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ASSIMILATE STORAGE IN VEGETATIVE ORGANS OF COCONUT (*Cocos nucifera*)

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SUMMARY

Assimilate storage in vegetative organs is an essential buffer for the source–sink imbalances that inevitably occur in perennial plants. In contrast to temperate trees, little information is available on such storage in tropical perennials, and almost none for *Cocos nucifera*. This paper describes the chemical nature, quantity and distribution of carbohydrate reserves in coconut plants grown in an environment favourable to production. The study was carried out on the island of Santo (Republic of Vanuatu, Southern Pacific) on twelve 17-year-old adult plants, representative of a large population, which were felled and characterized for root, trunk and crown dry matter, and contents of soluble sugars and starch. Roots were divided into three diameter classes and distal/proximal portions, the trunk into three axial and three or four radial zones, and the crown into petiole, rachis and leaflets for various leaf ages. The aggregate reserve pool size was compared with estimates of incremental demand for assimilates for growth and fruit production. Plants contained little starch but large quantities of sucrose were found, mainly located in the trunk. Less sucrose was present in roots and little in leaf blades. Large glucose and fructose pools were found in leaves, near the apex of the trunk and in the terminal portions of large roots. Aggregate soluble and non-soluble sugar pools were about equivalent to six months of copra production or 51 days of crop growth. More studies are needed on the dynamics of these sugars to evaluate their physiological role, particularly with regards to stress periods and fluctuating demand for fruit filling.

INTRODUCTION

Assimilate reserves are defined as resources accumulated in mobilizable form to sustain growth and other functions of the plant that may temporarily demand more assimilates than are being produced (Chapin *et al*., 1990; Kozlowski, 1992). The reversibility of the storage process within one generation distinguishes vegetative storage from reserves invested in fruits and seed (Ho, 1988). Perennial plants accumulate non-structural carbohydrates during periods of excess production of photoassimilates and use them when demand exceeds production, resulting in a high utilization ratio (Chapin *et al*., 1990; Dickson, 1991; Kozlowski, 1992).

The subject is well documented for temperate forest and fruit-bearing species. According to Bory and Clair-Maczulajtys (1988, 1991), however, little is known about

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vegetative reserves in tropical, perennial species. Among the Arecaceae, oil palm and the sago palm have been studied in detail (Van Die, 1974; Wardlaw, 1990; Henson *et al*., 1999). For coconut, we found only the work of Riejne (1948, cited by Van Die, 1974).

Coconut is an arborescent, monocotyledoneous species with indeterminate growth, producing nuts continuously over several decades (Jayasekara *et al*., 1995). The fruits, which have a high caloric content because of stored lipids constituting 68–70 % in the mature kernel (dry weight) (Shivashankar *et al*., 1999), are nearly uniform in size and develop over 12 months, resulting in a substantial drain on the plant's assimilates. This continuous demand needs to be met with the production of photoassimilates, which is subjected to intra- and inter-annual climatic variations (Jayasekara *et al*., 1996). It is therefore likely that the plant buffers these imbalances with a dynamic pool of reserves.

The objective of this study was to characterize the chemical nature, quantity and localization of such vegetative storage in coconut, as a first step towards a fuller comprehension of how assimilate source and sink relationships are regulated, and how important they are for continuous fruit production in variable conditions.

MATERIALS AND METHODS

Experimental site and plant material

The experiment was conducted on the coconut plantation of the Vanuatu Agricultural Research and Training Centre (VARTC), which covers about 400 ha in Saraoutou, (Espiritu Santo, Vanuatu, Southern Pacific, lat. 15°26.7′S; long. 167°11.5′E). The climate is tropical oceanic and favourable for the growth of coconut palm. Rainfall averages 2745 mm $year^{-1}$ (1989–2000). Rainfall peaks during the hot and rainy season (December–April), with a monthly average of 335 mm. A drier season usually occurs from July to September, with a monthly average rainfall of 117 mm. Average daily global radiation during the dry season (wet season in brackets) is 20.0 MJ m^{-2} day^{-1} (14.5 MJ m^{-2} day^{-1}); mean temperature is 27.6 °C (30.3 °C); mean relative air humidity is 89 % (86 %); the mean maximum vapour pressure deficit is 10.8 hPa (8.1 hPa); and the mean daily potential evapotranspiration (Priestley-Taylor) is about 5.4 mm (3.5 mm). The soil, according to Bonzon *et al*. (1991) and Quantin (1978), is ferralitic, weakly desaturated and of good nutritional quality. The experimental stand was located on a 1–2.5 m deep, volcanic, silty clay soil, covering a limestone plateau at 80 m altitude. Gravimetric soil water content (kg of H_2O/kg of soil) is 35 % at pF 4.2 and 50 % at pF 2.5, with an extractable water content less than 15 % (Bonzon *et al*., 1991).

