MODELLING THE EFFECTS OF 'HAZE' ON OIL PALM PRODUCTIVITY AND YIELD

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An increasing incidence of atmospheric pollution in the Southeast Asian region leading to substantial reductions in solar radiation has promoted concern over the possible long term effects on oil palm yields. Previous models of oil palm growth and production have emphasized the importance for yield of adequate radiation but effects of reduced radiation on yield are not immediately apparent due to the long time required for bunch morphogenesis, the complexity of the process and the presence of assimilate stores which serve to buffer the palm against periods of adverse conditions.

Because climatic factors other than radiation influence the physiological processes on which productivity is dependent, models were developed to take into account the other main factors, namely, temperature, atmospheric vapour pressure deficit (VPD) and soil water availability. Temperature had only a small effect because variations in mean temperatures were small. Soil water availability had a larger influence but VPD was the most important factor influencing yields. A lower VPD, lower temperature and improved soil water supply associated with reduced radiation tended to offset yield reductions due to lower light intensity. Under certain conditions, predicted yields were higher under low or moderate than under high radiation. High radiation was associated with high euapotranspiration (ET) rates and lower rainfall, leading to increasing likelihood of soil water

deficits and drought-induced yield reductions.

The results of the modelling exercise are related to palm performance in other regions with contrasting radiation receipts.

INTRODUCTION

Among the many environmental factors that affect crop growth and yield, solar radiation frequently exerts a major influence. It is generally considered that dry matter production is directly proportional to the amount of photosynthetically active radiation (PAR) intercepted by the crop canopy (Monteith, 1977). Thus, the intensity and duration of radiation received during the growing season can be expected to have a large bearing on crop productivity. In oil palm, bunch yield is thought to be largely source, rather than sink limited (Corley, 1976; Squire and Corley, 1987) and bunch yield per palm is positively related to the amount of intercepted radiation (Squire, 1984).

Solar radiation received at a site is mainly a function of latitude, time of year and cloud cover; all factors which lie outside the control of the grower. Recently, however, radiation levels in Southeast Asia have been additionally subjected to periodic reductions as a result of events such as forest fires, volcanic eruptions and increasing industrial and automobile-generated pollution. Some particularly severe periods of reduced radiation or 'haze', lasting at times for several weeks, have been observed during the past decade.

The effects of reduced radiation on oil palm growth and yield are difficult to determine directly as the large size and perennial nature of the crop limits experimental approaches. Comparisons can be made before and after haze events or between sites but interpretation is complicated and uncertain due to the long developmental time over which yield processes can be influenced, the possible intervention and interaction of several periods of low radiation over this period, and the frequent fluctuations in yields due to other causes. Long term records are usually needed to reliably gauge effects.

The radiation requirements for oil palm to achieve adequate yields are not known precisely but Hartley (1977) considered that in combination with suitable temperatures and rainfall, sunshine hours (SH; the most common form of radiation measurement available in oil palm growing regions) should amount to at least 5 day^{-1} rising up to 7 day^{-1} in some months of the year. However, he also noted that in general, similar yields could be obtained in areas which differed appreciably in radiation levels, and that in certain areas with very low radiation but well distributed and adequate rainfall (such as the Pacific coast of northern South America), yields could be higher than those in regions with much higher radiation but with seasonal dry periods. An example of this is seen in mean FFB and oil yields in regions of Colombia which contrast markedly in daily SH (*Table 1*). On one plantation in the southwest of Colombia, annual FFB yields of 27-30 t ha^{-1} and oil yields of over 6.5 t ha^{-1}, have been obtained with daily SH as low as 2.2.

TABLE 1. CLIMATE AND MEAN BUNCH YIELDS IN THREE REGIONS OF OIL PALM CULTIVATION IN COLOMBIA[1]

Region	Sunshine ($hr\ day^{-1}$)	FFB yield ($t\ ha^{-1}\ yr^{-1}$)	Oil yield	Main limiting factors
west	3.18	14.77	3.12	Low radiation
East	4.70	14.14	2.99	Dry season; disease
North	6.96	16.63	3.38	Long dry season, high temperatures

Notes: [1]Sunshine hours are means for two (west), three (east) or five (north) sites averaged over 4-28 years.
Yield data (FEDEPALMA, 1998) are for all crops in each region and are means for the years 1992.1997. Note that irrigation is widely practised during the dry season in both east and north regions.

