Carbohydrate Differences in Strawberry Crowns and Fruit (*Fragaria* × *ananassa*) during Plant Development

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Carbohydrates accumulation and mobilization are highly relevant in plants because they have been related to yield and quality. Therefore, the aims of this work were to determine soluble carbohydrates and starch in strawberry (*Fragaria* × *ananassa* cv. Camarosa) crown sections (basal, middle, and upper) at three different plant growth stages (vegetative, blooming, and fruiting), and in fruit varieties (cv. Camarosa, Seascape, and Oso Grande) grown on the same field and in a different geoclimate. The main soluble carbohydrates found were glucose, sucrose, and fructose. Concentration differences were found among crown sections and time. The lowest levels of glucose, fructose, and sucrose were present at the beginning of fruit formation (6.2, 1.8 mg/g, and trace, respectively). Starch increased in basal and middle sections at the same time (8.6 to 109.6 and 6.6 to 93.5 mg/g, respectively). There appears to be a relationship between crown and fruit soluble carbohydrates. The most abundant fruit monosaccharides in all varieties were glucose (160−190 mg/g), fructose (90−180 mg/g), and sucrose (30−120 mg/g), followed by *myo*-inositol (10−23 mg/g). Strawberry crowns are an important source of carbohydrates and they might play a role during plant development specifically related to fruit sweetness. Fruit quality is highly influenced by a combination of several factors such as genotype, geoclimate, and probably carbon partitioning.

KEYWORDS: Soluble carbohydrates; starch; strawberry; *Fragaria* × *ananassa*; crown; fruit; GC−MS

INTRODUCTION

Strawberry (*Fragaria* × *ananassa* Duch.) is one of the most popular fruits worldwide. Traditionally, Mexico has been considered an important strawberry producer and exporter, and in order to maintain its position in the international market there exists an interest to improve fruit production as well as quality. A number of components have been shown to influence fruit yield, including the number of leaves per plant, rooting date, leaf photosynthetic rate, and plant density (*1*). However, much of the variation in fruit production among cultivars has been attributed to two factors: the carbohydrates content in various parts of the plant (leaves, petioles, crowns, and roots) and temperature during growth (*2*). Strawberry plants stored at cold temperatures before planting favor starch accumulation in roots. Starch is the most significant form of carbon reserve in plants; it has been reported that an excellent adaptation and an increase in fruit yield have been obtained in plants with high starch content in their roots (*2, 3*).

Strawberry crowns (considered as modified stems) represent an important reservoir of carbohydrates in the plant (116.4 and 124.3 mg/g of total carbohydrates were reported for Earliglow

and Kent varieties, respectively) (*2*); despite this relevance, there are few studies related to the significance of the plant crowns with development and fruit yield. Le Mière et al. (*1*) studied the effect of strawberry crown size on Elsanta variety growth and yield; they concluded that berry number and average berry weight were positively correlated to crown size.

In another study, Ofosu-Anim and Shohei (*4*) described strawberry quality as the amount and composition of carbohydrates accumulated in the fruit. Meanwhile, the relationship between carbohydrates and sensory attributes such as fruit sweetness has been well studied (*5−7*). Glucose, fructose, and sucrose are regarded as significant quality factors by both consumers and the food industry (*5*), and it is well-known that the content of these compounds in the fruit is affected by ripeness stage, genotype variety, geographic origin, and temperature during growth (*2, 5, 8*). On the other hand, it is possible that the components that determine fruit yield might also participate in the quality of the final product, the strawberry fruit.

Therefore, the aims of this work were to establish carbohydrates differences (soluble and starch) in strawberry crowns (cv. Camarosa) during plant development (vegetative, blooming, and fruiting stages) and to compare soluble carbohydrates of Camarosa strawberries with Seascape and Oso Grande cultivars grown on the same field and in a different geoclimate.

