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ANALYSIS OF OIL PALM PRODUCTIVITY. III. SEASONAL VARIATION IN ASSIMILATE REQUIREMENTS, ASSIMILATION CAPACITY, ASSIMILATE STORAGE AND APPARENT PHOTOSYNTHETIC CONVERSION EFFICIENCY

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Total productivity of oil palm growing at two sites in West Malaysia was assessed on a monthly basis over three to four years aided by a method for calculating monthly bunch dry matter production. The level and seasonal variations in production were compared with those predicted by a simulation model of oil palm growth which used solar radiation and leaf area index as the main inputs. Deviations between measured and modelled productivity were catered for by invoking changes in assimilate storage. The contribution to the seasonal yield pattern, by changes in assimilation capacity (via changes in radiation and leaf area index) and storage pool size were assessed for each site. The influence of variations in sink strength on the system is discussed.

INTRODUCTION

Although oil palm can grow and produce fruit throughout the year, there are, in common with other tropical fruit crops, regular seasonal variations in yield (Corley, 1977; Corley and Gray, 1976; Corley and Teo, 1976; Foster, 1985). Although especially marked in seasonally dry environments, these yield fluctuations occur even in climates with adequate uniformly distributed rainfall, on sites with an accessible ground water supply and on sites where water deficits are prevented by irrigation (Chan *et al.,* 1985; Chang, 1985 and unpublished results). The basis for such yield 'cycles' in oil palm under these circumstances is often explained as being due to a negative 'feed-forward' influence of current levels of cropping on future fruit bunch production (Breure and Corley, 1992; Corley and Breure, 1992). This is achieved mainly by effects on bunch number, which is determined by frond number, the

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proportion of inflorescences developing as 'females' (sex ratio), the extent of inflorescence abortion and rate of bunch development (Corley 1976a; Chang *et al.,* 1993,1995).

While interest has understandably been concentrated on explaining yield variation in terms of the developmental processes, less attention has been given to examining the consequences of yield fluctuations for the carbon economy in terms of supply of photosynthetic assimilates and need to meet assimilate demands during peak periods of production. To examine this, measurements are needed of short-term variation in total palm dry matter production. Few such data have been presented. An assessment based on the variation in fresh fruit bunch (FFB) production alone is not adequate for this purpose, firstly because of the lag between bunch dry matter production and FFB harvest (Henson, 1997) and secondly because of the possibility of seasonal variation in growth of other parts of the palm.

In the present investigation an attempt was made to assess dry matter production on a monthly basis at two sites over several seasons with the aid of a simple bunch growth model (Henson, 1997) and periodic palm measurements. In the analysis, account is taken of the higher energy content of bunches using the concept of non-oil equivalent dry matter (DM*; Squire, 1985).

An oil palm simulation model based on that of van Kraalingen (van Kraalingen, 1985; van Kraalingen *et al.,* 1989) is used to determine theoretical dry matter production. Where differences occur between actual and modelled production, leading to excesses or deficits of currently produced assimilates, these are added to or deleted from, an assimilate storage pool. Changes in pool size are modelled assuming the trunk to be the most likely site of such a reserve.

MATERIALS AND METHODS

Experimental Sites

Data were obtained from two sites in West Malaysia, one coastal and one inland, selected as representing the two main oil palm 'environments' found in the central west area of the Peninsular. The 'coastal' site was a 94 hectare field planted in 1983 with 136 palms/hectare and the inland site a 104 hectare field planted in 1985 with 148 palms/hectare. For further details of these sites see Henson (1997). Both sites were part of large estates and subject to standard commercial management practice.

Assessment of Dry Matter Production

Individual palm measurements commenced in September 1991 at the coastal site and in August 1993 at the inland site, using five 20-palm plots per site, distributed in representative sectors within each field. Most measurements were made at three-monthly intervals ending March (coastal) and November (inland) 1995.

a) Above-ground vegetative dry matter

Standard 'non-destructive' measurements and counts were made of frond numbers and dimensions as described by Hardon *et al.* (1969), Corley *et al.* (1971) and Corley and Breure (1981). Frond 17 was used as the standard on which calculations of whole palm dry weight and leaf area were based. At each quarterly measurement 'round', counts were made of the number of newly 'emerged' fronds. At the coastal site from July 1993 onwards, counts of newly emerging fronds were also made monthly. These counts were used to calculate frond dry matter production (DMP) on a monthly basis assuming mean frond dry weight to be constant during the quarter. Where monthly frond counts were not available, monthly frond DMP was taken to be one-third of the quarterly value.

Trunk DMP was assessed as the difference between total standing trunk biomass present on successive occasions. The latter was calculated from measurements of volume and calculated density. Volume was determined from trunk height and diameter measurements. Trunk height was measured each quarter from soil level to the base of a standard frond. Trunk diameter was measured once at each site on a sample of four palms per plot (*i.e.* 20 per site) and the mean value used as a constant in calculations of trunk volume. Trunk density was calculated from the formula of Corley *et al.* (1971). Monthly trunk DMP was taken to be one-third of the quarterly value.

b) Root dry matter

Only two annual assessments for each site of root standing dry matter and one of root DMP were available, being obtained as described by Henson and Chai (1997). As there was no reliable information regarding possible seasonal variation in root growth, the rate of increase in root biomass was taken to be constant throughout the period of study. Productivity of roots was taken as the sum of the increase in standing biomass plus turnover. The latter was estimated from 'ingrowth core' samples and, for the coastal site, additionally by a 'carbon balance' method. The balance method gave a value for root turnover very close to that of the core method. The mean value of the two methods was used when calculating production. Monthly root production was calculated from the annual value assuming it to be a constant fraction of standing biomass.

At the inland site no net root increment was observed and any new growth was therefore lost in turnover. Turnover measured by the core technique was adjusted slightly, based on results for the two assessment methods used at the coastal site.

c) Male inflorescence and bunch dry matter

Dry matter incorporated into male inflorescences was determined from quarterly counts of inflorescence numbers assuming a mean dry weight each of 0.5kg (coastal site) or 0.4kg (inland). Monthly DMP was taken to be one-third of the quarterly value.

Dry matter (non-oil equivalent) incorporated into bunches (BDM*) was calculated from monthly FFB yields for each site, using the procedure described previously (Henson, 1997).

d) Total dry matter production (TDMP)*

Total palm DMP* for the two sites was calculated on a monthly basis by summing the above components.

