Journal of Oil Palm Research Vol. 11 No, 2, December 1999, p. 98-113

THE OIL PALM TRUNK AS A CARBOHYDRATE RESERVE

Keywords: Oil palm, trunk carbohydrates, assimilate reserves, bunch yields.

HENSON, I E*; CHANG, K C
SITI NOR AISHAH, M**; CHAI, S H**;
HASNUDDIN MHD, Y** and ZAKARIA, A****

Samples of oil palm trunk tissues were analysed for their contents of soluble sugars (SS), starch and acid-hydrolysable polysaccharides (PS). Starch was found in high concentrations only in samples taken near to the trunk apex of young palms, while SS and PS were present in appreciable amounts throughout the trunk.

The total amounts of carbohydrates present in the trunk of an eight-year-old palm were calculated as being sufficient to sustain the production of up to 38 kg of FFB.

Chromatographic and enzymatic analysis of the carbohydrates showed that sucrose was the main form of SS, followed in descending order by glucose and fructose. Acid hydrolysis of the polysaccharide fraction released mainly glucose together with appreciable proportions of a material with the chromatographic properties of xylose, together with some fructose.

Three trials were conducted to monitor variation in trunk carbohydrates in relation to bunch load, genotype and time of year. In the first trial, trunk carbohydrate levels were compared in selected low and high yielding tenera *palms, High yielding palms had higher SS levels, lower PS levels and a higher proportion* of *carbohydrate in the form of SS (%S) than low yielding ones. In the second trial, trunk carbohydrates were measured in 20 mature commercial* teneras *over a period of more than two years. Mean PS levels were again negatively correlated with bunch yield while %S was positively correlated*

* Present address: 21 Hurrell Road, Cambridge CB4 3RQ, UK.
** Palm Oil Research Institute of Malaysia, P.O. Box 10620, 50720 Kuala Lumpur. Malaysia.

with yield. The third trial made use of infertile pisiferas, *fertile* pisiferas *and* tenera *sibling progenies from a breeding population.* Tenera *palms had lower PS levels and more of the trunk carbohydrates present in the form of SS than did* pisiferas. *Infertile* pisiferas *had higher PS levels* and *a lower proportion of SS than did fertile* pisiferas.

The results are discussed in relation to the possible role of trunh carbohydrates as a source of assimilates during periods of peak bunch production.

INTRODUCTION

The considerable variation which occurs in bunch yields both during the year and between years has favoured the idea that oil palms contain a reserve supply of assimilates which can be drawn upon during periods of high sink demand, and be replenished when current assimilation exceeds the demands of bunch production and vegetative growth. Indeed, reductions in yields under conditions of apparently minimal environmental limitations are often explained as due to the 'exhaustion' of palm reserves as a consequence of a preceding period of high productivity (*e.g.* Foster et *al.*, 1985). The ability of palms to continue yielding after their photosynthetic capacity has been drastically reduced by severe frond pruning (Corley, 1976) further points to exploitation of reserve assimilates.

The trunk has generally been regarded as the most likely site of reserve assimilates in the oil palm. Firstly, in mature palms, it forms the largest single component of the 'permanent' palm biomass (e.g. *Table 1*). Secondly, the oil palm trunk, in contrast to the trunks of dicotyledonous trees, does not exhibit secondary thickening and contains a high proportion of parenchymatous ground tissue (Lim and Khoo, 1986; Killman and Lim, 1987). Early measurements (Gray, 1969) showed that the trunk contained high proportions of water soluble and acid-hydrolysable carbohydrates which might be sufficient, were they to be made available, to sustain the production of bunches for a significant period (Corley, 1976).

Starch was initially envisaged to be the most likely form of trunk reserve. While it has been reported that the trunk might contain as much as 24% starch (Killman and Lim, 1987, quoting Simatupang), other studies have shown levels which are lower (PORIM, 1983). Eater analysis (Abdul Rashih Ahmad, 1988) confirmed this, and showed that other forms of carbohydrate might be quantitatively more important.

In the present study, we aimed to reinvestigate the carbohydrate content of the oil palm trunk, by examining both the nature of the "reserve' carbohydrates and by monitoring variations in concentrations in relation to bunch production and environmental conditions. Variation in carbohydrate content was examined in relation to seasonal differences, differences between palm fruiting types and differences

TABLE 1. RELATIVE AMOUNTS OF DRY MATTER PRESENT IN TRUNK, PETIOLES AND PRIMARY ROOT STANDING BIOMASS OF TEN-YEAR-OLD PALMS PLANTED AT TWO SITES

Component	Dry biomass			
	t ha^{-1}		Relative amounts	
	Site A	Site B	Site A	Site B
Trunk	24.24	20.20	100	100
Petioles	10.48	8.01	43	40
Primary roots	4.87	7.66	20	38

Note: sites A and B correspond respectively to sites 4 and 5 described by Henson and Chai (1997).

between individual palms varying in bunch yield.

MATERIALS AND METHODS

Sampling of Trunk Tissue

In initial studies which involved determination of carbohydrate contents close to the trunk apex, palms were destructively sampled by felling at the trunk base and sequentially removing the fronds and adhering petiole bases to expose the trunk and its apex. Samples were then taken at defined positions in relation both to distance below the apex and position across the trunk radius.

In the alternative approach, small plugs of tissue were extracted from the trunks of standing palms These were taken with the aid of a drill bit which removed a 12 mm diameter portion of tissue to a depth of approximately 200 mm, roughly equivalent to the trunk radius. Old frond bases were removed when necessary prior to drilling. Samples were placed in plastic bags which were sealed and packed in ice prior to transport to the laboratory, where they were stored at -80°C prior to analysis

In addition to the exploratory studies, two major 'surveys' of trunk reserves were carried out:

1. Beginning in August in the seventh year after planting, a group of 20 randomly chosen commercial *tenera* palms growing on an inland soil in Selangor were sampled monthly for trunk carbohydrates. From the beginning of the eighth year, they were also individually yield recorded. Soil moisture at the site was monitored using tensiometers and gypsum blocks and daily rainfall was recorded at a site nearby. Sunshine hours (from which solar radiation could be calculated) were recorded daily at a station about 10 km distant.

2. This investigation used *pisifera* and *tenera* sibling progenies from a breeding population. Two groups of 10 *pisifera* palms, one group infertile and one fertile, were compared with a group of 10 randomly selected (fertile) *teneras*. The palms were planted on an inland soil in Johore. Sampling commenced in the tenth year after planting.

In both the above studies, samples were taken midway between ground level and the base of frond 34 and, in some cases, additional samples were taken just below the base of frond 34. Comparison of *tenera* palms, which had trunk samples removed monthly over more than 20 months, with an equal number of undisturbed neighbouring palms showed there to be no effect of the repeated trunk sampling on FFB yields.

Quantitative Analysis of Carbohydrates

All samples were divided into two approximately equal portions which served as replicates of the analytical procedure. From each replicate, further subsamples were taken, one to determine dry matter content and one for carbohydrate analysis. The first was weighed, then oven dried for 24 hr at 80°C prior to measuring dry weight.

Samples for carbohydrate analysis were first extracted in 70% ethanol using 10 ml to 1 g fresh weight. The samples were homogenized and incubated at 80°C for 20 min. The extracts were filtered and any evaporative losses made up with further solvent. Two aliquots of each extract were then diluted 20-fold with distilled water and a four-fold volume offreshly prepared anthrone reagent was then added (Yem and Willis, 1954). After incubation in a boiling water bath for 10 min followed by cooling, the ethanol soluble sugars were quantified by measuring absorbance against a sample blank at 625 nm. Glucose was used as a standard and the results expressed as glucose equivalents.

