Genetic Control of Fruit Sugar Accumulation in a Lycopersicon esculentum × L. hirsutum Cross

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Abstract. Fruit of the cultivated tomato (Lycopersicon esculentum Mill.) store predominantly glucose and fructose whereas fruit of the wild species L. hirsutum Humb. & Bonpl. characteristically accumulate sucrose. Reducing sugar and sucrose concentrations were measured in mature fruit of parental, F1, F2, and backcross (BC1) populations derived from an initial cross of L. esculentum 'Floradade' × L. hirsutum PI 390514. Generational means analysis demonstrated that additive effects were equal to dominance effects for percentage of reducing sugar. It was determined that a single major gene, dominant for a high percentage of reducing sugar, regulates the percentage of reducing sugar in tomatoes. We propose that this gene be designated sucr. Only additive effects were demonstrated to be important for glucose : fructose ratios.

Using L. hirsutum as a donor parent for increasing total soluble solids concentration in the cultivated tomato is discussed.

Sugars are an important component of tomato flavor and processing quality. Tomato flavor is a complex characteristic to measure and involves the perceived tastes and aromas of many chemical compounds. Stevens et al. (1977) determined that variation in sugar and acid concentration were significant contributors to genotypic flavor differences in tomato, with more intense flavor tion in sugar and acid concentration were significant contributors to genotypic flavor differences in tomato, with more intense flavor

Materials and Methods

Plant material. The populations used in this study were derived from two parental lines—L. esculentum 'Floradade' (female parent, P1) and L. hirsutum f. typicum PI 390514 (male parent, P2). Lycopersicon hirsutum seeds were obtained from the U.S. Dept. of Agriculture, Northeast Regional Plant Introduction Station, Geneva, N.Y. Plants were grown in the greenhouse to produce seeds of the F1, F2, and backcross (BC1) generations. Plants were grown in 5-liter pots in a mixture of 6 steam-treated soil : 3 peat : 2 perlite (by volume), with regular applications of soluble fertilizer. The green-
house day and night temperature cycle was maintained at a minimum of 21 and 16°C, respectively. Controlled crosses were made using standard emasculation and pollination methods to produce the F$_1$, F$_2$, and BC$_1$ generations. *Lycopersicon esculentum* "Floradade", was used as the recurrent parent to produce the BC$_1$ generation.

Fruit sampling. At harvest, representative portions (P$_1$ and BC$_1$, =5 g; P$_2$, F$_1$ and F$_2$ =1 to 3 g) of whole ripe fruit from each plant were frozen at -20°C to determine sugar concentration. For each plant, samples from three individual fruit were bulked before performing the sugar analysis. Three additional samples (*L. esculentum*, quartered fruit; *L. hirsutum*, whole fruit) were frozen at -20°C for use in determining the percentage TSS concentration.

Sugar and TSS determinations. Tomato sugar analyses were performed as described previously (Stommel, 1992), with minor modifications. Samples were homogenized in a homogenizer (Kinematica; Brinkman Instruments, Westbury, N.Y.) at 4°C in five parts distilled water containing 3% (by volume) saturated benzoic acid solution (to inhibit enzyme activity and microbial contamination). Homogenates were centrifuged at 20,000×g for 15 min at 4°C, and the supernatant was filtered using Whatman no. 2 filter paper. Filtered supernatants were eluted through a C18 water as the mobile phase (2 ml·min$^{-1}$ flow rate) in conjunction with a refractometer (model 410; Waters).

TSS percentage was determined by crushing thawed fruit samples and measuring the refractive index of the expressed juice with a refractometer (Abbe model 32; Bausch and Lomb, Rochester, N.Y.).

Data were analyzed using Hayman’s generational means analysis (Hayman, 1958, 1960). Due to unequal population sizes and heterogeneous variance between populations, the generational means were weighted by the reciprocal of the variance of the mean for each generation. When a population had a variance of zero, the variance was replaced by one.