The experimental plot, which was part of a larger genetic experiment, covered 7.7 ha. Population density was 160 plants ha^{-1}, in an 8.5 m equilateral, triangular planting pattern. Thus, each plant is surrounded by six other plants forming a hexagon. Plants were 17 years old at the beginning of our study. The cultivar studied was a hybrid between the Vanuatu Red Dwarf (VRD, female parent, short-statured, bearing a large number of small-sized fruits) and the improved Vanuatu Tall (VTT, male parent, tall

stature, having a high number of large-sized fruits). Details of the parental germplasm are given in Calvez *et al*. (1985) and Nucé de Lamothe *et al*. (1982).

At the beginning of our study, the population was in a sub-optimal phytosanitary state with attacks of *Graeffea crouani* and *Corticium penicillatum*, controlled from October 2001 onwards by chemical treatment. During sampling in March 2002 and October 2002, the plants were in good health.

Sampling procedure

Trunk, root and leaf samples were taken in the morning on several days during October 2001, March 2002 and October 2002 on 12 non-neighbouring plants (four for each sampling date) selected randomly from a large population of plants with a known individual production history. These 12 plants measured 10.2 ± 0.3 m (*s.e.*) trunk height and had produced 12.7 ± 0.4 (*s.e.*) fertile inflorescences year^{-1} and 153.8 ± 7.5 (*s.e.*) mature nuts year^{-1} during a previous monitoring period of nine years (between 1988 and 1996). No correlation was observed between trunk height and production history. Plants were felled and roots dug up for sampling. On the trunk, radial cores samples were taken at the top (sub-apical area), at mid-height and at the base (200 mm from ground). On each level, one or two cores were taken using a Pressler drill (6.6 mm diameter × 300 mm length). The cores were placed in an ice box until further processing in the laboratory. Each core was divided into four subsamples ('bark', outside, middle and 'heart') at the base and mid-height or three ('bark', outside and 'heart') at the top, from which 0.5–1 g (fresh weight) cubes were cut, representing the three or four radial zones that have a decreasing density of woody, vascular strands from periphery (i.e. 'bark') to centre (i.e. 'heart').

Leaves on one of the five spirals were collected, corresponding to rank 4, 9, 14, 19, 24 and (if present) 29 (leaf 1 being the youngest full expanded leaf out of about 30 leaves present on the plant). They were collected in the morning to avoid periods of transient sugar accumulation that may occur later in the day following sustained photosynthesis. Subsamples of 20–30 g (fresh weight) were taken from the base, middle portion and end of the petiole; from middle and end portions of the rachis; and from leaflets situated at the base, middle portion and end of the rachis.

On the root system, large roots (R1, 10 mm < diameter < 15 mm), medium size roots (R2, 1 mm < diameter < 9 mm) and fine roots (R3, diameter ≤ 1 mm) were distinguished; samples were taken from the white portion in the course of differentiation located close to the meristem (zone 1) and the mature, differentiated zone that includes a suberified rhizodermis and a lignified endodermis (zone 2).

Samples were stored at − 20 °C until freeze-drying using a Cryodos − 50 °C lyophilizer (Telstar, Spain), and then kept in vacuum-sealed bags at − 20 °C until chemical analysis.

Estimate of plant total dry matter by type of organ

Trunk dry matter was calculated from trunk dimensions (thickness and height) and specific mass (dry weight volume^{-1}) at the base, mid-height and top. The dry

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matter content of the petioles, rachis and leaflets was estimated by weighing the entire organs after drying at 104 °C, then multiplying by the total number of such organs present on the plant. Root sampling was performed for one-twelfth of the theoretical, hexagonal soil surface available to a plant, measuring 5.20 m^2. Roots were collected from a 1-m deep excavation, sieved, sorted by type, dried at 104 °C, weighed, and their weight extrapolated to the full hexagon associated with the plant. The result was multiplied by 1.1 in order to take into account deep roots, based on previous observations made on the same plot (C. Jourdan, CIRAD, personal comment).

Estimate of growth rates by type of organ

On four non-neighbouring plants selected randomly from the same plot that served for the carbohydrate reserve study, trunk growth rate was estimated from the height increment during one year, the specific mass and the trunk thickness at the top. The growth rate of leaves was estimated from the number of new leaves that appeared during one year multiplied by their dry mass, and the growth rate of roots from the number of new roots of each type that appeared during one year multiplied by their dry matter. Throughout the year, each mature bunch was harvested and the nuts counted. The dry mass of all nuts harvested was estimated from the dry matter of the husk, shell, copra and milk (for four nuts) by weighing after drying at 104 °C, then multiplying by the total number of nuts in a bunch.