The efficiency of the procedure for quantifying soluble sugars was checked by adding known amounts of glucose in aqueous solution to tissue samples immediately after their removal from the palm. These treated samples were handled and processed in parallel with untreated ones and recovery of the added glucose was calculated by difference. Eight or nine pairs of samples taken each month over a 13-

month period gave an average recovery of 97.0% with a 5.6% coefficient of variation.

Tissue acid-hydrolysable polysaccharide content was determined in the solid residue remaining after ethanol extraction. The residue was resuspended in distilled water (10 ml g-1 initial fresh weight) to which 0.1 ml ml^{-1} of concentrated HCl was added. The mixed extract was incubated for two hours at 80°C, then cooled, and a one millilitre aliquot taken and neutralized using saturated NaOH. Samples of the neutralized solution were then treated with anthrone reagent and the sugars released by acid hydrolysis quantified as described above.

Starch was determined on separate subsamples using the method described by Hirowaka *et* al. (1982). Soluble sugars were first removed by ethanol extraction and, after removal of residual ethanol by mild heating, the samples were homogenized in 0.5 M formic acid (6 ml g^{-1} initial fresh weight) to which was added a further two millilitres of 25% perchloric acid. After incubation for 50 min at 45°C, the sample was filtered and aliquots treated with a solution of iodine in potassium iodide and absorbance measured at 550 nm. Samples of soluble potato starch were used as a standard.

Qualitative Analysis of Carbohydrates

The probable identity of the ethanol-soluble sugars and those released from trunk samples by acid hydrolysis was checked using a combination of standard chromatographic and enzymatic methods. Samples were separated by paper and thin-layer chromatography (PC and TLC) using several solvent systems and by gas-liquid chromatography (GLC), and their retention properties compared with those of known monosaccharide and disaccharide standard samples.

Paper and silica gel TLC was carried out using a range of solvent systems as recommended by Harborne (1984). Sugar spots were visualized using anthrone reagent or analine hydrogen phthalate. Standard compounds were run either side ofextracts on each chromatogram.

Samples for gas chromatography were initially extracted in ethanol as described above. The ethanol-soluble fraction was partitioned against petroleum ether to remove lipids, the aqueous phase evaporated and the residual sugars converted to their trimethylsilyl ethers prior to GLC. The acid hydrolysed fraction, after neutralization with NaOH, was treated similarly. Derivatisation was performed using a pyridine/HMDS/TMCS mixture incubated for one hour at 60°C.

GLC was carried out using a dual column Perkin-Elmer Sigma 300 gas chromatograph equipped with a dual flame ionization detector. Separation was achieved on a capillary column, 1.0 m x 0.53 mm, of bonded FSOT RSL-150 1.2 pm polydimethylsiloxane with nitrogen as the carrier gas. The initial column temperature of 140°C was increased to 200°C at 3°C min^{-1} then to 250°C at 10°C min^{-1}. The flow rate:split injector ratio was 1:60. Retention times and areas of peaks were automatically determined using an attached computer.

The following sugars were used as chromatographic standards: arabinose, fructose, galactose, glucose, maltose, mannose, rhamnose, ribose, sorbitol, sucrose and xylose. Standards were run both singly and as mixtures. GLC separated the alpha and beta isomers generated in samples of glucose, maltose, mannose and xylose. All standards were adequately resolved by GLC with the exception of the pairs sucrose and alpha-maltose and fructose and galactose. The latter pair could be separated by paper chromatography while 'the identity of sucrose was confirmed by the release of glucose and fructose following treatment with invertase.

The presence of glucose in the samples was verified by treating paper and thin Bayer chromatograms with glucose oxidase (Raabo and Terkildsen, 1960; Sigma Diagnostics, 1987).

RESULTS

Distribution of Carbohydrates within the Trunk

Concentrations of carbohydrate were first examined in samples from the apical region of the trunk (top 90 mm) taken from palms of three different ages. Samples taken from various locations across and within the apex were analysed separately. Mean data are presented in *Table* 2. Soluble sugars were the main form

month period gave an average recovery of 97.0% with a 5.6% coefficient of variation.

Tissue acid-hydrolysable polysaccharide content was determined in the solid residue remaining after ethanol extraction. The residue was resuspended in distilled water (10 ml g^{-1} initial fresh weight) to which 0.1 ml ml^{-1} of concentrated HCl was added. The mixed extract was incubated for two hours at 80°C, then cooled, and a one millilitre aliquot taken and neutralized using saturated NaOH. Samples of the neutralized solution were then treated with anthrone reagent and the sugars released by acid hydrolysis quantified as described above.

Starch was determined on separate subsamples using the method described by Hirowaka et al. (1982). Soluble sugars were first removed by ethanol extraction and, after removal of residual ethanol by mild heating, the samples were homogenized in 0.5 M formic acid (6 ml g^{-1} initial fresh weight) to which was added a further two millilitres of 25% perchloric acid. After incubation for 50 min at 45°C, the sample was filtered and aliquots treated with a solution of iodine in potassium iodide and absorbance measured at 550 nm. Samples of soluble potato starch were used as a standard.

Qualitative Analysis of Carbohydrates

The probable identity of the ethanol-soluble sugars and those released from trunk samples by acid hydrolysis was checked using a combination of standard chromatographic and enzymatic methods. Samples were separated by paper and thin-layer chromatography (PC and TLC) using several solvent systems and by gas-liquid chromatography (GLC), and their retention properties compared with those of known monosaccharide and disaccharide standard samples.

Paper and silica gel TLC was carried out using a range of solvent systems as recommended by Harborne (1984). Sugar spots were visualized using anthrone reagent or analine hydrogen phthalate. Standard compounds were run either side of extracts on each chromatogram.

Samples for gas chromatography were initially extracted in ethanol as described above. The ethanol-soluble fraction was partitioned against petroleum ether to remove lipids, the aqueous phase evaporated and the residual sugars converted to their trimethylsilyl ethers prior to GLC. The acid hydrolysed fraction, after neutralization with NaOH, was treated similarly. Derivatisation was performed using a pyridine/HMDS/TMCS mixture incubated for one hour at 60°C.

GLC was carried out using a dual column Perkin-Elmer Sigma 300 gas chromatograph equipped with a dual flame ionization detector. Separation was achieved on a capillary column, 1.0 m x 0.53 mm, of bonded FSOT RSL-150 1.2 µm polydimethylsiloxane with nitrogen as the carrier gas. The initial column temperature of 140°C was increased to 200°C at 3°C min^{-1} then to 250°C at 10°C min^{-1}. The flow rate:split injector ratio was 1:60. Retention times and areas of peaks were automatically determined using an attached computer.

The following sugars were used as chromatographic standards: arabinose, fructose, galactose, glucose, maltose, mannose, rhamnose, ribose, sorbitol, sucrose and xylose. Standards were run both singly and as mixtures. GLC separated the alpha and beta isomers generated in samples of glucose, maltose, mannose and xylose. All standards were adequately resolved by GLC with the exception of the pairs sucrose and alpha-maltose and fructose and galactose. The latter pair could be separated by paper chromatography while the identity of sucrose was confirmed by the release of glucose and fructose following treatment with invertase.

The presence of glucose in the samples was verified by treating paper and thin Bayer chromatograms with glucose oxidase (Raabo and Terkildsen, 1960; Sigma Diagnostics, 1987).

