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NOTES ON OIL PALM PRODUCTIVITY.

V. EVALUATION OF ALTERNATIVE MECHANISMS FOR SUPPORTING SEASONAL VARIATION IN DRY MATTER PRODUCTION

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Three alternative mechanisms leading to seasonal variations in bunch and total dry matterproduction commonly found in stands of oil palm, were examined using a simulation model. The alternatives were: (i) the use of a store of reserve assimilate to accommodate both shortfalls and excesses in current assimilate production, (ii) variation in response to sink demand in the light-saturated rate of grossphotosynthesis (AMAX), and (iii) variation in the proportion of gross assimilates consumed in dark respiration (%R). The alternatives were tested using data from three palm populations for one of which, trunk carbohydrate concentrations had also been measured.

The results show that with certain assumptions, any of these processes could account for the seasonal variations in productivity recorded. However, certainperiods ofrelatively high or low productivity required extreme variations in AMAX, which were considered unlikely. The variations in %R which were needed were also thought unlikely as periods of high productivity required %R to decrease, whereas the opposite trend was more probable. Thus, of the three processes, the utilization of storage reserves appeared the most likely means of accommodating variations in sink demand. However, a model based solely on use of assimilate storage was not entirely consistent with measured changes in trunk reserves and changes in AMAX and /or use of reserves, located in other parts of the palm may be involved.

Further research needed to resolve this issue is suggested.

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INTRODUCTION

In previous studies, total dry matter production of oil palm and production of bunch dry matter (TDMP* and BDMP* respectively1 have been assessed in detail on a monthly basis at several sites (Henson, 1997; 1998; Henson and Chai, 1998). In one such exercise (Henson and Chai, 19981, the levels and seasonal variations in production were compared with those predicted by a simulation model of oil palm growth derived from that of van Kraalingen (1985). The model uses incident radiation and crop leaf area index as the main inputs and assumes leaf photosynthetic capacity and crop respiratory activity to be constant. Variations in sink demand (represented mainly by seasonal changes in fruit bunch production), were accommodated by utilization of storage reserves, assumed to be mainly located in the trunk. Measurements of trunk carbohydrate contents (Henson et al., 1999) have revealed seasonal changes and between-palm variation in concentrations of soluble sugar and polysaccharide fractions which are partly related to bunch load. The contribution to the seasonal yield pattern, of possible changes in leaf photosynthetic capacity or in crop respiration rates has not been explored. The variations in these parameters needed to account for the observed changes in productivity and palm sink strength are examined in this report.

MATERIALS AND METHODS

Experimental Data

Detailed data on monthly changes in total dry matter production and leaf area index (LAI) over several seasons were available for two sites, one coastal and one inland, both in West Malaysia (Henson and Chai, 1998). For a third site (inland), measurements of bunch production and trunk carbohydrate concentrations were acquired over a two-year period (Henson et al., 1999). Above-ground vegetative dry matter production (VDMP), LAI and root dry matter production were measured concurrently on a sample of adjacent palms. The vegetative measurements were only made annually and thus, seasonal variation in TDMP* at this site was ascribed solely to BDMP*. For convenience, the above sites are referred to furthe as Sites 1, 2 and 3 respectively.

Daily totals of incoming solar radiatio needed to run the simulation model were eithe measured at the sites (Sites 1, 2) or wer available from a regional meteorological statio (Site 3).

Simulation Modelling

The simulation model GHPOT (Henson 1989; 1992) is based on the model of va Kraalingen (1985) and the work of Breur (1988). It was modified to produce monthl estimates of VDMP, BDMP* and TDMP* an in the standard form, uses total daily sola radiation (MJ m^{-2}), LAI and single frond dr weight as inputs. The model calculates tota assimilate production and above-ground VDM is obtained by regression from single frond dr weight (PORIM, 1994). VDMP and (measured root dry matter production are subtracted fro TDMP* to give BDMP*. (The * superscrip indicates that values are in 'non-oil dry matte equivalents; Squire, 1985).

Parameter values used in the 'standard model were as given earlier (Henson and Chai 1998) and were:

AMAX (photosynthetic rate at saturatin radiation): 24µmol m^{-2} s^{-1}, Site 1; 22µmol m^{-2} s^{-1}, Sites 2 and 3.

EFF (photosynthetic efficiency at lo irradiance): 0.25µmol J-i.

K (extinction coefficient of canopy for PAR 0.45.

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

Calculation of Trunk Assimilate Concentrations

For Sites 1 and 2, for which direct measurements of trunk carbohydrates were lacking, the initial starting concentration of total carbohydrate reserves was assumed to be 186m glucose equivalents g^{-1} dry weight (Henson an Chai, 1998). For Site 3, the starting concentration was that measured. Subsequent change in assimilate reserves were then calculate based on the difference between observed TDMP* and modelled assimilate production.

RESULTS AND DISCUSSION

Variation in AMAX

One mechanism by which the supply of assimilates could be varied to meet the demands of growth centres in the palm would be for frond photosynthetic activity to increase in line with demand. Total photosynthate production is dependent on environmental factors (principally radiation levels and water supply), frond area, canopy light extinction coefficient (the last two determining radiation interception) and leaf photosynthetic rate. The photosynthetic rate can be characterized in terms of the photosynthesis-light response curve as defined by two characteristic parameters; the initial slope at low radiation intensities (the photosynthetic efficiency or quantum yield) and the assimilation rate at saturating light intensity (maximum assimilation rate or AMAX). The simulation model takes account of variations in radiation and leaf area/light interception but assumes water to be non-limiting and uses fixed values for the leaf photosynthetic parameters. The quantum yield generally shows little variation whereas AMAX is more plastic and could well be amenable to sink influence.