Biochemical analyses

The samples were ground with liquid nitrogen to 100 μm particle size using a knife grinder (Thomas Scientific, U.S.A.) for the larger samples or a ball grinder (Mixer Mill MM 200, Retsch, Germany) for the smaller core samples. Soluble sugars were extracted from 30 mg aliquot samples with 1 ml 80 % EtOH for 30 min at 80 °C, then centrifuged. This procedure was repeated once with 80 % EtOH and once with 50 % EtOH and the supernatants pooled. Soluble sugars were contained in the supernatant and starch in the sediment. The supernatant was filtered in the presence of polyvinyl polypyrrolidone and activated carbon to eliminate pigments and polyphenols. After evaporation of ethanol using a Speedvac (Jouan, RC 1022 & RCT 90), soluble sugars were quantified by high performance ionic chromatography (HPIC, standard Dionex) with pulsated amperometric detection (HPAE-PAD), with sugars being considered to behave as weak acids (Pka > 11).

Starch in the sediment was solubilized with 0.02N soda at 90 °C for 2 h and then hydrolysed with α-amyloglucosidase at pH 4.2 for 1.5 h. Glucose was quantified as described by Boehringer (1984) using hexokinase and glucose-6-phosphate-dehydrogenase, followed by spectrophotometry of NADPH at 340 nm (spectrophotometer UV/VIS Jasco, V-530). The results were expressed either as bulk organ or plant concentrations (mg g^{-1} dry matter) or the total contents for each organ (g) on a single-plant basis.

Table 1. Concentrations (mg g^{-1}) of total sugars in various components of the coconut trunk in October 2001, March and October 2002. *s.e.* = standard error of the mean of four replications.

Total sugar concentration												
	October 2001				March 2002				October 2002			
	'bark'	outside	middle	'heart'	'bark'	outside	middle	'heart'	'bark'	outside	middle	'heart'
base	70.4	91.1	89.5	103.8	99.7	103.3	134.8	167.5	55.6	67.4	90.6	115.8
s.e.	6.3	26.9	9.0	5.6	13.9	7.1	20.8	39.3	7.6	5.1	8.2	10.9
mid-height	76.8	82.9	97.9	122.1	71.6	104.4	168.3	240.4	66.1	95.3	142.7	205.5
s.e.	4.9	10.7	10.9	8.7	13.2	9.8	21.3	28.4	20.6	29.7	48.7	73.9
top	133.5	170.6	–	195.4	88.5	196.1	–	313.0	76.6	194.3	–	339.2
s.e.	11.7	23.3	–	7.0	17.4	36.1	–	66.0	6.7	50.4	–	51.6

RESULTS

Sugar concentrations

The soluble sugars showing the highest concentrations in coconut tissues were glucose, fructose and sucrose. Fructose and glucose will be referred to collectively as monosaccharides. The glucose/fructose concentration ratio was generally between 1 and 1.6 in all organs. Soluble sugars and starch combined are referred to as total sugar (TS). An overview of TS concentrations observed on the three consecutive sampling dates is presented in Table 1. Concentrations were generally lower in October 2001 than in March and October 2002, possibly due to phytosanitary problems prior to the onset of the experiment as detailed in the Materials and Methods section. They were similar on the second and third sampling dates, possibly indicating that plants had attained a physiological equilibrium. We focus on the analyses for the second (March 2002) sampling occasion, with occasional reference to the other dates.

The trunk

Sucrose was the most dominant reserve substance in the trunk, by far, followed by starch and monosaccharides (Figure 1). Sucrose and TS concentrations increased from bottom to top and from the periphery to the centre of the trunk, although the concentration gradient was not steep in either direction (radial or axial), suggesting that all parts of the trunk serve as a storage organ. These results are consistent with the October 2001 and October 2002 observations (Table 1). Total sugar concentrations ranged from 56 mg g^{-1} ('bark' at trunk base) to 339 mg g^{-1} ('heart' at trunk top) on a dry weight basis. Sucrose accounted for 70 % or more of TS concentration in all parts of the trunk except the inner fractions of the tops (Figure 1), where monosaccharides accounted for up to 27 % (October 2001). Starch was nearly absent in the lower parts of the trunk but attained a concentration of 64.5 mg g^{-1} at mid-height (March 2002), although this value varied considerably among plants.