RESULTS

Distribution of Carbohydrates within the Trunk

Concentrations of carbohydrate were first examined in samples from the apical region of the trunk (top 90 mm) taken from palms of three different ages. Samples taken from various locations across and within the apex were analysed separately. Mean data are presented in *Table* 2. Soluble sugars were the main form

TABLE 2. CONCENTRATIONS OF ETHANOL-SOLUBLE SUGARS, STARCH AND OTHER ACID-HYDROLYSABLE POLYSACCHARIDES (OP) IN TRUNK APICAL TISSUES OF VEGETATIVE PALMS AND FRUITING PALMS OF THREE AGES

Palm age (years in field)	sugars	Starch	OP	% Free sugars
	(mg g^{-1} dry weight)			
Vegetative				
2	216 (15)	124 (28)	58 (10)	54.3
Fruiting				
2	234 (9)	73 (13)	60 (11)	63.8
4	275 (11)	43 (4)	29 (4)	79.3
8	285 (5)	24 (3)	39 (5)	81.9

Notes: data are means of four to 16 samples; numbers in brackets are standard errors of the mean. Sugars and OP are glucose equivalents; % sugars = free (ethanol-soluble) sugars as a percentage by weight of total carbohydrates (sugars + starch + OP).

of carbohydrate. Levels of starch were substantial only in the youngest palms sampled, were higher in vegetative than in fruiting palms, and decreased with age. Detailed analysis of the apical region of the four-year-old palm showed starch levels to be highest (77 mg g-1 dry weight) at the apical meristem itself, declining to about half this level 80 mm below the meristem. Levels of other acid-hydrolysable polysaccharides in apical tissues were generally lower or similar to those of starch (*Table* 2).

Samples taken at various heights up the trunk of the palm about eight years old showed (*Table* 3) that 'free' sugars were the predominant form of extractable carbohydrate throughout the trunk and that levels increased with height, being highest at the apex. The Power levels of starch and other polysaccharides showed no marked gradients but their combined levels were highest about half way up the trunk. A radial analysis of the same samples, but excluding apical ones (*Table 4*), showed that highest sugar concentrations were present in the centre of the trunk, while starch and other polysaccharide levels were highest in the outer cortex. Averaged over all positions, free sugars comprised 71%, starch 15% and other polysaccharides, 14% of total extractable carbohydrates.

TABLE 3. CHANGES WITH HEIGHT UP THE TRUNK IN THE CONCENTRATION OF ETHANOL-SOLUBLE SUGARS, STARCH AND OTHER ACID-HYDROLYSABLE POLYSACCHARIDES (OP)

Height above ground (m)	Sugars	Starch	OP	% Free sugars
	(mg g^{-1} dry weight)			
1.06	**137**	19	50	66.5
1.46	141	24	34	70.9
1.86	178	67	53	59.7
2.26	200	77	34	64.3
2.66	235	40	39	74.8
3.08	249	41	41	75.2
4.60	285	24	39	81.9

Notes: data are means of five samples per height taken across the trunk radius except for the 4.6 m (apex) data which are means of four. Sugars and OP are glucose equivalents; % sugars = free (ethanol-soluble) sugars as a percentage by weight of total carbohydrates (sugars + starch + OP).

TABLE 4. CHANGES ACROSS THE TRUNK IN THE CONCENTRATION OF ETHANOL-SOLUBLE SUGARS, STARCH AND OTHER ACID-HYDROLYSABLE POLYSACCHARIDES (OP)

Distance from trunk centre as fraction of trunk radius	Sugars	Starch	OP	% Free sugars
	(mg g-1 dry weight9			
0.1	**233**	**35**	**35**	**76.9**
0.3	**229**	**30**	40	76.6
0.5	216	39	39	73.5
0.7	161	39	37	67.9
0.9	112	80	55	45.3

Notes: data are means of six samples taken from 1.06 to 3.08 m height up the trunk. Sugars and OP are glucose equivalents; % sugars = free (ethanol-soluble) sugars as a percentage by weight of total carbohydrates (sugars + starch + OP).

It is likely that carbohydrate levels in all parts of the trunk will vary with age and condition of the palm. Samples taken near to the trunk base of a 13-year-old palm (*Table* 5) contained lower concentrations of free sugars and starch than the eight-year-old palm, but levels of other polysaccharides were similar. In nine-year-old palms from a different site, concentration gradients of free sugars the reverse of the above were observed *(Figure la),* while no marked gradients in polysaccharide concentrations occurred *(Figure lb).*

The total extractable carbohydrate present in the entire trunk of the eight-year-old palm amounted to almost 37 kg *(Table 6),* equivalent to the production of about 20 kg bunch dry matter or 38 kg FFB. This is of a similar order to the 47.9 kg total carbohydrate found in an 8.5-year-old palm in the early study of Gray (1969) as summarized by Corley (1976). In contrast, an average sago palm trunk of the same fresh weight is expected to contain as starch, about 93 kg of carbohydrate (Flach and Schuiling, 1989).

Nature of the Carbohydrates

Initial PC and TLC analysis indicated that sucrose was the major form of ethanol-soluble sugar in the trunk. This conclusion was supported by results of TLC before and after acid hydrolysis and by GLC which showed three major peaks from the ethanol-soluble fraction with retention times corresponding to sucrose, glucose and fructose (*Table 7*).

The higher level of glucose compared with fructose indicated that at least some of the former was probably present naturally in the trunk as a free sugar and had not simply arisen due to sucrose hydrolysis following sampling.

TABLE 5. THE CONCENTRATION OF ETHANOL-SOLUBLE SUGARS, STARCH AND OTHER ACID-HYDROLYSABLE POLYSACCHARIDES (OP) IN CORE SAMPLES TAKEN AT ONE METRE ABOVE-GROUND FROM THE TRUNK OF A 13-YEAR-OLD OIL PALM

Sample number	Sugars	Starch	OP	% Free sugars
	(mg g-1 dry weight9			
1	94.3	4.2	66.5	57.2
2	**95.3**	7.9	54.0	60.7
3	91.6	10.4	46.6	61.5

Notes: data are means of one to four subsamples. Sugars and OP are glucose equivalents; % sugars = free (ethanol-soluble) sugars as a percentage by weight of total carbohydrates (sugars + starch + OP).

