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ASYMMETRIC DISTRIBUTION OF SUGARS IN CITRUS FRUITS: POSSIBLE PHYSIOLOGICAL CAUSES

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Abstract. **Sugars and related enzymes were determined at three stages of development in the stem and the blossom halves of 'Valencia' oranges (*Citrus sinensis* [L] Osbeck). The blossom half contained significantly higher concentrations of sugars at later stages of development. Neither the enzyme marker for sucrose synthesis (sucrose-phosphate synthase, SPS) nor enzymes of CO_2 fixation (NADP-malic enzyme, PEP carboxylase and PEP carboxykinase) were significantly different between the halves. Sucrose synthase (SS), a marker of sink strength, had significantly higher activity in the blossom half during later stages of fruit development when rapid sugar accumulation takes place. The data suggest that differential distribution of sugars between the stem and the blossom halves of citrus fruits is, in part, the result of differential sink strength.**

Soluble solids in citrus fruits are distributed unevenly both at the tree level (Syvertsen and Albrigo, 1980), and within the individual fruit as well (Bartholomew and Sinclair, 1946; Ting, 1969). Inside the fruit, soluble solids and total sugars are found in an increasing gradient towards the blossom end (Bartholomew and Sinclair, 1946; Ting, 1969), and on a outwardly radial direction. Bartholomew and Sinclair (1946) reported that mature oranges and grapefruits had considerably higher concentrations of soluble solids in the blossom halves than in the stem halves. Ting (1969) also observed an increase in the concentration of non-reducing sugars and total sugars along the axis of the mature fruit from the stem end to the blossom end. Unequal sugar distribution has also been reported for other mature fruits (Martin, 1954).

In citrus fruits, sugar content increases rapidly during development (Lowell et al., 1989) resulting from an increase in

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photoassimilate supply and a decrease in sugar consumption. Despite the fact that most photoassimilates that accumulate in the juice cells come from photosynthetic source leaves (Yen and Koch, 1990), several intracellular processes could affect the ultimate concentration of stored sugars.

Despite the long recognition of uneven distribution of soluble solids and sugar in citrus fruits, there are no reports, to our knowledge, examining potential factors involved. This study investigates possible causes for unequal sugar distribution in 'Valencia' oranges by examining the allocation of enzymes determinant of sink strength, sucrose synthesis, and CO_2 fixation. Sink strength at the enzyme level (as discussed in this work) refers to the series of enzymatic reactions associated with sucrose storage or its interconversion.

Materials and Methods

Plant material. 'Valencia' oranges (*Citrus sinensis*) were obtained from mature trees at the Citrus Research and Education Center, Lake Alfred, FL, during the 1995 and 1996 growing seasons. All fruit were sampled from the outside southern canopy and used immediately for enzyme extraction and sugar analysis. Sampling was conducted at three arbitrary stages of fruit development separated by two months each, starting in September; September fruit: green (not final size); November fruit: green (final fruit size attained, yellow inside); January fruit; yellow (faster rates of sugar accumulation).

For enzyme extraction, fruits were washed, cut equatorially, peeled, and separated into individual segments or segment halves. Juice sacs were separated from the segment wall, rinsed, and blotted dry prior to homogenization. For sugar analysis, fruit halves were squeezed separately and the extract immediately neutralized with 1N NaOH.

Sugar analysis. Sugar analysis was accomplished by HPLC as described by Lee and Nagy (1988), but purification with Chrom-prep mixed resin was omitted.

Enzyme extraction and assays. Four g of juice sac tissue were homogenized in a pre-chilled mortar and pestle with 10 ml of a buffered solution described by Echeverria and Salerno (1994). The resulting mixture was centrifuged for 5 min at 13,000 *g*, filtered through glasswool, and centrifuged again for 15 min at 25,000 *g*. Of the supernatant, 2.5 ml were desalted through a Sephadex G-25 column pre-equilibrated with 20 mM Hepes/KOH buffer (pH 7.2), 10 mM $MgCl_2$, 10% (v/v) glycerol, and 5 mM mercaptoethanol. Enzyme extractions were carried out at 4°C.

