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Inheritance of High Sugars from Tomato Accession PI 270248 and Environmental Variation between Seasons

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Abstract. **Small-fruited cherry tomato accession PI 270248 [*Lycopersicon esculentum* Mill. var. *cerasiforme* (Dunal) A. Gray] with high fruit sugars was crossed to large-fruited inbred line Fla.7833-1-1-1 (7833) (*L. esculentum*) that had normal (low) fruit sugars. The F_1 was crossed to PI 270248 and 7833 to obtain BCP_1 and BCP_2, respectively, and self-pollinated to obtain F_2 seed. The resulting population was used to study the inheritance of high sugars from PI 270248. Continuous sugar level frequency distributions of BCP_1, BCP_2, and F_2 suggest that the trait is under polygenic control. Additive variation was significant, but dominance variation was not. There was a heterozygote × heterozygote type of epistasis present that likely caused the F_1 sugar level to skew nearly to the level of the high sugar parent. The F_2 mean sugar level was lower than the midparent level. Broad-sense heritability was 0.86. There was a significant line × season (fall, spring) interaction where lines with higher sugars were affected more by seasons than lines with lower sugars. Sugar level, in general, was higher in spring. Higher solar radiation in spring than in fall may explain the sugar level difference between the seasons.**

There is general agreement that flavor of commercial fresh-market tomatoes could be improved if their fruit sugar concentration was increased (Jones and Scott, 1984; Malundo et al., 1995; Stevens, 1972). There are several small-fruited accessions with high fruit sugars and these can be used as donor parents. These include accessions of *L. chmielewskii* Rick et al. (Chetelat et al., 1995), *L. hirsutum* Humb. & Bonpl. (Hadas et al., 1995; Schaffer et al., 1998; Stommel and Haynes, 1993), and various cherry tomatoes (Saliba-Colombani et al., 2001). The small-fruited cherry accession PI 270248 'Sugar' was originally of interest in our breeding program because it had a high level of resistance to bacterial spot [*Xanthomonas campestris* Dye pv. *vesicatoria* (Doidge) Dye] on its fruit but not foliage (Scott et al., 1989). More recently, we have been interested in using PI 270248 as a source of high sugars for transfer to large-fruited tomato inbreds. Georgelis et al. (2004) identified six randomly amplified polymorphic DNA (RAPD) markers from PI 270248 that were linked to high sugars in at least three linkage groups. Unfortunately, five of these markers were also linked to small fruit size and the sixth was linked to indeterminate plant habit. These results confirmed earlier work showing sugars (or soluble solids) to be higher in small fruit (Goldman et al., 1995; McGillivary and Clemente, 1956; Saliba-Colombani et al., 2001) and in indeterminate plants over determinate plants (Emery and Munger, 1970). Thus, the transfer of high sugars from small-fruited accessions to large-fruited, determinate recurrent parents will be difficult because of the associations mentioned and the quantitative control of high sugars. The RAPD markers identified (Georgelis et al., 2004) might be helpful, but only if they can be used to select for sugars without either small fruit or indeterminate plant habit. Thus, further work is needed to determine their breeding value. It also will be helpful to know the inheritance of the high sugar trait from PI 270248 so an effective breeding strategy can be employed. The objectives of this report are 1) to determine the inheritance of high sugars from PI 270248 and 2) to elucidate some of the environmental effects on sugars that might affect the selection process.