Measurement of Radiation

Total incoming solar radiation (300nm-1000 nm) was measured by a Kipp solarimeter (Kipp and Zonen, Delft, The Netherlands) and a silicon cell 'energy' sensor (Skye, UK), and photosynthetically-active radiation (400nm-700nm; PAR) by a quantum sensor (Licor Inc, Nebraska, USA). All sensors were mounted ca. four above the canopy on masts located centrally at each site. Outputs from the sensors were recorded continuously using data loggers.

Modelling Production of Assimilates

The simulation model, GHPOT (Henson, 1989; 1992), based on the model of van Kraalingen (1985) and the work of Breure (1988), was modified to produce monthly estimates of VDM, BDM* and total dry matter production (TDMP*) using mean monthly solar radiation, leaf area index (LAI) and frond dry weight as inputs. The model calculates total assimilate production 'mechanistically' while giving above-ground VDM from a regression on single frond dry weight (PORIM, 1994).

The main parameter values used in the model (Henson, 1989; 1992) were determined from previous measurements (AMAX, EFF, K) or estimates (%R) and were:

AMAX (photosynthetic rate at saturating radiation): 24 μmol/m^2/s, coastal site; 22 μmol/m^2/s, inland site.

EFF (photosynthetic efficiency at low irradiance): 0.25 μmol/J.

K (extinction coefficient of canopy for PAR): 0.45.

%R (per cent of gross assimilates consumed in respiration): 60.3.

Calculation of Assimilate Storage Pool

Any differences between measured and modelled productivity can theoretically be accounted for by increases or reductions in the size of an assimilate storage pool. The trunk represents the most probable site of such a store (Henson *et al.*, 1998) and the size of this was calculated from the trunk mass and the percentage of 'available' carbohydrates. An estimate of the latter was obtained from analysis of carbohydrate levels in trunk samples of *tenera* palms growing on an inland site in Johore (Henson *et al.*, 1998) which gave a mean ethanol-soluble plus acid-hydrolysable carbohydrate content of 18.6% of dry weight.

Calculation of E*

Photosynthetic conversion efficiency (E*, g/MJ) was calculated in the standard way as:

$$E(*) = TDMP(*)/PAR \times f$$

where PAR is assumed to be half of total solar radiation on an energy basis and *f* is the fractional interception of PAR calculated from LAI following Squire (1985).

RESULTS

Seasonal Changes in Measured Productivity

Changes in the productivity of above-ground palm components are shown in *Figures 1a* and *1b*. Although BDMP* was by far the major contributor to the seasonal variation in total production, smaller changes were also apparent in frond and trunk growth. At the coastal site there were three peaks and four 'troughs' in BDMP*. During three of the troughs (nos. 1,3 and 4) there were small compensating increases in VDMP, largely due to increased frond production. There was, however, also a rise in VDMP during the first, though smallest BDMP* peak. At the inland site two peaks and three troughs in BDMP* could be discerned. VDMP increased during the second and third trough. However, VDMP decreased during the first trough when total productivity was at its lowest. This reduction in total DMP* may have been a response to water deficit (see Discussion).

Simulation of Productivity

Output of BDMP* and TDMP* from the simulation model is plotted alongside measured values of BDMP* and TDMP* in *Figures 2a* and *2b*. Generally, the simulated values showed similar cyclic patterns to the observed ones. The largest discrepancies occurred at the beginning and end of the periods of measurement and were more evident for the inland than for the coastal site.

Annual totals of BDMP*, TDMP* and TDMP* above-ground are presented in *Tables 1* and *2* together with modelled values. Values for incomplete years have been adjusted, though because of the cycling in yield these should be regarded as indicative only. The data indicate those years during which the best (and worst) agreement occurred between measured and modelled values.

The overall means and variation in modelled versus measured values are presented in *Table 3*. The model slightly overestimated bunch production at both sites but more so at the inland site where BDMP*(measured) was 90% of the modelled value, it being 94% at the coastal site. The variation in modelled monthly production at the coastal site was less than the variation in measured values for both BDMP* and TDMP*, but the opposite was true at the inland site where CV's were highest for modelled values.

Note that different values for AMAX were used for the two sites. Values of AMAX were adjusted to optimize agreement between measured and modelled values. The lower AMAX appropriate to the inland site is consistent with the lower values of AMAX measured at this site using gas exchange equipment (PORIM, 1994), its lower E* value (see below) and its lower productivity (Henson, 1998).

Photosynthetic Conversion Efficiency

The apparent efficiency of radiation use, the photosynthetic conversion efficiency (E*) (Squire, 1985), calculated monthly, showed a similar %CV to that of TDMP* (10.9% to 12%). However, variation in E* did not follow closely that of TDMP* except at the inland site during the first 20 or so months of measurements

