COCOS, 2010: ***19:*** *77-91*
Printed in Sri Lanka
RESEARCH ARTICLE

Transitory Carbohydrate Reserves in Vegetative Organs of Coconut Under Different Growth Conditions and Its Relation with Reproductive and Vegetative Growth of The Palm

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ABSTRACT

The study evaluated the non structural carbohydrate reserves in vegetative organs and vegetative and reproductive growth rates of a 25 year old Tall x Tall coconut (*Cocos nucifera L*) during the peak season of coconut yield (May/June) under S_2 and S_4 Land Suitability Classes (LSC) in three Agro Ecological Regions (WL_3, IL_{1a} and DL_3). Trunk (inner and outer), root (new roots and mature roots) and leaf samples (petiole, leaf blade and leaf ekel from 9th, 14th and 22nd fronds) were collected, total soluble sugars (TSS) and starch concentrations were analyzed and TSS and starch reserves at palm level were estimated. Growth rate of trunk and leaves (vegetative) and developing nuts of all bunches of a palm (reproductive) were measured.

The highest (3.86 kg month^{-1}) and the lowest (0.81 kg month^{-1}) reproductive growth rates and the highest (3.8 kg month^{-1}) and the lowest (2.1 kg month^{-1}) vegetative growth rates were found in the palms grown under S_2 and S_4 LSC in the DL_3, respectively. There was a constant vegetative growth rate of 3.3 kg month^{-1} for the palms in WL_3 and IL_{1a} irrespective of the AER or LSC. The most dominant nonstructural reserve substance in the vegetative organs of coconut was soluble sugars (TSS) and the starch concentration was approximately half the TSS concentration in all vegetative parts irrespective of the AER or the LSC. TSS and starch showed a marked pattern of distribution, with highest concentration in trunk (114-134 mg g^{-1} TSS and 60-83 mg g^{-1} starch), intermediate in leaves (69-117 mg g^{-1} TSS and 33-69 mg g^{-1} starch) and lowest in roots (22-79 mg g^{-1} TSS and 17-33 mg g^{-1} starch). The highest TSS and starch reserves in leaf compartments (kg per palm) were found in the S_2-grown palms of the DL_3 which had the highest reproductive and vegetative growth rates during May-June season.

Key words: coconut, reproductive and vegetative growth, starch and soluble sugars

INTRODUCTION

Coconut (Cocos nucifera L.) is an arborescent, monocotyledonous species with indeterminate growth, producing nuts continuously over several decades. Coconut yield mainly depends on the efficiency of dry matter supply into economic produce; a phenomenon applicable to any crop. In higher plants, assimilate for growth is mainly supplied by current photosynthesis and transitory carbon reserve pools in vegetative organs. It is accepted that medium-term transitory reserves (in stems and leaf petioles) are used during periods of increased internal demand or low assimilation rate (under stress conditions), and short-term storage reserves (in leaf blades) function mainly to buffer diurnal and sub-diurnal fluctuations in assimilation rates (Chapin et al. 1990; Kozlowski, 1992; Legros et al. 2009a; 2009b). However, the chemical nature and physiological role of the transitory reserves vary with the variety. Soluble sugars, mainly sucrose was found to be the main storage carbohydrate in vegetative organs of coconut (Mialet Serra et al. 2005; Ranasinghe and Silva, 2007) and sugarcane (Komor, 2000), whilst starch was found to be the main reserve in many dicotyledonous tree species. In oil palm (*Elaeis guineensis*), glucose is an important reserve sugar, followed by starch and sucrose (Legros et al. 2009a; 2009b). The physiological role of transitory non-structural carbohydrate reserves has been studied in annuals (Liu et al. 2004) and perennials (Dickson, 1991; Kozlowski, 1992; Mialet-Serra et al. 2008; Legros et al, 2009a; 2009b). In oil palm, source-sink imbalances were mainly buffered by fluctuations in non-structural carbohydrate reserves in the stem (Legros et al, 2009a; 2009b) whereas in coconut it was partly compensated by transitory reserves in leaf petiole (Mialet-Serra et al. 2008). The variation in the non-structural carbohydrates with tapping (artificial stimulation) was demonstrated in coconut (Ranasinghe and Silva, 2007) and rubber (Silpi et al. 2007).

