CARBON ASSIMILATION, RESPIRATION AND PRODUCTIVITY OF YOUNG OIL PALM (*Elaeis guineensis*)

Keywords: *Elaeis guineensis*; Carbon assimilation; Respiration; Dry matter production.

I E HENSON *

Standing dry matter, dry matter production, leaf area, leaf photosynthetic parameters, and dark respiration rates of main plant organs were measured for palms in the third year after planting on two adjacent sites ('dry' and 'wet') differing in ground water supply. The wet site had the higher productivity.

Gross assimilation of CO_2 (GA) was obtained (i) from the sum of dry matter production (DMP) and total respiration (R); (ii) from DMP alone, assuming this to be 1/4 of GA; and (iii) as the output of a simulation model of canopy photosynthesis. All three methods resulted in similar GA values, but some adjustment of light interception parameter values was needed to obtain realistic model output.

Respiration was partitioned into growth and maintenance components and general carbon budgets were constructed for the two sites.

INTRODUCTION

With annual crops, productivity can be measured by harvesting a portion of the entire canopy and determining dry matter increases over time. With perennial tree crops this is not feasible and alternative non-destructive methods need to be employed. With oil palm the single stem and single vegetative growing point, and the regular arrangement of the fronds have facilitated the development of standard systems of measurement for assessing above-ground productivity and standing dry matter (Hardon *et al.*, 1969; Corley *et al.*, 1971a; Corley and Breure, 1981). Only root growth is not examined in these procedures but it can be allowed for, generally by adding an extra 5%-10% to the total above-ground values (Squire and Corley, 1987).

* Palm Oil Research Institute of Malaysia,
P O Box 10620, 50720 Kuala Lumpur.

Original manuscript received on 29 June 1991

In addition to productivity, it is valuable to assess the gross photosynthetic activity of a crop and the amounts and proportions of carbon used in respiratory processes. If respiration can be minimized without affecting gross assimilation, or if gross assimilation can be increased without increasing respiration, then it follows that dry matter production will be raised.

Again with annual crops, or other plants of small stature, it is feasible to measure gross canopy photosynthesis and dark respiration directly, by enclosing the plants in a chamber or growing them in an enclosed structure such that CO_2 exchanges can be measured. Again, this is not feasible with oil palm.

In the following exercise an attempt has been made to evaluate productivity and gas exchange on a canopy scale for young palms in the third year after planting (first cropping year). The palms were grown on two adjacent sites differing in ground water supply. Details of the sites, and results of previous physiological and growth measurements have been given elsewhere (PORIM 1989; 1990; Henson and Chang, 1990; Henson, 1991c).

METHODS

There were three main parts to the analysis.

Estimation of annual dry matter production

This was based on annual measurements of:

i) frond dimensions
ii) frond production
iii) trunk biomass
iv) root biomass
and periodic harvests of fruit bunches.

Standard methods referred to in the Introduction were used for i) and ii) except that appropriate calibration factors for relating linear dimensions to frond dry weight and laminar area were first determined by destructive sampling. Details of the methods and the derived factors were as given in Henson (1991a). Because of the small size of the trunk it was not possible to assess its dry matter production by the standard methods of height and diameter measurements. Trunk biomass production was therefore assumed to represent the same fraction of frond biomass production as reported by previous workers (Ng *et al.*, 1968; Corley *et al.*, 1971b) for similarly aged palms.

Root biomass was determined using an auger method as described by Chan (1977). Samples 11 cm in diameter were taken to a depth of one metre, at 50 cm intervals along three axes radiating from the palm 'centre' 120° apart. The roots present in successive 10 cm depth increments were sorted into primary, secondary and tertiary (plus quaternary) classes and their dry weights determined. Root sampling was carried out at eight months after the first annual assessment of above-ground dry matter. To obtain estimates of mean standing root dry mass and net root dry matter production during the study year, the following procedure was adopted.