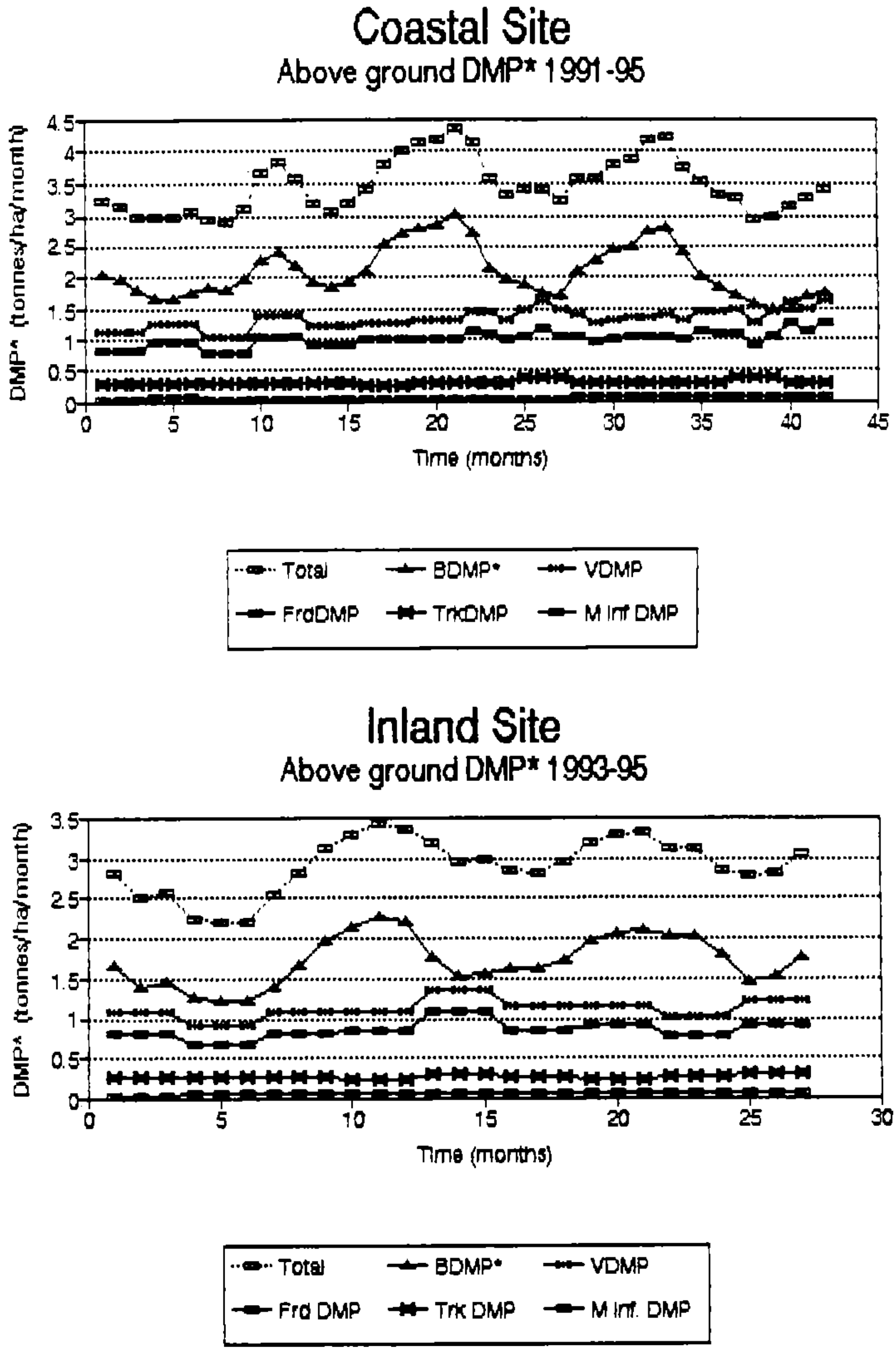
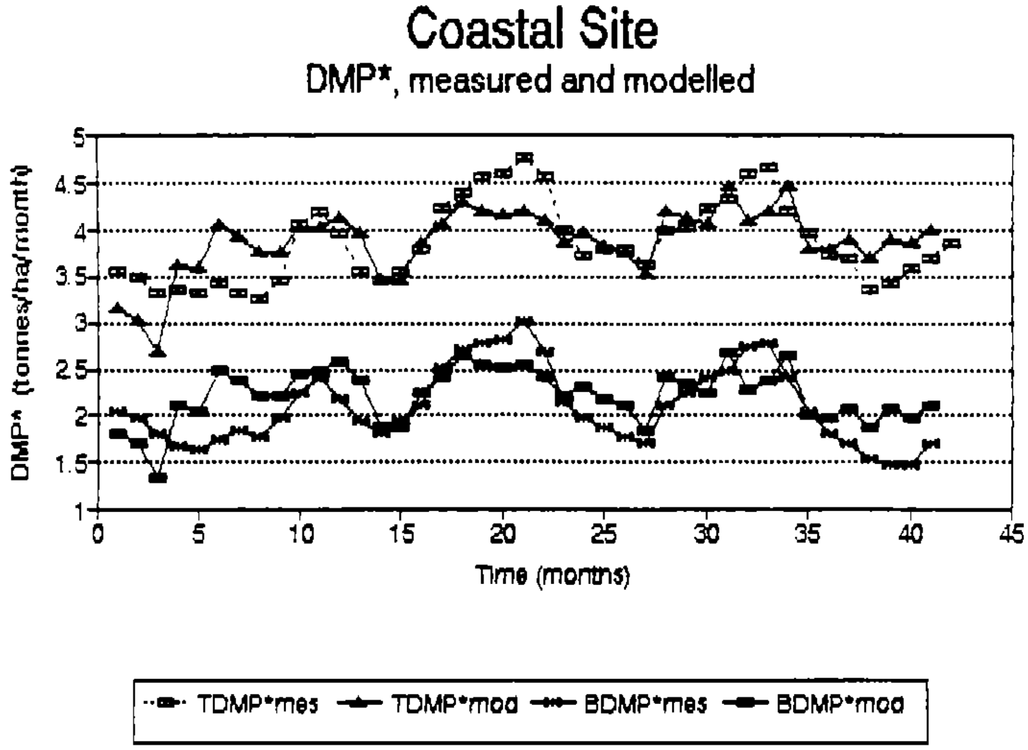


Figure 1. Monthly changes in above-ground dry matter production (non-oil equivalents; DMP) at the (a) coastal and (b) inland sites. Changes are shown in total above-ground (Total), bunch (BDMP*), vegetative (VDMP), frond (Frd DMP), trunk (Trk DMP) and male inflorescence (M inf. DMP) productivity*



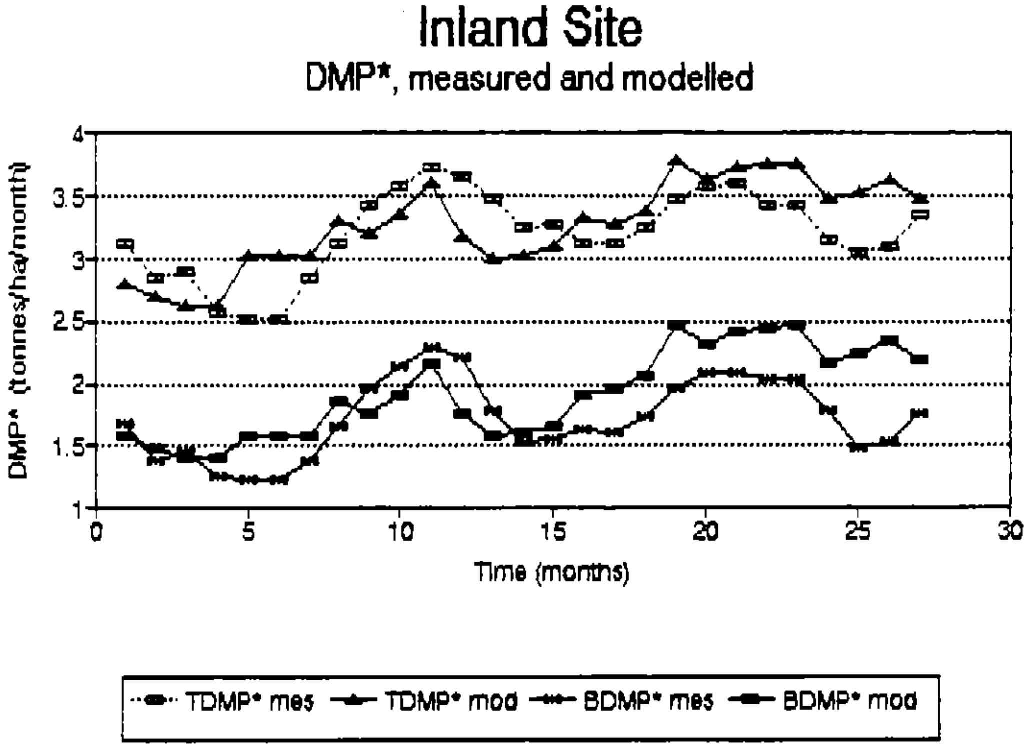


Figure 2. Comparison of observed and modelled, total and bunch DMP at the (a) coastal and (b) inland sites.*