Figure la-c show the values of AMAX which would be required at the three sites for the attainment of measured TDMP* based on measured LAI and radiation, a fixed respiratory loss and no use of storage reserves. As expected, AMAX generally increased with TDMP* but the correlations between the two were less than perfect due to the variable influence of changes in LAI and solar radiation. Thus, as LAI or radiation increase, the need to vary AMAX with TDMP* diminishes. Nevertheless, there were significant positive

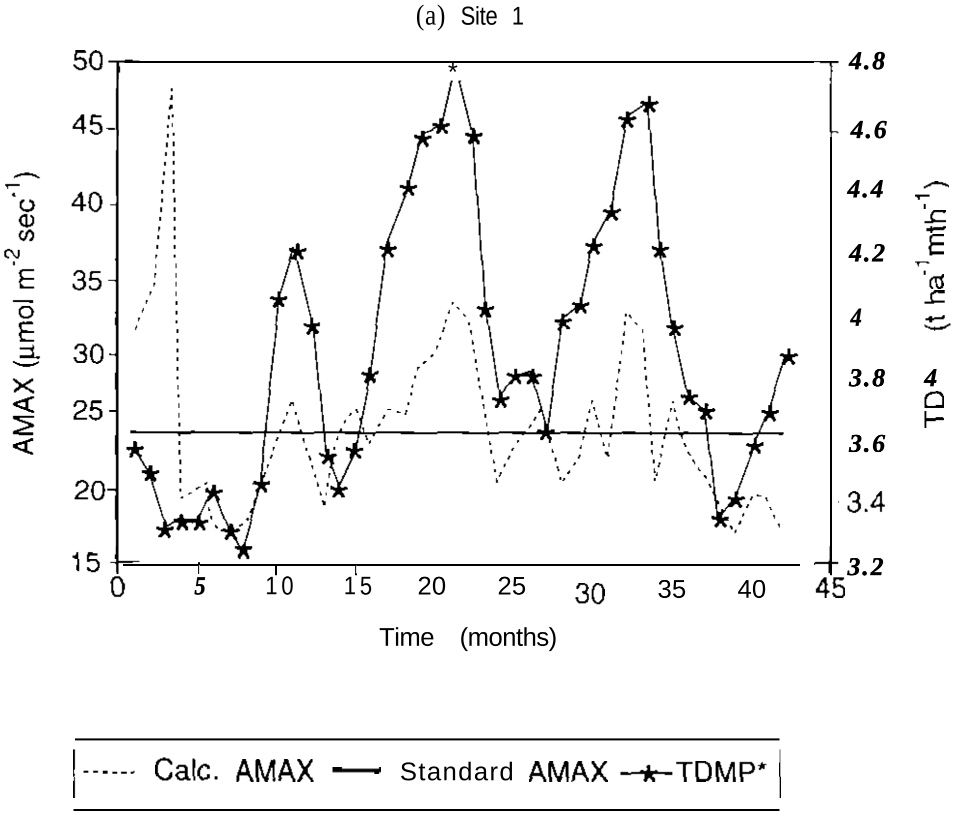
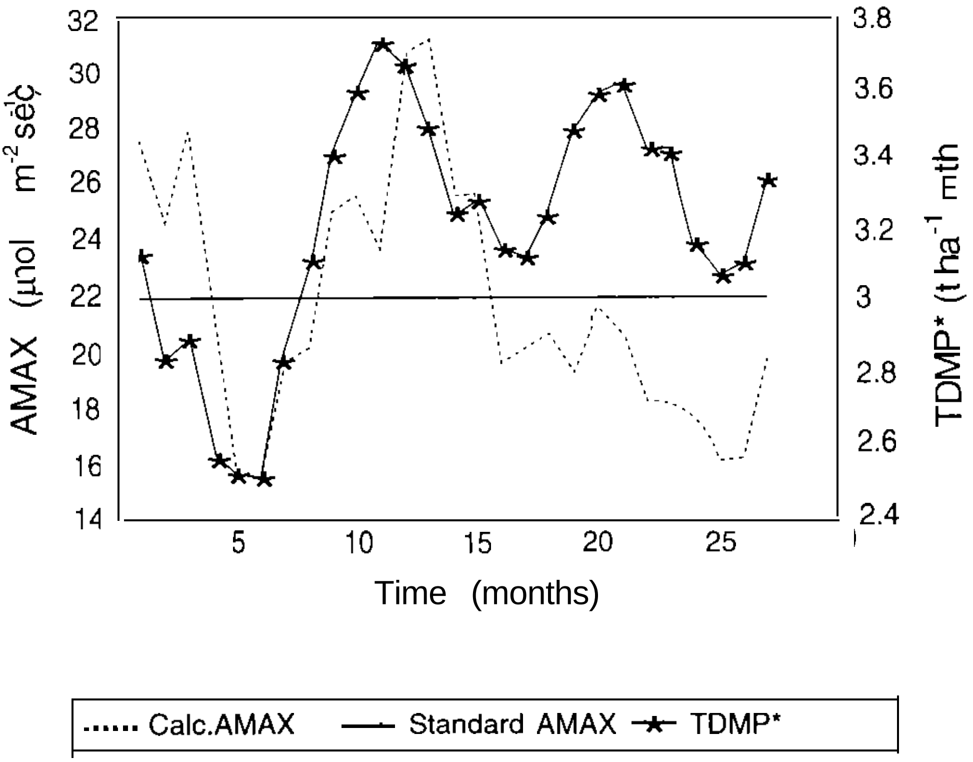
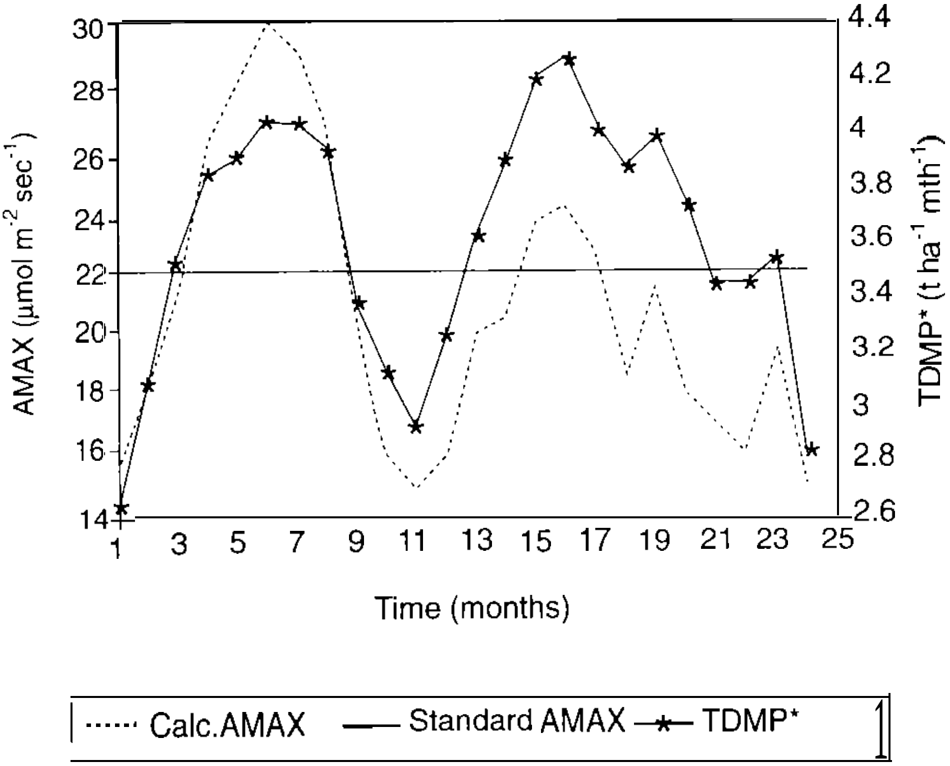