In Sri Lanka, coconut is cultivated in three agro climatic zones (ACZ), comprising about 30% in the wet zone, 50% in the intermediate zone and 20% in the dry zone. Within these ACZ, coconut is concentrated in seven Agro-ecological Regions (AER), namely, low country intermediate zone (IL_{1a}, IL_3), low country wet zone (WL_2, WL_3, WL_4), low country dry zone (DL_3 and DL_5). The total extent under coconut as at 2008 is 395,000 ha (MPA, 2008). Coconut can tolerate ranges of climate conditions, but performs well under mean annual temperature of 27^0C – 29^0C and rainfall of 1250-2500 mm per year (Liyanage, 1999). The rate of photosynthesis of coconut increases with light intensity up to 1000 -1200 µmol m^{-2} s^{-1} (Jayasekara et al. 1996). There is a variation in rainfall, temperature and solar radiation intensity within a year and this pattern differs with the AER. The annual rainfall of the dry zone in the coconut triangle is between 1000 mm and 1250 mm which can be regarded as the lower limit for coconut. However, solar radiation intensity in this area promotes high productivity when soil moisture and soil depth are not limited. In the wet zone of the coconut triangle, the mean annual rainfall is between 2250 mm to 2500 mm which is quite adequate for coconut. But the solar radiation intensity in wet zone is lower compared to the dry zone. The intermediate zone of the coconut triangle has the best combination of rainfall and solar radiation for the performance of coconut (Liyanage,

1999; Peiris et al. 2007). Within a region of fairly uniform climate, soil is the main cause of differences in the productivity of a particular crop. Coconut performs best in well drained, deep sandy loam soils. Coconut growing lands have been classified in to five main land suitability classes (LSC) ranging from highly suitable (S_1, S_2), suitable (S_3), moderately suitable (S_4) and marginally suitable (S_5). A high percentage of major coconut growing soils belong to S_2 and S_4 LSC. S_2 lands are deep to very deep (> 120 cm), sandy loam, imperfectly drained and highly fertile whilst S_4 lands are moderately deep (30-60 cm), sandy loam with gravel, well drained and less fertile soils. Potential yield in S_2 and S_4 lands are 12,500-15000 and 5000-10,000 nuts/ha/yr (Somasiri et al. 1994).

Coconuts are harvested at two-monthly intervals giving six picks per year. Out of six picks, ranking of the best crop follows the order; pick 3 (May/June)> pick 4 (July/August)> pick 2 (March/April)> pick 5 (September/October)> pick 1 (January/February)> pick 6 (November December). This pattern of crop fluctuation is regular and consistent over the three agro-climatic zones. The information on the non-structural transitory carbohydrates of vegetative organs of coconut in different agro-ecological regions and land suitability classes, during different seasons of the year (under naturally imposed varying source-sink ratios) and its relation with reproductive and vegetative growth of coconut palm is not available todate. Therefore, the objectives of this study were to compare the carbohydrate reserves (medium-term and short-term, concentrations and bulk content at palm level) and vegetative and reproductive growth rates of coconut palms under two land suitability classes (with different potential for growth of coconut) in three Agro Ecological Regions (where there are distinctive differences in climate conditions for coconut), during the peak period for coconut yield (May/June season).

MATERIALS AND METHODS

The experiment was conducted in six sites (part of large coconut plantations which covered more than 25 ha) representing three AER; low country wet (WL_3), low country intermediate (IL_{1a}) and low country dry (DL_3). In each AER, palms from two land suitability Classes (LSC), S_2 and S_4, were selected within a distance of less than 5 km (Table 1). Eight coconut palms were randomly selected from each site. The plantations were of uniform age (25-26 years) and density (160 palms / ha), and receiving uniform agronomic and cultural practices. The coconut variety was Tall X Tall, above a grass understory which was maintained by regular slashing. The sample collection was conducted during May/June, 2009.

