Carbohydrate-Related Changes in Sweetpotato Storage Roots during Development

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Abstract. The quantity and pattern of carbohydrate-related changes during storage root development differed among six sweetpotato cultivars [Ipomoea batatas (L.) Poir. ‘Beauregard’, ‘Heart-o-Gold’, ‘Jewel’, ‘Rojo Blanco’, ‘Travis’, and ‘White Star’]. Measurements were taken for individual sugars, total sugars, alcohol-insoluble solids (AIS, crude starch), and dry weight (DW) at 2-week intervals from 7 to 19 weeks after transplanting (WAT) in two separate years. Sucrose was the major sugar during all stages of development, representing at least 68% of total sugars across all cultivars and dates. Pairwise comparisons showed ‘Heart-o-Gold’ had the highest sucrose content among the cultivars. Sucrose content increased by 56% for ‘Heart-o-Gold’ over the 12 weeks of assay, ranking first among the cultivars at 17 and 19 WAT and possessing 27% more sucrose than the next highest ranking cultivar, ‘Jewel’, at 19 WAT. Fructose content profiles varied among and within cultivars. ‘Beauregard’ showed a consistent increase in fructose throughout development while ‘White Star’ showed a consistent decrease. The other cultivars were inconsistent in their fructose content profiles. Glucose content profiles were similar to those for fructose changes during development. The relationship between monosaccharides was fructose = 0.7207 × glucose + 0.0241. Cultivars with the highest fructose and glucose content could be selected by breeders after 13 WAT. Early clonal selection for high sucrose and total sugars is less promising because substantive changes in clonal rank occurred for sucrose and total sugars after 15 WAT. Cultivars ranking the highest in total sugars had either more monosaccharides to compensate for a lower sucrose content or more sucrose to compensate for a lower monosaccharide content. The relationship between DW and AIS was similar (AIS = 0.00089 × DW), and DW and AIS increased with time for most cultivars. Cultivars with high DW and AIS can be selected early during storage root development.

Sweetpotato (Ipomoea batatas) is an important staple food crop grown throughout the tropics. It is the fourth most important food crop produced in these regions (Food and Agr. Organization, 1993). Low sugar types generally predominate in the tropics. A high starch content is a desired attribute of this staple food (Mok et al., 1997). In the United States, and to a lesser extent in Japan, the sweetpotato is grown as a table vegetable. The North American market prefers high sugar, orange flesh dessert types.

Carbohydrate-related profiles of processed and baked sweetpotatoes have been reported for a wide range of genotypes (Kays, 1992; Lewthwaite et al., 1997; Morrison et al., 1993; Palmer, 1982; Picha, 1986). Little information is available on the carbohydrate composition of raw roots, especially during development. Postharvest carbohydrate changes in U.S. no. 1 grade raw roots (5.1 to 8.9 cm diameter; 7.6 to 22.9 cm long) have been documented (Picha, 1985, 1987). Staple sweetpotato types typically have a white to cream flesh with dry weight (DW) contents ranging from 25.0% to 35.0% based on 1999 U.S. Germplasm Resources Information Network data. The DW in sweetpotato is correlated with starch content (Li and Liao, 1983). DW content in excess of 35.0% is desired as a raw material in the starch processing industry (Mok et al., 1997). However, as DW content increases, there is a corresponding decrease in acceptability as a table food (Lin et al., 1995). Total sugars in stored, raw staple sweetpotato types range from 2.9% to 3.2% on a fresh weight (FW) basis (Picha, 1985). Corresponding sucrose, fructose, and glucose contents range from 1.3% to 2.5%, 0.4% to 0.7%, and 0.4% to 1.0%, respectively.

Dessert sweetpotato types generally have a cream colored to orange flesh and DW content ranging from 17.7% to 26.3% with starch contents ranging from about 13.0% to 22.0% (Picha, 1987). Total sugars in stored, raw dessert sweetpotato types range from 4.6% to 5.5% on a FW basis (Picha, 1985). Corresponding sucrose, fructose, and glucose contents range from 2.8% to 4.1%, 0.3% to 1.2%, and 0.2% to 1.5%, respectively.