Figure la-c. Monthly changes at Sites 1, 2 and 3 in total dry matter production (non-oil equivalents; TDMP) and in AMAX (light-saturated rate of photosynthesis) needed to sustain TDMP? Standard AMAX is also indicated. Respiration losses were held constant.*

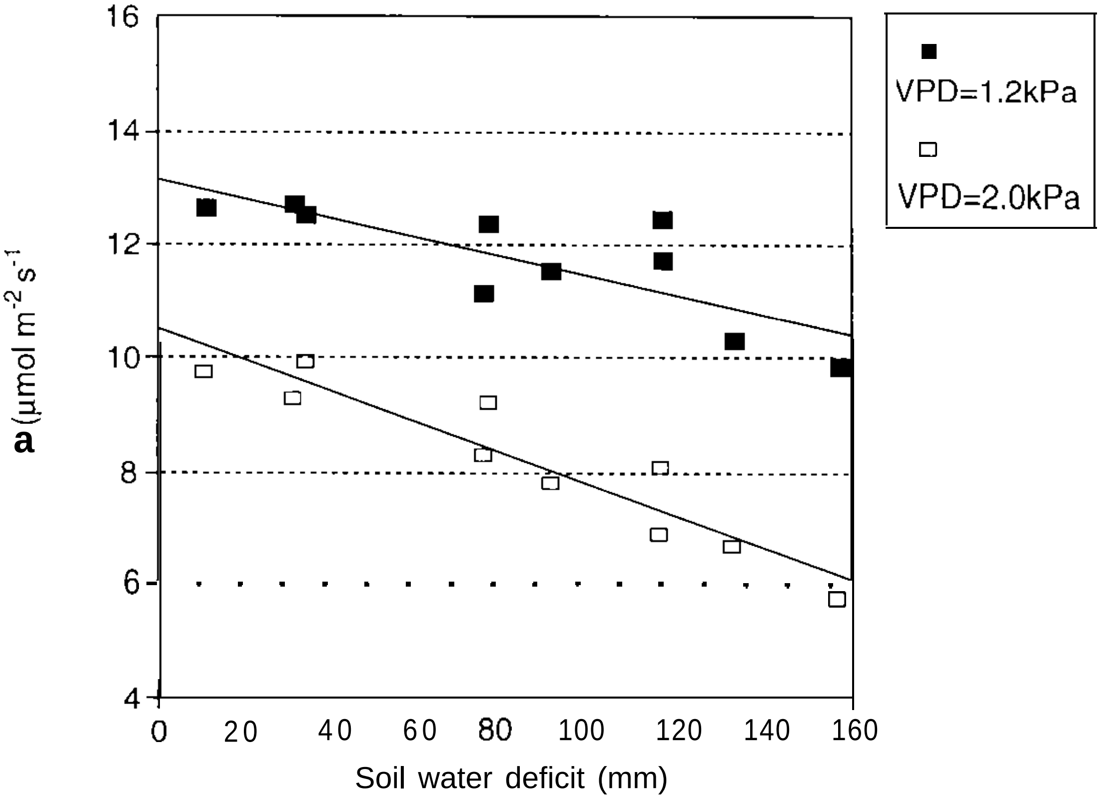
(b) Site 2



(C) Site 3



(a) Response to soil water deficit



(b) Response to VPD

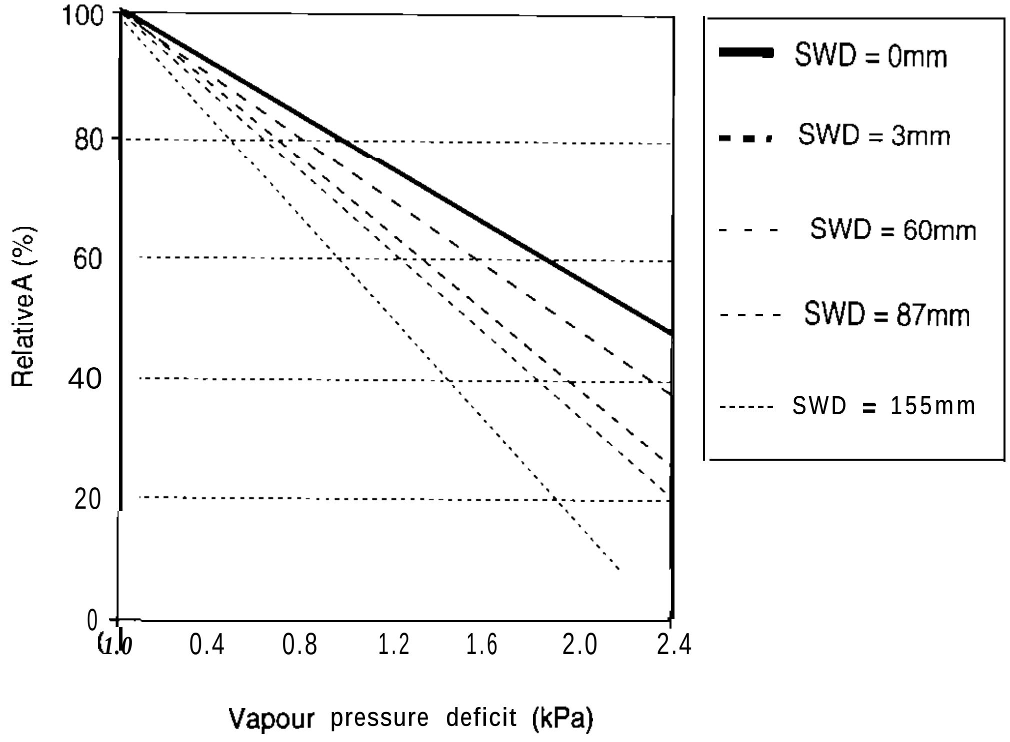


Figure 2. (a). Relationships at Site 3 between photosynthetic rates of upper fronds and soil water deficit at two levels of atmospheric vapour pressure deficit (VPD). (b). Relationships between relative photosynthetic rates and atmospheric vapour pressure deficit at various levels of soil water deficit (SWD).

correlations at all three sites between the required AMAX and TDMP*.

At Sites 1 and 2, the overall correlations between AMAX and TDMP* were significant at $P<0.05$ while that at Site 3 was significant at $P<0.001$.

The range of AMAX needed to meet sink requirements varied from 15 to 48µmol m^{-2} s^{-1}; the latter value, for Site 1, being a single exception with the next highest being 34.5 µmol m-2 s^{-1}. This range contrasts to standard AMAX values based on in situ measurements of 22 to 24µmol m^{-2} s^{-1}. While some variation in AMAX is not improbable and there is evidence in oil palm for increase in photosynthetic rate with sinkdemand (Henson, 1990), theextreme values noted here have not previously been encountered experimentally within individual palm stands, though appreciable variation is possible with a range of palm ages and growing conditions (Henson, 1991; Lamade *et* al., 1996; Smith, 1989).