Table 1: Location, soil characteristics and agro-climatic conditions of the sites

Location	Soil type and LSC	AER
Urapola (Gampaha District)	Pallama series – S_2	WL_3
	Boralu series – S_4	
Wellawa (Kurunegala District)	Kurunegala series – S_2	IL_{1a}
	Kuliyapitiya series – S_4	
Mangala Eliya & Madurankuliya	Mavillu series – S_2	DL_3
(Puttlam District)	Mampuri series – S_4	

The mean annual rainfall of WL_3, IL_{1a} and DL_3 was around 2224, 1662 1193 mm, respectively. Sri Lanka receives rainfall throughout the year, with a bimodal seasonal distribution. The seasonal peak vary by region with the peak of the main rainfall season occurring in October, November or December and the subsidiary peak occurring in April, May or June. Generally, the coconut growing areas may be prone to droughts during January to March and July to September (Peiris et al. 2007). The average maximum temperature ranges from 32-35 ºC, 29-35ºC and 29-38ºC, in WL_3, IL_{1a} and DL_3, respectively, and the highest values are recorded during February to May. The average minimum temperature ranges from 22-24 ºC, 20-26 ºC and 20-26 ºC in WL_3, IL_{1a} and DL_3, respectively, and the lowest are observed during December to February. The climatic condition of the three AER during the experimental period is given in Fig. 1.

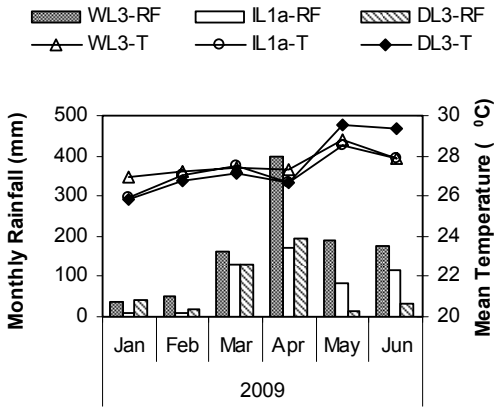

Fig. 1: Mean Temperature (T, ºC) and Monthly Rainfall (RF, mm) of three sites (WL_3), intermediate (IL_{1a}) and dry zones (DL_3) during January to June, 2009.

Characteristics of the selected soils

WL_3 Pallama Series : Imperfectly drained to poorly drained, deep sandy loam, sandy clay loam to clay loam or sandy clay soil with few fine quartz, manganese nodules and plinthied (S_2)

Boralu Series : Well drained, moderately deep, sandy loam , sandy clay loam to clay loam soil mixed with 40-50% ironstone gravel and few quartz gravel in sub soil (S_4)

IL_{1a} Kurunegala series : Imperfectly drained, deep, sandy loam to sandy clay loam soil with few fine quartz, feldspar & occasionally ironstone grand (S_2)

Kuliyapitiya Series :Well drained, moderately deep to deep, sandy loam to sandy clay loam soils with some quartz. Ironstone gravel and few feldspar in the sub soils (S_4)

DL_3 Mavillu series : Imperfectly drained, very deep, sandy loam to sandy clay loam soil (S_2)

Mampuri Series : Excessively drained , deep, coarse sand or sandy soil (S_4)

Estimation of above-ground vegetative and reproductive growth rate of palms: The palms were climbed every month to count the number of nuts in each developing bunch (14-16 bunches / palm) and to measure the length of nuts along the long axis (two nuts / bunch). In each bunch, the dry weight / nut was estimated non-destructively according to Ranasinghe, (2008). The growth (GR) of nuts in a given bunch between time t_1 and t_2 was estimated using the following equation (Navarro et al., 2008). The growth of all nuts on a palm was obtained by summing the growth of all bunches.

$$GR_{bunch} = N_{bunch(t2)}\left(\frac{DM_{nut(t2)} - DM_{nut(t1)}}{t_2 - t_1}\right)$$

DM_{nut} : Dry weight of a nut at time t_1 and t_2

$N_{bunch(t2)}$: Total number of nuts in a bunch at time t_2

Stem density was estimated using the dry weight of stem core samples of a known volume (density = weight/volume). The bulk stem dry weight of a palm was estimated by multiplying the volume of the stem with the density. Vertical growth of stem was monitored by marking a line just below the leaf crown. The increased volume of the stem over the period (considering that there is no detectable increase in stem circumference over time) and density were used to determine the growth rate of the stem (Friend and Corley, 1994). The most mature frond of each palm was collected and the actual dry weights of petiole, mid ribs (ekels) and leaf blades of the frond were taken. Dry weight of total leaf components of a palm was estimated by using the actual dry weight (dry) of leaf components and the crown leaf load (the variation in leaf weight with age is negligible). The number of new leaves emerged per month was nearly one for each palm. Therefore, the dry weight of mature frond (leaf) was used as the leaf growth rate per month.