TABLE 1. MEASURED AND MODELLED PRODUCTIVITY AT THE COASTAL SITE

	Tonnes DMP*/hectare/year				
	1991(a)	1992	1993	1994	1995(b)
Bunch DMP*	23.34	23.19	28.16	25.84	19.72
Total above ground DMP*	37.37	38.49	45.14	43.12	39.36
Total DMP*(c)	41.61	42.93	49.48	48.18	44.62
Modelled BDMP*	19.50	27.13	28.05	27.01	26.90
Modelled TDMP*	35.49	45.78	47.84	48.72	49.49

(a) final quarter of year x 4 (b) first quarter of year x 4
(c) shoot plus root

TABLE 2. MEASURED AND MODELLED PRODUCTIVITY AT THE INLAND SITE

	Tonnes DMP*/hectare/year		
	1993(a)	1994	1995(b)
Bunch DMP*	17.35	20.61	21.99
Total above-ground DMP*	30.57	34.95	36.44
Total DMP*(c)	34.28	38.50	39.75
Modelled BDMP*	17.59	20.98	27.32
Modelled TDMP*	32.14	38.09	42.91

(a) last 4 months of year x 3
(b) first 11 months of year x 1.0909
(c) shoot plus root

TABLE 3. SEASONAL VARIATION IN MEASURED AND MODELLED DRY MATTER PRODUCTION (tonnes/ha/month)

Site	Monthly mean	std dev	%CV
Coastal, n=42			
BDMP* (measured)	2.09	0.413	19.8
BDMP* (modelled)	2.23	0.295	13.2
TDMP* (measured)	3.87	0.433	11.2
TDMP* (modelled)	3.89	0.368	9.5
Inland, n=27			
BDMP* (measured)	1.72	0.313	18.2
BDMP* (modelled)	1.92	0.354	18.4
TDMP* (measured)	3.20	0.340	10.6
TDMP* (modelled)	3.26	0.351	10.8

(Figure 3b). E* at the coastal site changed rather erratically and showed little apparent relation to TDMP* *(Figure 3a)*. E* was higher at the coastal than at the inland site in all years, whether calculated on a total or on an above-ground DMP* basis *(Table 4)*. Including roots in the calculation of E* raised values by some 10%-12% *(Table 4)* (Henson and Chai, 1997).

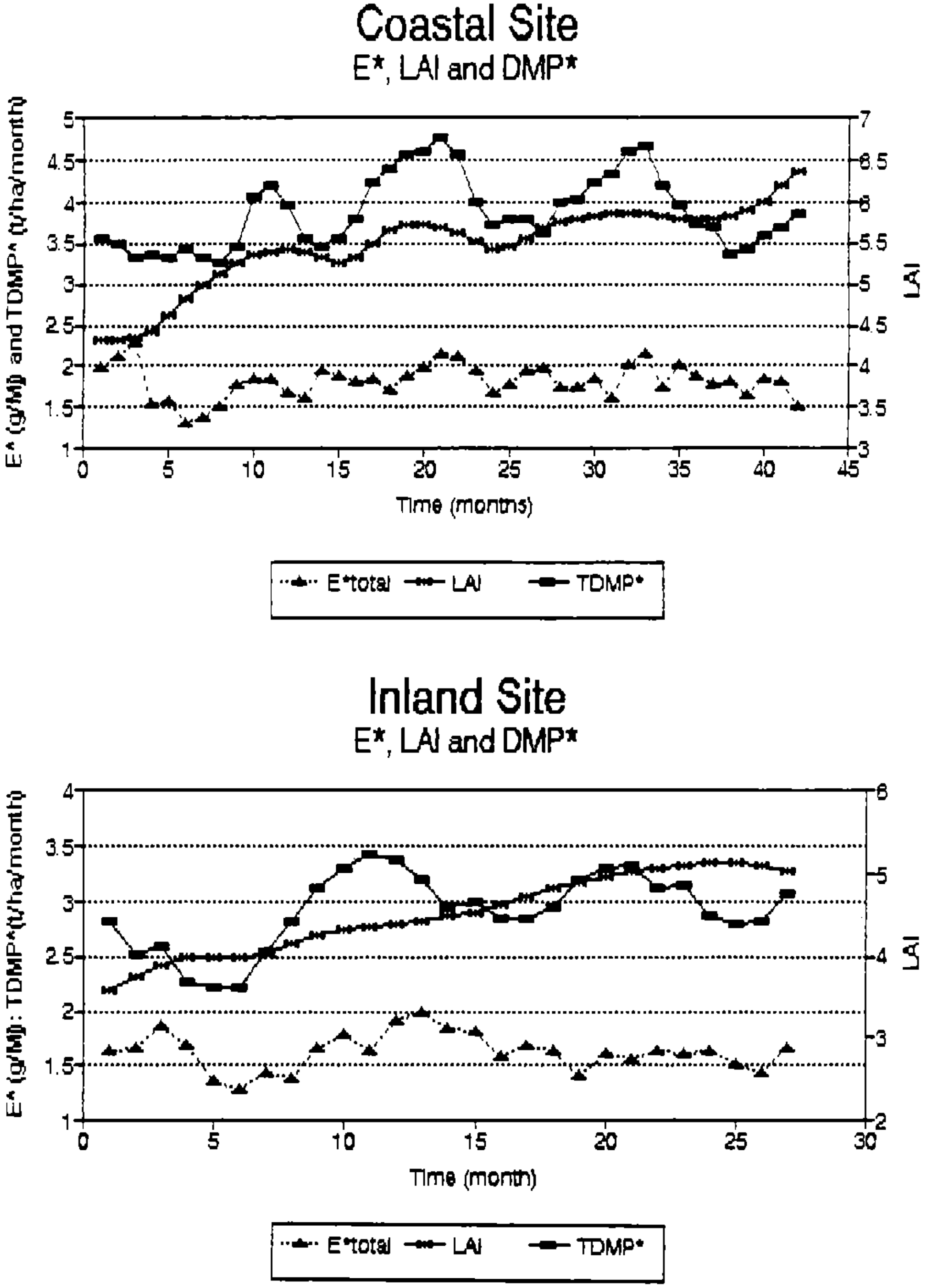


Figure 3. Changes in photosynthetic conversion efficiency (E) and leaf area index (LAI) in relation to total DMP* (TDMP*) at the (a) coastal and (b) inland sites.*