Our interest is to develop cultivars with a higher sugar content. Sweeter progeny from our breeding program are found routinely in field taste test screenings of raw roots. These often possess a significantly higher sugar content when baked and compared with control cultivars (Romaine, 1997). A strong linear relationship exists between fructose, glucose, and sucrose content in raw and baked roots (Lewthwaite et al., 1997). Concomitantly, a need exists to increase DW/starch content in sweetpotato for industrial use. No previous reports document clonal differences in sugar or DW/starch content profiles during growth and development. We were also interested in determining if compositional changes during development could be used in predicting final storage root, carbohydrate content. The present study was undertaken to document these carbohydrate-related changes in six sweetpotato cultivars.
Materials and Methods

Two white-flesh cultivars (‘Rojo Blanco’ and ‘Whitestar’) and four orange-flesh cultivars (‘Jewel’, ‘Beauregard’, ‘Travis’, and ‘Heart-o-Gold’) were evaluated for carbohydrate-related changes during storage root development. These cultivars encompass a broad spectrum of sweetpotato genotypes. ‘Jewel’ and ‘Beauregard’ are former and current mainstays, respectively, in the United States sweetpotato industry. ‘Travis’ is an early maturing cultivar, requiring 90 instead of the normal 110 to 120 d growing period to mature, and ‘Heart-o-Gold’ is an heirloom cultivar that is putatively sweeter raw and as a noncured baked product at harvest (Romaine, 1997). ‘Rojo Blanco’ and ‘Whitestar’ are high DW types. Field experiments were conducted at the Burden Research Station, Baton Rouge, Louisiana in 1991 and 1993. The soil was an Olivier silt loam (Aquic Fragiudalf) with <1% organic matter and pH 6.5.

The experimental design was a randomized complete block with four replications of each cultivar where year was the blocking factor. The plots consisted of 30 m long rows with 1.2 m between rows and each row contained 100 plants spaced 0.3 m apart. Commercial sweetpotato cultural practices were followed as recommended (Boudreaux, 1994). Slips (adventitious shoots) were transplanted in late May 1991 and early June 1993. Four plants of each cultivar were randomly selected from each replication for harvest between 8 and 10 AM beginning 7 weeks after transplanting (WAT) in both years. Harvests continued at 2 week intervals up until 19 WAT.

Analyses of alcohol-insoluble solids (AIS, crude starch) and sugar content in raw roots from each cultivar were made the day of harvest as described previously by Picha (1987). Briefly, unpeeled roots were halved longitudinally and uniformly grated over the entire surface to a depth of ≈3 mm. The grated tissue from each of the four roots per replication was combined and 10 g was homogenized in 80% ethanol, boiled, and filtered through Whatman no. 4 filter paper. The filtrate was adjusted to a final volume of 100 mL. The AIS content was determined by the weight of the insoluble residue retained on the filter paper after drying. Sugar content of the filtrate was determined by high performance liquid chromatography and results were expressed on a mg g−1 FW basis. DW of the raw roots was determined after forced air drying duplicate 10 g samples of grated tissue at 70 °C for 48 h. Due to missing values, 19 WAT was not considered in analysis of DW and alcohol-insoluble solids.

All data were analyzed by standard analysis of variance techniques for a randomized complete block design using Proc GLM (SAS Institute Inc., 1987). Blocking removed variation due to the year effect. We used $P \leq 0.05$ as our test of significance in all analyses presented. Only cultivars with a significant date effect based on F values for cultivar × date effect slices were considered for pairwise tests for date × cultivar interactions. These profile differences, i.e., date × cultivar interactions, between cultivars were determined by simultaneous contrast F tests on cultivar pairs. DW, AIS, fructose, glucose, and sucrose content were first analyzed using the Wilks’ Lambda statistic for multivariate analysis of variance (SAS Institute Inc., 1987). AIS, DW, fructose, and glucose data were combined across dates and cultivars and analyzed by simple linear regression to determine changes in AIS as a function of DW and changes in fructose as a function of glucose.