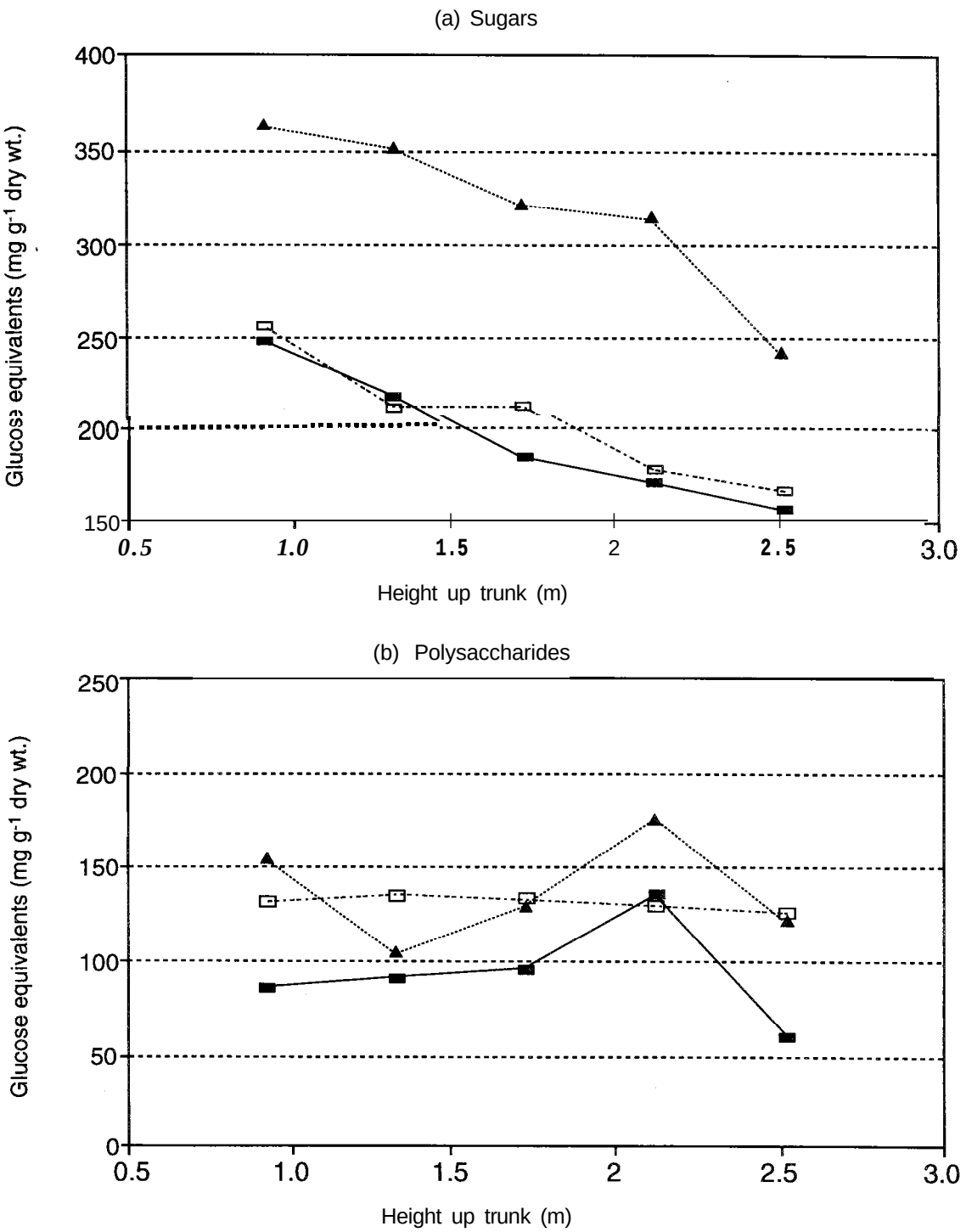

Figure 1. Changes with height up the trunk in concentrations of (a) ethanol-soluble sugars, and (b) total acid-hydrolysable polysaccharides as sampled on three separate occasions during the seventh year after planting.

TABLE 6. TOTAL AMOUNTS OF CARBOHYDRATES IN THE TRUNK OF AN EIGHT-YEAR-OLD OIL PALM

	Dry weight (kg)	% of total carbohydrates
Total dry matter	132.1	-
Free sugars	25.1	68.6
Starch	6.0	16.3
Other polysaccharides	5.6	15.1
Total carbohydrates	36.6	100.0
BDM equivalent of		
i) free sugars	13.8	
ii) starch	3.3	
iii) OP	3.0	
iv) total	20.1	

Notes: sugars and OP are glucose equivalents, the BDM (bunch dry matter) equivalent was calculated assuming 1.818 g glucose was required per g BDM (Corley, 1976). The calculation ignores weight changes during hydrolysis of di- or polysaccharides. At 53% dry matter, the FFB equivalent weight = 37.9 kg.

TABLE 7. GLC ANALYSIS OF SUGARS PRESENT IN ETHANOL-SOLUBLE AND ACID-HYDRBLYSED FRACTIONS OF OIL PALM TRUNK SAMPLES

	Ethanol-soluble fraction	Acid hydrolysed fraction
a) pm g^{-1} Fresh weight		
Sucrose	43.54	nd
Glucose	34.94	9.78
Fructose	1.28	0.94
Xylose	nd	4.11
b) % Mass		
Sucrose	69.60	nd
Glucose	29.40	69.10
Fructose	1.10	6.70
Xylose	nd	24.20

Note: nd = not detected.

After invertase treatment, the fructose:glucose molar ratio of samples separated by GLC increased from 0.04 to 0.2 while the sucrose:fructose molar ratio decreased from 34 to 4.6.

TLC and GLC of the acid-hydrolysed fraction indicated the major sugar to be glucose. This was confirmed by glucose oxidase treatment of samples separated by PC and TLC. In addition to glucose, the presence of small amounts of fructose and of xylose was suggested following GLC. The presence of xylose was suggested both by retention times and by the alpha/beta peak area ratios in comparison with standard xylose. The xylose:glucose mass ratio averaged 0.35 and was quite constant in different samples.

Quantitative Analysis: Experiment 1

In this experiment, the five highest and the five lowest yielding palms from a population of 100 commercial *tenera* palms, individually yield recorded, were compared for their mean trunk carbohydrate contents on two separate occasions during the ninth year after planting. (Starch was not determined separately and any starch present would be included in the polysaccharide fraction).

The high and low yielding palms initially differed more than six-fold in FFB production, largely due to differences in bunch numbers (*Table* 8). While sampling revealed no significant differences between the two groups in leaflet sugar concentration (results not presented), trunk sugar concentrations were higher in the high than in the low yielding group. Polysaccharide levels showed the reverse trend and, while differences in polysaccharide concentrations on a dry weight basis did not reach statistical significance, they did so on a fresh weight basis ($P<0.02$). The net result of these differences was that the percentage of total carbohydrates present as 'free' sugars was significantly greater ($P<0.01$) in the high yielding palms.

Quantitative Analysis: Experiment 2

In this experiment, 20 commercial *tenera* palms were sampled monthly for over two years beginning in the seventh year after planting with yield recording from the eighth. The results were examined in two ways, *vis:*

a) Monthly mean values of trunk carbohydrates for all 20 palms were plotted against time and related to seasonal changes in mean bunch load and environmental factors (soil water, radiation).

b) Single palm mean values of trunk carbohydrates for the 20 palms were regressed against individual bunch yields.

Figure 2 shows the variation in mean soluble sugar and polysaccharide levels over 29 months. Concentrations of 'free' sugars were generally higher than those released by hydrolysis. There

TABLE 8. YIELD CHARACTERISTICS AND CONCENTRATIONS OF ETHANOL-SOLUBLE SUGARS AND ACID-HYDROLYSABLE POLYSACCHARIDES IN TRUNK SAMPLES FROM LOW AND HIGH WELDING *tenera* PALMS

	Low yielding	High yielding	Sig. level (P)
Yield levels:			
FFB (kg palm^{-1} yr^{-1})	*34.8*	*222.6*	0.01
Bunch No. palm^{-1} yr^{-1}	1.4	11.0	0.02
			ns
Black bunch No. (palm^{-1}	*24.9*	*20.7*	0.02
Trunk carbohydrate content:			
(mg g^{-1} dry weight)			
Ethanol-soluble sugars	*205.1*	*261.1*	0.01
Polysaccharides	269.9	198.0	ns
Total carbohydrates	*475.0*	*459.1*	ns
% Sugars	*44.0*	*57.6*	*0.01*

Notes: yield data are for the year preceding collection of trunk samples; black bunch numbers were recorded at time of collecting trunk samples. Data are means for five palms per group. Four separate trunk samples were taken and analysed per palm. ns = not significantly different.