Variation in AMAX at the 'dry' inland Sites 2 and 3 could have arisen due to variation in soil water supply (Figure *3a*). The response of AMAX to soil water deficit (SWD) at Site 3 was therefore modelled based on observed regressions at the site of photosynthetic rates (A) on SWD at various humidities (Figure 2). At a mean vapour pressure deficit of 1.6kPa, A was found to decline linearly by 0.192% per mm increase in SWD. Adjusting AMAX for effects of SWD resulted in only minor changes to TDMP* compared with use of a fixed value of AMAX, mainly because quite severe droughts were needed to substantially affect AMAX. (AMAX proved more sensitive to change in vpd than in SWD; Figure 26). TDMP* calculated using the water deficit model was reduced at Site 3 in 1990 by only 3.2% and in 1991 by only 5.7%, compared with TDMP* calculated ignoring water deficit, while the water-deficit dependent TDMP* still failed to match the actual TDMP* (Figure *3b*).

Variation in %R

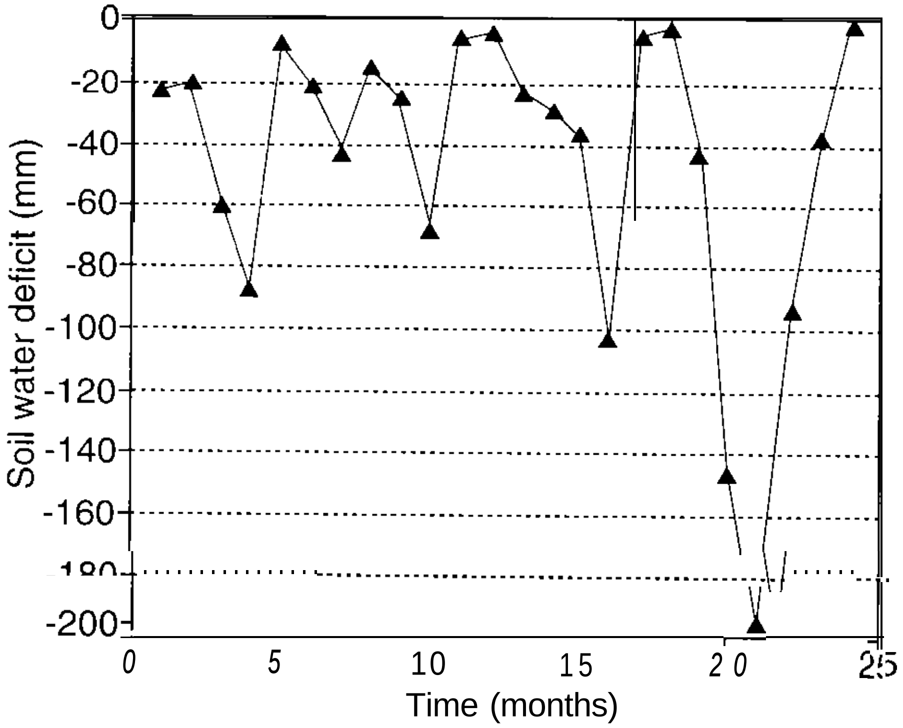
Adjustment in the proportion of gross assimilates consumed in respiratory processes could also **be** made to account for seasonal variation in TDMP* (Figure *4a-c*). At the three sites, the range of %R required for this varied from around 50% to 68% and averaged slightly higher for the two inland sites than for the coastal site. Although variation in %R could adequately accommodate the changes in productivity, there are several factors rendering such a mechanism rather unlikely. There are two components to total respiration, namely growth respiration (GR) and maintenance respiration (MR). The first type of respiration is directly coupled to growth and therefore would be expected to increase in direct proportion to TDMP*. This is the reverse of the changes in %R required to accommodate variation in TDMP*. Admittedly for mature palms, GR is normally the smaller of the two components; constituting from 22% to 29% of total respiration (Breure, 1988; Henson, 1992) and so could be counterbalanced by changes in maintenance respiration. However, rather large reductions in MR would be needed, which seem unlikely.