Materials and Methods

Inheritance study

Field design. PI 270248 was crossed to 7833 to obtain F_1 seed. Subsequently, the F_1 was self-pollinated to obtain F_2 seed and crossed to PI 270248 and 7833 to obtain BCP_1 and BCP_2 seed, respectively. In Spring 2002, 30 seeds of PI 270248, 38 of 7833, 35 of F_1, 35 of BCP_1 (limited seed available), 93 of BCP_2 and 198 of F_2 were sown in the greenhouse in Black Beauty spent coal (Reed Minerals Division, Highland, Ind.) medium on 11 Jan. and seedlings were transplanted into Todd planter flats (3.8 cm^3 cell size)(Speedling, Sun City, Fla.) on 25 Jan. Plants were transplanted to the field on 6 Mar. on 20-cm-high, 81-cm-wide beds of EauGallie fine sand that had been fumigated with 67% methyl bromide : 33% chloropicrin at 392 $kg \cdot ha^{-1}$ and covered with black polyethylene mulch 2 weeks before transplanting. All generations were arranged in a randomized complete-block design with four blocks. PI 270248, 7833, F_1, and BCP_1 entries had 10 plants per plot, while the BCP_2 and F_2 had 24 and 50 plants per plot, respectively. Plants were spaced 46 cm apart within plots that were 91 cm apart in rows, with 152 cm between rows. Recommended fertilizer and insecticide programs were followed (Olson et al., 2004). Plants were grown with stake culture and irrigated by seepage from ditches adjacent to the six experimental beds.

Fruit preparation. Fruit, ranging from 3 to 15 in number depending on fruit size, were harvested on 23 May then ground

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using a blender (Waring Products, Torrington, Conn.) and the fruit homogenate was stored in polyethylene bags at –20 °C until use. Fruit homogenate (40 g) was added to 70 mL of 80% ethanol, boiled for 15 min (with a loose-fitting cover), cooled, and vacuum-filtered through Whatman #4 filter paper (Whatman plc, Brendford, Middlesex, U.K.). The resulting extract was brought up to 100 mL with 80% ethanol, and 12 mL then was passed through a C-18 Sep Pak (Waters Corp., Milford, Mass.) and a 0.45-μm Millipore filter. The filtered extract was injected using a Bio-Rad AS-100 high-performance liquid chromatography (HPLC) autosampler (Bio-Rad, Richmond, Calif.), fitted with a 20-μL sample loop, into a Perkin Elmer Series 410 HPLC system (Perkin Elmer, Wellesley, Mass.). Sugars were analyzed using a Waters Sugar Pak column at 90 °C with a mobile phase of 100 μM ethylenediamine-tetraacetic acid disodium-calcium salt (CaEDTA) and a flow rate of 0.5 mL·min^{-1}. A Perkin Elmer LC-25 refractive index detector was used to measure sugars. Filtered analytical grade reagents were used for standard preparation to establish HPLC retention times and calibration. Determination of purity of individual peaks was accomplished by absorbance index (all wavelengths monitored simultaneously) on a Perkin Elmer LC-235 diode array detector. Values for sucrose, glucose, and fructose were added and presented as total sugars.

Data analysis. The generation means analysis of Mather and Jinks (1982) was used to estimate genetic and environmental effects on fruit sugar level. In this procedure, the adequacy of the additive-dominance model was tested using the joint scaling test (Cavalli, 1952), which uses weighted least square estimates based on the generation means. The generation means analysis was based on the mean and standard deviation of PI 270248, 7833, and the respective F_1, F_2, BCP_1, and BCP_2 according to Mather and Jinks (1982). The analysis was calculated using a spreadsheet program (Ng, 1990). This program estimates the number of effective factors (k) (Wright, 1934), the broad-sense heritability (Mahmud and Kramer, 1951), and, in the absence of epistasis, the narrow-sense heritability (Warner, 1952). The sugar level frequency distribution of plants, for each generation, was done using Excel 2000 (Microsoft Corp., Redmond, Wash.).

Environmental effects among seasons

Fall 2001. Seed of PI 270248, 7833, and their F_1 were sown in the greenhouse on 27 July, transplanted into Todd planter flats on 6 Aug., and transplanted to the field on 30 Aug. Beds were covered with white polyethylene mulch 2 weeks before transplanting. The entries were arranged in a randomized complete-block design with three blocks and 10 plants per plot. On 10 Dec., ≈15 table-ripe fruits per plant from PI 270248, 10 from F_1, and 3–4 from 7833 plants were harvested. The different number was due to fruit size differences. Fruits from each plant were ground and the fruit homogenate was stored in bags at –20 °C until use. Using the same procedures as described previously, sugar concentrations were measured. All other procedures were the same as previously described.