Estimates were first made of the root : frond dry matter ratio, the frond dry matter at the time of root sampling being obtained by linear interpolation between the annual measured values. The root: frond dry matter ratios, obtained separately for each site, were then used to produce from the frond dry weight data, values for root dry mass at the start and end of the study period. Net root dry mass production was obtained as the difference between the two.

The measurements of above-ground biomass, including bunch production, were carried out for 36 palms on each site. Root sampling was confined to five palms per site, randomly located.

Estimation of annual respiration

Total respiration per palm was calculated from dry weights of component parts of the palm and measured respiratory coefficients. The respiration was estimated separately for the standing dry matter at the end of the second and third years of planting and the mean of the two values was used in the annual production models.

Respiration was measured as CO_2 evolution by infra-red gas analysis using an open flow 'steady-state' system, and 'respiratory coefficients' were established for the main plant organs, namely, leaflets, petioles and rachises, trunk, roots and fruit bunches (*Table 1*).

The respiratory coefficient for leaflets was obtained in the course of determining photosynthesis-light response curves using a CO_2 gas analyzer

(Henson, 1991b), by extrapolating the linear portion of the curve at low light intensities back to zero irradiance. The coefficient differed between sunlit and shaded fronds and is likely to be influenced, as are all the coefficients, by temperature. A weighted value, representative of these variations, was therefore used. As it was determined on a leaf area basis it was necessary to determine also the dry mass per unit area.

Coefficients for other palm parts were also determined by CO_2 gas analysis, but using detached samples. Coefficients for the root differed for the various root orders (primary, secondary, tertiary plus quaternary) and the value given in *Table 1* has been appropriately weighted for the different contributions to the total mass by each order. These contributions were identical for the two sites and so the same weighted coefficient could be used.

The coefficient for the trunk was a mean of values obtained for different distances from the apex. The relatively high coefficient reflects the fact that the trunk tissue was entirely within the 'active' crown region of the palm.

The coefficient for bunches was determined from gas exchange measurements on individual spikelets and fruits. Respiration rates were found to decline during bunch maturation and the coefficient of 38.83 g CO_2 kg^{-1} day^{-1} (*Table 1*) represents an average value for the period from anthesis to maturity (about 160 days). Total bunch respiration per palm (BR) was calculated as:

$$BR = 38.83 \times BFWH \times 0.5 \times 0.5 \times BBN$$

where BFWH = mean bunch fresh weight at harvest, and BBN = mean black bunch number per palm; 0.5 is the factor converting fresh weight to dry weight and the second 0.5 is needed to give the mean bunch weight averaged over time.

Estimation of gross assimilation

From the mean respiration (R) and the measured dry matter production (DMP), the canopy gross assimilation (GA) over the year was assessed as:

$$GA = R + DMP$$

As an alternative approach, DMP was assumed to be 25 per cent of gross assimilation so that:

$$GA = DMP \times 4$$

It therefore follows that:

$$R = DMP \times 3$$

Finally, gross assimilation was computed using the canopy photosynthesis model of Goudriaan and van Laar (1978) which also forms the photosynthetic sub-routine of the larger oil palm simulation model (OPSIM) of van Kraalingen (1985) and van Kraalingen *et al.*, (1989).

Estimates of GA from the model can be compared with GA values calculated as above. Alternatively, the modelled GA can provide estimates of R or DMP as:

$$R = GA - DMP$$
$$\text{and} \quad DMP = GA - R$$

The main input parameters of the model are:

(i)	AMAX	- light saturated value of gross leaf photosynthesis
(ii)	EFF	- photosynthetic efficiency at low irradiance
(iii)	LAI	- leaf area index of canopy
(iv)	K	- extinction coefficient of canopy for photosynthetically active radiation
(v)	LAT	- latitude at site
(vi)	AVSUN	- average sunshine hours at site
(vii)	DL	- day length - specified by LAT and DOY (day of year)

Parameter values were either measured (AMAX, EFF, LAI) or taken from published values or records (K, AVSUN, DL).

RESULTS

The approaches outlined above were applied to the two groups of palms growing on adjacent wet and dry sites during the third year after planting.