Leaves

Monosaccharide concentrations were higher in leaves (especially in the petiole) than in the trunk and varied little between the rachis (7.9 mg g^{-1}) and leaflets (9.7 mg g^{-1}) (March 2002: Figure 2). In contrast to monosaccharides, sucrose showed a marked

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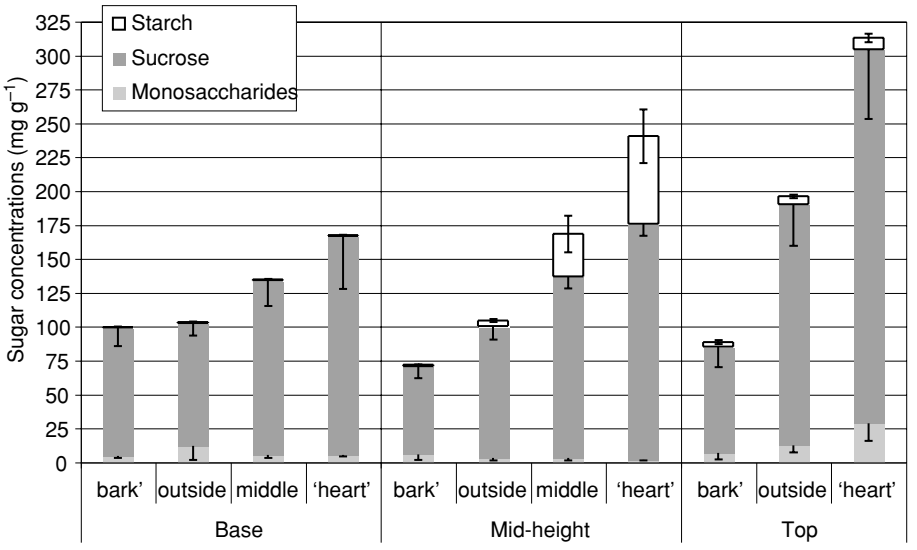

Figure 1. Concentration of sugars in various compartments of the coconut trunk in March 2002. Vertical bars indicate standard error of mean (*s.e.*) of four replications.

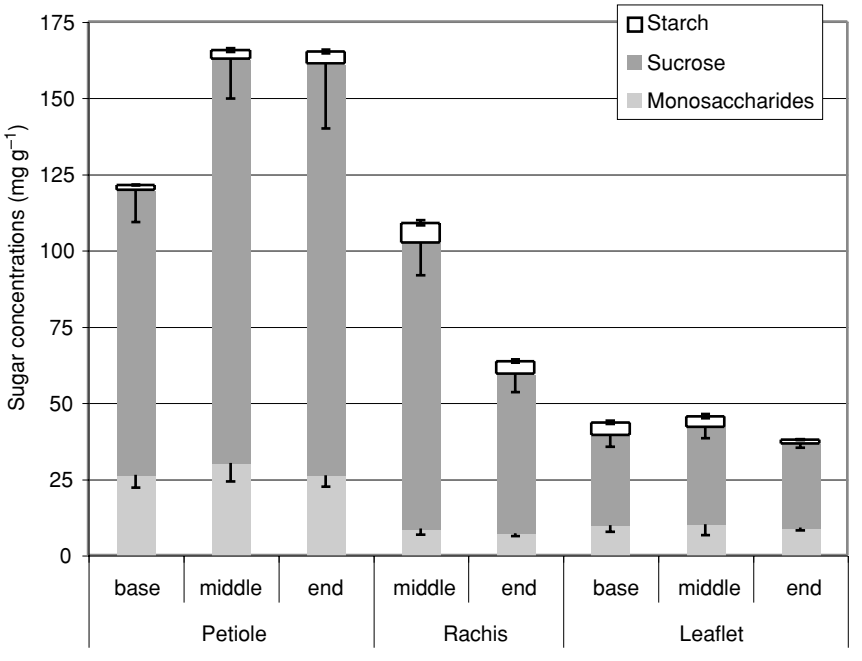

Figure 2. Concentration of sugars in various compartments of coconut leaves in March 2002. Vertical bars indicate standard error of mean (*s.e.*) of four replications.

pattern of distribution, with concentrations low in leaflets (29.7 mg g^{-1}), intermediate in the rachis (73.2 mg g^{-1}) and highest in the petiole (120.4 mg g^{-1}). Starch concentrations were generally low. Sucrose concentration in leaves depended not