Both seasons. Total sugars were measured separately from 21 plants of PI 270248, 30 of 7833, and 25 of F_1 in fall. The design was a 2 × 3 factorial, with two seasons (fall and spring) and three lines (PI 270248, 7833, and F_1). The significance of each effect along with their interaction was analyzed by SAS (SAS Institute, Cary, N.C.), using the General Linear Model procedure PROC GLM. The effects of season on each line, were also estimated by PROC GLM (SAS). The sugar concentrations for each season were compared using Duncan's multiple range test. The average monthly temperature (°C), rainfall (centimeters), solar radiation (watts per square meter), and average daily rainfall (cm) were obtained from the Florida Automated Weather Network facility of the Univ. of Florida.

Results and Discussion

Inheritance of high sugars

The frequency distribution of total sugars shows that the sugar concentration of PI 270248 was higher than that of 7833 and there was no overlap (Fig. 1). The F_1 was highly skewed toward the high sugar parent PI 270248 and their values overlapped to a considerable extent. The F_1 was compared to the parents in this experiment and two others and in each case was found to be significantly different than both parents but much closer to PI 270248 in value (data not shown). This might be due to (partially) dominant gene action. However, dominance would also be expected to skew the F_2 sugar mean [3.50 g/100 g fresh weight (FW)] in the same direction, but it was nearly equal to the midparent value (3.58 g/100 g FW). If only indeterminate F_2 plants were considered, the total sugars would be 3.68 g/100 g FW, which is not much more than the midparent value. Thus, the trend for indeterminate plants to have higher sugars (Emery and Munger, 1970; Georgelis et al., 2004) does not account for the much higher sugar levels seen in the F_1 (4.68 g/100 g FW) and does not support a model with dominant gene action. The BCP_2 mean was between the F_1 and 7833 as expected. Surprisingly, the BCP_1 mean was lower than both PI 270248 and the F_1. If dominance effects were present it would be expected that BCP_1 would be between PI 270248 and the F_1. Accordingly, the joint scaling test worksheet using the chi-square goodness of fit test, showed that the additive–dominance model was inadequate (Table 1). Additive effects and the heterozygote × heterozygote interaction were found significant at the 5% level and dominance was not significant (Table 2). Thus, there were nonallelic genes, affecting sugars that were interacting with each other in heterozygous condition. The significance of the heterozygote × heterozygote interaction may explain the above results that could not be explained by dominance. This type of interaction would be expected to exert its maximum effects in the F_1, where the genes affecting sugar differences in the parents were in heterozygous condition. Apparently, these epistatic effects boosted F_1 sugars well above the midparent value. Heterozygosity is greatly reduced in BCP_1, BCP_2, and F_2 generations, especially if the number of interacting genes is higher than two, and thus the epistatic effects would be reduced in these generations compared to the F_1. Epistasis will hinder selection if high sugars are contingent upon it, and it would be difficult to fix high sugars if based on heterozygosity. In a previous report, several RAPDs linked to high sugars from PI 270248 (Georgelis et al., 2004) were found. RAPDs are usually dominant markers that do not distinguish between homozygotes and heterozygotes. The existence of epistasis may mean that these markers must be converted to co-dominant sequence characterized amplified region (SCAR) markers that will allow the identification of heterozygotes. On the other hand, additive variance was significant, dominance was not and broad sense heritability was high (0.86). This suggests selection progress should be effective in F_2 and subsequent generations. Progeny testing would verify if a selection had high sugars due to the heterozygote × heterozygote interaction or from additive gene action. Unfortunately, epistasis prevented the estimation of narrow-sense heritability. Our results are in agreement with those