Several reasons can be advanced for the possible maintenance of yields under low radiation or conversely, for limits to yield under high radiation. High radiation is frequently associated with higher air temperature and lower relative humidity, both contributing to higher VPD. Higher temperatures may increase maintenance respiration while higher VPD leads to greater VPD-induced stomata1 closure, lower leaf conductance and lower leaf and canopy photosynthetic rates (Smith, 1989; Dufrene, 1989; Henson, 1991; 1995a; Setyo et al., 1996). It is also possible that extreme leaf temperatures reached with high radiation loads may also directly reduce photosynthesis rates (Hong and Corley, 1976).

With low radiation under cloudy conditions, a higher proportion of radiation will be diffuse as opposed to direct, and this may lead to a better light distribution within the canopy and a more efficient conversion of radiation to dry matter. Finally, lower radiation and temperature together with lower VPD reduces ET and decreases the possibility of soil water deficit reaching a level where it can affect yield.

In view of the impracticality of directly determining radiation effects on oil palm yields and the need to collect extensive data over long periods before reaching any conclusions based on yield trends, an attempt was made to predict effects of reduced radiation using a revised mechanistic 'simulation' model. The model used is based on the OPSIM model of van Kraalingen (van Kraalingen. 1985; van Kraalingen et al., 1989) which is similar to that of Dufrene (1989). But unlike those models and earlier versions used in previous studies (Henson, 1992; 1995h; Henson and Chai, 19981, all of which assume no limitations to growth other than radiation, the present model has been modified to provide versions incorporating effects of temperature, VPD and soil water supply.

EXPERIMENTAL DATA

Detailed stand, growth and meteorological data were available from two sites on the west coast of Peninsular Malaysia, as described previously (Henson, 1997). One was on a coastal, and the other, on an inland soil. The coastal site was a 94 ha field planted in 1983 and the inland site, a 104 ha field planted in 1985. The two sites were chosen for their contrasting yields in order to determine whether the same conclusions could be drawn for low, as for high yielding, palms. A full array of meteorological instruments was located in the middle of each site.

Levels of incident short-wave solar radiation, PAR, air temperatures within and above the canopy, relative humidity, wind speeds, net radiation and rainfall above the canopy, were recorded at both sites as hourly means (Henson, 1995a; Henson and Chai, 1998). VPD and potential evapotranspiration (PET) were calculated from meteorological readings above the canopy whilst actual evapotranspiration (AET) was determined from Bowen ratio or eddy correlation measurements (Henson, 1995a).

MODEL STRUCTURE AND DEVELOPMENT

The general structure of the model follows that described for OPSIM by van Kraalingen *et al.* (1989) and the main components are outlined in ***Figure 1.*** Parameter values in the model apply to climatic conditions on the west coast of West Malaysia.

The model calculates dry matter and bunch production on a daily basis and then sums these to give yearly totals. However, it does not aim to accurately simulate seasonal yield trends (which depends additionally on inflorescence development and partitioning of assimilates between bunch sinks and storage sites, (e.g. Henson and Chai, 1998).

The main steps in the model are as follows:

i) Calculation of gross canopy CO, assimilation (GA) based on daily incident PAR, LAI, foliar light extinction coefficient (K) and leaf photosynthetic parameters (quantum yield and the light-saturated rate of photosynthesis, A_{max}). The procedure used was that described by Goudriaan and van Laar (1978).