Results and Discussion

Striking differences in sugar concentration were evident between the parent species used in this study (Table 1). Typical of the cultivated tomato, the *L. esculentum* parent, "Floradade" (P$_1$), stored sugars in the form of reducing sugars. No sucrose was detectable in mature fruit of this cultivar. In contrast, fruit of *L. hirsutum* PI 390514 (P$_2$) contained predominantly sucrose, with reducing sugars comprising only 13% of the total sugars in mature fruit. These results are consistent with previous studies that have examined sugar accumulation during fruit development in wild and cultivated tomatoes (Davies and Kempton, 1975; Miron and Schaffer, 1991; Stommel, 1992; Yelle et al., 1988). The wild, green-fruit ed tomato species *L. chmielewskii, L. hirsutum,* and *L. peruvianum* characteristically accumulate high concentrations of sucrose during the latter phases of fruit development, with low concentrations of glucose and fructose present during the period. In *L. esculentum,* reducing-sugar concentration steadily increases during fruit development, with little or no detectable sucrose.

To characterize genetic components of storage-sugar type, F$_1$, F$_2$, and BC$_1$ populations were developed from an initial cross of the parent (P$_1$) with a high percentage of reducing sugar (*L. esculentum* ‘Floradade’) and the parent (P$_2$) with a low percentage of reducing sugar (*L. hirsutum* PI 390514). Hayman’s generational means analysis revealed that additive (a = 43.11, se = 1.77) and dominance (d = 43.31, se = 1.83) effects were about the same for percentage of reducing sugar. Fruit within respective F$_1$, F$_2$, and BC$_1$ populations were categorized as containing a high or low percentage of reducing sugar, based on the percentage of reducing sugar characteristic of the parental lines (Fig. 1, Table 2). All fruit of the 20 F$_1$ plants and 93 BC$_1$ plants from the backcross to the high-reducing-sugar parent (P$_1$) contained a high percentage of reducing sugar, a result suggesting that additive and dominance effects were similar for percentage of reducing sugar. A good fit to an expected 3:1 ratio of tomatoes with a high to low percentage of reducing sugar was observed in F$_2$ progeny (P > 0.1). These results suggest that a single major gene, dominant for a high percentage of reducing sugar, regulates this characteristic in tomatoes. Variation evident for percentage of reducing sugar in fruit of P$_2$ and segregating F$_2$ and BC$_1$ populations suggests the presence of potential modifiers of storage-sugar concentration contributed by P$_2$. For future reference and consistent with current rules for nomenclature in tomato genetics (Clayberg et al., 1970, 1973), we propose that the major gene regulating the percentage of reducing sugar in tomatoes be designated *sucr*.

In addition to differences in the percentage of reducing sugar in the parental lines, large differences in the glucose : fructose (G : F) ratios were also evident. G : F ratios of 0.06 and 0.90 were observed in fruit of *L. hirsutum* (P$_2$) and *L. esculentum* (P$_1$), respectively (Table 1). Slightly higher amounts of fructose than glucose are typical of ripe *L. esculentum* fruit and normally result in G : F ratios of 0.8 to 1.0 (Davies, 1966). In fruit of sucrose-containing wild species, however, glucose concentrations are commonly low relative to those of fructose and result in much lower G : F ratios than those typically noted in *L. esculentum*. The influence of the

### Table 1. Sugar concentrations in tomato populations derived from an initial cross of *L. esculentum* ‘Floradade’ and *L. hirsutum* f. *typicum* PI 390514.