TABLE 4. APPARENT PHOTOSYNTHETIC CONVERSION EFFICIENCY (E*; g/Mj), MEAN ANNUAL VALUES

Year	Coastal site	Inland site	Inland/coastal
i) Above-ground biomass production			
1991	1.91(a)	—	—
1992	1.49	—	—
1993	1.72	1.53(d)	0.89
1994	1.64	1.49	0.91
1995	1.51(b)	1.44(e)	0.95
mean	1.61(c)	1.45(f)	0.90
ii) Total biomass production			
1991	2.13(a)	—	—
1992	1.66	—	—
1993	1.90	1.71(d)	0.90
1994	1.83	1.64	0.90
1995	1.72(b)	1.58(e)	0.92
mean	1.82(c)	1.62(f)	0.89

Notes:
(a) last quarter only
(b) first quarter only
(c) 42 months
(d) last four months only
(e) first 11 months only
(f) 27 months

Leaf Area Index

There was a tendency for LAI also to exhibit 'cyclic' changes *(Figure 3a)*. The increase in LAI with time was not continuous but there were periods when the increase was slowed or LAI underwent reductions. These 'troughs' in LAI followed peaks in TDMP* and coincided with peaks both in harvested bunch numbers *(Figure 4a)* and in numbers of fronds removed during harvesting *(Figure 4b)*. The variation in LAI would have contributed to the variation in modelled DMP*.

Storage Reserves

The calculated changes in assimilate storage reserves resulting from imbalance in demand and supply are shown in *Figures 5a* and *5b*. The size of the storage pool was assumed to be directly proportional to standing trunk biomass and the linear increase in pool size which would occur if no 'withdrawals' or additions were made to the assimilate bank is contrasted with the dynamic changes resulting from withdrawals and additions to the pool. (Note: In calculating these, no allowance has been made for possible additional metabolic costs of interconversions.) The fluctuations in the reserves ranged at the coastal site from -63.7% to +47.9% of the 'nominal' amounts, and at the inland site from -63.2% to +66.9%.

Sink Demand

As the major component of seasonal variation in productivity resides in bunch production *(Figure 1)*, the strength of the bunch 'sink' may at times be a more important factor in determining total productivity than are current environmental conditions. BDMP* is a function of both number and individual weights of

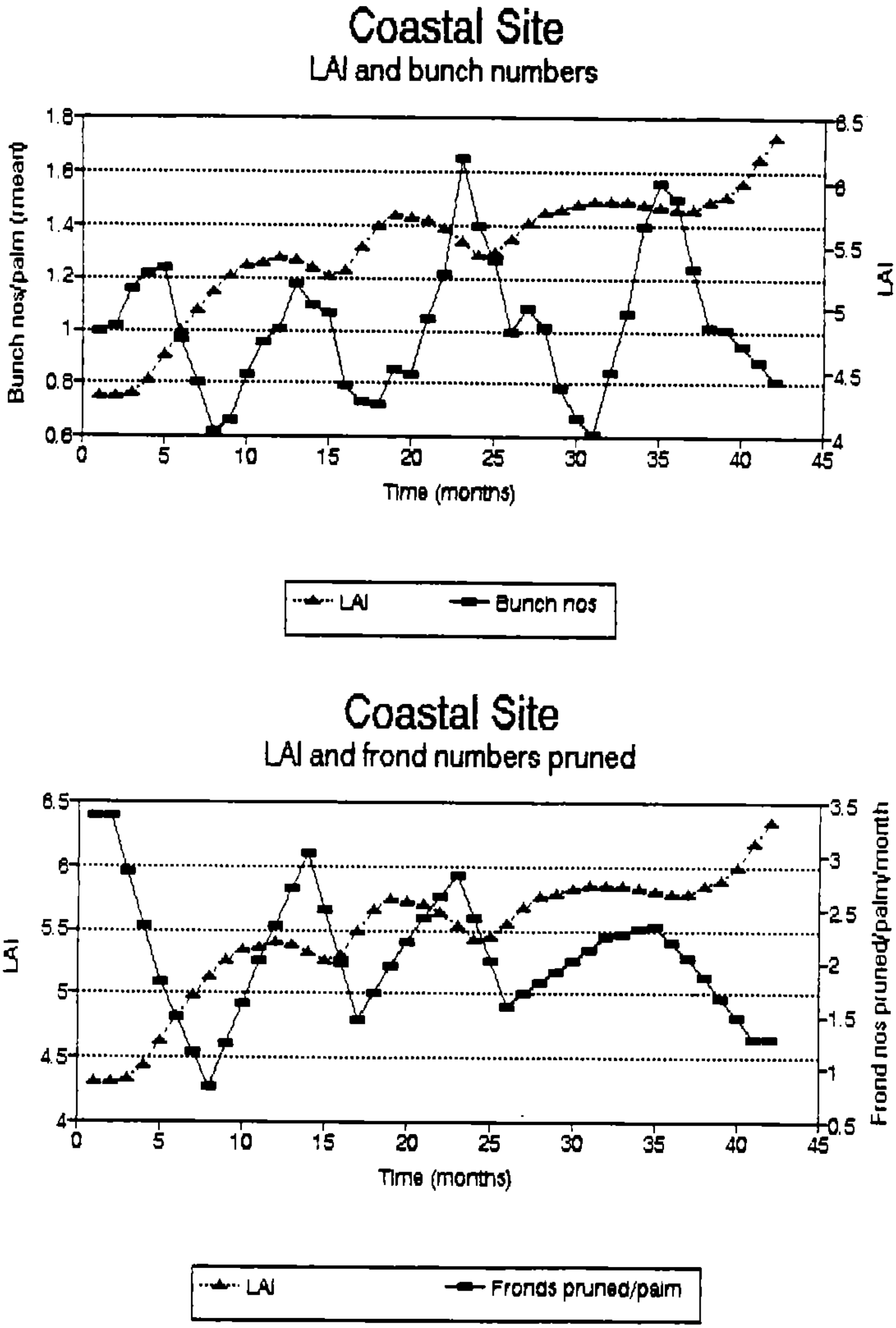


Figure 4. Changes at the coastal site in (a) leaf area index and numbers of bunches harvested (running means) and (b) leaf area index and numbers of pruned fronds (running means derived from quarterly counts).