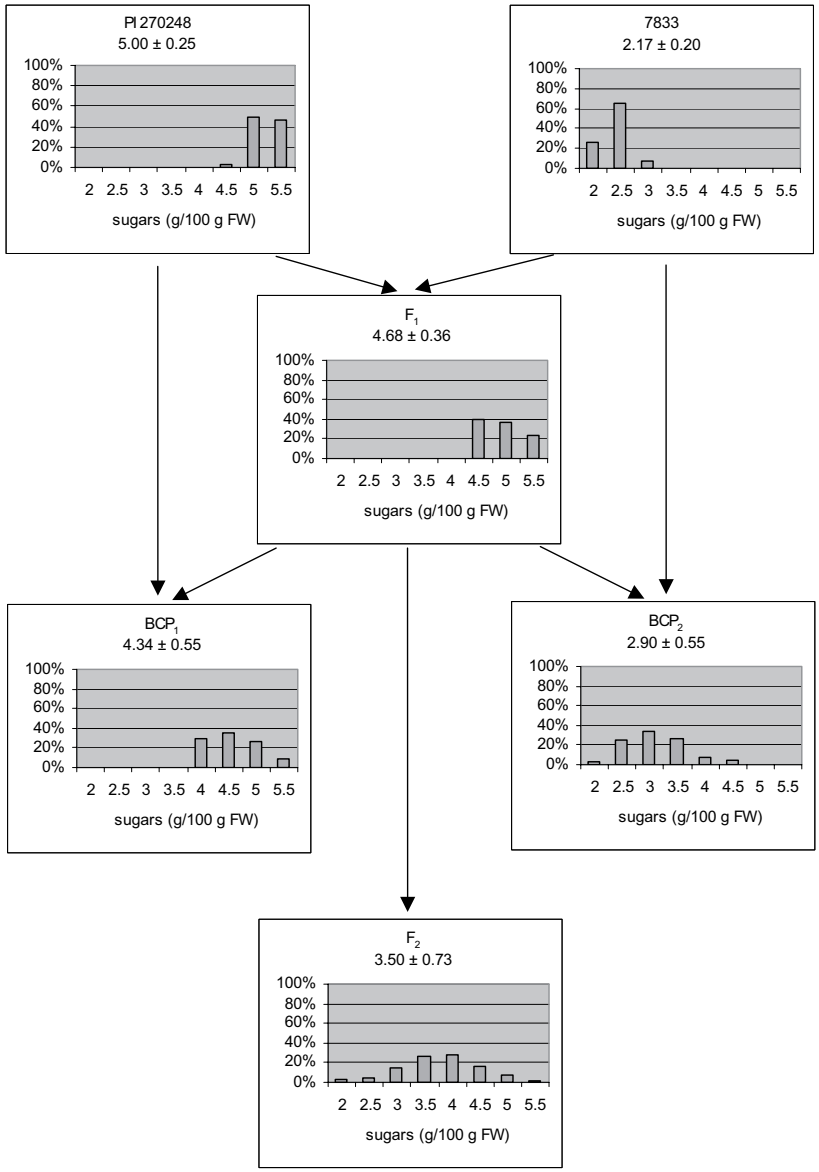

Fig.1. Frequency distribution of tomato fruit sugar concentrations for PI 270248 (*Lycopersicon esculentum* var. *cerasiforme*), 7833 (*L. esculentum*), F_1, F_2, BCP_1, and BCP_2 generations in Spring 2002. The sugar mean (±SD) for each generation is shown above their respective diagram.

Table 1. Total sugars for fruit of PI 270248 (*Lycopersicon esculentum* var. *cerasiforme*) (Parent 1), 7833 (*L. esculentum*) (Parent 2), F_1, F_2, and backcross generations grown in Spring 2002 and joint scaling test for goodness of fit to an additive–dominance model.

	Plants	Mean sugars (g/100 g FW)			Goodness
Generation[z]	(no.)	Observed	Expected	Variance	of fit
PI 270248	30	5.00	4.90	0.01	4.44
BCP_1	35	4.34	4.57	0.05	5.87
F_1	35	4.68	4.23	0.20	53.29
F_2	198	3.50	3.86	0.13	48.98
BCP_2	93	2.90	3.16	0.07	20.76
7833	38	2.17	2.09	0.01	5.72
Midparent		3.58			$\chi^2 = 139.07$
					$P < 0.001$

[z]BCP_1 = PI 270248 × F_1, BCP_2 = 7833 × F_1.