Sucrose-phosphate synthase (SPS, EC. 2.4.1.14) reactions were assayed as described by Salvucci et al. (1990). For sucrose synthase (SS, EC. 2.4.1.13), the reaction consisted of 10 mM fructose, 5 mM $MgCl_2$, 2 mM UDP-glucose, 100 mM Hepes/KOH (pH 7.2) and enzyme extract in a final volume of 1 ml. Reactions were terminated by boiling 60 µl aliquots for 2 min. The product sucrose was measured by the anthrone method of Van Handel (1968); UDP was measured as described by Salvucci et al. (1990). Malic enzyme activities (NAD-malic enzyme, EC 1.1.1.38; and NADP-malic enzyme, EC 1.1.1.40) were measured at 340 nm by following the continuous reduction of NAD^+ or $NADP^+$, respectively, as in Cook et al. (1995). PEP carboxylase (EC 4.1.1.39; Zhang et al., 1995) and PEP carboxykinase (EC 4.1.1.49; Ray and Black, 1976) were determined by coupling the formation of the product oxaloacetate with commercial malic dehydrogenase (EC 1.1.1.37; Sigma M-9004). The spectrophotometric method of Ishibashi et al. (1996) was used for Rubisco (EC 4.1.1.39) measurements. All reactions were carried out at 30°C. Protein was determined by the coomassie blue method of Bradford (1976). Data values are from five separate experiments. Each experiment was conducted in triplicates and consisted of combined extracts of two fruit.

Results and Discussion

Total sugar increased over 50% in the stem half and about 85% in the blossom half of Valencia oranges between September and January (Table 1). At all three developmental stages, the blossom half contained higher levels of total sugars than the stem half, although only the last two stages were statistically different ($P < 0.05$). In January, the blossom half contained 24% more total sugars than the stem half. In comparison, the differences in total sugars between the blossom and stem half were only 4% in September and 12% in November.

The concentrations of all three individual sugars increased during development in both halves. Overall, sucrose increased an average of 130% whereas hexoses increased approximately 30%. At maturity (January), each sugar was found at higher concentrations at the blossom half (Table 1). There were no significant differences in total or individual sugars between the sunny side and the shady side of the fruit (Table 2). The lack of differences in sugar composition between the sunny and shady side regardless of any light intensity variations, and the fact that peel photoassimilates are not transported inward into the juice cells (Yen and Koch, 1990) eliminate fruit photosynthesis as a possible cause of unequal sugar distribution.

The activities of SPS and SS, established as the major mechanisms for sucrose synthesis (Huber and Huber, 1996) and determinant of sink strength (Black et al., 1995), respectively, are presented in Table 3. There was a continuous decline in the specific activity of SPS (µmol sucrose synthesized·min^{-1}·mg $prot^{-1}$) during development of both halves. Nevertheless, there were no significant differences in the levels of SPS activity at maturity. Protein content (total protein) was similar in both halves. In contrast, the activity of SS was consistently higher at the blossom half throughout fruit development. While SS activity remained fairly constant in stem half, it increased continuously in the blossom half

Table 1. Sugar content in the stem and blossom halves of 'Valencia' orange fruit at three stages of development. Each value is the mean of 5 experiments ± SD.

	Date of sampling		
Sugars	September	November	January
Stem half	(g·100 ml tissue $extract^{-1}$)		
Fructose	1.63 ± 0.14	1.86 ± 0.19	2.07 ± 0.10
Glucose	1.51 ± 0.15	1.66 ± 0.21	1.75 ± 0.12
Sucrose	2.04 ± 0.28	3.24 ± 0.40	4.16 ± 0.40
Total	5.18 ± 0.28	6.75 ± 0.48	7.96 ± 0.38
Hexoses/sucrose	1.54	1.09	0.92
Blossom half			
Fructose	1.79 ± 0.12	2.23 ± 0.16*[z]	2.58 ± 0.14*
Glucose	1.70 ± 0.12	2.06 ± 0.13*	2.32 ± 0.10**
Sucrose	1.87 ± 0.22	3.30 ± 0.39	4.95 ± 0.37*
Total	5.36 ± 0.43	7.59 ± 0.27*	9.85 ± 0.42**
Hexoses/sucrose	1.87	1.30	1.02

[z]*, **Significance at $P < 0.05$ and $P < 0.01$, respectively.