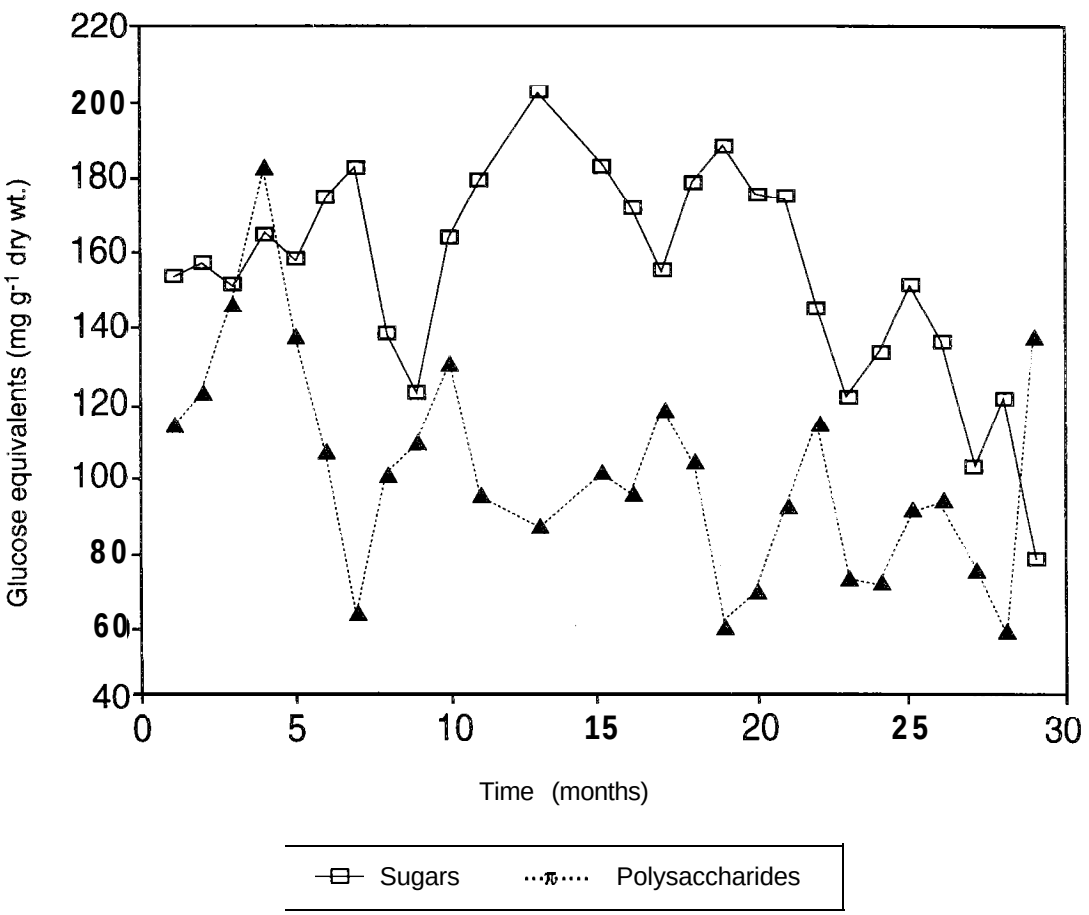

Figure 2. Changes with time in concentrations of ethanol-soluble sugars and acid-hydrolysable polysaccharides in trunk samples of tenera *palms. Sampling commenced in the seventh year after planting. Each point is a mean for 20 palms.*

was a tendency for increases in soluble sugars to be accompanied by decreases in polysaccharides and vice versa, but the total carbohydrate level also varied (results not presented). Although at first glance rather irregular, there was a pattern to the changes in both fractions" There were two maxima annually in free sugar concentrations (in February and August),' and two minima (in December and in April or June). Peak polysaccharide levels occurred in December and May and minimum levels in February and July-August.

Neither variation in solar radiation or in soil water deficit (Figures *3a* and *b)* fully accounted for changes in free sugar concentration,

FFB harvest data, available only from the seventh month from the start of trunk sampling onwards, allowed calculation of changes in fruiting activity (FA: dry weight of bunches developing on the palm) (Corley and Breure, 1992) and bunch dry matter production (BDMP*, non-oil equivalent) (Henson, 1997). Soluble sugar levels were significantly correlated with FA ($P<0.05$) but the correlation with BDMP* just failed to reach significance at this level, as did the correlations between the fraction of total carbohydrate in the form of free sugars and FA and BDMP*. Nevertheless, it is apparent from Figure 4 that, in general, a positive relationship existed between sugar levels and fruit bunch production.

Analysis of single palm values averaged over 20 months of sampling showed that there were significant negative correlations between polysaccharide and total carbohydrate levels and the total FFB yield palm-1 *(Figure 5).* By contrast, the fraction of carbohydrate in the form of free sugars was significantly positively correlated with the FFB yield *(Figure 6),* though the absolute level of free sugars was not.

Quantitative Analysis: Experiment 3

This study investigated further the relationship between yield and trunk carbohydrate content by comparing infertile, (virtually non-yielding) *pisifera* palms (IP) with related fertile *pisiferus* (FP) and *teneras* (T). The cumulative yields of these groups from the fourth to eleventh year after planting differed as much as 11-fold *(Table 9).*

In these samples, the mean content of ethanol-soluble sugars differed little between the three groups and was noticeably lower than in the commercial *tenera* palms sampled previously. Polysaccharide levels were substantially lower in *tenera* than in *pisifera* palms and were highest in the infertile *pisiferas* which consequently had the highest total carbohydrate levels. The proportion of carbohydrate in the form of ethanol-soluble sugars was lowest in infertilepisiferas, intermediate in fertile *pisiferas* and highest in *tenera* palms.

DISCUSSION

Even when experiencing conditions conducive to continuous growth and production, the oil palm still exhibits marked seasonal changes in bunch production (Corley, 1977; Chan *et al.,* 1985) and in total productivity (Henson and Chai, 1998). Such variation implies comparable changes in the provision of assimilates which must either be met from current photosynthesis or by mobilization of storage reserves. A role for reserves has been strongly indicated from pruning experiments (Corley, 1976) while a recent case study (Henson and Chai, 1998) has demonstrated how seasonal variation in dry matter production could be met from a combination of reserve mobilization and current photosynthesis.

The trunk has long been favoured as a site of assimilate reserves and data in *Table I* indicate its quantitative importance in mature palms over other plausible sites.

Information on the nature of the trunk reserves is still rudimentary. Starch was initially envisaged as the likely form of storage reserve but the reporting of high starch concentrations in the oil palm trunk (Killmann and Lim, 1987; quoting Simatupang, 1985) was not supported by results of other work (PORIM, 1983; Abdul Rashih Ahmad, 1988; Normah et al., 1994), nor by the results of the present study in which highest starch concentrations were found in the apical region of the trunk in young palms but appeared to decline with age and were low in mature palms (*Table 2).*

Although only a small fraction of carbohydrate may be partitioned into starch, large