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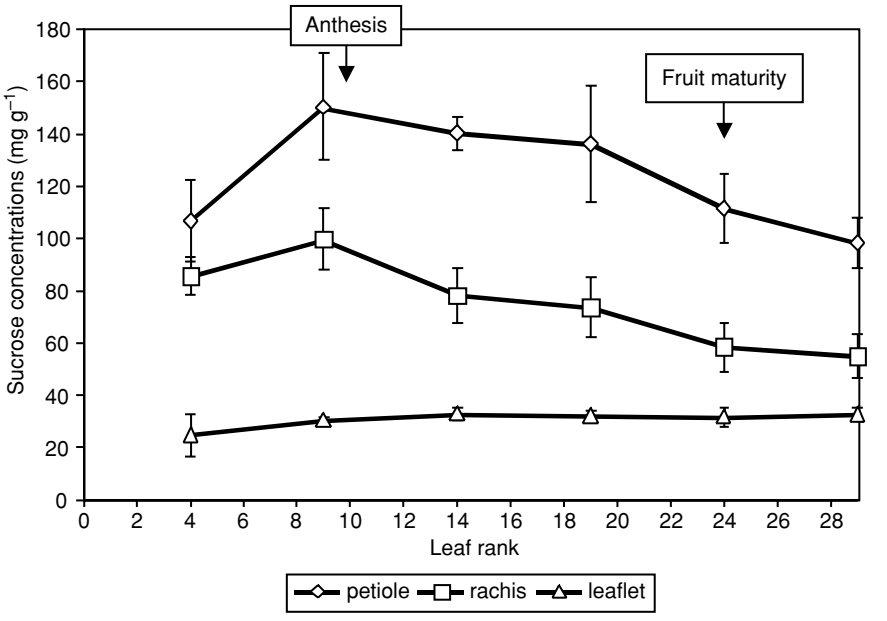

Figure 3. Sucrose concentration in leaf petiole, rachis and leaflets of coconut as a function of leaf position (1: youngest fully expanded) in March 2002. Vertical bars indicate standard error of mean (*s.e.*) of four replications.

only on the organ compartment but also on leaf position, which is related to appearance time and therefore, age (March 2002: Figure 3). Petioles and rachises showed the highest sucrose concentrations just before anthesis of the corresponding axillary inflorescence (rank 9). Thereafter, sucrose reserves in these organs gradually decreased. No such patterns were observed in leaflets, which had nearly constant sucrose concentrations regardless of age.

Roots

Total sugar concentration exhibited a strong gradient from large to fine roots, the latter having very low concentrations (March 2002: Figure 4). These concentrations were almost entirely made up of soluble sugars; starch occurred only in traces. Marked differences in sugar concentrations were observed between zone 1 (near the meristem) and zone 2, with monosaccharides dominating in zone 1 and sucrose in zone 2. Overall, roots had much lower sugar concentrations than the trunk, leaf rachis and petiole and varied markedly among plants. Similar observations were made on the two other sampling dates.

Organ dry matter, growth rate and sugar content at the plant and population scales

Standing dry matter. Mean total plant dry mass including roots and fruits across all sampling dates and replications was 346 kg (Table 2), corresponding to 55 360 kg ha^{-1} for the population. With 134.3 kg, the trunk accounted for 39 % of the total dry matter.

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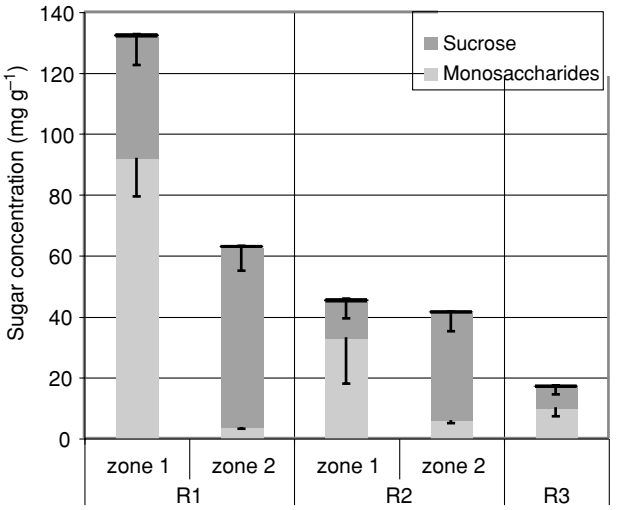

Figure 4. Concentration of sugars in various compartments of coconut roots in March 2002. R1, R2 and R3 represent root diameter classes in decreasing order. Zone 1 is distal (sub-apical) and zone 2 proximal. Vertical bars indicate standard error of mean (*s.e.*) of four replications.

Table 2. Mean standing biomass (kg) of coconut plants by type of organ and by sampling date. *s.e.* = standard error of mean for four replicates.