   Incident PAR, K, and leafphotosynthetic parameters were measured at each site; LAI was calculated in the model from the regression of LAI on Frond 17 dry weights (*Appendix 1*) determined at the beginning and

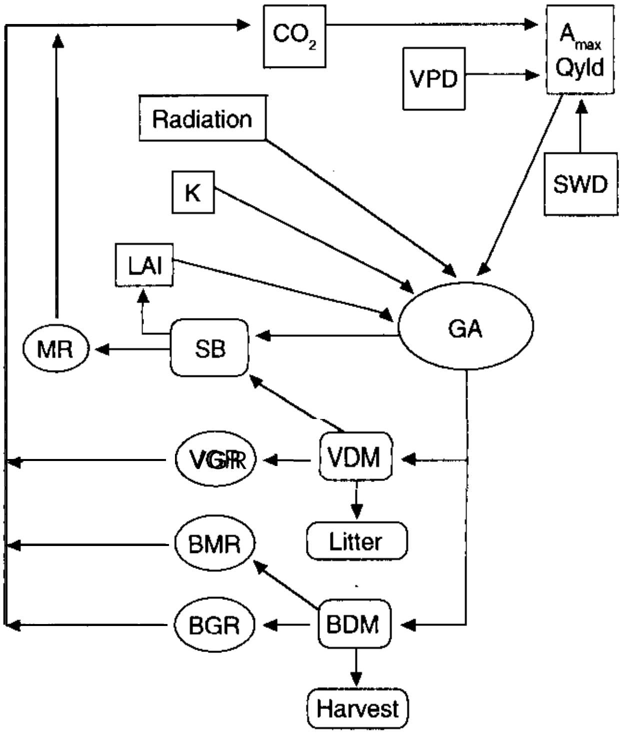

Figure 1. Main components of the simulation model. GA (gross CO, assimilation) is influenced by level of radiation, CO, concentration, atmospheric vapour pressure deficit (VPD), soil water deficit (SWD), leaf area index (LAI), leafphotosynthetic (A_{max}, quantum yield) and light interception (K) characteristics. Assimilates are used in order of priority for maintenance respiration (MR) of standing biomass (SB), vegetative dry matter (VDM) production and vegetative growth respiration (VGR) and bunch dry matter (BDM) production, bunch maintenance respiration (BMR) and bunch growth respiration (BGR). VDM either adds to SB or contributes to litter (e.g. pruned fronds). Male inflorescences make only a small contribution to dry matter production and are omitted for clarity. SB influences GA via LAI. In the diagram rectangles represent factors influencing GA, ovals represent processes and rounded rectangles represent assimilate pools.

end of each year. LAI was increased daily assuming the rate of increase to be constant over the year.

GA was corrected daily for VPD based on the regression of 'relative' (radiation-adjusted) above-canopy CO, assimilation (measured at the sites using the eddy correlation method; Henson, 1995a) on maximum daily VPD (*Appendix 1*). The effect of VPD was slightly greater on the inland than on the coastal site (PORIM, 1995). Regressions of CO, flux on mean daytime VPD gave similar results to regressions on maximum VPD but the latter was more convenient to use. Although the regressions were based only on the above-canopy CO, flux, a separate study (Henson, 1999) showed that above- and below-canopy fluxes were closely correlated such that total fluxes are expected to follow an identical trend.

GA was also corrected for soil water availability by reference to the daily ratio of actual to potential evapotranspiration (AET/PET) following the approach of Gerritsma and Wessel (1994). This was considered to be a more reliable method than adjustments based on soil water deficit, the determination of which was only possible for the inland site as on the coastal site, ground water also contributed significantly to total water use.

ii) Calculation of maintenance respiration (MR) of standing biomass from mean standing biomass of the main organs and MR coefficients. Biomass of roots, trunk, fronds, male inflorescences and bunches was determined as previously described (Henson and Chai, 1997; 1998). Partitioning of frond dry matter into leaflets, petioles and rachis was additionally determined on sub-samples. Pruned frond bases adhering to the trunk, while known to show respiratory activity (PORIM, 19921, were not included for the purpose of determining MR on the assumption that their respiration largely represented microbial decomposition and did not comprise a drain on newly assimilated carbon.