Maintenance respiration, and hence total respiration, is sensitive to variations in temperature. However, there was no significant correlation between %R and mean air temperatures at any of the sites. Also, variation in mean monthly air temperature was small; being less than 1.4°C at the coastal site and 1.8°C and 1.7°C at inland Sites 2 and 3. Assuming a respiratory quotient of two, a 1.8°C temperature rise would increase MR by less than 14% and total respiration (assuming MR to be 75% of total) by less than 11%. This restricts the probable change in the median value of %R with temperature to a maximum of plus/minus 3.3%; considerably less than was needed to account for changes in TDMP*.

Use of Trunk Reserves

Previous calculations (Henson and Chai, 1998) suggested that use of trunk carbohydrate reserves provided a plausible mechanism for resolving discrepancies between assimilate demands and current assimilate production. This presupposes that at least part of the acid-hydrolysable polysaccharide fraction is available for conversion into monosaccharides which are capable of being translocated to growth sinks, and that the reverse process can operate

(a) Site 3; soil water deficit



(b) Site 3; TDMP*

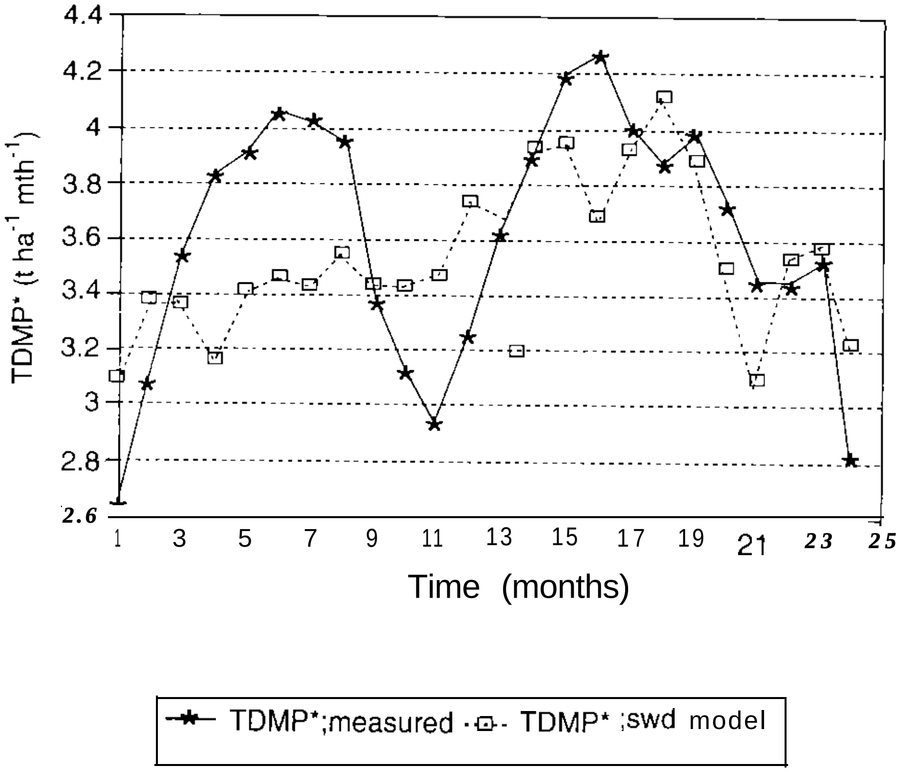
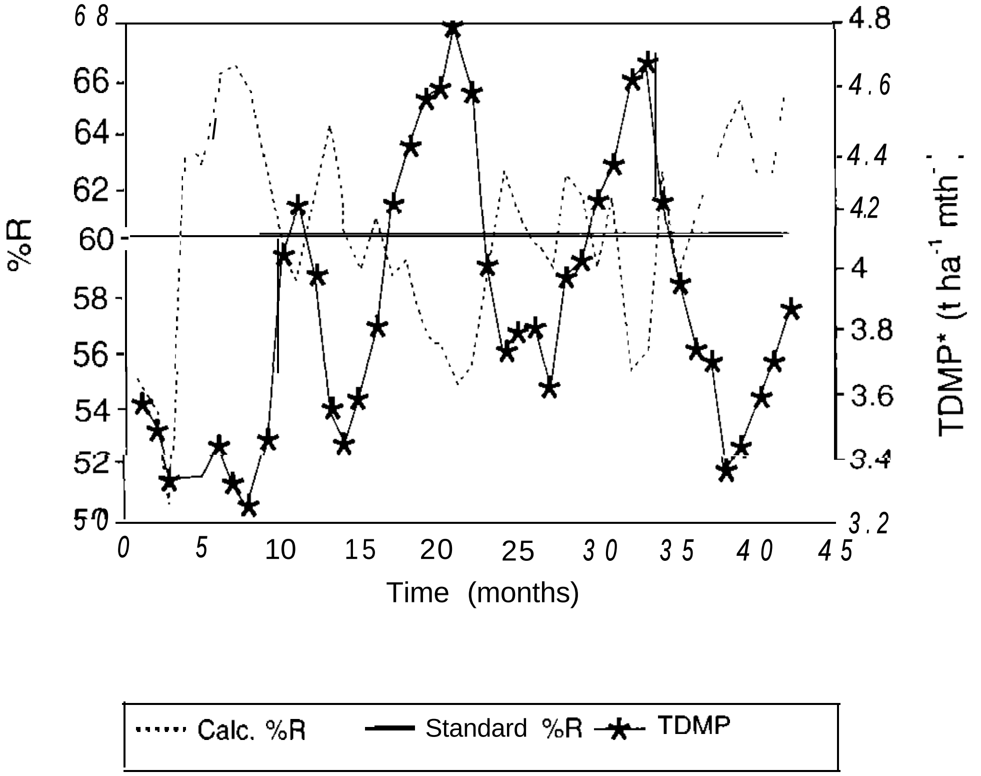