	Roots	Trunk	Crown	Fruits	Total
October 2001	81.3	124.4	88.7	44.0	338.3
s.e.	11.8	4.2	2.7	5.6	13.7
March 2002	75.7	134.3	94.5	25.0	329.6
s.e.	4.9	10.8	3.0	2.0	11.3
October 2002	100.6	144.2	86.6	38.7	370.1
s.e.	17.4	12.0	4.5	4.0	15.3
Mean	85.9	134.3	89.9	33.1	346.0
s.e.	7.3	5.6	2.1	3.2	8.8

The leaf crown contributed 26 % and the root system 25 % to the total. Fruit and root mass were most variable whereas crown and trunk mass varied little.

Vegetative and reproductive dry matter growth rates. Annual dry matter production rates were estimated for a separate set of plants belonging to the same population and having about the same total biomass as the plants sampled for carbohydrate reserve analyses (Table 3). Total plant growth rate including roots and fruits was 153.2 kg y^{-1}, corresponding to 24.5 t ha^{-1}y^{-1} for the population. The genotype studied has greatly improved yield due to a high number of fruits (12.8 fertile inflorescences and 188.2 nuts palm^{-1} year^{-1} under the experimental conditions, with a copra content of 120.3 g per nut on average). This corresponded to 3.6 t ha^{-1} y^{-1} copra production and a remarkably high harvest index of 66 % (HI, defined here as the ratio of nut dry weight to total dry matter production).

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Table 3. Growth rates (kg y^{-1}) of coconut plants and harvest index (HI, nut production divided by total dry matter production expressed as percentage), *s.e.* = standard error of mean for four replicates.

	Vegetative growth rates			Yield			
	Roots	Trunk	Leaves	Nuts incl. copra	Copra	Total	HI
Plant (kg y^{-1})	23.9	5.7	38.6	85.0	22.6	153.2	
s.e.	–	0.3	1.6	–	–	–	
Population (t ha^{-1} y^{-1})	3.8	0.9	6.2	13.6	3.6	24.5	65.7

Source: C. Jourdan and O. Roupsard, CIRAD, personal comment, for data on roots and trunk.

Table 4. Mean bulk sugar content (g) of coconut plants by type of organ and campaign and by plant. *s.e.* = standard error of mean for four replicates.

	Roots	Trunk	Crown	Total
Monosaccharides (*s.e.*)				
October 2001	910 (131)	1003 (140)	3578 (257)	5491 (361)
March 2002	1230 (224)	586 (203)	1390 (106)	3309 (478)
October 2002	1851 (523)	915 (294)	2309 (448)	5075 (671)
Sucrose (*s.e.*)				
October 2001	1434 (463)	9878 (748)	3147 (211)	14 459 (1033)
March 2002	3873 (613)	15 316 (1190)	6261 (516)	24 757 (942)
October 2002	5445 (893)	13 996 (2889)	3923 (186)	23 364 (2830)
Starch (*s.e.*)				
October 2001	25 (9)	827 (399)	285 (26)	1137 (418)
March 2002	13 (2)	2006 (299)	342 (48)	2374 (274)
October 2002	51 (10)	1220 (482)	281 (29)	1552 (501)
Total (*s.e*)				
October 2001	2369 (600)	11 708 (1119)	7010 (353)	21 087 (1468)
March 2002	5115 (613)	17 908 (1427)	7993 (511)	30 441 (1360)
October 2002	7347 (1407)	16 131 (3542)	6514 (577)	29 991 (3911)

Plant and population sugar content. Sugar reserves in the plant, excluding fruits (the reserves of which are considered here as not being mobilizable for plant growth), were predominantly located in the trunk, constituting between 12 and 18 kg $plant^{-1}$ in the trunk alone, depending on sampling date, or 1.9 to 2.9 t ha^{-1} (Table 4). Total sugars accumulated in vegetative organs were 21 kg $plant^{-1}$ in October 2001, when the plants were still affected by previous phytosanitary problems, and about 30 kg $plant^{-1}$ in March 2002 and October 2002. If these sugars can be considered globally as reserves, and if the relatively stable concentrations through 2002 represent a state of equilibrium, the population had a capacity of storing about 4.8 t ha^{-1} total sugars in vegetative tissues. A sizeable pool of starch was only observed in the trunk (up to 2 kg $plant^{-1}$), but it only constituted 3.9 to 6.6 % of the total sugar reserves, depending on the sampling date. By contrast, monosaccharides, present mainly in the crown, represented between 11 and 26 % of total sugars in the plant. Sucrose was the main reserve compound with 81 and 78 % of total sugars for the two 2002 sampling dates. This fraction was lower (69 %) in October 2001 when overall sugar contents

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were lower due to poor plant health, possibly indicating that sucrose reserves indeed act as a physiological buffer.