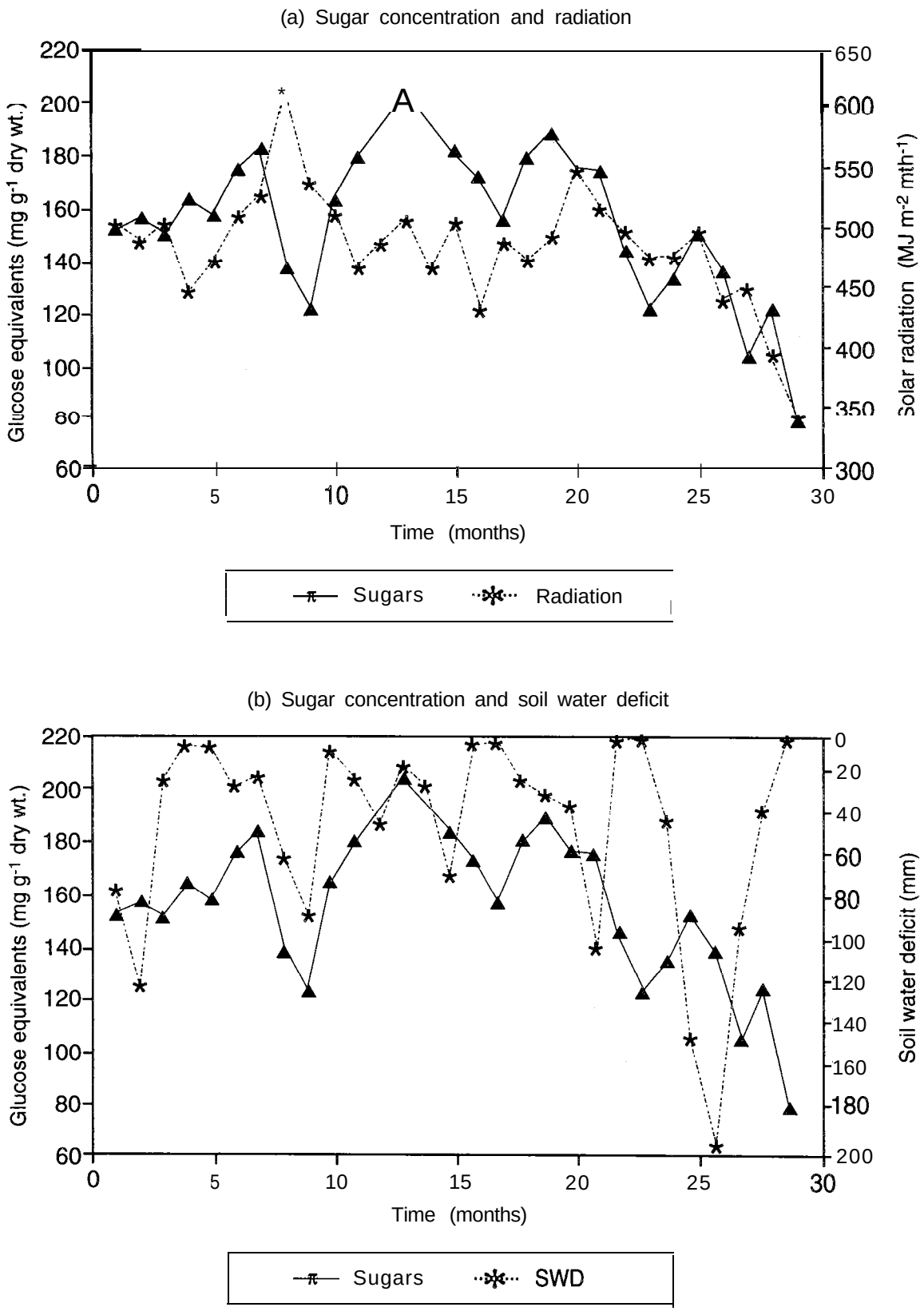

Figure 3. Changes with time in (a) concentrations of ethanol-soluble sugars and solar radiation, and (b) concentrations of ethanol-soluble sugars and soil water deficit (SWD). Other details are as for Figure 2.

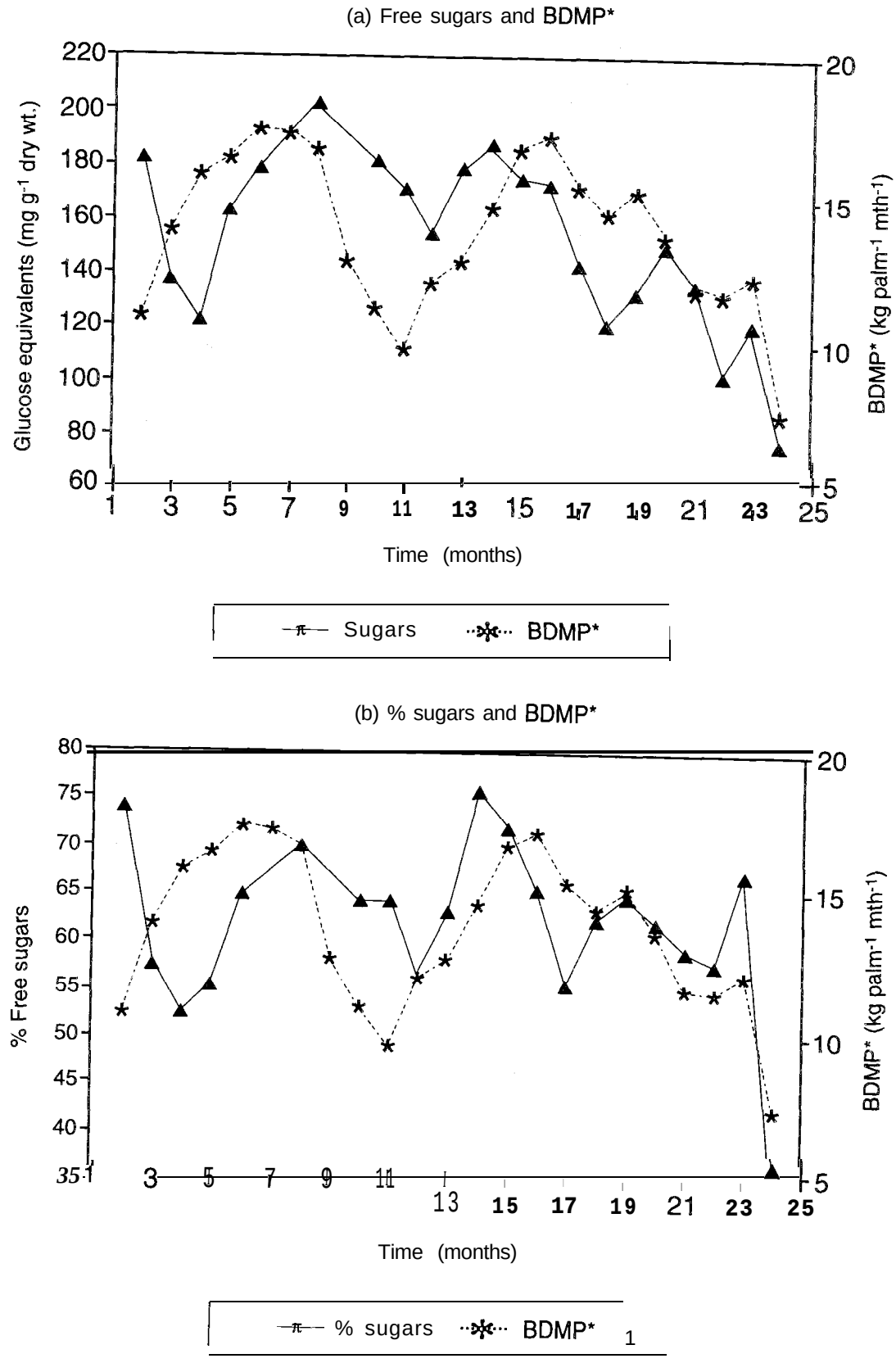

Figure 4. Changes with time in (a) concentrations of ethanol-soluble sugars and non-oil equivalent bunch dry matter production (BDMP*), and (b) the fraction of total carbohydrate present as ethanol-soluble sugars and BDMP*. Data starts in the eight year after planting. Other details are as for **Figure 2.**