The MR coefficients needed for each major organ were either calculated as described by van Kraalingen *et* al. (1989) and Dufrene (1989) or taken directly from those sources. Nitrogen (N) and mineral (Min) contents needed for the calculations were taken from Ng *et* al. (1968). For the trunk, N and Min contents vary with age, decreasing linearly between two and 15 years, and this was taken into account in deriving the coefficients. Values for other organs show no age trends.

While Dufrene (1989) used a single MR coefficient for the whole trunk (determined by measuring the gas exchange of a mature section enclosed in a plastic 'sleeve'), van Kraalingen (1985) argued for a division between an upper metabolically 'active' portion of trunk with a 'normal' MR rate and a remaining inactive portion with a much lower respiration rate. Subsequent calculations (Breure, 1988) and measurements (PORIM, 19921 support the validity of this approach.

Two sets of MR calculations were performed, the first using the coefficients and approaches ofvan Kraalingen (1985) and the second, of Dufrene (1989). As there was no way of knowing which was the more accurate, the means of both were used in the model.

MR is temperature sensitive. Because mean temperatures vary little in most oil palm growing regions, previous models have ignored temperature effects. The effect of temperature was incorporated in the model by assuming the calculated coefficients to apply to a temperature of 25°C (Dufrene, 1989) and the respiratory quotient (Q_{10}) to equal 2.0. The calculated daily MR was then adjusted using mean daily air temperatures measured within the canopy.

iii) Estimation of total vegetative dry matter production (VDMP). This was calculated from an empirical regression of VDMP on Frond 17 dry weight ***(Appendix 1). The*** regression includes an allowance for root productivity.

iv) Calculation of growth respiration of vegetative biomass (VGR) from VDMP and GR coefficients. Coefficients of GR are temperature insensitive, depending only on organ biochemical composition. As with the MR coefficients, those for GR given by van Kraalingen (1985) and Dufrene (1989) differ; thus two sets of calculations were performed and the mean values used in the model.

v) Calculation ofassimilates allocated to bunch growth (BA). In line with previous models, BA was taken as the residual after subtracting MR, VDMP and VGR from GA.

vi) Calculation of bunch dry matter production (BDMP). BDMP was calculated from BA and the ratio between BDMP and bunch GR determined using the GR coefficients.

. Several versions of the model were prepared:

i) Uncorrected, with yield determined solely by radiation;
ii) With correction of MR for temperature;
iii) With correction of GA for VPD;
iv) With correction of GA for soil water supply;
v) With correction of MR for temperature and GA for VPD; and .
vi) With correction of MR for temperature and GA for VPD and soil water supply.

PREPARATION OF CLIMATE DATA SETS

Daily values of solar radiation, maximum VPD, mean canopy-space air temperature, rainfall, AET and the AET/PET ratio, covering a full year for each site, were assembled into files suitable for processing by the models. Data from these 'real data' files were then sorted in order of radiation level and three subsets extracted corresponding to low, medium and high radiation. Each subset was then replicated to produce a full year's data set for processing by the various versions of the model.

The high correlation between radiation and most other climatic variables (Table 2) led to radiation-related differences between the data sets in VPD, temperature, AET, AET/PET and rainfall (Tables *3a* and *3b*).

The data sets were run with the different versions of the model to examine the effects of corrections for temperature, VPD and soil water supply (the latter assessed from the AET/PET ratio), either singly or in combination, on bunch yield. Because the association between haze and rainfall may, in practice, differ from that obtained when radiation varies solely due to natural cloud cover, a model version was also run which ignored possible effects of variation in soil water supply.