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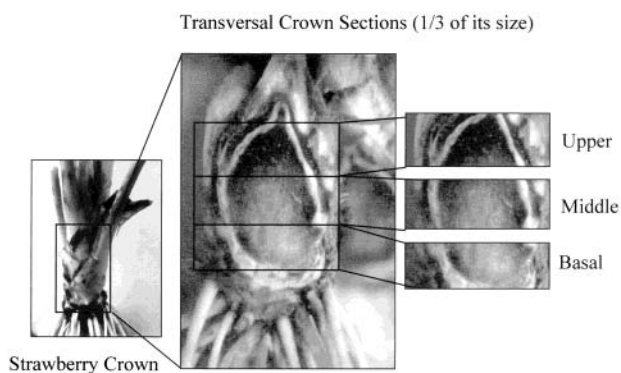‡ Instituto Tecnológico Superior de Uruapan.

Figure 1. Transversal sections from strawberry crown (*Fragaria × ananassa* cv. Camarosa) before carbohydrate analysis.

MATERIALS AND METHODS

Samples. *Crowns*. Strawberry (*Fragaria × ananassa* Duch. cv. Camarosa) nursery crowns (2,000 plants with a diameter of 12−15 mm) were cultivated on September 20, 1998 in Zamora, Michoacan, Mexico. Crowns were collected in a random way (150 plants) at 3, 5, 7, 9, and 11 weeks from planting. On the basis of physiologic developmental characteristics of this crop, sampling weeks were divided into three different growth stages: vegetative, comprising nursery crowns and 0−3 weeks from planting; blooming, crowns with 5 to 7 weeks growth; and fruiting, crowns 9 to 11 weeks old. Crowns harvesting finished on December 5, 1998 and on this date, fruits were picked. Crowns were frozen with liquid nitrogen and stored at −80 °C for a day. After lyophilization (Labconco), crowns were transversally sectioned into three parts: basal, middle, and upper sections (**Figure 1**). Samples were stored under vacuum at −20 °C until use.

Strawberries. Strawberry plants (cv. Camarosa, Seascape, and Oso Grande) were cultivated also on September 20, 1998 in the same field under a latin square statistical design and strawberries were picked in December. To compare the geoclimatic effect on the carbohydrate content of Camarosa fruits, strawberries were also cultivated and picked in Irapuato, Guanajuato, Mexico. All fruits were frozen (−80 °C), lyophilized, and stored under vacuum at −20 °C until use.

Reagents. All reagents were analytical reagent grade. Helium used during chromatographic analyses was of high-purity grade.

Soluble Carbohydrate Analysis in Crowns. *Extraction Technique*. Sample extraction was conducted as follows: 250 mg of crown sections plus perseitol (internal standard, 1.5 mg) were extracted with 20 mL methanol/chloroform/water (48:20:12, v/v) at room temperature for 12 h and reextracted with 20 mL of water for 4 h (*9*). The extracts were combined and diluted to 50 mL. Aliquots of 25 mL were purified with 25 mL of chloroform, concentrated to 5 mL with a rotary evaporator at 65 °C, and passed through a 10-cm Bio-Rad resin H⁺ 200−400-mesh column. A neutral fraction was collected where mainly carbohydrates were eluted with 50 mL of 0.01 N HCl and 10 mL of deionized water. All neutral fractions were concentrated again to 5 mL and then derivatized.

Derivatization. A 1 mL aliquot of each sample was evaporated to dryness under a steam of nitrogen, then diluted in 1 mL of dichloromethane and redried; this procedure was repeated three times. The extracts were first treated with 1.5 mL of a hydroxylamine chloride−pyridine solution (53 mg/3 mL) to prepare the oxime derivatives. The samples were sonicated for 30 min and then heated for 1 h at 85 °C. After cooling, the solutions were converted to their aldonitrile peracetylated derivatives using acetic anhydride (1 mL) and pyridine (500 μL) at 85 °C for 20 min. The derivatized samples were diluted with 1 mL of chloroform and washed with deionized water three times. The organic phase was recovered, dried over anhydrous Na₂SO₄, evaporated, and redissolved in 50 μL of chloroform.

GC−MS. Aldonitrile peracetylated derivatives were separated in a HP5890 Series II gas chromatograph from Hewlett-Packard, equipped with a HP-MS detector 5972, and a 30 m × 0.2 μm × 0.25 mm 5% phenyl methyl silicone capillary column (HP-5 MS). Operating conditions were as follows: Helium was the carrier gas, 0.25 mL/min;

detector, 300 °C; injector, 270 °C; injected volume, 1 μL. The column was held for 3 min at 150 °C and programmed at 10 °C/min to a final temperature of 270 °C for 35 min.