Sample collection for determining non-structural carbohydrates in vegetative organs: Trunk (stem), root, leaf blade, leaf ekel (mid rib) and leaf petiole samples were collected in the morning on several days during May / June 2009. Trunk samples were taken at mid-height of the palm, at a depth of six cm from the surface, using an electric drill. Outermost bark tissues was removed and the sample was divided into two sub samples; trunk-outer and trunk- inner. Samples of leaf petiole, mid rib of leaflet (ekel) and leaf blade were collected from three fronds; 9^{th},14^{th} and 22^{nd}, representing three levels of the canopy (taking the youngest fully opened leaf as number one and counting downwards). Petiole samples were collected from the distal part of the frond. For leaf blade and mid rib (ekel) sampling, two leaflets were removed from the mid portion of each frond and leaf blade and ekel were separated. Newly formed roots (8-20 cm length) and mature roots were sampled at the manure circle. New root was divided in to two sub samples; root-distal and root-proximal. Collected samples were put in to labeled, clear, transparent polythene bags, immediately stored in ice and taken in to the laboratory for analysis. Then the samples were oven dried for 48 hrs at 60ºC in a fan forced oven and powdered using a high speed micro mill (Model: Retsch-MS, Laboratory supply company, Germany).

Determination of carbohydrate (total soluble sugar and starch) content : A sample of 0.5g was placed in 10ml of 80% ethanol (prepared using analytical reagent, BDH laboratory supplies, UK) for 15 minutes in a water bath at 60 ºC and transferred to a centrifuge tube with subsequent washing with 2ml of 80% ethanol. The solution was then centrifuged (Kubota 5100 table top centrifuge, Kubota corporation, 29-9, Tokyo, Japan) for 10 minutes at 3500 rpm in a centrifuge tube and the supernatants was decanted. The residue was extracted again with another 5ml of 80% ethanol for 10 minutes in a water bath at 60 ºC and the supernatant was collected by centrifugation for 10 minutes at 3500rpm, and the two supernatants were combined. The residue was kept aside for analysis of starch. The supernatants of trunk and root samples were concentrated to a volume of 5ml, in a rotoevaporator (Rotavator RE-111 with Bchi 461 water bath Laboratorium-Technik, Flawil, Swistzerland) for sugar analysis. The consolidated supernatants of leaf components (petiole, mid rib and leaf blade) were mixed with 5.0 ml of chloroform (Analytical reagent, RDH Laboratory supplies, UK) and 10ml of distilled water, shaken well and kept for 10 minutes for separation of the aqueous layer and the organic layer containing chlorophyll. The organic layer was discarded and the aqueous layer containing all the water soluble compounds in leaf and ekel samples was concentrated to a volume of 5ml using rotoevaporator for sugar analysis. The total sugar content was determined by Phenol Sulphuric method (Dubois et al. 1956; Ranasinghe and Silva, 2007).

The residue was suspended in 10 ml of distilled water, boiled for 20 minutes in a water bath and allowed to cool at room temperature. Two ml of 1% α-amylase (1g of α-amylase from Bacillus subtilis ,Fluka chemical, Switzerland, dissolved in 100ml of 0.2M sodium acetate having PH 4.5) was added to the suspension and

allowed to stand over night at 42^0C in a water bath. The suspension was then centrifuged at 3500 rpm for 10 minutes and the supernatant was analyzed for total sugars (Dubois et al. 1956) to determine the starch content (mg/g dry weight).

Estimation of carbohydrate reserves of the total palm : Using the trunk carbohydrate concentration (mean value of inner and outer tissue of trunk) and trunk dry weight, the carbohydrate content of the total trunk was estimated. Using the mean carbohydrate concentration of different leaf components of the 9^{th}, 14^{th} and 22^{nd} fronds, the weight of leaf components of a single frond and total number of fronds in the canopy, the carbohydrate reserves of the total leaf canopy was estimated. Due to practical difficulties the dry weight of total root system of a palm and the carbohydrate reserves in the root system was not estimated.

The data were analysed with two-way ANOVA, using the SAS statistical package. The difference between means was compared using Duncan's multiple range test.