Figure 3. (a). Soil water deficit at Site 3. (b). Comparisons for Site 3 of measured TDMP, and TDMP* calculated assuming AMAX to vary in response to soil water supply (SWD model).*


(a) Site 1

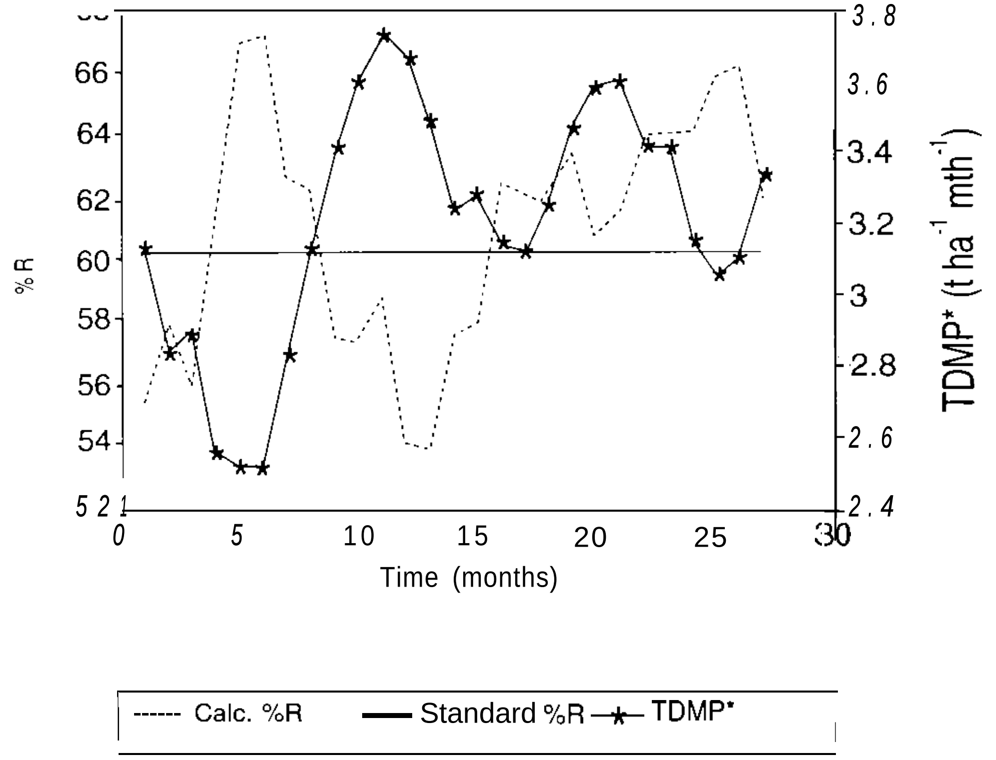
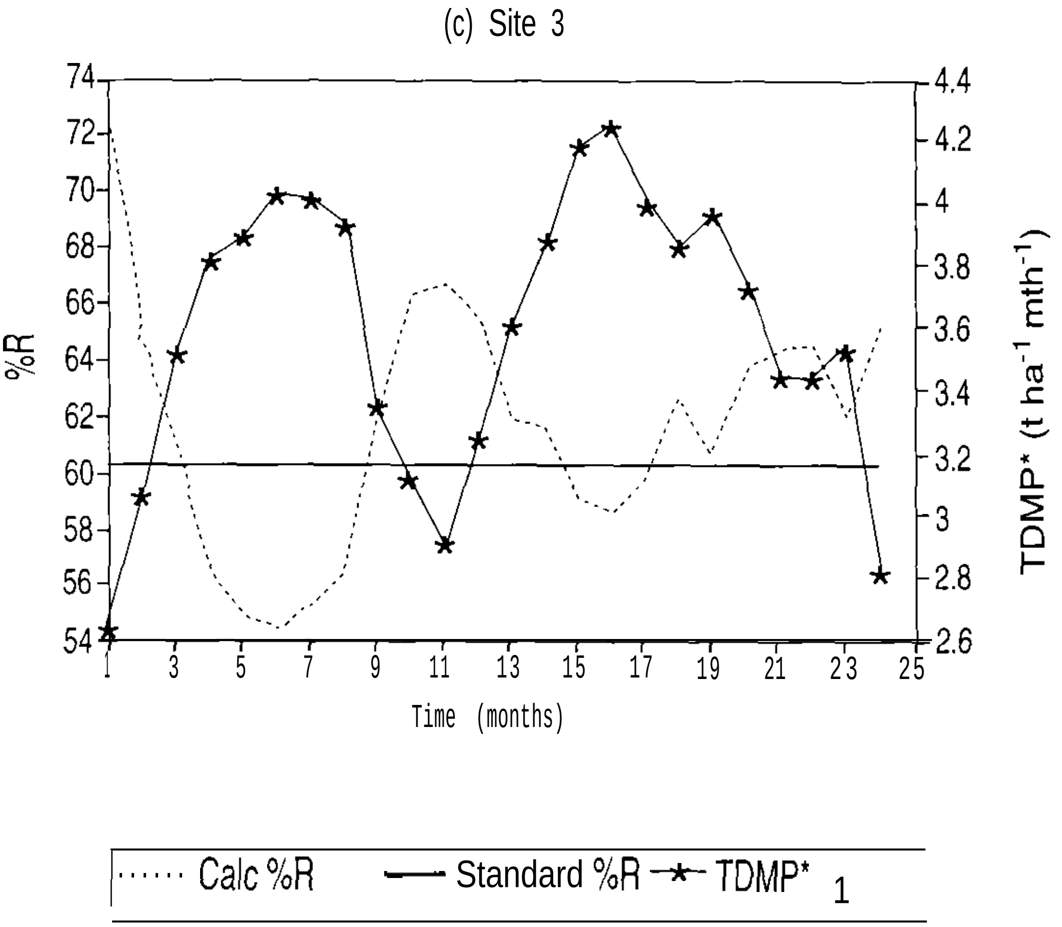

