Introgressions from *Lycopersicon pennelli* can improve the soluble-solids yield of tomato hybrids. Theor Appl Genet 88:891–897

Goldman IL, Paran I, Zamir D (1995) quantitative trait locus analysis of a recombinant inbred line population derived from a *Lycopersicon esculentum*×*Lycopersicon cheesmanii* cross. Theor Appl Genet 90:925–932

Jones RA, Scott SJS (1993) Improvement of tomato flavor by genetically increasing sugar and acid contents. Euphytica 32: 845–855

Lower RL, Thompson AE (1966) Sampling variation of acidity and solids in tomatoes. Proc Am Soc Hortic Sci 89:512–522

McKendry AL, Tague DN, Miskin KE (1996) Effect of 1BL.1RS on agronomic performance of soft red wheat. Crop Sci 36:844–847

Rick CM (1974) High soluble-solids content in large-fruited tomato lines derived from a wild green-fruited species. Hilgardia 42:493–510

SAS Institute (1991) SAS user's guide: statistics, version 6, 1st edn. SAS Institute, Cary, N.C.

Stevens MA (1986) Inheritance of tomato fruit quality components. Plant Breed Rev 4:273–311

Stevens MA, Kader AA, Albright M (1979) Potential for increasing tomato flavor via sugar and acid contents. J Am Soc Hortic Sci 104:40–42

Tanksley SD, Hewitt J (1988) Use of molecular markers in plant breeding for soluble solids content in tomato – a re-examination. Theor Appl Genet 75:811–823

Tanksley SD, Ganal MW, Prince JP, de Vicent, Bonierbale MW, Broun P, Fulton TM, Giovannoni JJ, Grandillo S, Martin GB, Messeguer R, Miller JC, Miller L, Paterson AH, Pineda O, Roder MS, Wu W, Young ND (1992) High density molecular linkage maps of the tomato and potato genomes. Genetics 132:1141–1160

Tanksley SD, Grandillo S, Fulton TM, Zamir D, Eshed Y, Petiard V, Lopez J, Beck-Bunn T (1996) Advanced backcross QTL analysis in a cross between an elite processing line of tomato and its wild relative *L. pimpinellifolium*. Theor Appl Genet 92:213–224

Thompson AE, Lower RL, Helper RW (1964) Increasing acidity content of tomatoes by breeding and selection. Proc Am Appl Genet 75:811–815

Toojinda T, Baird E, Booth A, Broers L, Hayes P, Powell W, Thomas W, Vivar H, Young G (1998) Introgression of quantitative trait loci (QTLs) determining stripe rust resistance in barley: an example of marker-assisted line development. Theor Appl Genet 96:123–131

Triano SR, St. Clair DA (1995) Processing tomato germplasm with improved fruit soluble solids content. HortScience 30:1477–1478

Wang S-S (1997) Epistasis and other factors influencing the detection of marker-QTL associations. PhD thesis, University of Illinois at Urbana-Champaign, Ill.

Wood M (1992) Solid future for tomatoes. Agric Res 40:4–5

Young TE, Juvik JA, Sullivan JG (1993) Accumulation of the components of total solids in ripening fruits of tomato. J Am Soc Hortic Sci 118:286–292

Zehr BE, Dudley JW, Chojecki J (1992) Some practical considerations for using RFLP markers to aid in selection during inbreeding of maize. Theor Appl Genet 84:704–708