RESULTS

Reproductive (fruit) and vegetative growth rates : Fruit growth rate (dry matter accumulation rate of coconuts) and above-ground vegetative growth rate (leaf and trunk) during the peak period (May/June) were not affected by the LSC or the AER in WL_3 and IL_{1a}. The highest and the lowest reproductive and vegetative growth rates were observed in the palms of S_2 and S_4 soils in the DL_3, respectively and the rates were significantly different to that of WL_3 and IL_{1a} (Table 2).

Carbohydrate concentration in different organs of the palm : Total Soluble Sugar (TSS) concentration in all vegetative parts of coconut

Table 2: Growth rate of reproductive (nuts) and vegetative (trunk and leaf) organs of palms during May/June period, in three AER under two LSC.

AER	LSC	Reproductive Growth Rate (kg month^{-1})	Vegetative Growth Rate (above ground) (kg month^{-1})		
			Trunk	Leaf	Total
WL_3	S_2	2.22 ± 0.25	0.651 ± 0.14	2.65 ± 0.17	3.30
	S_4	1.75 ± 0.25	0.670 ± 0.11	2.60 ± 0.14	3.30
IL_{1a}	S_2	2.27 ± 0.35	0.507 ± 0.07	2.72 ± 0.10	3.23
	S_4	2.56 ±0.28	0.518± 0.05	2.78 ± 0.17	3.30
DL_3	S_2	3.86 ± 0.55	0.715 ± 0.10	3.08 ± 0.19	3.80
	S_4	0.812 ± 0.14	0.212 ±0.03	1.90 ± 0.16	2.11

Values are mean ± SE.

palm was significantly higher compared to starch concentration therein irrespective of the AER, LSC, location of trunk or the age of the leaf. Whilst the concentration of TSS and starch of trunk did not vary with the AER or LSC (Tables 3a and 3b), it varied with the location of the trunk (Fig. 2). Both TSS and starch concentration increased from the periphery to the centre of the trunk. TSS concentration of leaf-petioles was significantly higher in the DL_3 than that of WL_3 and IL_{1a} whilst the starch concentration of the petioles in DL_3 and WL_3 were significantly higher than that of IL_{1a} irrespective of the LSC. A significantly higher TSS concentration of leaf mid rib (ekel) and leaf blade was found in S_4–grown palms in the DL_3 compared to other palms (Tables 3a and 3b).

Moreover, TSS and starch concentration in leaves varied with the position of leaves in the canopy (age). Irrespective of the AER or LSC, a significantly higher TSS concentration was found in 9th leaf compartments (petiole, mid rib and leaf blade) compared to 14th and 22nd, of which the former had a significantly higher concentration of TSS than the latter. The starch concentration of the petioles of 9th and 14th fronds was significantly higher compared to 22nd (data not presented). TSS or starch concentration of new roots did not vary with the AER, LSC or position of the root (proximal or distal end). However, both TSS and starch concentration of mature roots in the WL_3 was significantly higher than that of IL_{1a} and DL_3 whilst they were unaffected by the land suitability class (data not presented).

Table 3a: Total Soluble Sugar (TSS) concentration in trunk and leaf components of coconut palms in three AER under two LSC.

AER and LSC		Trunk (mg/g dw)	Leaf petiole (mg/g dw)	Leaf mid ribs (mg/g dw)	Leaf-blade (mg/g dw)
WL_3	S_2	113.80±8.17	89.53±6.30	86.56±6.35	98.28±5.13
	S_4	129.98±8.75	98.81±6.46	83.94±5.77	89.53±7.60
IL_{1a}	S_2	134.68±6.73	86.57±6.20	69.23±5.15	88.48±4.83
	S_4	131.11±7.05	95.14±4.81	71.00±6.58	82.54±4.57
DL_3	S_2	131.75±5.48	115.14±6.04	92.81±5.28	98.58±4.29
		130.07±3.88	116.66±5.24	116.27±4.34	113.65±4.86

Values are mean ± SE.

Table 3b: Starch concentration in trunk and leaf components of coconut palms in three AER under two LSC.