| Population$^1$ | No. of individuals | Sugar concn (mean ± SE) (mg g$^{-1}$ fresh wt) | Reducing sugar (of total) | Glucose : fructose ratio |
|----------------|--------------------|-----------------------------------------------|--------------------------|-------------------------|
| P$_1$          | 6                  | Fructose 14.0 ± 1.3 | Glucose 12.5 ± 1.2 | Sucrose 0.0 ± 0 | 100 ± 0 | 0.90 ± 0.03 |
| P$_2$          | 20                 | Fructose 4.0 ± 0.3 | Glucose 0.3 ± 0.2 | Sucrose 31.7 ± 2.6 | 13.4 ± 1.7 | 0.06 ± 0.03 |
| F$_1$          | 20                 | Fructose 27.0 ± 1.2 | Glucose 10.2 ± 0.5 | 0.0 ± 0 | 100 ± 0 | 0.38 ± 0.01 |
| F$_2$          | 1/4                | Fructose 16.9 ± 0.7 | Glucose 7.5 ± 0.7 | Sucrose 1.1 ± 0.9 | 9.1 ± 2.4 | 0.40 ± 0.01 |
| BC$_1$         | 93                 | Fructose 18.8 ± 0.8 | Glucose 14.1 ± 0.7 | Sucrose 1.2 ± 0.5 | 97.4 ± 0.8 | 0.73 ± 0.02 |

$^1$P$_1$ = *L. esculentum* ‘Floradade’; P$_2$ = *L. hirsutum* f. *typicum* PI 390514; BC$_1$ = backcross; P$_1$ was used as the recurrent parent in the BC$_1$ generation.
parental phenotypes ($P_1$ and $P_2$) on fruit $G:F$ ratios was evident in $F_1$, $F_2$, and $BC_1$ progeny, a result suggesting a genetic basis for glucose and fructose concentrations. Hayman’s generational means analysis revealed that additive effects ($a = 0.47$, SE = 0.06) were important for $G:F$ ratios but that dominance effects were not ($d = -0.11$, SE = 0.071). A relationship between fruit $G:F$ ratios and storage-sugar type was not evident since sucrose was not detectable in $F_1$ or $BC_1$ fruit (Table 1). These results suggest that $G:F$ ratio and percentage of reducing sugar are under separate genetic control. Thirteen of 174 ($\approx 1/13$) $F_1$ plants were noted with a $G:F$ ratio of 0.85 to 1.02 ($G:F$ range for $P_1$). An equal number of $F_2$ plants was observed with a $G:F$ ratio of 0 to 0.37, a result consistent with the $G:F$ ratio observed in $P_1$. The observed segregation patterns for parental extremes within this $F_2$ population suggests that the $G:F$ ratio in tomato is controlled by at least two genes (Rothwell, 1979; Sinnott et al., 1950).

Considerable variation for fruit TSS and sugar concentration

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**Table 2. Chi-square analysis of percentage of reducing sugar in tomato parental ($P_1$ and $P_2$), $F_1$, $F_2$, and backcross ($BC_1$) populations.**

| Population | Reducing sugar (%) | Ratio | Chi-square |
|------------|-------------------|-------|------------|
|            | High | Low | Total | tested |                       |
| $P_1$      | 6    | 0   | 6     | 1:0    | 0                       |
| $P_2$      | 0    | 0   | 0     | 0:1    | 0                       |
| $F_1$      | 20   | 0   | 20    | 1:0    | 0                       |
| $F_2$      | 139  | 35  | 174   | 3:1    | 2.3*                    |
| $BC_1$     | 93   | 0   | 93    | 3:1    | 0                       |

*Fruit of respective progeny were classified as containing a high (>37%) or low (<37%) percentage of reducing sugar based on the percentage of reducing sugar in parental lines.

$P_1 = Lycopersicon esculentum 'Floradade'; P_2 = L. hirsutum f. typicum PI 390514; P_1$ was used as the recurrent parent in the $BC_1$ generation.

*P > 0.1; probability values >0.05 suggest that observed values do not differ significantly from the expected values.*

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was observed within the populations developed (Table 3). *Lycopersicon hirsutum* PI 390514 is higher in total sugar and TSS concentration relative to the *L. esculentum* cultivar used in this study, yet lower in TSS and sugar concentration compared to many other *L. hirsutum* accessions (J. Stommel, unpublished data). Despite this fact, sugar and TSS concentration in fruit of parental, *F₁*, *F₂*, and *BC₁* generations indicated a positive effect of the *L. hirsutum* parent (*P₂*) on total sugar and TSS concentration in *F₁* progeny and subsequent generations. *F₂* and *BC₁* progeny with TSS and total sugar concentrations equal to or greater than those observed in the high-TSS *L. hirsutum* parent were noted. Relative to *P₁*, overall increases in total sugar and TSS concentration of 28% and 18%, respectively, were realized in the *BC₁* generation, a result suggesting that improved breeding lines can be developed using this and other *L. hirsutum* accessions as high-TSS donor parents.