Response Factors Determination. Individual carbohydrates were derivatizated and analyzed in the GC−MS following the same methodology mentioned above to determine the response factors for accuracy and precision on carbohydrates quantitation: arabinose, 0.73; xylose, 0.74; glucose, 0.74; inositol, 0.99; fructose, 0.21; and sucrose, 0.09.

Starch Analysis in Crowns. The starch content was determined only in crowns (basal, middle, and upper sections) using a total starch assay kit (Megazyme Co.) based on the use of thermostable α-amylase and amyloglucosidase enzymes. Starch hydrolysis proceeded in two phases: phase I, starch is partially hydrolyzed and totally solubilized; and phase II, starch dextrins are quantitatively hydrolyzed to glucose by amyloglucosidase. The colored reagent was GOPOD (glucose determination reagent) which contains glucose oxidase, peroxidase, and 4-aminoantipyrine. Spectroscopic readings were made at λ 510 nm. Before the enzymatic determination, free carbohydrates were extracted from the samples (100 mg) with 5 mL of aqueous ethanol (80% v/v); this step was repeated twice.

Soluble Carbohydrate Analysis in Strawberries. Soluble carbohydrates from strawberries of Camarosa (Zamora and Irapuato), Seascape, and Oso Grande (Zamora) were also analyzed following exactly the same methodology mentioned above.

Statistical Analysis. *Crowns*. Statistical analysis was performed using SAS statistical computer program (SAS Institute Inc. version 6.12, 1996; Cary, NC). Significant differences in each soluble carbohydrate and starch contents were tested by a factorial analysis with crown section and time as the factors in a completely randomized design. Least significant difference (LSD) was used for multiple means comparison ($\alpha = 0.05$).

Strawberries. Significant differences in carbohydrates content among varieties were tested by a factorial analysis with one factor (variety) in a completely randomized design. In the case of the carbohydrate content comparison in Camarosa from Zamora and Irapuato, the factor was geographic origin. Minimal significance difference (MSD) was used for multiple means comparison ($p < 0.05$).

RESULTS AND DISCUSSION

Soluble Carbohydrate in Crowns. In this study, strawberry crown (upper, middle, and basal transversal sections) carbohydrates were determined at three different plant growth stages (vegetative, blooming, and fruiting). The main soluble carbohydrates found in strawberry crowns are shown in **Table 1**. Arabinose, xylose, glucose, *myo*-inositol, fructose, and sucrose were the most abundant carbohydrates in all sections. Arabinose was present in trace content in the basal and middle crown sections at 9 weeks but a large increment was observed at 11 weeks (1.3 and 1.9 mg/g, respectively). Xylose levels were practically the same from 0 up to 7 weeks (middle and upper sections), but at the beginning of the fruiting stage (9 weeks) xylose increased considerably (4.6 and 7.1 mg/g, respectively). This remarkable change was statistically significant, $\alpha = 0.05$; LSD (**Table 1**), however, after this point, its concentration dropped again to the original level. It is worth mention that xylose was the only carbohydrate that showed this behavior. The observed changes in pentoses levels might indicate that their metabolisms during strawberry development, specifically at fruit formation, are very active and might be related to the plant requirement for glycosyl units for polysaccharide biosynthesis as cell wall form like L-arabanes and D-xylanes (*10*) which participate in the formation of rhizomes, leaves, roots, and fruit structures. *Myo*-inositol, on the other hand, was the only compound that showed a concentration gradient in crown sections at all growth stages; inositol increased from basal to upper sections (**Table 1**). One of the many *myo*-inositol