of Lower and Thompson (1967) who studied soluble solids. They crossed two small-fruited tomato lines and also found epistasis that boosted the F_1 close to the high-solids parent, and additive effects were also significant. Interestingly, they also reported that the backcross of the high soluble solids parent with the F_1 had lower soluble solids than both of them, as in this research. Similarities between the two studies may relate to the high positive correlation between soluble solids and sugars (Georgelis et al., 2004; Jones and Scott, 1984; Kader et al., 1977; Malundo et al., 1995; Saliba-Colombani et al., 2001; Stevens, 1972; Stevens et al., 1977). The epistatic effects on the high F_1 sugars (or solids) seen in both studies have interesting implications for hybrid breeding provided that these effects are retained once higher sugars are incorporated into improved parental lines. If they are retained, a hybrid between high sugar and normal sugar parents will have high sugars. If the epistasis is lost in elite lines then the hybrid will likely be intermediate due to additive gene action.

Due to epistasis, an estimate of the number of genes affecting sugars could not be obtained. However, continuous frequency distributions of sugar level in F_2, BCP_1, and BCP_2 are consistent with polygenic control as was the discovery of several RAPD markers linked to high sugars from PI 270248 (Georgelis et al., 2004). As mentioned, broad-sense heritability was 0.86. Previous research on the broad-sense heritability of sugars or soluble solids has been highly variable. Conti et al. (1988) found that soluble solids broad sense heritability was 0.13. Saliba-Colombani et al. (2001) used the cherry tomato 'Cervil' as a source of high sugars and showed that the broad-sense heritability was 0.61, while Lower and Thompson (1967) reported the narrow-sense heritability of soluble solids content was 0.75, indicating that the broad-sense heritability would be higher. Differences may be explained by different genotypes and/or environments. Whereas, the genetic analysis suggests selection progress will be effective, the major difficulty may be in obtaining determinate plants with large fruit and high sugars since high sugars were associated with small fruit and/or indeterminate plants (Georgelis et al., 2004). It may not be physiologically possible to obtain large fruits with the high sugar levels of PI 270248 or other cherry type tomato sources. Stevens (1986) suggested that cells in large fruit contain more water and thus sugars would be diluted. Nevertheless, such sugar levels are probably not needed and the transfer of only a portion of the sugars would likely have a positive impact on tomato flavor. Of course sugars are only one component of flavor as acids and volatiles are also important to tomato flavor (Baldwin et al., 2000; Jones and Scott, 1984, 2002; Stevens, 1972; Stevens et al., 1979). Stevens et al. (1977) found locules contain more acids than pericarp and the locule:pericarp ratio in cherry tomatoes like PI 270248 is higher than that of large fruited cultivars. PI 270248 had higher titratable acidity

Table 2. Estimates of additive, dominance, and interaction parameters for the PI 270248 (*Lycopersicon esculentum* var. *cerasiforme*) × 7833 (*L. esculentum*) family in Spring 2002.

Parameter[z]	Estimate (±SE)	*t* test
[d]	1.415 ± 0.028	50.92***
[h]	0.015 ± 0.783	0.02NS
[i]	0.480 ± 0.301	1.59NS
[j]	0.050 ± 0.226	0.22NS
[l]	1.550 ± 0.502	3.19*

[z][d] = difference of AA and aa from midparent (additivity), [h] = difference of Aa from midparent value (dominance), [i] = homozygote × homozygote interaction, [j] = homozygote × heterozygote interaction, [l] = heterozygote × heterozygote interaction.

NS, *, ***Nonsignificant, significant at $P \leq 0.05$, or significant at 0.001, respectively.

than large fruited Fla. 7833 and for anatomical reasons it might be difficult to transfer.