Previous studies have focused on the potential for increasing TSS in tomato by incorporating sucrose accumulation from wild tomato species into cultivated types that store predominantly reducing sugars (Stommel, 1992; Yelle et al., 1988, 1991). The results of the current study suggest that factors in addition to the storage of sucrose, as opposed to reducing sugars, positively influence TSS concentration. *F₁* and *BC₁* progeny contained higher concentrations of TSS and total sugar relative to the *L. esculentum* parent (*P₁*), yet stored free sugars as glucose and fructose (Tables 1 and 3). Thus, the higher TSS and total sugar concentration in these progeny may be conditioned by a positive effect of the *L. hirsutum* parent on TSS and total sugar concentration, irrespective of storage-sugar type; elevated concentrations of additional components including organic acids or water-soluble polysaccharides, which influence TSS concentration; or both.

The benefits to be realized in increasing tomato sugar concentration are substantial for processed and fresh tomato markets. Increases in total sugar concentration are correlated with increased TSS concentrations in tomato, thus reducing the energy inputs required to produce processed tomato products. Current estimates indicate that a 1% increase in tomato TSS concentration could be worth $70 million to $80 million a year to the tomato processing industry (Wood, 1992). A negative relationship between TSS and yield, however, has limited past efforts to increase TSS (Stevens and Rudich, 1978). The relationship between yield and increased TSS concentrations conditioned by sucrose accumulation has not been determined in advanced populations derived from *L. esculentum × L. hirsutum* crosses. Since sugars, together with acids, are also the principal flavor components of tomatoes (DeBruyn et al., 1971; Stevens et al., 1977), an increase in total sugar concentration will also enhance tomato flavor. Flavor and market quality of fresh tomatoes have been the subject of substantial criticism recently (Sokolov, 1989). Although the relative perceived sweetness is fructose > sucrose > glucose (Shallenberger and Birch, 1975), the overall increase in total sugar concentration likely would negate any net loss in sweetness due to decreased fructose concentrations.

In summary, this report provides evidence indicating that the regulation of sugar type in tomato is controlled by a simply inherited major gene, designated suc, dominant for a high percentage of reducing sugar. The G : F ratio in these populations seems to be under separate genetic control and is influenced by at least two pairs of alleles. High TSS and sugar concentrations in tomato populations with a high percentage of reducing sugar suggests that components in addition to sucrose accumulation contribute to the high TSS concentrations conditioned by *L. hirsutum* accessions. In considering the simply inherited nature of sugar type in tomatoes, the potential benefits to be realized in fruit of new tomato cultivars that store sugars as sucrose may have practical applications in improving tomato quality components.

### Table 3. Total sugar and soluble solids concentrations in parental (*P₁* and *P₂*), *F₁*, *F₂*, and backcross (*BC₁*) populations.

| Population | Total soluble solids (%) | Total sugar (mg g⁻¹ fresh wt) |
|------------|--------------------------|-------------------------------|
| *P₁*       | 5.6 ± 0.2 (4.7–6.2)      | 26.5 ± 2.5 (16.2–34.9)       |
| *F₁*       | 7.5 ± 0.3 (5.3–10.4)     | 36.0 ± 2.0 (17.4–60.3)       |
| *F₂*       | 6.9 ± 0.2 (5.2–8.3)      | 37.2 ± 1.7 (24.6–54.5)       |
| *BC₁*      | 6.5 ± 0.1 (4.0–12.9)     | 31.5 ± 1.0 (5.7–73.0)        |

*P₁ = Lycopersicon esculentum “Floradada”; *P₂ = L. hirsutum f. typicum* PI 390514; *BC₁ = backcross; *P₁* was used as the recurrent parent in the *BC₁* generation.

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