TABLE 2. REGRESSION ANALYSIS OF RELATIONSHIPS AT THE TWO STUDY SITES BETWEEN DAILY TOTAL SOLAR RADIATION (MJ M^{-2}) AND (a) MAXIMUM DAILY VPD (kPa), (b) MEAN DAILY WITHIN CANOPY TEMPERATURE (°C), (c) DAILY AET (mm), (d) DAILY AET/PET RATIO AND (e) DAILY RAINFALL

	Site	Intercept	Slope	*r*	*P*
VPD us. radiation	Coastal	0.331	0.066	**0.71**	**0.001**
	Inland	0.425	0.068	0.70	0.001
Temp. us. radiation	Coastal	23.84	0.105	0.60	0.001
	Inland	23.93	0.134	0.60	0.001
AET us. radiation	Coastal	0.522	0.217	0.91	0.001
	Inland	0.315	0.219	0.94	0.001
AET/PET us. radiation	Coastal	1.159	-0.011	-0.43	**0.001**
	Inland	1.039	-0.007	-0.34	0.001
Rain vs. radiation	Coastal	19.17	-0.855	-0.29	0.01
	Inland	19.39	-0.805	-0.23	0.05 .

TABLE 3. CHARACTERISTICS OF THE DATA SETS USED TO TEST MODEL OUTPUT

a) Coastal site measured during 1993; 10 years after planting.

	Data set (radiation level)			
	LOW	Medium	Real	High
Daily total short-wave radiation (MJ m^{-2} day-?	10.64	14.02	15.88	21.20
Maximum daily vapour pressure deficit (kPa)	1.059	1.227	1.383	1.736
Mean canopy air temperature (°C)	24.95	25.25	25.51	26.02
Mean daily evapotranspiration (mm)	2.79	3.62	3.97	5.10
Mean daily AET/PET	1.047	1.009	0.991	0.945
Mean daily rainfall (mm)	10.57	5.07	5.59	2.09

b) Inland site • measured during 1994; 9 years after planting.

	Data set (radiation level)			
	LOW	Medium	Real	High
Daily total short-wave radiation (MJ m^{-2} day^{-2})	10.49	14.01	15.55	21.27
Maximum daily vapour pressure deficit (kPa)	1.135	1.393	1.487	1.802
Mean canopy air temperature (°C)	25.33	25.86	26.01	26.74
Mean daily evapotranspiration (mm)	2.58	3.42	3.73	4.85
Mean daily AET/PET	0.959	0.934	0.926	0.883
Mean daily rainfall (mm)	12.12	6.28	6.87	2.41

RESULTS: MODEL OUTPUT

In order to 'fine-tune' the model, the fully corrected version (version vi) was first run using the 'real' data set with A_{max} adjusted to give a BDM yield at each site within 0.1% of the actual yield. These A,, values were then used with all other model versions and data sets. The results for the two sites are shown in *Table 4.*

In the uncorrected model, in which BDM was dependant only on radiation, BDM increased at a rate of 2.09 t ha^{-1} yr^{-1} MJ^{-1} ($r=0.995$; $P<0.01$) at the coastal site and 1.7 t ha^{-1} yr^{-1} MJ^{-1} ($r=0.995$; $P<0.01$) at the inland site. Correction for temperature affected MR, which was reduced if mean temperatures were below 25°C (as with the low radiation data set at the coastal site) but increased iftemperatures exceeded this (as they did for all other data sets). The outcome was for BDM to be increased in the first case but decreased in the others. However, the daily mean temperature ranges were not large and differed between data sets by only about 1.1°C and 1.4°C for coastal and inland sites respectively. Thus, the effects of temperature correction were correspondingly small: less than 5% at the coastal and 8% at the inland site *(Table 5).*

TABLE 4. BUNCH DRY MATTER YIELD (t ha^{-1} yr^{-1}) PREDICTED FOR FOUR CLIMATIC CONDITIONS AT TWO SITES, USING MODELS WITH OR WITHOUT CORRECTIONS FOR EFFECTS OF CANOPY AIR TEMPERATURE, VAPOUR PRESSURE DEFICIT AND. SOIL WATER AVAILABILITY

a) Coastal site measured during 1993; 10 years after planting.