Table 2. Sugar content in the 'sunny' and 'shaded' halves of 'Valencia' orange fruit at three stages of development. Each value is the mean of 5 experiments ± SD.

Sugars	Date of sampling		
	September	November	January
Sunny half	(g·100 ml tissue extract^{-1})		
Fructose	1.64 ± 0.08	2.10 ± 0.18	2.19 ± 0.23
Glucose	1.54 ± 0.07	1.89 ± 0.17	1.93 ± 0.25
Sucrose	1.70 ± 0.16	3.06 ± 0.57	4.34 ± 0.39
Total	4.88 ± 0.21	6.97 ± 0.76	8.46 ± 0.46
Hexoses/sucrose	1.87	1.30	0.95
Shady half			
Fructose	1.57 ± 0.06	2.02 ± 0.17	2.19 ± 0.22
Glucose	1.49 ± 0.07	1.81 ± 0.08	1.96 ± 0.21
Sucrose	1.69 ± 0.17	3.26 ± 0.38	4.70 ± 0.27
Total	4.65 ± 0.43	7.05 ± 0.52	8.85 ± 0.48
Hexoses/sucrose	1.81	1.17	0.88

throughout development. Specific activities of both enzymes were very similar to those reported by Lowell et al. (1989) for grapefruit juice cells.

Of the five enzymes with capacity to fix CO_2, Rubisco and NAD-malic enzyme were not detected in juice tissue. The remaining enzymes (NADP-malic enzyme, PEP carboxylase and PEP carboxykinase; Table 4) showed declining levels of activity from green fruit to maturity. NADP-malic enzyme had the highest maximal activity. In all instances, there were no differences between the blossom and the stem halves in any of these three enzymes.

Although sucrose enters citrus juice cells without significant levels of apoplastic inversion (Koch and Avigne, 1990), several intracellular events may affect the final concentration of stored assimilates. Our data indicate that in 'Valencia' orange fruits the activity of SS in the juice cells of the blossom half is significantly higher than in the stem half (Table 3). The difference in SS activity is notable since it indicates a higher sink strength during the stages of sugar accumulation. Sink strength encompasses the collective capacity for sucrose breakdown which includes SS, total invertase activity, and in the case of acidic cells, vacuolar acid hydrolysis (Echeverria and Burns, 1989). In sucrose importing organs the regulation of sucrose cleavage within the cells constitutes the biochemical marker of sink strength (Ho et al., 1991). Our evidence is in agreement with this concept. The higher levels of SS activity in the juice cells at blossom half of 'Valencia' oranges are paralleled by significantly higher levels of stored sugars (Table 1). The fact that the hexoses/sucrose ratio always remained higher in the blossom half supports this contention.

Table 3. Activities of enzymes of sucrose synthesis (SPS) and sink strength (SS) at the stem and blossom halves of 'Valencia' juice tissue. Values are the mean of 5 experiments ± SD.

Enzyme	Date of sampling		
	September	November	January
	Activity (μmol sucrose synthesized or hydrolyzed·min^{-1}·mg protein^{-1})		
Stem half			
SPS	*25.64 ± 0.60	22.75 ± 2.65	18.36 ± 1.39
SS	25.94 ± 0.99	26.35 ± 1.24	26.43 ± 1.45
Blossom half			
SPS	23.80 ± 1.04	21.70 ± 2.50	18.22 ± 1.62
SS	26.17 ± 0.47	*28.01 ± 1.77	**29.97 ± 0.64

*, **Significance at $P < 0.05$ and $P < 0.01$, respectively.

Table 4. Activities of enzymes of CO_2 fixation from 'Valencia' orange juice cells at two stages of development. Values are the mean of 3 experiments ± SD.