Environmental effects between seasons

Analysis of variance indicated significance for season, line and their interaction at the 5% level (data not shown). Therefore, the effect of season was analyzed separately for each line (Table 3). The sugar means of PI 270248 and F_1 in spring were significantly higher than in the fall, while the sugar mean of 7833 did not differ significantly between the two seasons (Table 3). The cultural practices (irrigation, fertilization, disease and pest control) were the same in both seasons. However, temperature, rainfall and solar radiation were uncontrolled factors. Rainfall can affect sugar concentrations, especially if it occurs close to the date of fruit harvest (Brooks and MacGillivray, 1928). After a heavy rainfall (≈5 cm or more) tomato fruits can take up water and dilute sugars (J.W. Scott, personal observations). However, rainfall did not reduce sugars in the fall since there was no rainfall for at least 40 d prior to harvest. In the spring, there were 3.5- and 3.2-cm rainfalls 4 and 7 d, respectively, prior to fruit harvest that could have lowered the sugars, but they were still higher than in the fall (Table 4). Thus, rainfall was not a factor in the observed seasonal difference.

The average monthly temperatures in both seasons were favorable for growth of tomato plants (Table 4). In fall, these temperatures ranged from 20–23 °C and in spring, from 23–26 °C during most of the period of fruit development. The higher temperature in spring might have resulted in higher photosynthetic rates (increasing carbohydrate production), but also in higher respiration rates (increasing carbohydrate consumption). Taking these into account along with the fact that the temperature difference between seasons was small, it can be deduced that most of the sugar variation between seasons was not caused by temperatures.

Solar radiation in spring, was much higher than in fall (Table 4), and this could account for the sugar increase, since higher solar radiation means higher photosynthetic rates and more carbohydrates. A positive correlation between sugar and solar radiation has already been documented (Davies and Hobson, 1981; Forshey and Alban, 1954).

As mentioned above, the environment did not influence the sugar level of line 7833. This is consistent with the results obtained over the years with tomato cultivars that do not have elevated sugar levels. There was some variation in the sugar levels, but the variation did not relate to spring or fall seasons (Baldwin et al., 1996). One possible explanation is that line 7833 reached its maximum genetic potential to produce sugars in fall. Hence, solar radiation was not the limiting factor and increased solar radiation in spring did not affect the sugars of 7833. Another possible reason could be that, compared to PI 270248 and the F_1, line 7833 had larger fruits, much higher yield and lower leaf : fruit ratio. So, even if more carbohydrates were produced in spring, they would have to be distributed to much more fruit mass. Furthermore, PI 270248 and the F_1 are both indeterminate and more carbohydrates would be expected to be produced in spring since they had a higher leaf : fruit tissue ratio than the determinate 7833.

To summarize, the environmental differences between seasons in Florida influenced the concentration of sugars in tomato fruits for genotypes with genetically increased sugars. Factors like temperature, rainfall, and extreme environmental events cannot be controlled in the field and can affect sugar level either in spring or in fall. However, solar radiation will almost always be higher in spring and this will favor this season against fall in the production of more sugars, especially with high sugar plants. Also, knowing that there will be more variation in high sugar selections can be helpful in interpreting the value of selections made in breeding for high sugars.

Table 3. The effect of growing season on the fruit sugar concentrations for PI 270248 (*Lycopersicon esculentum* var. *cerasiforme*), 7833 (*L. esculentum*), and their F_1 grown in Fall 2001 and Spring 2002.

Line	Season	Plants (no.)	Sugar (g/100 g FW)
PI 270248	Spring	30	5.00***
	Fall	21	4.66
7833	Spring	38	2.17
	Fall	30	2.21
F_1	Spring	35	4.68*
	Fall	25	4.43

***, *Difference for a given genotype between seasons is significant at $P \leq 0.001$ and $P \leq 0.05$, respectively.

Table 4. Average monthly temperature, rainfall and solar radiation in Fall 2001 and Spring 2002.

Season	Month	Temp (°C)[z] Mean	Max.	Min.	Rainfall (cm)	Mean solar radiation (W·m^{-2})
Spring	March	21.0	31.7	9.4	0.4	242.9
	April	23.0	32.1	12.4	6.3	258.1
	May	26.0	34.3	16.7	6.7	271.3
Fall	September	25.0	34.7	17.7	25.5	180.1
	October	23.0	32.9	8.9	6.7	181.0
	November	20.0	30.0	10.7	0.0	161.4
	December	21.0	28.5	11.6	0.1	136.5

[z]Mean = average monthly temperature, Max. = maximum monthly temperature, Min. = minimum monthly temperature.

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