Results and Discussion

Fructose. Four of the six cultivars (‘Travis’, ‘Beauregard’, ‘Whitestar’ and ‘Heart-o-Gold’) showed significant differences in fructose content based on harvest date, i.e., fructose content changed significantly throughout development (data not presented). Cultivars also accumulated fructose differently from one another throughout development based on pairwise comparisons (Table 1). No cultivars were similar to one another in pairwise comparisons of fructose content profiles. ‘Beauregard’ was the only cultivar showing a consistent increase in fructose throughout development (Fig. 1A). ‘Travis’ was consistently the highest ranking cultivar across all dates; however, changes in fructose

Table 1. Pairwise comparisons of sweetpotato cultivars over 2 years showing significant changes (date × cultivar) in sugar, DW, and alcohol-insoluble solids (AIS) content patterns in fleshy roots during development.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Fructose</th>
<th>Glucose</th>
<th>Sucrose</th>
<th>Total sugars</th>
<th>DW</th>
<th>AIS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beauregard vs. Jewel</td>
<td>*</td>
<td></td>
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<td>NS</td>
<td>NS</td>
<td>NS</td>
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<tr>
<td>Beauregard vs. Travis</td>
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<td>Beauregard vs. Rojo Blanco</td>
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</tr>
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<td>Beauregard vs. Whitestar</td>
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<tr>
<td>Beauregard vs. Heart-o-Gold</td>
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<td>Jewel vs. Travis</td>
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<td>Jewel vs. Rojo Blanco</td>
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<td>Jewel vs. Heart-o-Gold</td>
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<td>Travis vs. Rojo Blanco</td>
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<td>Travis vs. Whitestar</td>
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<td>Travis vs. Heart-o-Gold</td>
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<tr>
<td>Rojo Blanco vs. Whitestar</td>
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<td>Rojo Blanco vs. Heart-o-Gold</td>
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<tr>
<td>Whitestar vs. Heart-o-Gold</td>
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</table>

*Pairwise comparisons were not made if one or both cultivars showed no significant date × cultivar interaction for a given variable. No significant quantitative changes in the variable from 7 to 19 WAT based on harvest date ($P \leq 0.05$) for ‘Rojo Blanco’, and ‘Jewel’ (fructose); ‘Rojo Blanco’, ‘Heart-o-Gold’, and ‘Jewel’ (glucose); ‘Rojo Blanco’, ‘Beauregard’, and ‘Whitestar’ (sucrose); ‘Rojo Blanco’, and ‘Whitestar’ (total sugars); ‘Travis’ and ‘Heart-o-Gold’ (DW); and ‘Travis’ (AIS).

Nonsignificant or significant at the $P < 0.05$, respectively.
content were inconsistent, showing significant sharp increases early and late and some significant decline during development. These results agree with those of Picha (1987) who reported that 'Travis' ranks highest in fructose in comparison to 'Whitestar', 'Jewel', and 'Rojo Blanco' at harvest, and after curing and storage for U.S. no. 1 grade roots. The fructose profile for 'Whitestar' was unlike the other cultivars and showed a consistent decline (73%) during development. Fructose in 'Heart-o-Gold' decreased from 9 to 11 WAT before increasing again at 17 and 19 WAT (Fig. 1A).

'Rojo Blanco' and 'Jewel' showed no significant quantitative changes in fructose throughout development based on harvest date (data not presented), i.e., no date-dependent profile exists. Both 'Rojo Blanco' and 'Jewel' ranked the lowest in fructose content for most evaluation dates (Fig. 1A).

**Glucose.** Three of the six cultivars ('Travis', 'Beauregard', and 'Whitestar') showed significant quantitative differences in glucose content based on harvest date (data not presented). In general, glucose content profiles and rank are similar to those for fructose (Fig. 1B). The relationship between fructose and glucose (across all cultivars and dates) is described by the following significant regression equation: fructose = 0.7207 × glucose + 0.0241 (r = 0.88; n = 305). This is consistent with previous results that showed the proportion of fructose to glucose was very stable across cultivars (Lewthwaite et al., 1997). 'Travis' and 'Beauregard' shared similar glucose content profiles that consistently increased during development (Table 1 and Fig. 1). 'Travis' shows no significant decline in glucose from 15 to 17 WAT, unlike the significant 29% decline observed for fructose over the same period. 'Travis' ranked the highest in glucose content of all cultivars at all harvest dates. These results agree with those of Picha (1987) who reported that 'Travis' ranks highest in glucose in comparison to 'Whitestar', 'Jewel', and 'Rojo Blanco' at harvest, and after curing and storage for U.S. no. 1 grade roots. The glucose profile for 'Whitestar' showed a decline during development (Fig. 1B) and was statistically different from the profiles of 'Travis' and 'Beauregard' (Table 1).