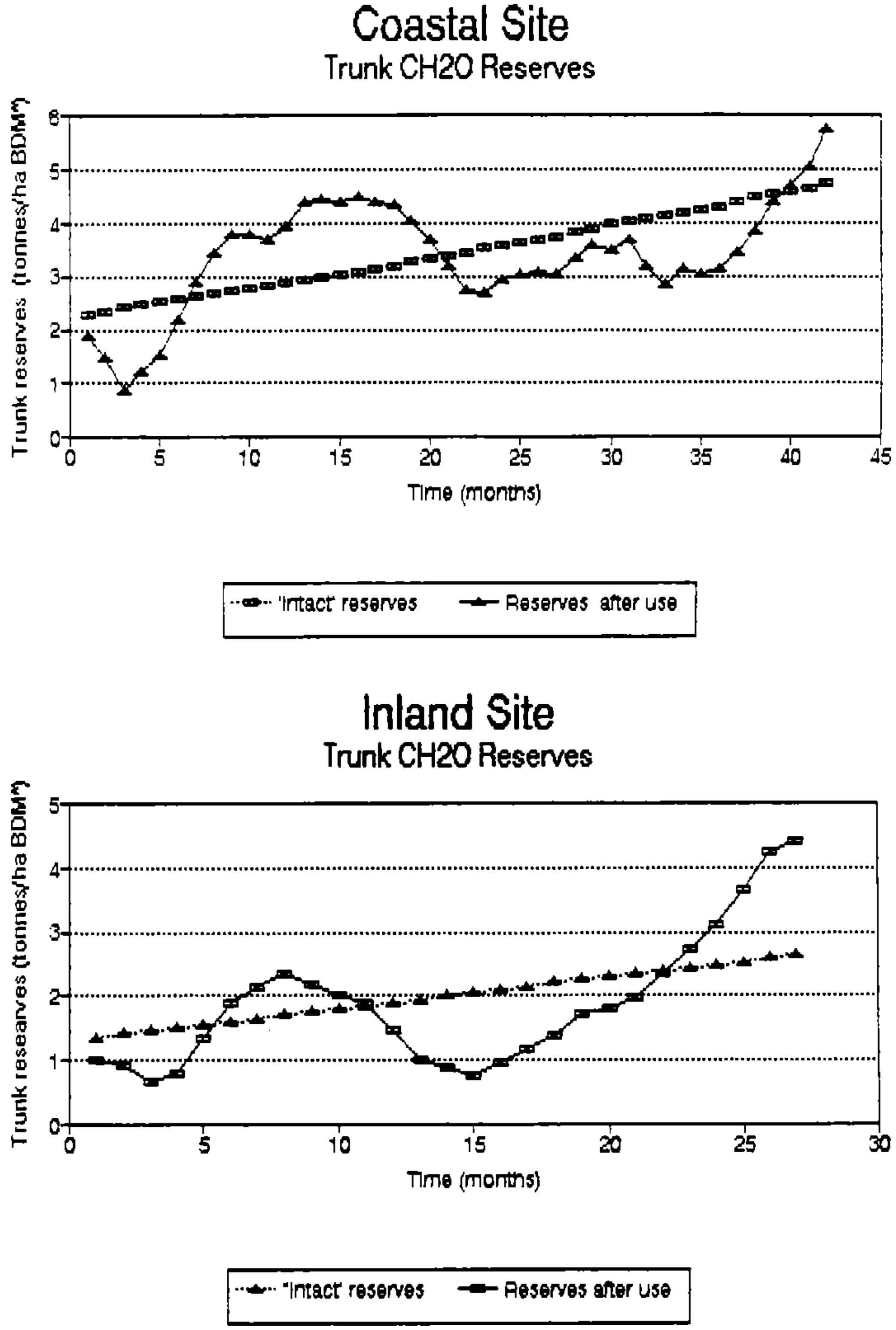
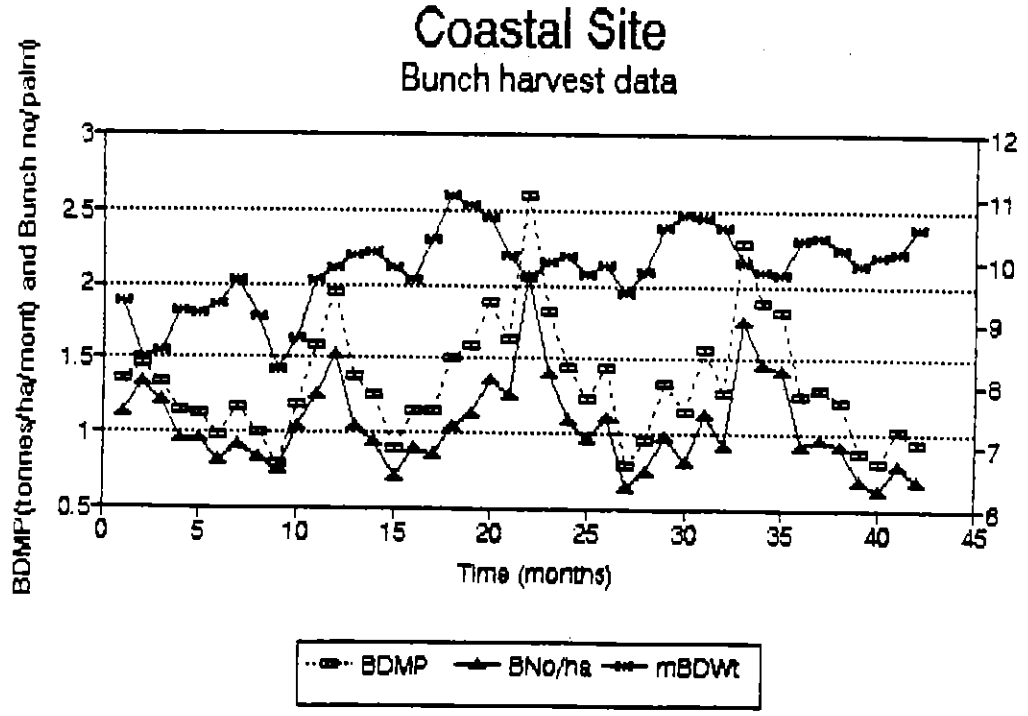


Figure 5. Calculated changes in trunk carbohydrate reserves at the (a) coastal and (b) inland sites. Changes occurring as a consequence of differences between the theoretical level of assimilate production and the assimilate requirements for growth (reserves after use) are contrasted with the level of reserves expected if no deletions or additions are made to them ('intact' reserves).

bunches. The manner in which these bunch components changed in relation to total bunch dry weight is shown in *Figure 6*. It is clear that at both sites, bunch number had the greatest influence on short-term variation in total bunch dry matter yield.