DISCUSSION

The Vanuatu hybrid produced less above-ground vegetative dry matter (7.1 t $ha^{-1}y^{-1}$, fractions for trunk and leaves in Table 3) than some other hybrids, for example, Chowgat Orange Dwarf × West Coast Tall (Kasturi Baï *et al*., 1996) at the same age. On the other hand, total dry matter growth rates reported by Corley (1983) for coconut populations grown with good management in favourable environments were nearly identical to the 24.5 t ha^{-1} y^{-1} reported here, although it is not clear if Corley's calculation included roots. It is evident that the population studied here allocated much more dry matter to fruit production than to plant growth, as indicated by the high harvest index, thus explaining the comparatively low standing biomass. In spite of comparatively low copra weight per nut (120.3 g as compared with 152.6 g reported for Indian hybrids by Kasturi Baï *et al*. (1996)), the observed yield was high, comparable with high-yielding hybrids like PB 121 or PB 111 from the Ivory Coast, currently the most widely grown genotypes worldwide (Nucé de Lamothe and Bénard, 1985). The biological material studied here had therefore high potential yields, possibly requiring large reserve pools to satisfy a high and continuous assimilate demand for fruiting while assimilation rates vary.

The largest fraction of sugars by far found in the vegetative organs of coconut were soluble sugars. Their dry weight-based concentration exceeded 300 mg g^{-1} in some parts of the trunk, and high concentrations were found in all plant parts except leaf blades and old roots. For oil palm, a related species, similar soluble sugar concentrations were found in the subapical area of the trunk (285 mg g^{-1}; Henson *et al*., 1999). In the same tissues, starch concentrations were quite low in both oil palm (24 mg g^{-1}) and coconut (between 11 and 40 mg g^{-1}). In contrast to the majority of higher plants (Glerum, 1980; Kozlowski, 1992), coconut thus does not use starch as a major form of carbohydrate storage.

Sucrose, the transport form for carbohydrates in many plants, was the dominant sugar in coconut, present in particularly high concentrations in the trunk. It therefore clearly serves as the principal reserve compound. Other monocotyledonous plants such as sugar cane (Komor, 2000) and oil palm (Henson *et al*., 1999) also store sucrose in vegetative tissues, whereas many Poaceae such as wheat and barley (Housley, 2000) store fructans, and many dicotyledonous tree species store starch. Sugar beet (*Beta vulgaris*), also a dicotyledonous species, however, uses sucrose as the main reserve substance (Getz, 2000). The chemical nature of carbohydrate reserves is therefore not strictly associated with biological groups.

Within the Arecaceae, Van Die (1974) identified three types: (1) species that do not store starch in the trunk or (2) store starch in small quantities (e.g. *Arenga* spp.), and (3) those that store large quantities of starch (e.g. *Corypha* and *Metroxylon* [sago palm]). The monocarpic sago palm tree can accumulate 600 kg ha^{-1} of starch during seven to fifteen years of vegetative growth, which is then mobilized and translocated to fill a single, massive inflorescence (Corley, 1983; Wardlaw, 1990). By contrast, the coconut

plant produces fruits continuously and thus does not require such a large reserve. We conclude that coconut is part of a biologically very heterogeneous group of plants that accumulate reserves mainly as sucrose, and only small quantities of starch, as a transient pool.

The distribution of sucrose in the coconut plant showed a number of topological gradients. Within the trunk, it increased axially from the bottom to the top where the apical meristem is located, and radially from the periphery to the centre where the bast density is greatest (M. Croisetu, CIRAD, personal comment). Despite these gradients, however, concentrations were high throughout, indicating that this organ as a whole has a storage function. Sucrose concentration gradients were also evident in the root system and the crown, with concentrations decreasing towards the distal portions (leaf blades and root tips). At these distal sites, monosaccharide concentrations were higher than in other parts of the plant. Particularly near the root apexes high monosaccharide concentrations were observed, possibly a result of invertase activity providing substrate to sites of high metabolic activity. These sugars therefore may not necessarily serve as storage for the whole plant.

In temperate trees, the temporal pattern and control of carbohydrate storage is complex, serving both as a buffer for intra-seasonal source-sink imbalances and re-growth after defoliation and dormancy (Sauter [1966], cited by Wardlaw [1990]). Only detailed studies on the histological location, as well as on the diurnal and seasonal dynamics, of the sugar reserves in coconut can tell us how transitional these pools are. Hypothetically, glucose and fructose may represent a short term reserve for local use that, as monomers, are protected from enzymatic attack and long distance transport systems (Richter, 1993). In oak trees, fluctuations in monosaccharide concentration were reported to be less regular than for sucrose (Gibbs [1940], cited by Kozlowski and Keller [1966]). In wood of young *Quercus robur* and *Robinia pseudoacacia* trees, in September, most of the soluble sugars were monosaccharides, followed by a two- to three-fold increase by January, associated with a 12-fold increase in disaccharide concentration (Roscina [1962], cited by Kozlowski and Keller [1966]). Seasonal and inter-annual dynamics of sugar reserves are likely to be different in tropical crops having continuous production such as coconut.