'Rojo Blanco', 'Heart-o-Gold', and 'Jewel' showed no significant quantitative changes in glucose throughout development based on harvest date (data not presented). These three cultivars also ranked among the lowest in glucose (Fig. 1).

**Sucrose.** Sucrose was the major sugar in all six cultivars at all stages of development. This was consistent with previous results for U.S. no. 1 grade roots (Picha, 1987). Three of the six cultivars ('Travis', 'Heart-o-Gold', and 'Jewel') showed significant quantitative differences in sucrose content based on harvest date (data not presented). Pairwise comparisons showed similarities existed between content profiles for 'Jewel' and 'Travis' (Table 1). In general, sucrose profiles were less varied across all dates for these six cultivars in comparison to the results for the monosaccharides. 'Jewel' showed the greatest increase in sucrose (28%) among these five cultivars from 7 to 19 WAT. The sucrose content profile for 'Heart-o-Gold' was distinct and significantly different from all others showing a date effect (Table 1). Sucrose content increased 56% during development for 'Heart-o-Gold' and contained 27% more sucrose than the next ranking cultivar, 'Jewel', at 19 WAT.

The white flesh cultivars, 'Rojo Blanco' and 'Whitestar', were consistently ranked the lowest in sucrose (Fig. 2A). These two cultivars and 'Beauregard' showed no significant quantitative changes in sucrose throughout development based on harvest date (data not presented).

**Total Sugars.** Four of the six cultivars ('Travis', 'Heart-o-Gold', 'Beauregard', and 'Jewel') showed significant quantitative differences in total sugars based on harvest date (data not presented). Pairwise comparisons showed similarities existed between total sugars profiles for 'Beauregard', 'Jewel', and 'Travis' (Table 1). In general, these three cultivars showed increases in total sugars from 7 to 19 WAT, e.g., 'Jewel' increased by 24% during development and 'Travis' by 36% (Fig. 2B). 'Beauregard' and 'Travis' were unique among all cultivars in that at least 39% of total sugars were monosaccharides. In contrast, only 6% of the total sugars for 'Jewel' was comprised of monosaccharides at 19 WAT. The higher levels of monosaccharides enabled 'Travis' to rank first across all dates for total sugars, even though it ranked third in sucrose. The total sugars profile for 'Beauregard' was highly influenced by significant increases in monosaccharides at 17 to 19 WAT (Fig. 1) that compensated for the corresponding decline in sucrose (Fig. 2A). 'Heart-o-Gold' had a profile distinct from all others in total sugars content which showed a date effect (Table 1). 'Heart-o-Gold' increased in total sugars by 48% over the 12-week assay period to reach a level comparable to 'Travis' at 19 WAT (Fig. 2B). 'Heart-o-Gold' also differed from 'Beauregard' and 'Travis' and had relatively low levels of monosaccharides, e.g., 15% at 19 WAT compared to 40% in 'Travis' and 'Beauregard'.

The white flesh cultivars, 'Rojo Blanco' and 'Whitestar', were consistently ranked among the lowest in total sugars (Fig. 2B).
These two cultivars showed no significant quantitative changes in total sugars throughout development based on harvest date (data not presented).

**Dry weight.** Four of the cultivars (‘Rojo Blanco’, ‘Whitestar’, ‘Jewel’, and ‘Beauregard’) showed significant quantitative differences in DW content based on harvest date (data not presented). DW exceeded 32% in the white flesh cultivars ‘Rojo Blanco’ and ‘Whitestar’ at 17 WAT, while ‘Travis’ was the lowest ranking cultivar at 19.9% DW after 17 WAT (Fig. 3A). ‘Whitestar’ and ‘Rojo Blanco’ shared a similar DW profile (Table 1). Pairwise comparisons also showed similarities in DW profiles for ‘Beauregard’, ‘Jewel’, and ‘Rojo Blanco’ (Table 1). In general, profiles among these cultivars showed a quantitative increase in DW during development. ‘Travis’ and ‘Heart-o-Gold’ showed no significant quantitative changes in DW throughout development based on harvest date (data not presented).