Table 1. Soluble Carbohydrate Contents[a] (mg/g dry weight) of Strawberry Crown Sections (cv. Camarosa) at Different Plant Growth Stages

crown section	vegetative stage (weeks)		blooming stage (weeks)		fruiting stage (weeks)	
	0	3	5	7	9	11
			Arabinose			
upper	0.5 ± 0.5^{BC}	1.2 ± 0.6^{AB}	1.3 ± 0.5^{AB}	0.9 ± 0.5^{ABC}	0.5 ± 0.3^{BC}	1.1 ± 0.3^{AB}
middle	t^{C}	0.6 ± 0.6^{BC}	0.8 ± 0.6^{BC}	0.6 ± 0.5^{BC}	t^{C}	1.9 ± 0.4^{A}
basal	0.4 ± 0.0^{BC}	1.4 ± 0.2^{AB}	0.6 ± 0.3^{BC}	0.8 ± 0.0^{BC}	t^{C}	1.3 ± 0.4^{AB}
			Xylose			
upper	2.1 ± 1.0^{DE}	1.5 ± 0.5^{DEF}	1.5 ± 0.2^{DEF}	1.2 ± 0.1^{EF}	7.1 ± 0.1^{A}	1.6 ± 0.4^{DEF}
middle	2.5 ± 0.5^{CD}	1.5 ± 0.5^{DEF}	1.5 ± 0.2^{DEF}	1.4 ± 0.2^{DEF}	4.6 ± 0.2^{B}	1.8 ± 0.3^{DEF}
basal	2.1 ± 0.1^{DE}	1.3 ± 0.4^{DEF}	0.8 ± 0.2^{F}	1.1 ± 0.6^{EF}	3.4 ± 0.3^{BC}	1.2 ± 0.4^{EF}
			Glucose			
upper	46.6 ± 2.3^{A}	34.5 ± 0.7^{CD}	39.9 ± 0.7^{BC}	35.5 ± 3.5^{CD}	22.8 ± 0.9^{GH}	31.4 ± 2.0^{DEF}
middle	39.2 ± 1.1^{C}	26.3 ± 1.3^{EFG}	25.1 ± 1.8^{FG}	23.2 ± 3.5^{GH}	11.5 ± 0.9^{JK}	39.8 ± 4.4^{BC}
basal	45.1 ± 0.5^{AB}	23.4 ± 1.3^{GH}	14.4 ± 0.5^{IJ}	18.2 ± 2.8^{HI}	6.2 ± 0.8^{K}	30.8 ± 2.0^{DEF}
			myo-Inositol			
upper	3.8 ± 0.8^{D}	3.0 ± 0.5^{DE}	5.0 ± 0.1^{BC}	7.9 ± 0.8^{A}	4.0 ± 0.4^{CD}	5.7 ± 0.7^{B}
middle	3.0 ± 0.5^{DEF}	2.4 ± 0.4^{EFG}	2.1 ± 0.5^{EFGH}	2.3 ± 0.1^{EFG}	1.9 ± 0.1^{FGHI}	3.0 ± 0.5^{DE}
basal	2.1 ± 0.5^{EFGH}	1.1 ± 0.2^{HI}	0.9 ± 0.2^{I}	1.4 ± 0.1^{GHI}	1.1 ± 0.1^{HI}	2.0 ± 0.3^{EFGHI}
			Fructose			
upper	30.0 ± 6.2^{ABC}	31.2 ± 4.5^{AB}	23.4 ± 9.7^{ABCD}	23.4 ± 5.8^{ABCD}	14.9 ± 8.6^{BCD}	35.3 ± 12.5^{AB}
middle	27.8 ± 8.0^{ABCD}	29.4 ± 6.8^{ABC}	36.9 ± 8.0^{AB}	37.4 ± 10.5^{AB}	1.8 ± 0.9^{D}	47.0 ± 20.7^{A}
basal	38.3 ± 14.0^{AB}	28.8 ± 8.5^{ABC}	12.4 ± 9.0^{BCD}	25.8 ± 12.6^{ABCD}	3.3 ± 2.6^{CD}	25.4 ± 8.4^{ABCD}
			Sucrose			
upper	29.3 ± 5.0^{D}	72.5 ± 6.1^{A}	39.2 ± 6.9^{C}	3.0 ± 1.3^{FGH}	0.4 ± 0.2^{H}	15.2 ± 1.9^{E}
middle	43.0 ± 8.0^{C}	6.3 ± 1.2^{FG}	5.1 ± 0.2^{FGH}	0.2 ± 0.0^{H}	t^{H}	2.0 ± 0.1^{GH}
basal	19.1 ± 1.0^{E}	8.0 ± 3.5^{F}	0.3 ± 0.1^{H}	0.3 ± 0.1^{H}	t^{H}	58.1 ± 0.0^{B}

[a] GC elution order. Using response factors (see methodology). Mean values and standard error of the sum of three independent determinations. Means with same letter ([A-L]) are not significantly different ($\alpha = 0.05$; LSD). t, trace. Statistical analysis of individual carbohydrates was performed.

functions is involved in the biosynthesis of phytic acid which is considered as an important source of phosphate in plants (*11*). On the basis of this knowledge, it is possible to assume that inositol in crowns might be considered as a carrier of phosphate in the form of phytic acid, which is pumped constantly from the crown to the aerial parts throughout plant development.