	November		January	
	Stem half	Blossom half	Stem half	Blossom half
	Activity (nmol·min^{-1}·mg protein^{-1})			
NADP-Malic enzyme	219.6 ± 20.5	239.4 ± 2.14	136.5 ± 23.4	145.3 ± 22.8
PEP-carboxylase	24.36 ± 1.4	26.9 ± 2.3	15.5 ± 2.7	15.7 ± 4.3
PEP-carboxykinase	29.8 ± 8.9	32.9 ± 7.3	16.2 ± 11.4	17.8 ± 0.9

Acid hydrolysis of sucrose in the vacuole plausibly contributes significantly to the production of hexoses considering the low vacuolar pH of orange juice cells (estimated at 2.8; Echeverria and Burns, 1989). In fact, such hydrolysis may account for most of the hexoses present in the vacuole but is an unlikely factor in differential sugar allocation since the acidity in citrus fruits is equally distributed between the stem and blossom halves (Ting, 1969). Other possible factors that may have contributed to differential sugar allocation between the two halves, such as higher rates of sucrose synthesis (Table 3) and dark CO_2 fixation (Table 4), were not significantly different (or in some instances, even higher in the stem half as for SPS). Both processes are known to take place in citrus juice cells (Lowell et al., 1989; Yen and Koch, 1990).

In conclusion, the higher levels of SS in the blossom half of Valencia orange juice tissue represent a stronger sink that consequently results in higher levels of stored sugars.

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VARIATION OF SUGAR CONTENT IN VARIOUS PARTS OF PITAYA FRUIT

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Abstract. **Pitaya (*Hylocereus undatus* Britt & Rose) belongs to the Cactaceae family and is native of arid and semiarid regions. Pitaya fruit are edible and juicy with solids content in the range of 17 to 19.5 degrees Brix in the core part of the fruit. The soluble solids and enzyme activities in core, stylar-end, stem-end, and peripheral parts of the fruit were determined for red and white pitaya species. The predominant sugars in the fruit are glucose and fructose with small amount of sucrose. The patterns of sugar distribution in various parts were closely related to invertase and amylase activities in the tissues. A high ratio of glucose to fructose was attributed to the hydrolysis of starch by amylase. Pitaya fruits are a good sources of minerals, glucose, fructose, dietary fiber, and vitamins. Because pitaya can withstand prolonged drought, it is considered a potential economic crop for semiarid regions.**

Pitaya (*Hylocereus undatus* Britt & Rose) is in the Cactaceae family and is native of arid and semiarid regions (Morton, 1987). The pitaya plant produces edible and juicy fruit. The fruit is a berry with a thick wall (or peel) enclosing delicately flavored and seedy pulp. The peel color can either be pink, red, or light yellow and the flesh is either white or red color. Pitaya fruit is nutritious, drought resistant, and can tolerate low storage temperature (Morton, 1987; Campos-Hugueny et al, 1986). Commercial production of pitaya fruit flourishes in Mexico, Central America, West Indonesia Island, and Vietnam.

Pitaya cultivation has been recently introduced and fruit consumption has gained popularity in Taiwan. Previous work on pitaya fruit (Chang and Yen, 1997) showed there were large differences in soluble solids among various parts of the fruit. Pitaya solids contents range from 17 to 19.5 degrees Brix in the core part of the fruit with the predominant soluble sugars being glucose and fructose. Sweetness is an important quality attribute for consumer preference. Acid and neutral invertase (β-fructo-furanoside fructohydrolase E.C.3.2.1.26) are widely distributed in higher plants (Bradshaw et al., 1970; Richardson et al., 1990). Increased invertase activity is usually associated with an increase in hexoses and a decrease in sucrose (Pressey and Shaw, 1996).

The objective of this study was to investigate sugar distribution in core, stylar-end, stem-end, and peripheral parts of the flesh and their relationships with invertase and amylase activities in the tissues for red and white species of pitaya fruits.

Material and Methods

Fruit samples. White pitaya fruits were harvested form an experimental orchard at the National Pingtung University of Science and Technology. Red pitaya fruits were harvested from a commercial orchard in Taichung. The fruits were hand picked 50 days after flowering and the flesh separated into core, stylar-end, stem-end, and peripheral parts. The test samples were taken from the 1.5 cm-diameter cylinders from each section, then weighed, frozen, and stored at -18°C. Flesh of core, stylar-end, stem-end, and peripheral parts (5 g each) were homogenized separately with 60 ml of 90% (V/V) ethanol and clarified by centrifugation. After standing for 2 wk at -12°C, a 10 ml aliquot of clear supernatant of the homogenized samples was evaporated to dryness under a stream of N2 and redissolved in 5 ml of deionized water. Triplicate samples were used for analysis.