**Alcohol-insoluble solids.** Profiles, ranks, and pairwise comparisons of AIS did not differ substantially from those described for DW (Table 1 and Fig. 3B). The only differences were 1) ‘Whitestar’ did not significantly differ in pairwise comparisons with ‘Beauregard’ and ‘Jewel’ (Table 1) and 2) ‘Heart-o-Gold’ showed no quantitative changes in AIS. Percent AIS values 17 WAT for ‘Travis’, ‘Jewel’, ‘Whitestar’, and ‘Rojo Blanco’ were similar to those obtained by Picha (1987) for U.S. no. 1 grade roots at harvest. The relationship between DW and AIS (across all cultivars and dates) is described by the following significant regression equation: AIS = 0.00089 × DW (r = 0.88; n = 274). These results are consistent with the significant linear correlation between DW and starch found by Li and Liao (1983) on mature fleshy roots. Our equation extends their results by including DW – AIS data throughout growth and development.

In conclusion, this study documents cultivars achieving the highest total sugars at normal harvest periods (17 to 19 WAT) have 1) higher levels of monosaccharides to compensate for a lower sucrose content or 2) higher levels of sucrose to compensate for a lower monosaccharide content. No cultivar contained high levels of both sucrose and monosaccharides, but these results do not preclude the existence of such a clone. Previous research on raw and baked sweetpotato supports these results (Lewthwaite et al., 1997; Picha, 1985). This study also documents cultivars with the highest fructose and glucose content could be selected by breeders after 13 WAT. Early clonal selection for high sucrose and total sugars is less promising because substantive changes in clonal rank occur for sucrose and total sugars after 15 WAT.

A number of factors complicate the ultimate selection of a sweeter sweetpotato. First, sugars are not equal in their contribution to sweetness in sweetpotato. When sucrose, fructose, and maltose (the main sugar in baked sweetpotato) are compared at similar levels of sweetness (sucrose equivalents), it takes more sucrose and fructose, in comparison to maltose, to achieve optimum sweetness (Koehler and Kays, 1991). Second, a higher sugar content in raw sweetpotato implies a sweeter baked prod-

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**Fig. 2.** (A) Sucrose and (B) total sugars in ‘Beauregard’, ‘Jewel’, ‘Travis’, ‘Rojo Blanco’, ‘Whitestar’, and ‘Heart-o-Gold’ sweetpotatoes on a FW basis in fleshy roots during development. Data were means ± SE averaged over 2 years. Legend in A applies to B also.

**Fig. 3.** (A) Dry weight and (B) alcohol-insoluble solids in ‘Beauregard’, ‘Jewel’, ‘Travis’, ‘Rojo Blanco’, ‘Whitestar’, and ‘Heart-o-Gold’ sweetpotatoes on a FW basis in fleshy roots during development. Data were means ± SE averaged over 2 years. Legend in A applies to B also.
uct. However, a high sugar content in a raw sweetpotato does not necessarily result in a higher sugar content in a baked sweetpotato. For example, this study documented a high level of total sugars in 'Travis'. However, this cultivar has a lower level of total sugars than 'Jewel' when baked (Picha, 1986). The low AIS content in 'Travis' implies a reduced amount of starch available for conversion to maltose by heat activated α- and β-amylase; and third, carbohydrate-related compositional changes are variable due to amylase-mediated starch hydrolysis. Staple-types often lack starch hydrolysis due to inhibition of β-amylase synthesis or a nonenzyme mediated mechanism (Morrison, et al., 1993). These authors also suggest the existence of high sugar, low starch hydrolysis cultivars. Baking trials are needed to determine sugar conversions in cultivars that possess both high total sugars and high AIS content.

Our results also demonstrated that DW is a quick, reliable estimator of AIS in sweetpotato. DW rankings remained constant for the high DW, white-flesh cultivars throughout the entire 12-week period. This implies breeders could compare and select high DW cultivars at early development stages.

**Literature Cited**