(b) Site 2

Figure 4a-c. Monthly changes at Sites 1. 2 and 3 in total dry matter production (non-oil equivalents; TDMP) and in %R (percentage of gross assimilates consumed in respiration) needed to sustain TDMP* with AMAX held constant. Standard %R is also indicated.*



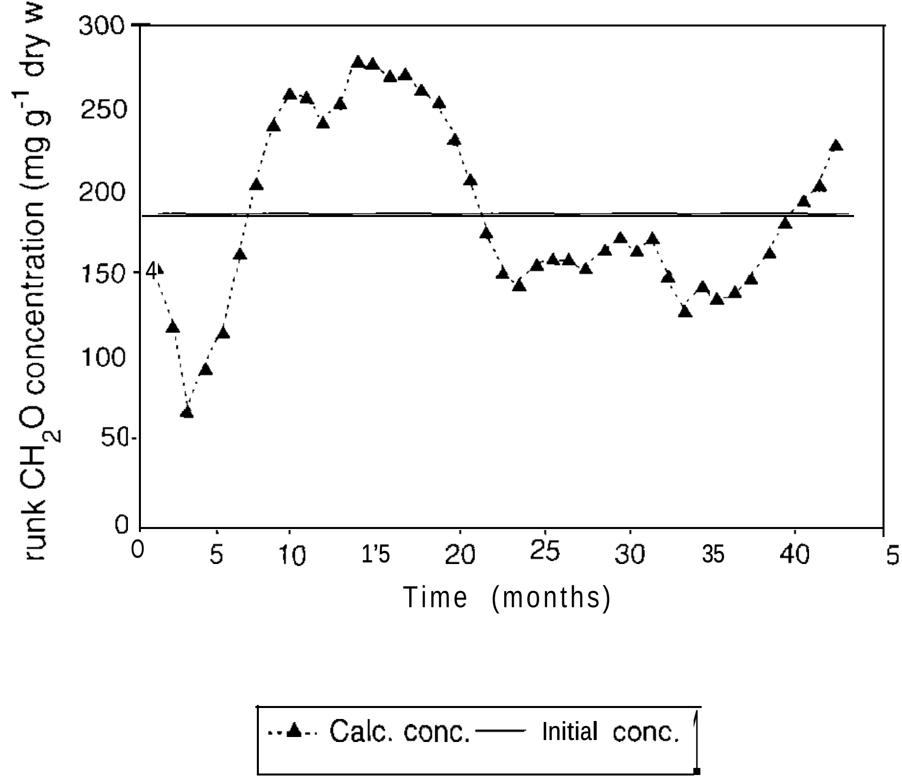
in times of excess assimilate production.

Calculated changes in trunk carbohydrate concentrations which would result from operation of the above mechanism are shown in Figure 5. It can be seen that provided the initial level of reserves are fully available and calculations of net assimilation are realistic, then the reserves were adequate to sustain the observed production. However, at Site 3, where concentrations of reserves were measured (Henson *et* al., 1999), the calculated changes did not match those measured (*Figure 5c*). This may suggest that reserves in other parts of the palm are being utilized or that the measured changes in the trunk samples were not representative of changes in the trunk as a whole. Alternatively, the use of trunk reserves might form only one of the several means whereby carbon demands of growth sinks are satisfied.