If carbohydrate reserves in vegetative tissues serve a buffer function, for example to bridge periods of low assimilation or of high demand for fruit growth, their potential pool size should be large compared to the crop's daily carbon demand for growth and fruit production. In coconut, about 2.83 g of glycosides are required to produce 1 g of copra. This coefficient takes into account the high energy costs of producing lipids as well as translocation and conversion costs (Penning de Vries *et al*., 1989). The TS accumulated in vegetative plant organs in March 2002 (30.4 kg plant^{-1}) would, on this basis, theoretically permit the production of 10.7 kg copra plant^{-1}, or 1721 kg copra ha^{-1}. Assuming an average production of 1.76 kg copra plant^{-1} month^{-1} at the experimental site according to our observations, this value corresponds to about six month's production seasonal fluctuations not being considered.

Another way of evaluating the potential physiological significance of the sugar reserve pool is to estimate the period during which it can theoretically substitute

for photo-assimilation. Daily dry matter production (dM_{dplant}) is calculated from the product of solar radiation (S), canopy light interception (f) and radiation use efficiency (e) and the ratio of total dry mass (Md_{plant}) and above-ground dry mass (M_{dag}):

$$dM_{dplant} = 0.5 \times S \times f \times e \times (M_{dplant}/M_{dag})$$

The calculation of e conventionally disregards root mass because data are rarely available. The coefficient of 0.5 represents the fraction of global radiation constituting photosynthetically active radiation PAR.

Assuming that mean daily S at the site is about 17 MJ m^{-2}, f is 0.74 according to measurements made on the same plantation, e is estimated to be 0.8 g MJ^{-1} on a global radiation basis (corresponding to the upper limit reported for coconut by Jayasekara *et al*., 1996) and the total/above-ground dry weight ratio is 1.33 (derived from Table 2), the total daily dry matter production of a coconut plantation would be 6.7 g m^{-2} d^{-1}, or 67 kg ha^{-2} d^{-1}. On a yearly basis, this results in 24 455 kg dry matter produced ha^{-1}, consistent with the empirical measurements presented in Table 3 and local estimates of 23 000 kg ha^{-1} per year made by an ongoing carbon balance research project using population-based gas exchange measurements in Vanuatu (O. Roupsard, CIRAD, personal comment). A similar estimate was made in Malaysia resulting in 24 000 kg ha^{-1} annual total dry matter production and 2500 kg ha^{-1} copra production (Chew and Ooi [1982], cited by Corley [1983]).

In order to compare plant sugar reserves with daily growth rates, we return to the scale of the individual plant which occupies 62.5 m^2 ground area (160 plants ha^{-1}), and consequently grows at an average rate of $6.7 \times 62.5 = 418.7$ g $plant^{-1}$. The observed reserves (30 440 g $plant^{-1}$ in March 2002) would theoretically sustain growth for 51 days, assuming that growth efficiency is 0.7. (This value is a crude estimate taking into account mobilization, translocation and conversion into various classes of compounds such as lignin and lipids, as well as maintenance respiration using the generic estimates of Penning de Vries *et al*. [1989]. This estimate remains uncertain because of the patchy information available on coconut.) We conclude that the mobilizable sugars accumulated in a healthy coconut plant of the type investigated here is theoretically sufficient to sustain full growth rates for one to two months in the absence of fresh assimilates, or to sustain a copra production for the equivalent of six months. In reality, the reserve pool would probably be able to bridge even longer periods of unfavourable conditions because demand for assimilates would be reduced as well. Consequently, the reserve pools are significant in size and are probably important in sustaining growth and production.

This study is the first of a series investigating the role of carbohydrate reserves in coconut. These results have established sucrose to be the species' main storage compound in non-reproductive organs, its distribution in the plant and its pool size in relation to the crop's approximate rate of growth and production. The next steps will be to characterize the annual and seasonal dynamics of the various reserve pools and to model their probable role as a physiological buffer as source and sink activities fluctuate. The hypothetical buffer role of assimilate reserves will be tested by the experimental

removal of sinks (fruits) and sources (leaves) and by the imposition of water stress by root pruning. This study thus lays the foundation for a larger study aiming at developing a coconut growth model capable of simulating attainable, climate-driven production while taking into account crop phenology, sink–source relationships, and in particular the effect of the carbon reserve status on the capacity of the plant to sustain production during periods of reduced assimilation.

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