AER and LSC		Trunk (mg/g dw)	Leaf petiole (mg/g dw)	Leaf mid ribs (mg/g dw)	Leaf-blade (mg/g dw)
WL_3	S_2	72.14±10.43	69.23±5.10	49.6±3.82	43.0±2.87
	S_4	64.53±8.04	60.69±4.48	54.70±3.99	47.29±5.01
IL_{1a}	S_2	59.60±2.90	49.80±2.12	43.97±2.23	44.25±2.37
	S_4	59.97±3.22	49.66±2.13	32.87±2.17	41.44±2.22
DL_3	S_2	82.32±11.21	60.43±3.86	51.95±2.94	59.49±2.28
	S_4	68.12±10.40	63.97±3.82	56.27±3.78	59.80±3.04

Values are mean ± SE.

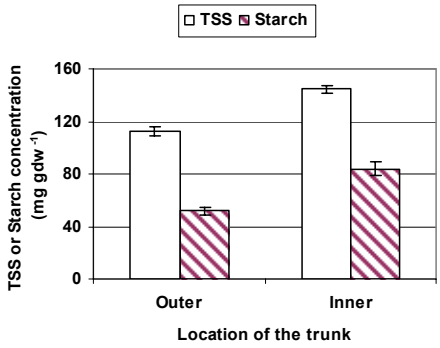

Fig. 2: Total soluble sugar (TSS) and starch concentrations of different location of the trunk. Error bars show the standard error of means.

Standing biomass and carbohydrate reserves of vegetative organs (above-ground) : Weight of the trunk was affected by the LSC in WL_3 and IL_{1a}. It was highest in the palms of S_2 LSC in the WL_3 and lowest in that of S_4 in the WL_3 and DL_3. In contrast, the trunk weight was unaffected by the LSC in the IL_{1a}. Both highest and the lowest weights of leaf compartments (petiole, mid rib and leaf blade) were observed in the palms of S_2 and S_4 LSC in the DL_3, respectively. Consequently, the total weight of above-ground vegetative dry matter in the S_2 of all three AER and S_4 of IL_{1a} were higher than that of S_4 in the WL_3 and DL_3 (Table 4).

Table 4: Mean standing biomass of above-ground vegetative components of coconut palms in three AER under two LSC

AER and LSC		Trunk (kg/palm)	Leaf petiole (kg/palm)	Leaf mid ribs (kg/palm)	Leaf-blade (kg/palm)	Total above ground vegetative organs (kg/palm)
WL_3	S_2	228.76±16.70	44.44±5.40	8.58±0.74	25.75±2.22	307.53±21.33
	S_4	145.89±7.26	39.33±2.42	9.16±3.30	27.51±0.91	221.90±7.91
IL_{1a}	S_2	199.66±14.15	49.49±4.16	12.08±0.62	36.25±1.86	297.48±16.67
	S_4	200.79±17.56	45.81±4.56	11.06±1.03	33.18±3.09	290.83±24.40
DL_3	S_2	175.73±10.97	55.26±5.80	13.77±0.64	41.31±1.92	286.08±14.56
	S_4	150.12±11.69	27.25±2.83	6.57±0.70	19.72±2.09	203.69±15.01

Values are mean ± SE.

Total Soluble Sugar reserves (TSS) : TSS reserves in all vegetative parts of coconut palm were approximately two fold higher than starch reserves therein irrespective of AER or LSC (Tables 5a and 5b). TSS reserves in the trunk of S_2- grown palms of all three AER and S_4- grown palms of IL_{1a} were significantly higher than that of S_4-grown palms in both WL_3 and DL_3. TSS reserves in leaf petioles and mid ribs were not affected by the LSC in WL_3 and IL_{1a}. However, the highest and the lowest TSS reserves of leaf petioles were found in S_2- and S_4–grown palms, respectively, in the DL_3 and the contents were significantly different to that of WL_3 and IL_{1a}. TSS reserves in leaf mid ribs of S_2-grown palms in the DL_3 were significantly higher than other palms whilst that in leaf blades of S_2- grown palms in IL_{1a} and DL_3 were significantly higher compared to other palms. Consequently, the total TSS reserves of above ground vegetative organs of S_2-grown palms were higher than that of S_4-grown palms in both WL_3 and DL_3 whilst it was unaffected by the LSC in IL_{1a} (Table 5a).

Table 5a. : Total soluble sugar reserves in trunk, leaf canopy and total palm (excluding roots) in three AER under two LSC.