CONCLUSIONS

Clearly, many assumptions are involved in assessing the probable mechanisms whereby seasonal fluctuations in the demand for carbon by growth centres are met. Of the three main mechanisms considered here, that involving the utilization of stored assimilate reserves is considered most likely. However, this should not preclude the possibility of several processes acting together to achieve the required effect. There is good evidence in other crop plants both for variation in AMAX and use of reserves to meet sink demands in different circumstances, though as far as the present writer is aware, there has been no single study demonstrating the operation of both mechanisms in concert. 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 oil palms (Henson, 1990). While 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

(a) Site 1



(b) Site 2

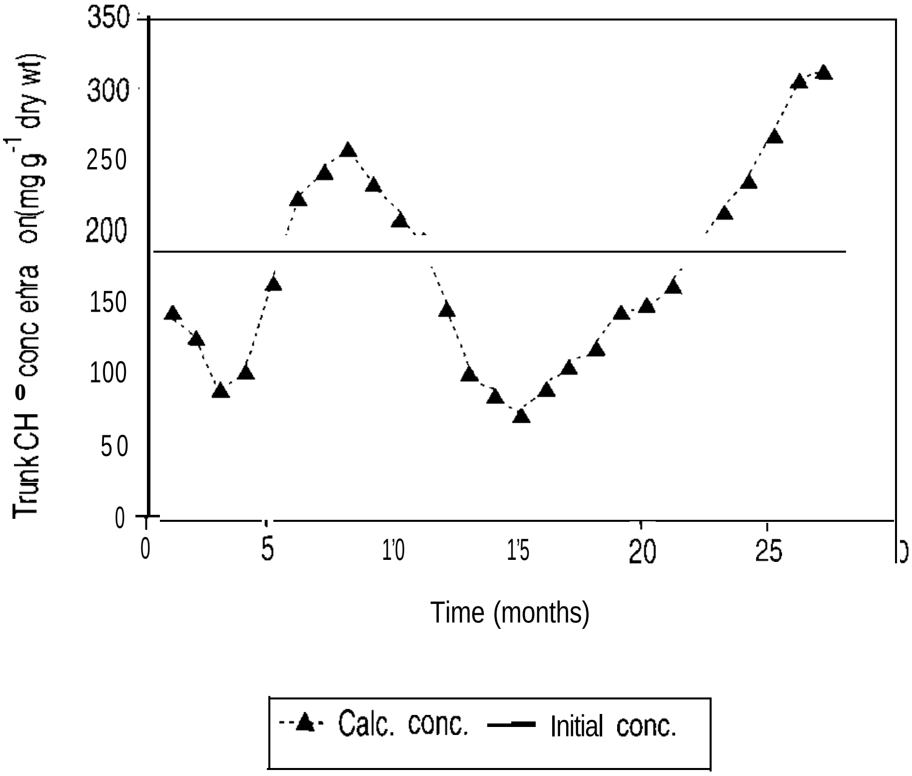
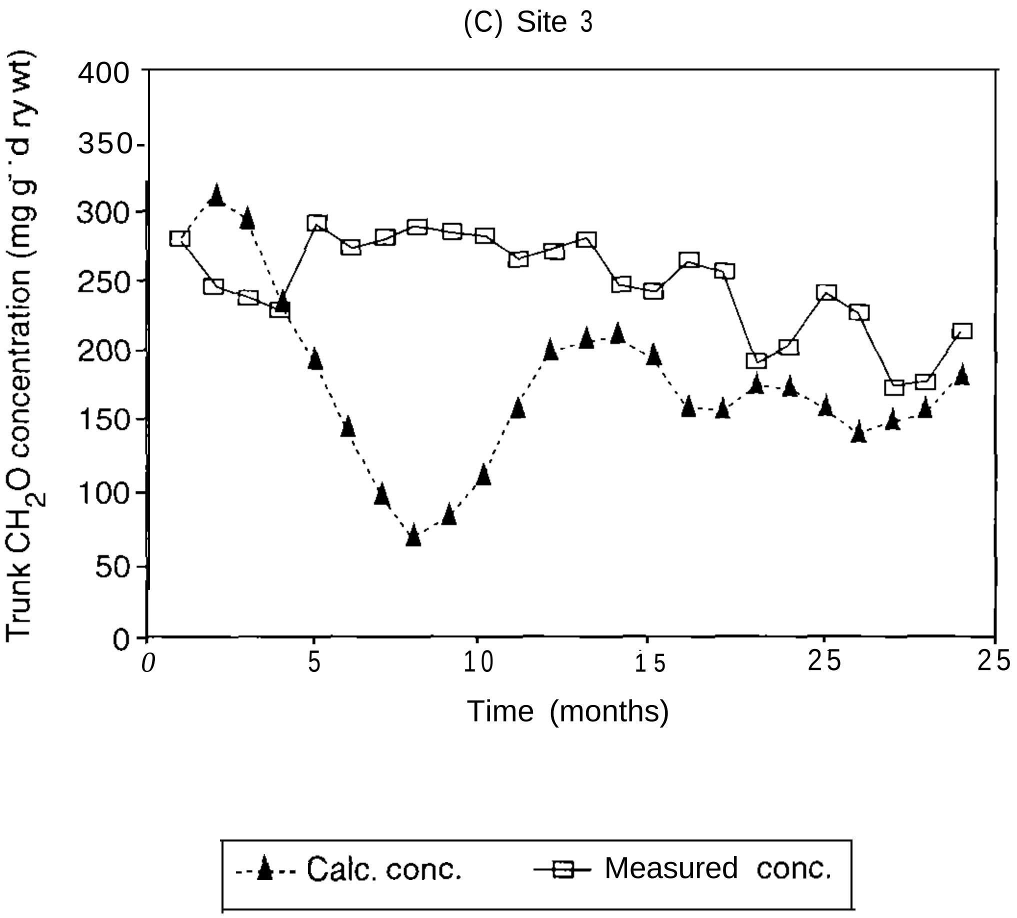


Figure 5a-c. Calculated changes in trunk carbohydrate reserves at Sites 1, 2 and 3 compared with the initial assumed (Sites 1 and 2) or measured (Site 3) concentrations.



bunch load of mature palms would still be worthwhile.

Although the use of trunk reserves seems feasible, a more chemically rigorous examination of the nature and availability of these reserves is required together with an examination of the endogenous enzyme systems which would be needed to ensure their availability. Possible involvement of other storage sites, such as frond petiole bases and large primary roots should also be examined.

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