Glucose, fructose, and sucrose are the prevalent constituents in strawberry crowns, and also the most abundant carbohydrates. Glucose fluctuation levels may be related to an active mobilization from basal to upper section and as a function of time (3, 5, 7, and 9 weeks); however, at the beginning of fruit formation (9 weeks) a decrement in the concentration of this compound was observed (22.8, 11.5, and 6.2 mg/g in upper, middle, and basal sections, respectively). This same behavior was also observed for fructose and sucrose. It is interesting to point out that at this week the fruiting stage begins, therefore the decrements may be related to formation of fruits.

Starch in Crowns. The observed 2-fold excess in the starch accumulation in the upper section (apical) at 0 week in strawberry crowns might be related to sucrose import from leaves at the vegetative stage (**Figure 2**). The interconversion of sucrose and starch occurs widely in plants, so it is posible that an excess sucrose can feedforward to stimulate sink process and feedback to down-regulate photosynthesis (*12, 13*). The lowest sucrose levels were observed in the basal section from 3 to 9 weeks, which indicates the hypermetabolic activity occurs in the middle and upper crown sections.

The highest sucrose level was found in the upper section at 3 weeks (**Figure 2**), suggesting that the plant needs to import sucrose to accumulate starch as a reserve carbohydrate to support the beginning of a high metabolic activity during blooming. In fact, starch levels increases in the middle and basal sections were observed at week 3, but then a drastic drop of starch occurred between weeks 5 and 7. Two important events take placed at 9 weeks: a regeneration of reserves in the basal and middle sections, and a fast mobilization of these reserves. Very low levels of glucose were detected at this week in all crown sections. On the other hand, at the end of the fruiting stage, starch content decreased but sucrose and glucose increased. This might indicate that a complete strawberry production cycle was achieved, and that translocation and distribution of photosynthates during plant growth is crucial for complete plant development (*14*).

Figure 3 shows total carbohydrates (soluble and starch) changes during strawberry crown development. A weekly carbohydrate analysis showed that accumulation took placed in the vegetative stage, followed by mobilization to the rest of the plant for blooming; at this stage the lowest total carbohydrate contents were observed. Finally, carbohydrate increases were observed again, which are needed for fruit formation (9 week) and maturation (11 week). These results might suggest that if the plant accumulates a large quantity of carbohydrates before blooming, the plant will have plenty of fuel to satisfy its own requirements to complete a fruit production cycle, and consequently more carbohydrates will be available for fruit formation, therefore a high-quality product will be obtained. This phenomenon is similar to that in other species such as *Trillium erectum* where carbohydrate accumulation in stems is essential to support a complete fruit development and maturation (*15*).

Forney and Breen (*16, 17*) mentioned that the rate at which carbohydrates (glucose, fructose, and sucrose, principally) are uptaken and accumulated in the fruit limits its growth and size. In this study, the last crown harvesting was done at 11 weeks (end of fruiting stage), at this same point, fruit collection was also carried out to determine glucose, fructose, and sucrose contents in both organs (crowns and strawberries) (**Figure 4**). Glucose, fructose, and sucrose levels were similar in the crown at 11 weeks, but a 2:1 ratio was observed for glucose/fructose in the fruit. Previous reports (*16, 17*) stated that glucose is uptaken more rapidly than fructose and sucrose. It is also

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Table 2. Carbohydrate Contents[a] (mg/g dry weight) of the Strawberry Fruits Harvested from Two Mexican Locations