AER and LSC		Trunk (kg/palm)	Leaf petiole (kg/palm)	Leaf mid ribs (ekel) (kg/palm)	Leaf-blade (kg/palm)	Total (kg/palm)
WL_3	S_2	26.02±2.27	4.08±0.67	0.73±0.07	2.55±0.32	33.38±2.25
	S_4	18.90±1.13	3.92±0.42	0.77±0.07	2.42±0.21	26.02±1.36
IL_{1a}	S_2	26.47±1.85	4.29±0.61	0.83±0.13	3.17±0.15	34.76±2.23
	S_4	25.80±1.43	4.30±0.38	0.81±0.13	2.79±0.37	33.71±2.11
DL_3	S_2	23.06±1.62	6.43±0.91	1.27±0.09	4.07±0.26	34.83±1.93
	S_4	19.36±1.22	3.03±0.35	0.75±0.07	2.22±0.23	25.35±1.68

Values are mean ± SE.

Starch reserves : Starch reserves in the trunk of S_2-grown palms were significantly higher than that of S_4-grown palms in both WL_3 and DL_3 AER. However, starch reserves of palms in the IL_{1a} was unaffected by the LSC. The highest and the lowest starch reserves of trunk were found in S_2- and S_4–grown palms, respectively, in the WL_3. The starch reserves of leaf compartments (petiole, mid rib and leaf blade) were highest in S_2-grown palms of DL_3 and the difference was significant only for the starch reserves in leaf mid rib and leaf blade. Consequently, the total starch reserves of above ground vegetative organs of S_2-grown palms were higher than that of S_4-grown palms in both WL_3 and DL_3 whilst it was unaffected by the LSC in IL_{1a} (Table 5b).

Since the total root biomass of the palms was not measured, the bulk TSS and starch reserves in the root system under two land suitability classes and three AER were not estimated.

DISCUSSION

Reproductive and vegetative growth rates: A constant vegetative growth rate of 3.3 kg $month^{-1}$ was recorded for the palms in WL_3 and IL_{1a} irrespective of the AER or LSC. A comparatively higher (3.8 kg $month^{-1}$) and a lower (2.1 kg $month^{-1}$) vegetative growth rates were recorded for palms grown under S_2 and S_4 LSC in the DL_3, respectively during the May/ June. In contrast, the fruit growth rate which was always less compared to the respective vegetative growth rates (except for S_2-grown palms in DL_3) was highly depended upon the LSC, specially in the DL_3. The highest (3.86

Table 5b. : Starch reserves in trunk, leaf canopy and total palm (excluding roots) in three AER under two LSC.

AER and LSC	Trunk (kg/palm)	Leaf petiole (kg/palm)	Leaf mid ribs (ekel) (kg/palm)	Leaf-blade (kg/palm)	Total (kg/palm)
WL_3 S_2	16.47±2.48	3.06±0.56	0.42±0.05	1.06±0.09	21.00±2.32
S_4	9.41±0.82	2.31±0.12	0.53±0.06	1.46±0.24	13.71±0.98
IL_{1a} S_2	11.71±0.79	2.41±0.17	0.54±0.05	1.58±0.08	16.24±0.82
S_4	11.89±0.81	2.13±0.20	0.37±0.06	1.40±0.18	15.79±1.05
DL_3 S_2	14.35±1.51	3.36±0.46	0.71±0.04	2.45±0.11	20.87±1.37
S_4	10.38±2.10	1.70±0.21	0.38±0.07	1.18±0.14	13.65±2.38

Values are mean ± SE.

kg month^{-1}) and the lowest (0.81 kg month^{-1}) reproductive growth rates in May/June were recorded in the palms grown under S_2 and S_4 LSC in the DL_3, respectively. Mialet Serra et al, (2008) reported a vegetative growth rate of 3.5 – 4.8 kg palm^{-1} month^{-1} for a coconut plantation under optimal conditions and there was no seasonal or intra annual variation in dry matter growth rates of above-ground vegetative organs.