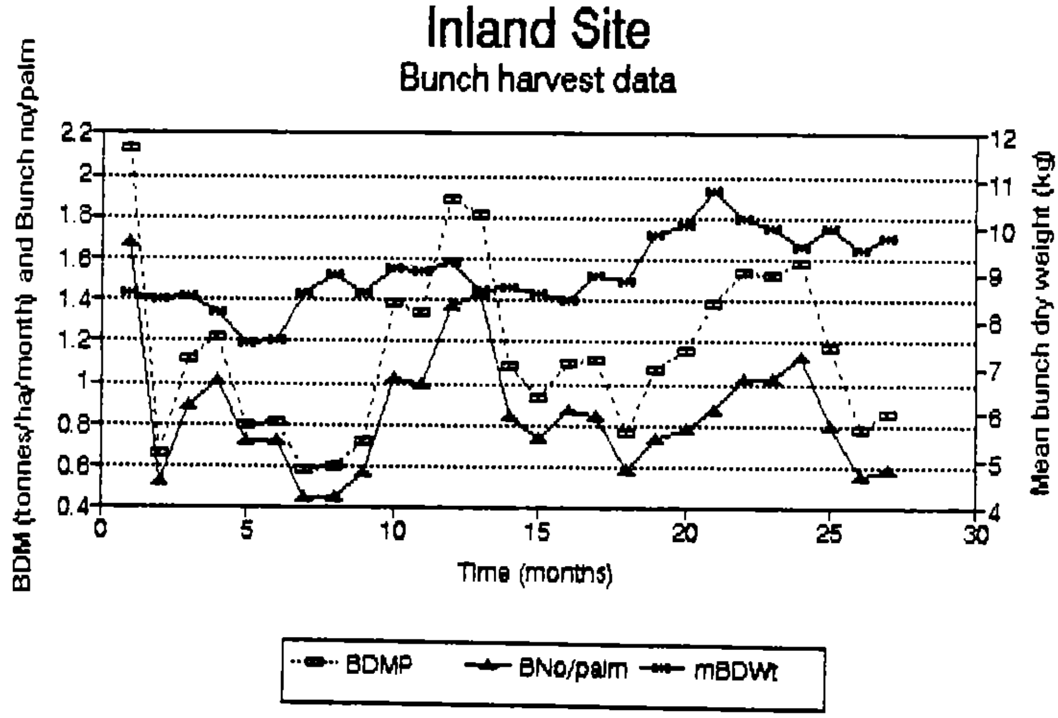
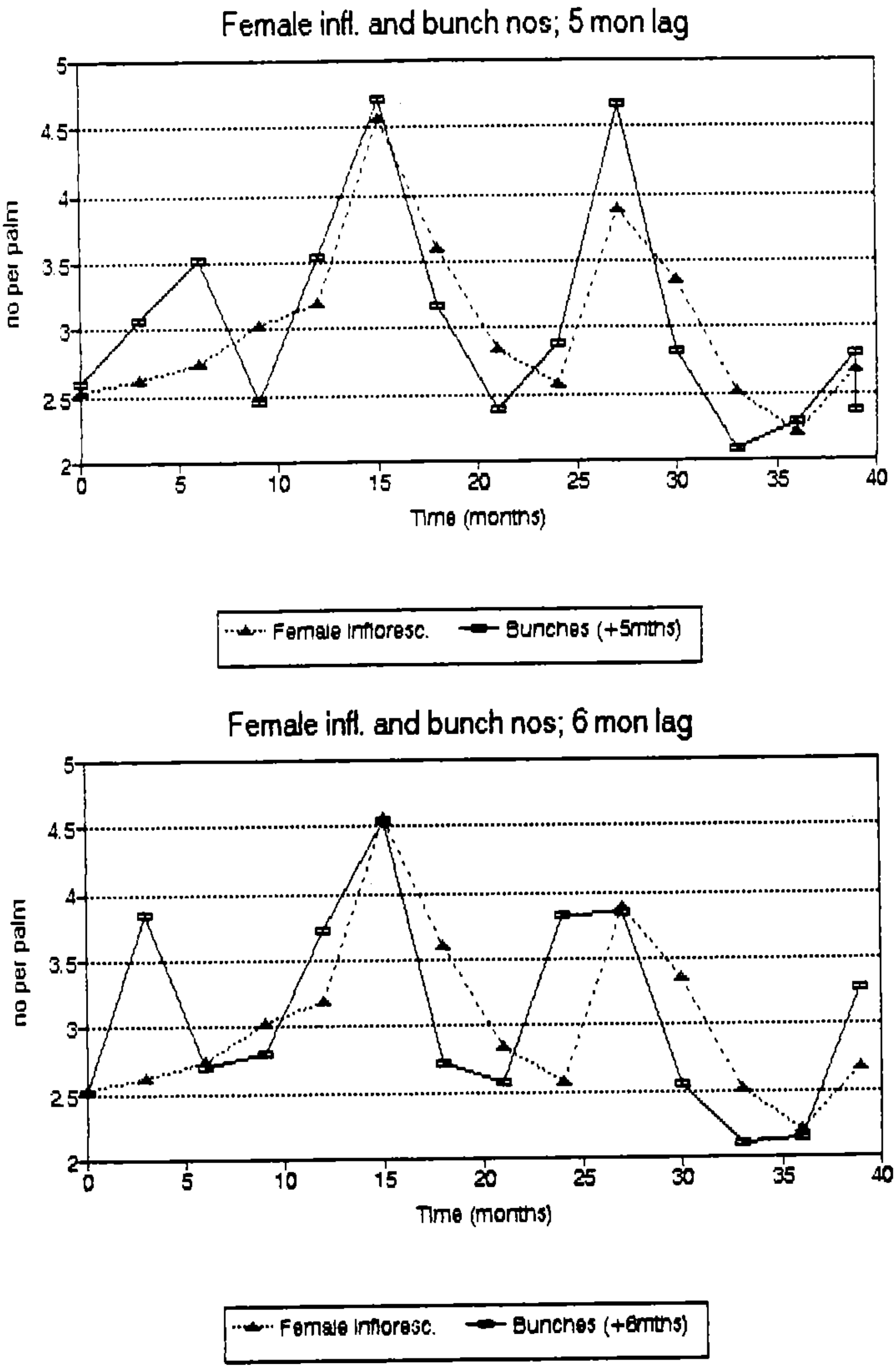


Figure 6. Changes in total harvested bunch dry matter, (BDMP), bunch numbers per palm (BNo/ palm) and mean dry weight per bunch (mBDWt) at the (a) coastal and (b) inland sites.