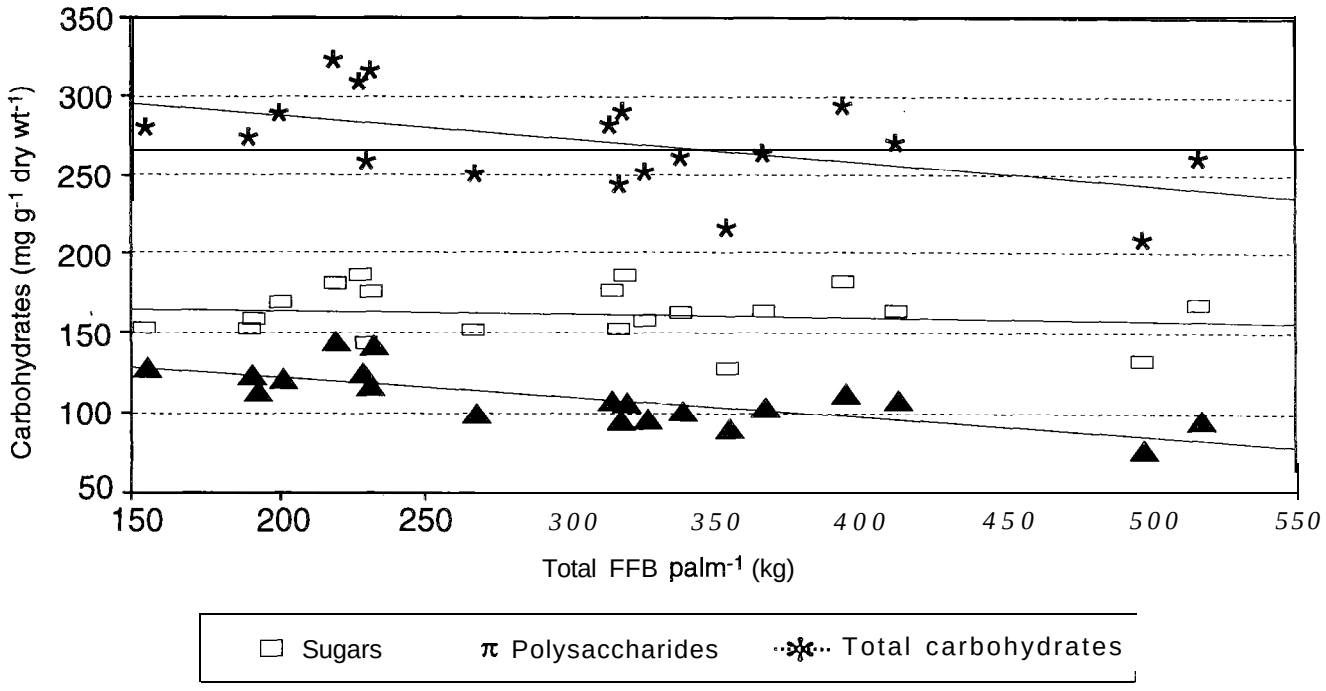

Figure 5. Relationships between concentrations of ethanol-soluble sugars, acid-hydrolysable polysaccharides and total carbohydrates in trunk samples of commercial tenera *palms, and their FFB yields. Data are for samples taken monthly over 20 months from the eighth year after planting. Each point is a mean for a single palm. Correlation coefficients (r) for regressions of sugar, polysaccharide and total carbohydrate concentrations against FFB yield were: -0.12, -0.74 and -0.50; the latter two values being significant at* $P< 0.001$ *and* $P< 0.05$ *respectively. Lines of best fit are shown.*

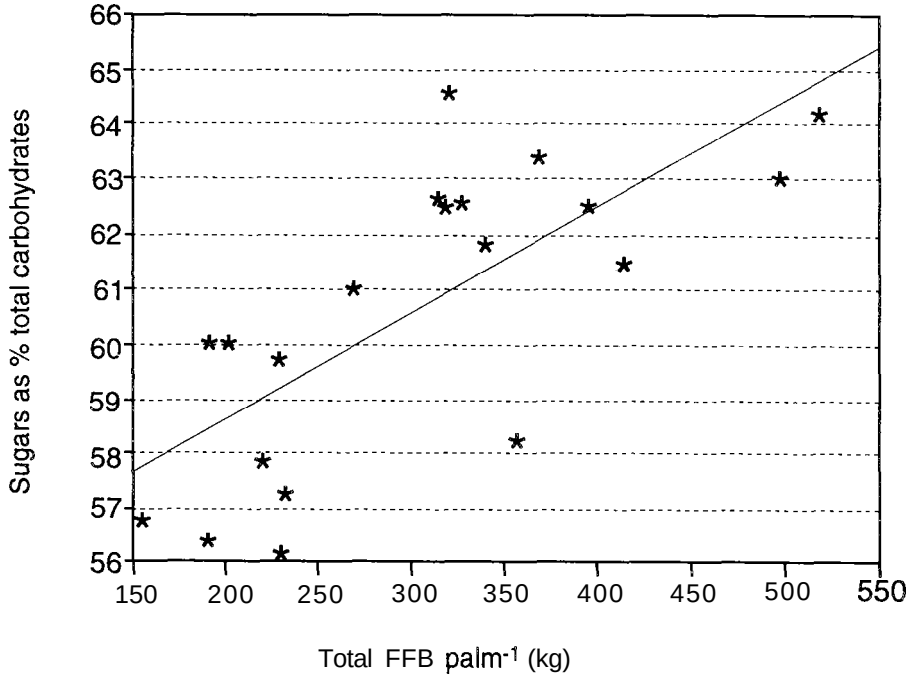

Figure 6. Relationship between percentage of total carbohydrate present as 'free' (ethanol-soluble) sugars in trunk samples of commercial tenera *palms, and their FFB yields. Data are for samples taken monthly over 20 months from the eighth year after planting. Each point is a mean for a single palm. The correlation coefficient (r) for the regression of percent sugar against FFB yield = 0.725, significant at* $P< 0.001$.

TABLE 9. YIELD CHARACTERISTICS AND CONCENTRATIONS OF ETHANOL-SOLUBLE SUGARS AND ACID-HYDROLYSABLE POLYSACCHARIDES IN TRUNK SAMPLES FROM INFERTILE pisifera, FERTILE *pisifera* AND *tenera* PALMS

	Infertile *pisifera*	Fertile *pisifera*	*Tenera*
FFB yield (kg palm^{-1} yr^{-1}):			
Years 4-11	9.0	91.7	101.8
Years 9-11	6.8	56.4	81.6
Trunk carbohydrate content[a]: (mg g^{-1} dry weight)			
Ethanol-soluble sugars	83.1	84.0	79.5
Polysaccharides	194.1	135.7	103.7
Total carbohydrates	277.2	219.7	183.2
% Sugars	34.0	40.5	44.9

Notes: [a]Data are means of ten palms per group, 18 monthly samplings and two separate assays per sample. Analysis of variance showed that the effect of palm group was highly significant ($P<0.001$) for polysaccharide, total carbohydrate and % sugars but non-significant for absolute sugar concentrations.

quantities of other polysaccharides as well as 'free' sugars may be present (Gray, 1969). The relative proportions of soluble and hydrolysable forms seems to vary, as well as their distribution within the trunk. Gray (1969) and Abdul Rashih Ahmad (1988) found concentrations of soluble sugars to be lower than those released by acid hydrolysis. This was found also to be the case with the palms examined in Experiment 3 (*Table* 9) but contrasts with the results shown in *Tables* 2, 3, 4, and 6 and *Figures* I, 2 and 5, in which soluble sugars were the dominant form. The reasons for these differences are not known; they could represent genotypic variation or be a response to differences in environment. However, in Experiment 3, polysaccharides were the dominant form in both *pisifera* and *tenera* palms while in Experiment 2, free sugar concentrations exceeded polysaccharides in all but two months over a course of more than two years despite variations in radiation and soil water supply.

