A study using *Lycopersicon cheesmanii* Riley LA 1449 (typicum), a low soluble solids content (SSC) accession, and *L. cheesmanii* f. minor LA 528 (minor), a high SSC accession, was undertaken to characterize the accumulation of starch, sugar, and total SSC. Fruit of each accession was sampled throughout development to identify differences in SSC, starch accumulation, and sugar distribution. Osmotic analysis indicated that the *minor* race had higher SSC content throughout the ontogeny of fruit development than the typicum. Typicum contained more starch than *minor*, and both accessions showed a rapid decline in percent starch as the fruit ripened. Sucrose remained low throughout all stages of fruit development for both accessions. Glucose increased in the *minor* and declined in the typicum. Fructose increased in both accessions. Total reducing sugar content at the full ripe stage was higher in *minor* than the typicum.

A survey of 30 accessions of *Lycopersicon cheesmanii* from the Galapagos Islands revealed that *L. cheesmanii* f. *minor* had a higher soluble solids content than *L. cheesmanii* typicum (Garvey and Hewitt, 1984). This difference prompted a series of developmental studies to analyze factors governing SSC content in the two races of *L. cheesmanii*.

Starch accumulation followed by hydrolysis to reducing sugars has been proposed as a mechanism contributing to high SSC (Walker and Ho, 1978; Yelle et al., 1988). Cultivated tomatoes that have higher total SSC when fully ripe were shown to have higher starch levels during early fruit development (Dinar and Stevens, 1981). Walker and Ho (1977) reported that starch and other insoluble are formed from the soluble sugars in the fruit, and a correlation was found between the rate of carbon import and the formation of insoluble residues. Fruits with the highest carbon import rates also had the greatest starch accumulation (Walker and Ho, 1977).

Furthermore, there was an increase in reducing sugar levels accompanying the breakdown of starch (Davies and Cocking, 1965; Davies and Hobson, 1981). Walker and Ho (1977) reported that sucrose was a principal transport assimilate but that its level in cultivated tomato fruit remained low. Developmental studies of the tomato revealed that fructose and glucose were accumulated rather than sucrose (Davies, 1966; Davies and Kempton, 1975) in the mature fruit. Experiments with 14C indicated that sucrose was hydrolyzed to reducing sugars once inside the tomato fruit (Walker and Ho, 1977).

Representative accessions of each race of *L. cheesmanii*, sampled throughout fruit development, were used in the present study to identify differences in SSC, starch accumulation, and sugar distribution.

**Materials and Methods**

**Fruit analysis.** Seeds of the *L. cheesmanii* accessions used in this study, LA 1449 (typicum) and LA 528 (minor) (kindly provided by C.M. Rick), were germinated and transplanted into 3.8-liter pots containing modified UC mix (Matkin and Chandler, 1957) and ammonium phosphate fertilizer (16N-20P-16K) at a density of two plants per pot. At full bloom, flowers were hand pollinated and marked to identify anthesis and day of pollination. Flowers not hand pollinated were removed from the truss. Marked fruits (150) from 20 plants were harvested at =7–day intervals for analysis. Fruits were weighed and frozen at –20C. Frozen samples were thawed, pureed, centrifuged for 10 min (4000 rpm, 1975 × g). A sample from the supernatant was saved and the remainder of the puree was lyophilized and weighed. Total solids were calculated from the dry weight : fresh weight ratio.

An 8-µl sample of centrifuged supernatant was analyzed for solute concentration using a Wescor Vapor Pressure Osmometer (Wescor, Logan, Utah). Solute concentration was calculated by comparison with sucrose standards.

**Starch analysis.** Tissue (25 mg) from the lyophilized pellets was ground using a mortar and pestle and was analyzed for starch using a coupled glucose oxidase and peroxidase reaction following procedures described by MacRae (1971). Absorbance of samples was read on a B&L 88 spectrophotometer (Bausch & Lomb, Rochester, N. Y.) at 540 nm. Percent starch was calculated as described by Hewitt (1981).

**Sugar distribution analysis.** Fruit (150) from a second planting of 40 plants of each accession were harvested at =10-day intervals following anthesis. Fruits were weighed, frozen in liquid N, and stored at –80C.

Frozen fruit were ground in 80% ethanol (1 ml·g⁻¹) using a large bore Tissuemizer (Tekmar, Cincinnati) for 1.5 min followed by a small bore Tissuemizer for 2 min. Samples were ground in a 15-ml Wheaton (Millville, N. J.) grinding tube for 2 min. A heated 80% ethanol extraction was conducted three times and the soluble fraction was saved.

The 80% ethanol supernatant was evaporated in a water bath at 50C under vacuum. Samples were resuspended in 1 ml of double distilled H₂O, filtered through a 0.45-micron Millipore (Bedford, Mass.) filter using a syringe, passed through 300-µg C₄ Maxi-clean column (Alltech, Palo Alto, Calif.), and frozen at –20C until analyzed by high performance liquid chromatography (HPLC).