Dry matter production

This is shown in *Table 2*. The two sites differed more in bunch dry matter production (wet site yield = 1.64 x dry site yield) than in vegetative dry matter production (wet site = 1.11 x dry site). Root dry matter production was identical on both sites.

TABLE 1. RESPIRATORY COEFFICIENTS FOR VARIOUS PARTS OF THE PALM, USED TO CALCULATE TOTAL RESPIRATION

	g CO_2 kg^{-1} dry matter day $^{-1}$
Leaflets	38.28
Petioles and rachises	9.35
Trunk [1]	30.41
Roots	15.04
Fruit bunches[3]	38.83

[1] within crown

[2] weighted for different root orders (see Methods)

[3] average for period from anthesis to maturity (see Methods)

Respiratory losses

Respiratory coefficients, measured for each major organ, are shown in *Table 1.* From the respiratory coefficients and the standing dry matter measurements and estimates, the current respiration of the canopy was calculated for the beginning and end of the production year. *Table 3* shows the mean of these values and the relative contributions made by the different organs to total palm respiration. Leaflets contributed most to total respiration losses followed by bunches (on the wet site), petioles and rachises (wet site) and roots.

Gross assimilation

Knowing the dry matter production and respiration the gross assimilation can be calculated. From *Table 4* gross assimilation is seen to be 47.6 and 59.7 tonnes CH_2O ha^{-1} an^{-1} for the dry and wet sites respectively, equivalent to 69.9 and 87.5 tonnes CO_2 ha^{-1} an^{-1}. Respiratory losses constituted 76.1 and 75.8 per cent of gross assimilation on dry and wet sites respectively. These values are similar to those derived by other workers (Corley, 1976; Breure, 1988 ; van Kraalingen *et al.*, 1989; Dufrene, 1989).

If the gross assimilation is taken as being four times the DMP (*i.e.* R = 75 per cent of GA), values of 45.5 and 57.7 tonnes CH_2O ha^{-1} an^{-1} for dry and wet sites are obtained, equivalent to 66.7 and 84.6 tonnes CO_2 ha^{-1} an^{-1} respectively. These values are only three to five per cent lower than those derived from measured DMP + R (*Table 5*).

Gross assimilation was also calculated using the canopy assimilation model. In the model, AMAX of the dry site was set to 90.6% of the wet site (90% of net photosynthesis plus the same dark respiration) to allow for lower rates during short dry periods. For the wet site, a value of GA comparable to those obtained by the preceding methods was produced (*Table 5*), though only after using a K value of -0.67 rather than the more commonly quoted one of -0.47 (Squire, 1984; Squire and Corley, 1987), and after substituting the measured LAI with an 'effective LAI' (based on the standard coefficients used to obtain 'true' frond area from 'relative' area; Hardon *et al.*, 1969). (The rationale for these modifications is discussed elsewhere: Henson, 1991a).

Carbon budget

From data in *Tables 2, 3* and *4* it was possible to construct an interim carbon budget for palms growing on the dry and wet sites. This is illustrated in *Figure 1*, where assimilate allocation to the main organs of the palm and its 'partition' between accumulating dry matter and respired material is outlined. Major differences are seen to occur between sites in the absolute assimilate 'flow' to fronds and bunches, which are the main carbon sinks on the plant. For the root sink, it must be remembered that no allowance has been made for loss of carbon in root exudate or in root turnover. Such processes may be quite significant quantitatively, but their measurement remains problematic.

Maintenance and growth components of respiration

From *Figure 1* it can be seen that the ratio between R and DMP varies between organs. This is mainly due to differences in 'turnover rate' of the organs together with differences in biochemical composition which affect respiratory needs. Thus fronds have a long life and continue to respire for at least a further year following the year of their 'production'. On the other hand fruit bunches are formed and mature within 6-7 months after anthesis. Long-lived organs such as fronds, trunk and part of the root system have a potentially greater mainte-

TABLE 2. DRY MATTER PRODUCTION AT DRY AND WET SITES DURING THE PERIOD NOVEMBER 1989 - OCTOBER 1990

	Dry matter production (tonnes ha^{-1} an^{-1})	
	Dry site	**Wet site**
Fronds	5.15	5.88
Trunk and male inflorescences	0.77	0.88
Roots	1.98	1.98
Total vegetative dry matter	7.90	8.74
Fruit bunches	3.47	5.68
Total	11.37	14.42

nance as opposed to growth component of respiration while the growth respiration requirement of bunches is high and that for maintenance low, because of the high cost of synthesizing lipids but low cost of maintaining them.