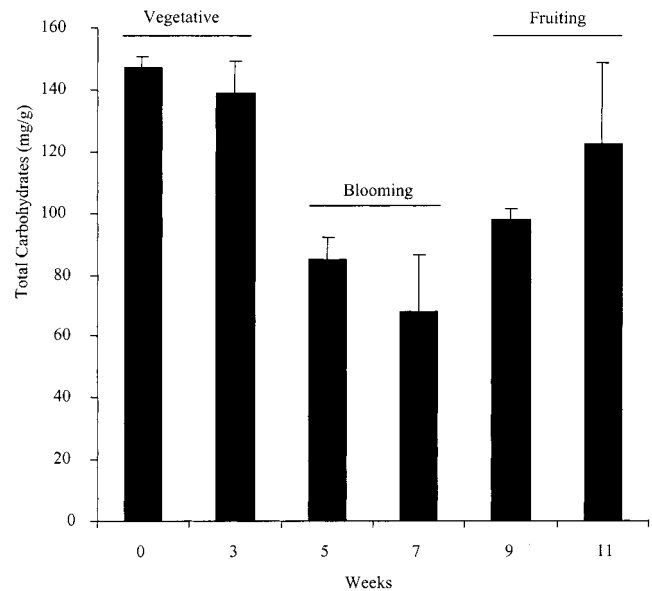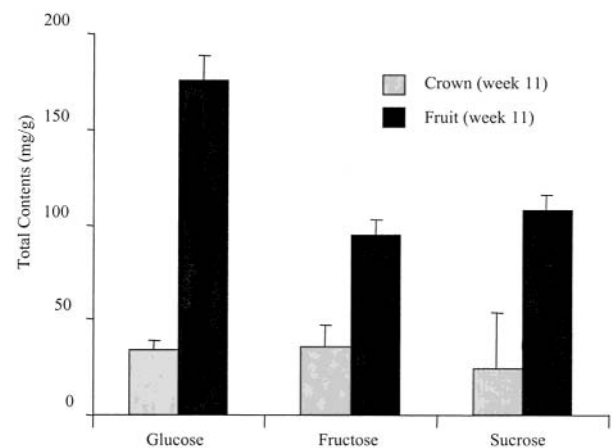|	arabinose	xylose	glucose	*myo*-inositol	fructose	sucrose	total
				Zamora Field			
Camarosa	9.7 ± 0.3^A	5.3 ± 0.2^A	175.6 ± 7.5^A	23.5 ± 2.5^A	93.9 ± 4.6^B	108.1 ± 4.7^{AB}	416.1 ± 16.9
Seascape	9.2 ± 1.5^A	4.9 ± 0.4^{AB}	173.5 ± 9.5^A	13.7 ± 3.9^B	109.4 ± 37.5^{AB}	122.2 ± 34.1^A	432.8 ± 18.9
Oso Grande	6.7 ± 0.2^A	4.1 ± 0.5^B	164.4 ± 7.1^A	10.5 ± 0.3^B	178.6 ± 9.4^A	27.5 ± 1.2^C	391.9 ± 2.3
				Irapuato Field			
Camarosa	7.2 ± 1.1^A	5.3 ± 0.0^A	187.4 ± 2.2^A	9.8 ± 1.8^B	140.7 ± 24.6^{AB}	53.3 ± 10.6^{BC}	403.7 ± 38.6