Variation in carbohydrate content with type of organ : The most dominant nonstructural reserve substance in the vegetative organs of coconut was soluble sugars (TSS) and the starch concentration was approximately half the TSS concentration in all vegetative parts irrespective of AER or LSC. TSS and starch showed a marked pattern of distribution, with highest concentration in the trunk (114-134 mg g^{-1} TSS 60-83 mg g^{-1} starch) and indicating that this organ has a primary storage function, intermediate in the leaves (69-117 mg g^{-1} TSS and 33-69 mg g^{-1} starch) and lowest in the roots (22-79 mg g^{-1} TSS and 17-33 mg g^{-1} starch). TSS concentration in fronds (leaves) depended not only on the organ compartment (petiole, leaf blade or mid rib), but also on leaf position which is related to age. Of the three fronds, the ninth frond which corresponds to the axillary inflorescence just before anthesis (opening) showed the highest TSS concentration in all leaf compartments. However, the starch concentration in leaf compartments did not vary with the position of the leaf in the canopy except in leaf petiole. These results confirm previous investigations of Mialet-Serra et al. (2005) who reported that sucrose is the dominant sugar in vegetative parts of coconut. Their study showed that under near-

optimal environmental conditions, high yielding hybrid, Vanuatu Red Dwarf (VRD) x Vanuatu Tall (VT) palms, contained little starch but had large quantities of sucrose, mainly located in the trunk. In addition to sucrose, they found large glucose and fructose pools in the leaves near the apex of the trunk, and the terminal portion of large roots. As in the present study, starch content in the trunk was quite low in VRD x VT hybrid coconut. TSS of leaf and trunk tissues was approximately twice their starch content in both nut producing and sap producing Tall x Tall coconut palms (Ranasinghe and Silva, 2007). The distribution of TSS in different organs of coconut palm showed a number of topological gradients. Within the trunk, it increased from the periphery to the centre and this may be attributed to the distribution of vascular bundles in the trunk (Menon and Pandalai, 1958). Mialet-Serra et al. (2005) also showed that soluble sugar concentration in the trunk increased axially from the bottom to the top where the apical meristem is located, and radially from the periphery to the centre.

Variation in medium-term carbohydrate reserves in stem and petiole : Similar to the trend in vegetative and reproductive growth rates, the highest and the lowest medium-term carbohydrate reserves (TSS and starch) of leaf petiole were found in S_2-grown palms and S_4-grown palms of DL_3, respectively. However, the patterns were not consistent in the trunk as in the petioles. The highest TSS and starch reserves of the trunk was found in the palms of IL_{1a} and S_2-grown palms of WL_3, respectively. The lowest carbohydrate reserves (TSS and starch) of the trunk were found in the S_4- grown palms of WL_3.

Variation in short-term carbohydrate reserves in leaf blade and ekel : Similar to the medium-term carbohydrate reserves in leaf petioles, the highest amount short-term carbohydrate reserves (TSS and starch) in leaf blade and mid rib (ekel) was also found in the S_2-grown palms of DL_3. Therefore, it is likely that palms in DL_3 produce and store high amount of carbohydrates in leaves when the soil conditions are favourable (S_2). Coconut performs poorly on non-friable soils in the dry zone such as Mampuri series (S_4) even during the favourable seasons for coconut (May/ June).

CONCLUSION

The fruit production in coconut is more plastic than vegetative organs and able to adjust to available resources by the reduction in number or size of nuts. This study provided new information on the nature of transitory carbohydrate reserve pool identifying its relation with reproductive and vegetative growth in coconut under different growth conditions. The reproductive and vegetative growth rates of palms have a very close relationship with carbohydrate reserves in leaf compartments. The data collection for the present study was undertaken in May / June season which is the peak period for coconut. As future studies, vegetative and reproductive growth rates and carbohydrate reserves during periods of low yield such as November/December (a period of low light intensity and high rainfall) and during March/April (a period with low rainfall and hight ligh intensity) will be assessed. A more comprehensive study on intra- and inter-annual dynamics of photosynthetic assimilation,

respiration, fruit set, fruit growth, final yield and fruit components of the same palms are carried out as a parallel study in the same laboratory. Finally, all these information will be used to understand yield fluctuation pattern, the role of carbohydrate reserves in vegetative organs on yield fluctuation and to develop process-based crop growth model for coconut.

ACKNOWLEDGEMENTS

Authors extend their sincere thanks to the Coconut Research Institute of Sri Lanka for financial Assistance, the staff of the Plant Physiology Division, Coconut Research Institute for their support in data collection and Dr A Nainanayake for his assistance in data analysis.

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