Because growth respiration is so tightly coupled to the growth process and is related in a highly predictable way to the chemical composition of growing organs (Penning de Vries, *et al.*, 1983), growth respiration can be computed from DMP and biochemical analytical data. Total respiration minus growth respiration then gives maintenance respiration. These were calculated using data in *Table 2* and growth respiration coefficients for the different organs as given by van Kraalingen *et al.* (1989).

It can be seen (*Table 6*) that fronds contributed most to palm maintenance respiration whereas the greatest growth respiration occurred in the bunches as a result of the high assimilate requirements for lipid synthesis. Overall, growth and maintenance respiration contributed 22% - 25% and 75% - 78% respectively to total respiration, and constituted about 18% and 58% respectively of gross assimilation. These overall values agree broadly with results of other studies (Breure, 1988; van Kraalingen *et al.*, 1989; Dufrene, 1989).

DISCUSSION

Of the alternative methods presented for estimating gross and net productivity of oil palm on a canopy scale, none is without some degree of uncertainty. Direct, but non-destructive measurements of canopy dry matter involve some approximations and are still not entirely adequate for estimating total dry matter production in young palms for which frond coefficients change with age (Henson, 1991a), and evaluation of trunk dry matter produc-

TABLE 3. RESPIRATION OF STANDING BIOMASS ON THE TWO SITES AVERAGED OVER THE PERIOD NOVEMBER 1989 - OCTOBER 1990

Organ	**Respiration rate (tonnes CO_2 ha^{-1} an^{-1})**		**% of total**	
	Dry site	**Wet site**	**Dry site**	**Wet site**
Leaflets	18.59	22.56	34.9	34.0
Petiole and rachises	8.82	10.71	16.6	16.1
Trunk	5.72	6.92	10.8	10.4
Roots	10.56	10.56	19.8	15.9
Bunches	9.51	15.60	17.9	23.5
Total	53.20	66.35	100.0	100.0

TABLE 4. RESPIRATION, DRY MATTER PRODUCTION AND CALCULATED GROSS CANOPY PHOTOSYNTHESIS AT THE TWO SITES OVER THE PERIOD NOVEMBER 1989 - OCTOBER 1990

	Tonnes CH_2O ha^{-1} annum^{-1}	
	Dry site	**Wet site**
Total respiration	36.27	45.24
Dry matter production	11.37	14.42
Gross assimilation	47.64	59.66

[a] Primary assimilate (CH20) = CO_2 x 30/44

tion is problematic before stem extension commences. In addition, there is the need for more adequate data on which to base estimates of root productivity.

There are similar problems in applying the canopy assimilation model. The original model caters best for crops with a fully developed canopy cover and a randomly distributed leaf area density, such that light intensity decreases exponentially with depth in the canopy. It is recognized (van Kraalingen, 1985; Gerritsma, 1990) that oil palm may not fulfill the latter criterion, even with full canopy cover, while for palms with incomplete canopy cover, as in the present study, interception of light by partially isolated plants is likely to be underestimated using the conventional approach and 'standard' K value. This may explain why values of GA comparable to those obtained from summing measured dry matter production and respiration

TABLE 5. COMPARISONS OF GROSS CANOPY PHOTOSYNTHESIS AS ESTIMATED BY A CANOPY ASSIMILATION MODEL AND OTHER METHODS FOR THE TWO SITES OVER THE PERIOD NOVEMBER 1989 - OCTOBER 1990