Female infl. and bunch nos; 5 mon lag

Female infl. and bunch nos; 6 mon lag

Figure 7. Quarterly changes in female inflorescence production and bunch numbers harvested (a) five, or (b) six months later at the coastal site. Inflorescence numbers were determined on a sample of 100 palms; bunch numbers from the whole field.

TABLE 5. CORRELATIONS BETWEEN FEMALE INFLORESCENCE AND LAGGED BUNCH NUMBERS.

Site	Months lag	df	r	P
Coastal	5	12	0.792	<0.001
	6	12	0.556	<0.05
Inland	5	7	0.223	ns
	6	7	0.606	<0.1

At neither site was there any evidence for any regular pattern in percentage abortion or in changes in sex ratio. Female inflorescence counts on the 100 palms sampled at the coastal site correlated well with bunch numbers harvested from the whole field five or six months later *(Figure 7; Table 5)*. Bunch yields at both sites showed a maximum inverse relationship with past yields when lagged 6-7 months (Henson, 1998).

DISCUSSION

In this study, data from coastal and inland sites were used to quantify the seasonal variation in the assimilates needed to support varying growth and FFB yield and to examine how this varying demand could be met. There were several stages in this analysis, the first being the use of a bunch production model (Henson, 1997) based on bunch analysis results for the two sites and new estimates of the dry weights and energy contents of bunch components. This model allowed calculation of the dry matter (in 'non-oil equivalents') incorporated into bunches (bunch dry matter production: BDMP*) during each month, on the basis of subsequent FFB harvests. It was superior to using the current FFB harvest as a measure of productivity, as only a fraction of FFB dry matter harvested in a particular month is actually formed in that month. Although based on a fixed bunch growth rate throughout the year, the results have been shown to be relatively insensitive to growth duration.

The next stage was to assess VDMP on a monthly basis. This is less satisfactory as frequent measurements on the same palms are not only costly in time but may also involve an unacceptable level of damage to the palms due to the need with tall palms to remove frond 17 for leaf area and petiole cross-section measurements. Quarterly measurements combined with monthly frond counts seemed a reasonable compromise.

Trunk growth was likewise difficult to assess over short intervals due to the slow vertical growth and imprecise height reference points. Here, quarterly measurements were considered the best that could be achieved. A greater uncertainty in the measurement of trunk DMP concerns the assumptions regarding density, which is taken to increase linearly with palm age (Corley *et al.*, 1971; Corley and Breure, 1981) but not to change otherwise. Obviously this is unlikely to be the case if dynamic changes were occurring in levels of reserve carbohydrates as proposed here. In future experiments it would be desirable to monitor trunk density directly and at frequent intervals by taking core samples.

No quantitative information was available on seasonal variation in root growth. However, as with the trunk, root production formed only a small proportion of total DMP* and was unlikely to have influenced significantly the seasonal variation in total productivity, which arose mainly from variation in bunch DMP* *(Figure 1)*.

Notwithstanding the above, variation in bunch yield could be augmented if partition ratios between BDM* and VDM were changed. There was some indication that VDMP aboveground increased during periods of minimum BDMP* and vice versa *(Figure 1)*. However, more data to confirm this would be desirable.

The trunk has long been considered as a possible site of reserve assimilates for bunch production (Corley, 1976b). It is here shown theoretically that such reserves could be sufficient to sustain bunch production during periods when current assimilation becomes inadequate and, conversely, for the trunk to act as a store of assimilates currently 'surplus' to requirements for growth. Other storage sites, such as frond petiole bases and possibly large primary roots cannot, however, be precluded.

An alternative to withdrawing assimilates from storage pools would be for photosynthetic activity (*i.e.* AMAX) to increase during periods of peak demand. The presence of a bunch sink in the first year of fruiting was found to be associated with higher rates of net photosynthesis in young palms (Henson, 1990). However, little data for mature palms are available. There was no evidence from eddy correlation measurements at the coastal site for any relationship between above-canopy gas exchange and bunch production (PORIM, 1994). However, attempts to determine if AMAX changes seasonally in relation to bunch load of mature palms would still be worthwhile.

While the present analysis satisfactorily explains how seasonal variation in carbon requirements can be met, the manner by which demand for assimilates on the one hand (represented primarily by the developing bunch load), and the expected supply of assimilates on the other (determined to a large extent by radiation levels) are synchronized, is still something of a mystery. Bunch yield is well known to be predetermined largely many months in advance of harvest and hence in advance of any coinciding periods of high radiation, by the differentiation and sustained growth of female inflorescences. The seasonal variation in yield was found largely to be a function of variation in numbers of bunches maturing (and hence of female inflorescence numbers determined at a much earlier stage) and did not appear to depend on any transient changes in mean bunch weight *(Figure 6)*. Although mean bunch weight increases in circumstances favouring increased assimilate supply (Corley and Gray, 1976; Breure and Menendez, 1990; Breure *et al.*, 1990), maximum frame weight is thought to be fixed at the onset of the rapid expansion phase of inflorescence growth ca. five months prior to anthesis. Mean bunch weight did not change after anthesis in response to a thinning of the stand (Breure and Menendez, 1990). Thus, apart from bunch failure or rot (which was not a significant event in the present experiments), the palm shows little ability to adjust rapidly its current sink demand in accordance with external conditions affecting CO_2 assimilation. A way to do this would be for oil content and hence O/B to fall at times of peak FFB yield. However, at the coastal site, no relationship was observed between O/B (which varied erratically over time) and yield over a two-year period of bunch analysis. This may have been because during the present studies, conditions favourable to high assimilation fortuitously coincided with the presence of peaks in numbers of developing bunches.

There were distinct differences in productivity of the two sites which can be attributed in part to periods of low soil water potential at the inland site (results not presented). The lower productivity of the inland site was reflected in both lower light interception and lower photosynthetic conversion efficiencies (E*). Further productivity comparisons are the subject of a following report (Henson, 1998).

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