Model version	Data set			
	LOW	Medium	Real	High
i Uncorrected	**9.66**	**18.79**	21.88	32.12
ii Corrected for temperature	9.72	18.40	21.10	30.56
iii Corrected for VPD	13.79	20.61	19.68	20.67
iv Corrected for AET/PET	11.57	19.30	21.03	28.40
v Corrected for temperature and VPD	13.84	20.23	18.90	19.11
vi Corrected for temperature, VPD and AET/PET	16.06	20.75	18.29	16.06
Combined effects of all corrections	+6.40	+1.96	-3.59	-16.06

b) Inland site - measured during 1994; 9 years after planting

Model version	Data set			
	LOW	Medium	Real	High
i Uncorrected	9.69	17.44	19.34	28.37
ii Corrected for temperature	9.31	16.42	18.14	26.29
iii Corrected for VPD	15.14	18.96	18.00	19.03
iv Corrected for AET/PET	8.08	14.47	15.65	21.85
v Corrected for temperature and VPD	14.76	17.95	16.80	16.95
vi Corrected for temperature, VPD and AET/PET	13.09	14.99	13.48	11.79
Combined effects of all corrections	+3.40	-2.45	-5.86	-16.58

TABLE 5. RELATIVE EFFECTS OF ADJUSTING BUNCH DRY MATTER YIELD FOR TEMPERATURE, VPD AND SOIL WATER AVAILABILITY UNDER FOUR CLIMATIC CONDITIONS AT THE TWO SITES. DATA ARE PERCENTAGE CHANGES TO UNCORRECTED YIELDS

Model version	Data set			
	LOW	Medium	Real	High
a) Coastal site				
ii Corrected for temperature	0.62	-2.08	-3.56	-4.86
iii Corrected for VPD	42.75	9.69	-10.05	-35.65
iv Corrected for AET/PET	19.77	2.71	-3.88	-11.58
v Corrected for temperature and VPD	43.27	7.66	-13.62	-40.50
vi All corrections	66.25	10.43	-16.41	-50.00
b) Inland site				
ii Corrected for temperature	-3.92	-5.85	-6.20	-7.33
iii Corrected for VPD	56.24	8.72	-6.92	-32.92
iv Corrected for AET/PET	-16.61	-17.03	-19.08	-22.98
v Corrected for temperature and VPD	52.32	2.92	-13.13	-40.25
vi All corrections	35.09	-14.05	-30.29	-58.44

Correction for soil water availability generally had a lesser effect than correction for VPD and was more important on the inland than on the coastal site. Combined corrections for the different factors were not strictly additive. Relative effects of the corrections also depended strongly on the radiation level.

The net results of all the corrections at the coastal site were to increase yields under ‘low’ and ‘medium’ radiation whilst decreasing them under ‘real’ and ‘high radiation, much more so in the latter case. At the inland site, yields were increased under low radiation and decreased under all other conditions. After all corrections, BDM yields were no longer correlated with radiation, with yields under medium radiation exceeding those under other conditions at both sites, This was also true when corrections were made only for VPD and temperature and corrections for soil water supply were omitted. The medium radiation levels represented an 11.7% (coastal) and 9.9% (inland) reduction in radiation over the real values which is similar to the maximum annual variation in sunshine hours for West Malaysia recorded between 1990 and 1997 (Chow and Chan, 1999).

The effects of the corrections on photosynthetic conversion efficiency (*e**; Squire, 1985) are shown in ***Table*** 6. In the absence of corrections, the highest efficiency for both sites was found with the medium radiation data set. After corrections, efficiency was inversely correlated with radiation at both sites.

CONCLUSION

The data sets produced for testing in the present exercise were designed to simulate varying degrees of radiation conditions together with the associated naturally occurring values of temperature, humidity and soil water availability found at the experimental sites. As the various conditions were deemed to persist for a whole year, some of the results are necessarily somewhat extreme but nevertheless serve to indicate the likely effects of differing radiation conditions as found on the west coast of Peninsular Malaysia.