Method	**gross assimilation**			
	(kg CO_2 ha^{-1} day^{-1})		**(tonnes CO_2 ha^{-1} an^{-1})**	
	dry site	**wet site**	**dry site**	**wet site**
i) DMP (measured) + R (measured)	191.4	239.7	69.88	87.50
ii) DMP x 4	182.7	231.8	66.70	84.60
iii) GPHOT[a]	159	237	58.03	86.50

[a]Main parameter values were:

Palm factors:
AMAX : 20.34, dry site; 22.44 µmol m^{-2}s^{-1}; wet site
EFF : 0.225 µmol J^{-1} ; both sites
LAI : 1. 523, dry site; 1. 935, wet site
K : -0.67; both sites

Climate factors:
LAI : 4°
DOY : 130
AVSON : 6. 0 hours

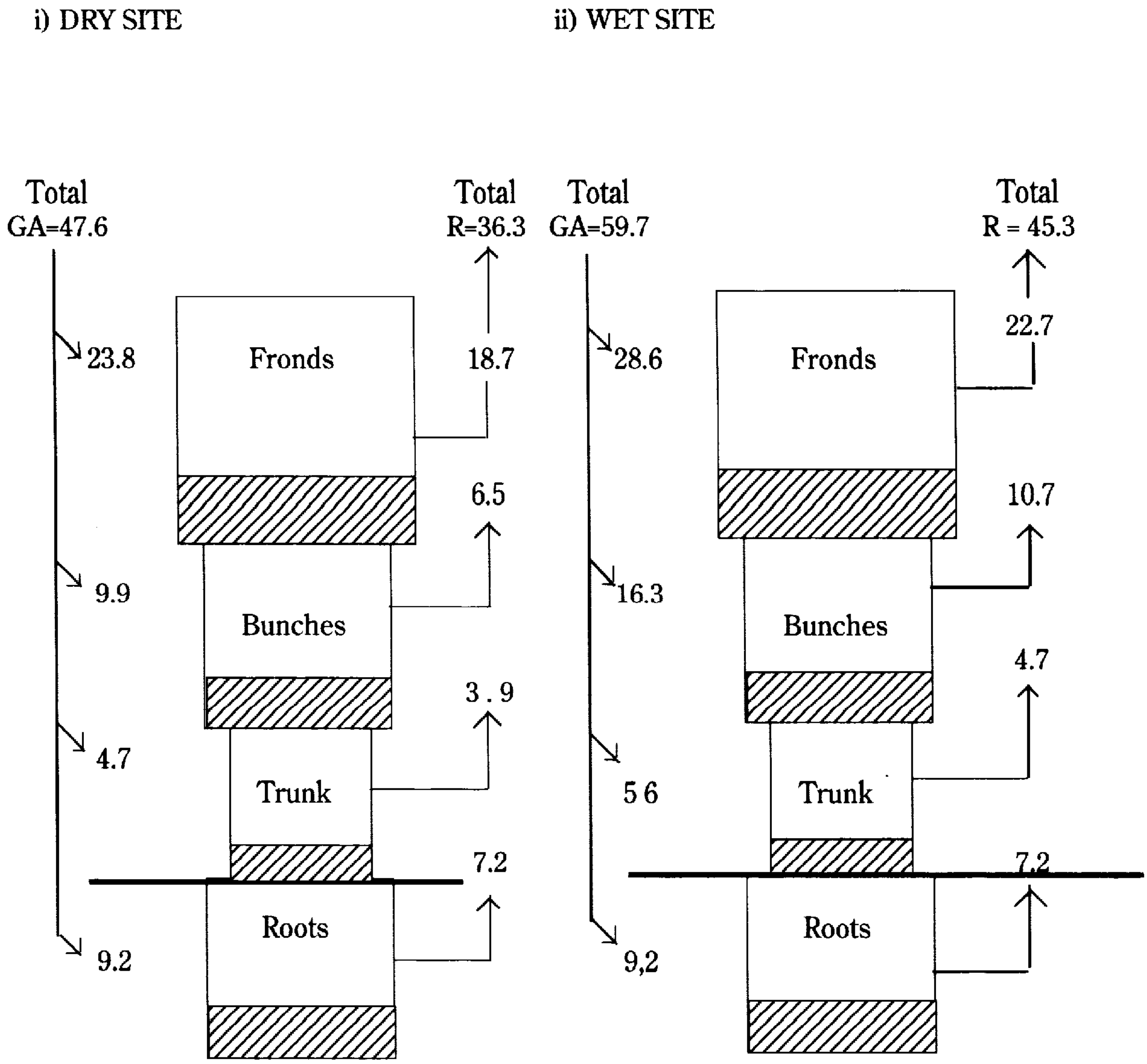

Figure 1. Carbon budgets for oil palms in the third year after planting on dry and wet sites. For simplicity, all data are in tonnes of assimilates (CH_2O) ha^{-1} $annum^{-1}$. (Amounts of respired CO_2 are obtained by multiplying amounts of assimilate by 44/30). Sizes of rectangles are proportional to amounts of assimilates; hatched areas represent dry matter produced and open areas, amount of assimilates lost in respiration (R). GA = gross assimilation. Downward arrows represent inputs and upward arrows outputs from the system.

were only obtained following adjustments to light interception parameters. Further refinements involving more complex light interception models (van Kraalingen, 1986; Gerritsma, 1990) and a taking into account of the differences between diffuse and direct components of radiation (Spitters, 1986) may prove to be more satisfactory.

Despite these uncertainties, the various estimates of GA, R and DMP were consistent with those of previous studies in demonstrating the large proportion of assimilate lost by respiration of oil palm, most of which was in the form of maintenance respiration to which the fronds contributed the bulk (about 59%: *Table 6*).

The usefulness of partitioning total respiration into growth and maintenance components lies in the possibility of reducing the latter via selection and breeding. This may not be easy with a perennial plant but is worth exploring in view of its expected benefits for productivity.