Although initial samples *(Table 3)* showed the highest carbohydrate levels to be present in the upper part of the trunk (a finding also made by Abdul Rashih Ahmad (1988); the opposite was found in a further sampling at a different site *(Figure 1)*. Gray (1969) reported a pattern of carbohydrate content similar to those in *Figure* 1. It is tempting to speculate that lower concentrations near to the crown indicate their active utilization for bunch growth.

The presence in the trunk of large quantities of soluble sugars is compatible with its anatomy; the inner part containing a substantial volume of living parenchymatous tissues in which scattered vascular and fibrous bundles are embedded (Lim and Khoo, 1986; Killman and Lim, 1987). That substantial quantities of free (non-polymerized) sugars were naturally present in the trunk was shown by the fact that the major form of soluble sugar was the disaccharide, sucrose, the form in which assimilate is normally translocated to growth centres via the phloem. Acid hydrolysis is expected to release only monosaccharides, which in this case comprised predominantly glucose (*Table 7*). The presence of a hydrolysis product with the characteristics of xylose indicated that hemicelluloses (xylans) were being degraded during acid treatment. Xylans are common components of monocot cell walls. Thus, the polysaccharide fraction may serve mainly a structural rather than a storage function. Nevertheless, the present data provided some evidence for a 'reserve' role also for the polysaccharide fraction, as indicated by the following:

i) Levels of free sugars and polysaccharides were often inversely related suggesting their interconversion *(e.g. Figure 2)*.

ii) Polysaccharide levels were highest in low yielding palms *(e.g. Figure 5; Tables* 8 and *9)* suggesting deposition of 'excess' assimilate in the form of polysaccharide and/or conversely, release of assimilates from polysaccharides with high sink demand.

It was not possible from the present data to determine how such interconversions were regulated, not what the precise factors were governing the levels of free sugars and other forms of carbohydrate. The situation is undoubtably a complex one as levels of free sugars could be influenced by both sink demand or source supply (photosynthesis), both in turn being sensitive to environmental factors such as radiation levels and soil water supply. This renders interpretation of seasonal changes especially difficult. An example is the reduction in sugar levels shown in *Figure 3b* during months S-10. This corresponded with a dry period which may have restricted photosynthesis but such a reduction was not found at the same time the following year (although this was also dry), nor during months 24-25 which experienced much greater deficits. Similarly, free sugar levels were only partly correlated with radiation *(Figure 3a).* It is suggested that sink demand may have had the greatest influence, causing sugar release by hydrolysis and resulting in a close relation between the percentage of free sugars and bunch dry matter production *(Figure 6).*

ACKNOWLEDGEMENTS

We are most grateful to the Managements of Dunlop Estates Sdn. Bhd., Industrial Oxygen Incorporated Bhd. and Kumpulan K.L. Kepong Sdn. Bhd. for allowing sampling and recording of palms on their estates. The co-operation and help of the Oil Palm Breeding Section and Statistics Unit of PORIM are also gratefully acknowledged. We thank the staff of the Physiology Section for field and laboratory work.

REFERENCES

ABDUL RASHIH AHMAD (1988). Personal Communication.

CHAN, K W; YEE, C B; LIM, K C and GOH, M (1985). Effects of rainfall and irrigation on oil palm yield production. In *Proc. of a Briefing on Oil Palm Yield Prediction for the MOPGC.* Malaysian Oil Palm Growers Council, Kuala Lumpur, p. 49-58.

CORLEY, R H V (1976). Photosynthesis and productivity. In (eds. Corley, R H V; Hardon, J J and Wood, B J) *Oil Palm Research.* Elsevier Scientific Pub. Co. Amsterdam. p. 55-76.

CORLEY, R H V (1977). Oil palm yield components and yield cycles In (eds. Earp, D A and Newall, W) *International Developments in Oil Palm.* Incorporated Society of Planters, Kuala Lumpur. p. 116-29.

CORLEY, R V H and BREURE, C J (1992). Fruiting activity, growth and yield of oil palm. I. Effects of fruit removal. *Experimental Agriculture, 28:*99-109.

FLACH, M and SCHUILING, D L (1989). Revival of an ancient starch crop: a review of the agronomy of the sago palm. *Agroforestry Systems, 7: 259-81.*

FOSTER, H L; BEALING, F J; MOHD TAYEB DOLMAT; SINGH, G; TAN, K S; SAID ISMAIL and SINASAMY, N (1985). The effect of the introduction of the weevil (*Elaeidobius kamerunieus)* on the yield performance, nutrition and physiology of the oil palm in Peninsular Malaysia. In *Proc. of the Symposium on Impact of the Pollinating Weevil on the Malaysian Oil Palm Industry.* Palm Oil Research Institute of Malaysia, Bangi. p. 339-54.

GRAY, B S (1969). A study of the influence of genetic, agronomic and environmental factors on the growth, flowering and bunch production of the oil palm on the west coast of West Malaysia. Ph.D thesis, University of Aberdeen. 947 pp.

HARBORNE, J B (1984). *Phytochemical Methods.* Second edition. Chapman and Hall, London.

HENSON, I E (1997). Analysis of oil palm

productivity. I. The estimation of seasonal trends in bunch dry matter production. *Elaeis, 9(2):*69-77.

HENSON, I E and CHAI, S H (1997). Analysis of oil palm productivity. II. Biomass, distribution, productivity and turnover of the root system. *Elaeis, 9(2):*78-92.

HENSON, I E and CHAI, S H (1998). Analysis of oil palm productivity. III. Seasonal variation in assimilate requirement, assimilation capacity, assimilate storage and apparent photosynthetic conversion efficiency. *J. Oil Palm Research, 10(1):*35-51.

HIROKAWA, T; I-IATA, M and TAKEDA, H (1982). Correlation between the starch level and the rate of starch synthesis during the developmental cycle of *Chlorella ellipsoides*. *Plant and Cell Physiology, 23:*813-20.

KILLMANN, W and LIM, S C (1987). Anatomy and properties of oil palm stem. In *Proc. of the National Symposium on Oil Palm By-products for Agro-based Industries.* Palm Oil Research Institute of Malaysia, Bangi, p. 18-42.

LIM, S C and KHOO, K C (1986). Characteristics of oil palm trunk and its potential utilization. *The Malaysian Forester, 49:*3-22.

NORMAH, A M; MOHD AZEMI, M N; SIMATUPANG, M H and MANAN DOS, A (1994). Extraction and characterization of oil palm starch. In *Abstracts of Third National Seminar on Utilization of Oil Palm Tree and Other Palms.* Oil Palm Fibre Utilization Committee, Malaysia. p. 24.

PORIM (1983). Mobilization of starch reserves in the trunk of mature palms. In *Annual Research Report 1982* (Biology Division). Palm Oil Research Institute of Malaysia, Bangi. p. 136-7.

RAABO, E and TERKILDSEN, T C (1960). On the enzymatic determination of blood glucose. *Scandanavian Journal of Clinical Laboratory Investigation, 12:*402.

SIGMA DIAGNOSTICS (1987). Glucose; quantitative, enzymatic (glucose oxidase) determination in whole blood, serum or plasma at 425-475 nm. (Procedure No. 510). Sigma Chemical Company, St Louis, USA. 11 pp.

YEM, E W and WILLIS, A J (1954). The estimation of carbohydrates in plant extracts by anthrone. *Biochemistry Journal, 57:*508-14.

ERRATUM

Please note that the key of ***Figure 2b*** on page 36 in the previous issue (Journal of Oil Palm Research Vol. 11 No. 1) should read as follows:

2100hr A

0100hr ❑

0500hr •!

The error is regretted.