There are several shortcomings to the present models. VDMP at a given age and site is assumed constant throughout but variation

TABLE 6. EFFECTS OF ADJUSTING BUNCH DRY MATTER YIELD FOR TEMPERATURE, VPD AND SOIL WATER AVAILABILITY UNDER FOUR CLIMATIC CONDITIONS AT THE TWO SITES ON PHOTOSYNTHETIC CONVERSION EFFICIENCY, e^*, WHERE e^* (g MJ^{-1}) = TOTAL NON-OIL EQUIVALENT DRY MATTER PRODUCTION/INTERCEPTED PAR

Model version	Data set			
	LOW	Medium	Real	High
a) Coastal site				
i Uncorrected	1.97	2.11	2.04	1.98
ii Corrected for temperature	1.98	2.08	1.99	1.92
iii Corrected for VPD	2.34	2.23	1.91	1.48
iv Corrected for AET/PET	2.14	2.14	1.99	1.82
v Corrected for temperature and VPD	2.34	2.20	1.87	1.41
vi All corrections	2.54	2.24	1.83	1.27
b) Inland site				
i Uncorrected	1.95	2.01	1.93	1.83
ii Corrected for temperature	1.91	1.94	1.85	1.73
iii Corrected for VPD	2.46	2.11	1.84	1.40
iv Corrected for AET/PET	1.80	1.80	1.69	1.53
v Corrected for temperature and VPD	2.43	2.04	1.77	1.29
vi All corrections	2.27	1.83	1.56	1.06

with climatic conditions is likely as low bunch production may result, at least in part, in some stimulation of vegetative growth. Also, the realized BDM production depends on the presence of sufficient sinks, i.e. female inflorescences, as well as sufficient assimilates, and possible climatic effects on sex ratio, inflorescence abortion, pollination efficiency, bunch rot and rates of bunch development need to be considered.

The models used are unable to satisfactorily simulate seasonal changes in bunch dry matter yield. Again, this is because actual BDMP depends on the presence of sufficient sinks and more sophisticated routines and inputs (e.g. Jones, 1997) are required to cope adequately with this level of complexity.

Despite such drawbacks, the present models have succeeded in demonstrating the feasibility of yields being sustained under low radiation in otherwise favourable environments and provide an explanation for the good yields reported for certain regions (e.g. *Table 1*) where such conditions exist normally. They also indicate that similar responses are to be expected irrespective of actual yield capacity. Further work is required to widen the applicability of such models and to reduce the level of empiricism within them.

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REFERENCES

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

CHOW, C S and CHANG, K C (1999). Effects of sunshine hours on oil extraction rate with special reference to the haze in recent years. In *Proceedings of the National Seminar on Opportunities for Maximizing. Production through Better OER and Offshore Investment in Oil Palm.* p. 244-253.

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

DUFRENE, E (1989). *Photosynthese, consommation en eau et modelisation de la production chez lepalmier a huile (Elaeisguineensis* Jacq.). These de Docteur en Sciences, Universite Paris-Sud Orsay. 154pp.

FEDEPALMA (1998). *Annuario Estadistics, 1997.* Federacion Nacional de Cultivadores de Palma de Aceite, Santafá de Bogota.

GERRITSMA, W and WESSEL, M (1994). Calculated yield trends of cocoa in different countries. Paper presented at MICC '94. 20-21 October 1994. Kuala Lumpur.

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

HARTLEY, C W S (1977). *The Oil Palm.* 2nd edition. Longmans, London. 806 pp.

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

HENSON, I E (1992). Carbon assimilation, respiration and productivity of young oil palm *(Elaeis guineensis). Elaeis, 4 (2):*51-59.

HENSON, I E (1995a). Carbon assimilation, water use and energy balance of an oil palm plantation assessed using micrometeorological techniques. In *Proceedings of 1993 PORIM International Palm Oil Congress - Update and Vision (Agriculture)* (Jalani, B S; Ariffin Darus; Rajanaidu, N, Mohd Tayeb Dolmat; Paranjothy, K; Mohd Basri Wahid; Henson, I E and Chang, K C eds.). Palm Oil Research Institute of Malaysia, Bangi. p. 137-158.