TABLE 6. GROWTH AND MAINTENANCE RESPIRATION (tonnes CO_2 ha^{-1} an^{-1}) FOR PALMS ON THE TWO SITES

		Dry site		**Wet site**	
		Growth	**Maintenance**	**Growth**	**Maintenance**
Fronds		3.32	24.08	3.80	29.46
Trunk		0.30	5.42	0.33	6.59
Roots		1.57	8.99	1.57	8.99
Bunches		6.67	2.85	10.91	4.69
Total		11.86	41.34	16.61	49.73
Growth or maintenance respiration as % of:	total respiration	22.3	77.7	25.0	75.0
	gross assimilation	17.0	59.2	19.0	56.8

From the present analysis, it is evident that increases in productivity occur even if the proportion of total assimilate used for respiration (%R), does not change. Conversely, a constant %R does not preclude there being differences in the efficiency of conversion of intercepted radiant energy to dry matter (*e*). Thus for the sites and year in question, *e* was calculated (after allowing for the higher energy content of oil, using the model of Squire (1984)), to be 1.51 and 1.70 g above-ground dry matter MJ^{-1} PAR for dry and wet sites respectively (Henson, 1991c). Nevertheless, it is self-evident that any reduction of respiration in the absence of a comparable change in GA will cause *e* to increase, while any factor which increases GA but not R at a given level of light interception will also increase *e*. Both are, therefore, possible avenues towards increased productivity, and hopefully, increased yields.

ACKNOWLEDGEMENTS

It is a pleasure to thank Mr Chai Seong Hong for his valuable assistance with this project.

REFERENCES

BREURE, C J (1988). The effect of palm age and planting density on the partitioning of assimilates in oil palm (*Elaeis guineensis*). *Experimental Agriculture, 24*, 53-66.

CHAN, K W (1977). A rapid method for studying the root distribution of oil palm, and its application. In D.A. Earp and W. Newall (eds). *International Developments in Oil Palm*. The Incorporated Society of Planters, Kuala Lumpur, pp. 131-151.