[a] GC elution order. Using response factors (see methodology). Mean values and standard error of the sum of three independent determinations. Means with same letter ($^{A-C}$) are not significantly different ($\alpha = 0.05$; LSD). Statistical analysis of individual carbohydrates was performed.
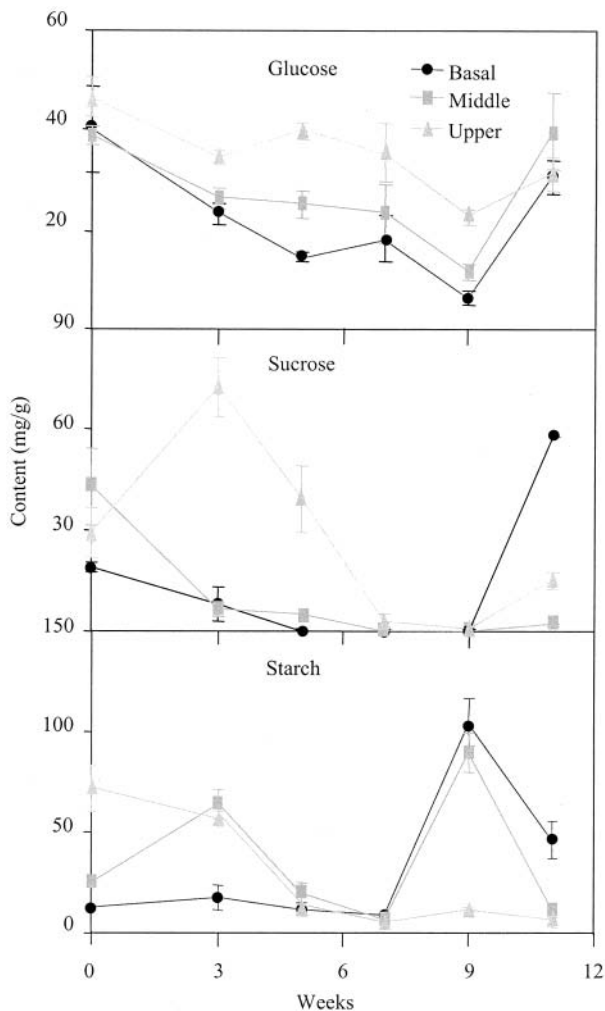
Figure 2. Glucose, sucrose, and starch accumulation and mobilization in strawberry crowns (cv. Camarosa) during plant growth.

Figure 3. Total carbohydrate (soluble and starch) content in strawberry crowns (cv. Camarosa) for all plant growth stages: vegetative (0–3 weeks), blooming (5–7 weeks), and fruiting (9–11 weeks).

Figure 4. Glucose, fructose, and sucrose contents in strawberry crowns and fruits (*Fragaria* × *ananassa* cv. Camarosa) harvested at fruiting stage.

worthwhile to mention that all soluble carbohydrate crown levels at 11 weeks were similar to those of nursery crowns (0 weeks); indicating that the plant carbohydrate status at the end of the fruiting stage (11 weeks) allows it to produce enough starch to begin a second fruit production cycle.

Soluble Carbohydrate Analysis in Strawberries. As mentioned earlier, glucose, fructose, and sucrose levels in strawberry are synonyms of quality. The carbohydrate contents of Camarosa fruit were compared to those of Seascape and Oso Grande varieties which were cultivated under exactly the same conditions (location and time) (**Table 2**). Glucose was the most abundant compound in all fruit varieties (160−190 mg/g), without significant differences among varieties ($\alpha = 0.05$; LSD). However, a higher level of fructose was found in Oso Grande (178.6 mg/g), but this variety also presented the lowest sucrose

content (27.5 mg/g). Arabinose, xylose, and inositol were also found in all fruits. Very similar quantities were observed for arabinose and xylose, and in the case of inositol Camarosa showed the highest content (23.5 mg/g).

When comparing carbohydrate of Camarosa growth under two geoclimatic conditions, there were no significant differences in soluble carbohydrate between locations except for inositol. The large carbohydrate differences seen among Camarosa fruits suggests that the genotype and environment interaction have a direct influence on the quality (sweetness) of this variety (*16*).

There is a worldwide interest in improving fruit quality, and based on this study it seems that one of the key considerations to achieve this might be a combination of cultivar and geoclimate, as well as cultural practices. The varieties tested in this study are widely used for fruit production in Mexico. In the case of fruit from Zamora, the Seascape variety showed more content of glucose, fructose, and sucrose (405.1 mg/g) than Camarosa (377.6 mg/g) and Oso Grande (370.5 mg/g). On the other hand, Camarosa fruit cultivated in Irapuato was sweeter (381.4 mg/g) than that grown in Zamora.

CONCLUSION

Carbohydrate differences were observed in strawberry crowns during plant development. An accumulation with subsequent mobilization of carbohydrates from the crown to other parts of the plant was observed in all stages; and among crown sections, the upper section presented the maximum metabolic activity. On the basis of these results it can be confirmed that strawberry crowns are an extremely high source of carbohydrates (solubles and storage) and therefore they play a relevant role during plant growth and fruit development. Comparison of soluble carbohydrates of Camarosa with Seascape and Oso Grande strawberries grown on two different fields indicated that fruit quality is highly influenced by a combination of several factors such as genotype, geoclimate, and probably carbon partitioning.

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