HENSON, I E (1995b). Photosynthesis, dry matter production and yield of oil palm under light-limitingconditions. In *Proceedings of 1993 PORIM International Palm Oil Congress - Update and Vision (Agriculture)* (Jalani, B S; Ariffin Darus; Rajanaidu, N; Mohd Tayeb Dolmat, Paranjothy, K; Mohd Basri Wahid; Henson, I E and Chang, KC eds.). Palm Oil Research Institute of Malaysia, Bangi, p. 525-541.

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 (1999). Notes on oil palm productivity. IV. Carbon dioxide gradients and fluxes and evapotranspiration, above and below the canopy. *Journal of Oil Palm Research, 11 (1):*33-40.

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 requirements, assimilation capacity, assimilate storage and apparent photosynthetic conversion efficiency. *Elaeis, 10 (1):*93-*109.*

HONG, T K and CORLEY, R H V (1976). Leaf temperature and photosynthesis of a tropical C3 plant, *Elaeis guineensis. MARDI Research* Bulletin, *4:*16-20.

JONES, L H (1997). The effects of leaf pruning and other stresses on sex determination in the oil palm and their representation by a computer simulation. *Journal of Theoretical Biology, 187:*241-260.

MONTEITH, J L (1977). Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society, B., 281: 277-294.*

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

PORIM (1992). *Annual Research Report for 1991.* Biology Division, Palm Oil Research Institute of Malaysia, Bangi. p. 5-15.

PORIM (1995). *Annual Research Report for* 1994. Biology Division. Palm Oil Research Institute of Malaysia, Bangi. p. 5-14.

SETYO, I E; SUBRONTO and LAMADE, E (1996). Photosynthetic rats of three different DxP clones: the sensitivity to vapour pressure deficit in North Sumatra. In *Proceedings of the 1996 PORIM International Palm Oil Congress, Agricultural Conference* (Ariffin Darus; Mohd Basri Wahid; Rajanaidu, N; Mohd Tayeb Dolmat; Paranjothy, K; Cheah, S C; Chang, K C; and Ravigadevi, S eds.). Palm Oil Research Institute of Malaysia, Bangi. p. 421-426.

SMITH, B G (1989). The effects of soil water and atmospheric vapour pressure deficit on stomata1 behaviour and photosynthesis in the oil palm. *Journal of Experimental Botany, 40:* 647-651.

SQUIRE, *G* R (1984). *Light Interception, Productivity* and *Yield of* Oil *Palm.* Occasional report, Palm Oil Research Institute of Malaysia, Bangi, 45pp.

SQUIRE, G (1985). A physiological analysis of oil palm trials. *PORIM Bulletin No. 12:*12-31.

SQUIRE, G R and CORLEY, R H V (19871. Oil palm. In *Tree Crop Physiology* (Sethuraj, M R and Raghavendra, AS eds.). Elsevier Science, Amsterdam. p. 141-167.

van KRAALINGEN, D W G (1985). Simulation of oil palm growth and yield. Doctoral thesis, Department of Theoretical Production Ecology, Agricultural University, Wageningen. 106pp.

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.

Appendix 1

Empirical regression equations used in the model

1. LAI versus Frond 17 dry weight (FDW) (kg).

$$LAI = 1.556 \times FDW - 0.3366$$

($n=21$; $r = 0.97$; $P<0.001$)

2. GA versus maximum VPD (kPa).

a) Coastal site:

$$GA_{corrected} = GA_{uncorrected} \times [1.4997 (0.3795 \times VPD_{max})]$$

($n=339$; $r = 0.67$; $P<0.001$)

b) Inland site:

$$GA_{corrected} = GA_{uncorrected} \times [1.7197 (0.492 \times VPD_{max})]$$

($n=89$; $r = 0.64$; $P<0.001$)

3. VDMP ($t\ ha^{-1}\ yr^{-1}$) versus Frond 17 dry weight (FDW) (kg)

$$VDMP = 4.302 \times FDW + 2.662$$

($n=17$; $r = 0.98$; $P<0.001$)