Sugars were analyzed on a Beckman (Fullerton, Calif.) 110A HPLC equipped with a Bio-Rad (Cambridge, Mass.) Anex HPX 87C column 300 × 7.8 mm, temperature-controlled at 60C, and equipped with a de-ashing precolumn (Bio-Rad) using HPLC water (VWR, Philadelphia) at 0.9 ml·min⁻¹ flow. A sample of 250 µL was injected, and components were detected on a temp-
perature-compensated refractive index detector (Altex 165, San Ramon, Calif.). Concentrations were determined relative to a mixed standard of sucrose, glucose, and fructose in the range of 0.5 to 8 mg·mL⁻¹.

Results

Fruit growth analysis. The average weights of typicum (LA 1449) fruit were higher at all stages relative to the minor (528) race (Fig. 1). Typicum reached maximum weight and size at 62 days (full ripe). For the first 10 days after anthesis, growth for both accessions was very slow. After day 10, fruits of typicum grew rapidly, while the growth of minor remained substantially lower. At 52 days, the maximum weight of the minor fruit was 35% that of typicum. At full ripe, the minor and typicum races had 21% and 11% total solids, respectively.

Soluble solids content. Osmotic solute concentrations are correlated with the refractive index of tomato serum (Mathews et al., 1987). Minor fruit had higher SSC throughout fruit development than typicum (Fig. 2). A decrease in SSC was noted at the end of the first 10-day period for typicum. Following this decrease, typicum SSC remained unchanged from the second sampling period until fully ripe, whereas minor continued to accumulate SSC between ≈40 and 60 days after anthesis. Both accessions reached maturity by day 50, determined by tan seed coat color.

Starch distribution. From the analysis of lyophilized fruit, typicum and minor had similar starch contents 7 days after anthesis (Fig. 3). Thereafter, typicum exhibited a rapid rise in starch content, reaching a maximum value of 25% on day 30, whereas the minor reached its maximal starch level (17%) on day 22. Starch content rapidly declined following each of these maxima, and there was no significant difference in starch content between the two accessions 35 days after anthesis.

Sugar concentration. In frozen samples of minor fruit, sucrose content remained constant and low throughout development (Fig. 4). Conversely, glucose and fructose increased beginning on the 42nd day after anthesis and reached a maximum when the fruit was fully ripe. The typicum fruits had a constant low sucrose level throughout ontogeny of the fruit (Fig. 5), glucose declined beginning at 40 days, and fructose continued increasing through day 62.

Discussion

High soluble solids L. cheesmanii races (minor LA 528 and typicum LA 1449) diverge from typical patterns that prevail in the cultivated tomato for sugar and starch accumulation. Both races of L. cheesmanii exhibit high total solids and SSC when compared to the cultivated tomato (Davies and Hobson, 1981; Garvey and Hewitt, 1984). Starch distribution was the inverse
of that in the cultivated tomato (Dinar and Stevens, 1981), with the low-SSC typicum having the higher starch content.

Starch is an important constituent of the developing tomato fruit (Hobson, 1967; Hobson and Davies, 1971). In the cultivated tomato fruit, starch levels reach a maximum 4 to 5 weeks after pollination and then decrease until the mature-green stage (Davies and Cocking, 1965; Dinar and Stevens, 1981; Ho and Hewitt, 1986; Hobson and Davies, 1971). This change was associated with a concomitant increase in reducing sugars and a decrease in sucrose levels (Davies and Cocking, 1965; Dinar and Stevens, 1981; Walker, and Ho, 1977).

The starch accumulation patterns in the two races of L. cheesmanii suggest that different mechanisms affecting SSC are operating in each race. Minor, although having a higher SSC at ripeness, had lower starch levels than a typicum. This difference is in contrast to a positive association between starch levels during fruit development and SSC of ripe fruit for several tomato cultivars (Dinar and Stevens, 1981). Davies and Cocking (1965) suggested that there is a correlation between the breakdown of starch and the rapid rise in sugars in tomatoes. Walker and Ho (1978) showed that starch and other insoluble materials accumulate in proportion to the carbon import rate in the cultivated tomato fruit.

There was a preferential accumulation of glucose and fructose in minor; in typicum, fructose levels increased while glucose levels in typicum were inconsistent with glucose levels in minor of that in the cultivated tomato (Robinson et al., 1988). The lower reducing sugar levels in L. cheesmanii may be partially explained by the high proportion of seed found in these accessions.

The present study indicates that L. cheesmanii differs in total solids content, SSC, and starch concentration from L. esculentum. Increased soluble and insoluble components increase the commercial value of the fruit and improve processing yields. The low starch level in minor indicates that an alternate mechanism is operating to elevate SSC in this accession. Decreased glucose levels in typicum were inconsistent with glucose levels in minor and L. esculentum. The increased total solids in L. cheesmanii will have practical application in the development of new tomato cultivars with improved quality characteristics.

**Literature Cited**


Hewitt, J.D. 1980. Physiological basis of genotypic variation for solids content of tomato fruits. PhD Diss. Univ. of California, Davis.