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

CORLEY, R H V and BREURE, C J (1981). Measurements in oil palm experiments. Internal report, Unilever Plantation Group, London.

CORLEY, R H V; HARDON, J J and TANG, Y (1971a). Analysis of growth of the oil palm (*Elaeis guineensis* Jacq.). I. Estimation of growth parameters and application in breeding. *Euphytica, 20*, 307-315.

CORLEY, R H V; GRAY, B S and NG, S K (1971b). Productivity of the oil palm (*Elaeis guineensis* Jacq.) in Malaysia. *Experimental Agriculture, 7,* 129-136.

DUFRENE, E (1989). Photosynthese, consommation en eau et modellisation de la production chez la palmier a huile (*Elaeis guineensis* Jacq.). Doctoral Thesis, Universite de Paris-Sud, Centre D'Orsay. 154pp.

GERRITSMA, W (1990). Light interception and productivity in oil palms and its simulation. Paper presented at *International Workshop on Yield Potential in Oil Palm,* Phuket, Thailand, 29-30 October 1990. (In press).

GOUDRIAAN, J and van LAAR, H H (1978). Calculation of daily totals of the gross CO_2 assimilation of leaf canopies. *Netherlands Journal of Agricultural Science, 26,* 373-382.

HARDON, J J; WILLIAMS, C N and WATSON, I (1969). Leaf area and yield in the oil palm in Malaya. *Experimental Agriculture, 5,* 25-32.

HENSON, I E (1991a). Assessing frond dry matter production and leaf area development in young field palms. Paper presented at *PORIM 1991 International Palm Oil/Oil Palm Development Conference,* 9-14 September 1991, Kuala Lumpur. (In press).

HENSON, I E (1991b). Adaptation to light environment by leaves of oil palm (*Elaeis guineensis*). *PORIM Bulletin, 22,* 1-8.

HENSON, I E (1991c). Limitations to gas exchange, growth and yield of young oil palm by soil water supply and atmospheric humidity. *Transactions of the Malaysian Society of Plant Physiology, 2,* 39-45.

HENSON, I E and CHANG, K C (1990). Evidence for water as a factor limiting performance of field palms in West Malaysia. In: *Proceedings of 1989 International Palm Oil Development Conference, Module II, Agriculture,* pp. 487-498.

van KRAALINGEN, D W G (1985). Simulation of oil palm growth and yield. M.Sc. Thesis. Agricultural University, Wageningen, The Netherlands. 106 pp.

van KRAALINGEN, D W G (1986). A three-dimensional light model for crop canopies. Internal Report 17. Department of Theoretical Production Ecology, Agricultural University, Wageningen. 106 pp.

van KRAALINGEN, D W G; BREURE, C J and SPITTERS, C J T (1989). Simulation of oil palm growth and yield. *Agricultural and Forest Meteorology, 46,* 227-244.

NG, S K; THAMBOO, S and de SOUZA, P (1968). Nutrient contents of oil palms in Malaya. II. Nutrients in vegetative tissues. *The Malaysian Agricultural Journal, 46,* 332-390.

PENNING de VRIES, F W T; van LAAR, H H and CHARDON, M C M (1983). Bioenergetics of growth of seeds, fruits, and storage organs. In: *Potential Productivity of Field Crops under Different Environments.* International Rice Research Institute, Manila, The Philippines.

PORIM (1989). Annual Research Report 1989. Biology. pp. 312- 325. (Internal).

PORIM (1990). Annual Research Report 1990. Biology. pp. 152-169. (Internal).

SPITTERS, C J T (1986). Separating the diffuse and direct component of global radiation and its implications for modelling canopy photosynthesis. Part II. Calculation of canopy photosynthesis. *Agricultural and Forest Meteorology, 38,* 231-242.

SQUIRE, G R (1984). *Light interception, productivity and yield of oil palm.* Internal Report. PORIM. 73 pp.

SQUIRE, G R and CORLEY, R H V (1987). Oil palm. In: *Tree Crop Physiology* (eds. M.R. Sethuraj and A.S. Raghavendra). pp. 141-167.