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Estimating Maintenance Respiration of Oil Palm

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ABSTRACT

Maintenance respiration (MR) is normally the largest fraction of dark *respiration in crop plants. MR of mature oil palm is difficult, if not impossible, to measure directly. However, it can be calculated from respiratory coefficients and standing crop biomass components. The derivation of the coefficients is described and examples are given of the MR of different organs and whole crops. Alternative derivations of MR are considered and an explanation provided for the observed declines in MR per unit biomass with increasing palm age and planting density.*

ABSTRAK

Respirasi penyelenggaraan (MR) biasanya adalah pecahan terbesar respirasi gelap. *MR sawit matang susah, jika tidak mustahil, diukur secara terus. Walau bagaimanapun, ia boleh dikira daripada pekali respirasi dan komponen biojisim tanaman. Cara pekali dihasilkan diterangkan dan contoh-contoh MR untuk keseluruhan pokok dan organ-organ berlainan juga diberi. Cara lain untuk mendapatkan MR dipertimbangkan dan penerangan diberi untuk penurunan MR seunit biojisim yang dilihat dengan peningkatan umur dan kepadatan tanaman sawit.*

Keywords: oil palm, maintenance respiration, tissue nutrient contents, simulation modelling.

INTRODUCTION

Crop physiologists recognize two main forms of respiration, namely growth respiration (GR) and maintenance respiration (MR) (Amthor, 1984). The former is the respiration associated with the formation of new biomass while MR is required for the maintenance of existing biomass. Maintenance activities include the replacement of enzymes and structural proteins, the maintenance of ion potentials across membranes and the uptake and active transport of ions. MR is the largest component of *dark* respiration and is considered to take precedence over other requirements in the utilization of assimilates produced by photosynthesis.

The amount of GR depends on the biochemical composition of the new tissue and the coefficients (g/g) are independent of temperature. GR can be defined in terms of the quantity of assimilate required for the formation of a given quantity of biomass without reference to time. MR represents an on-going requirement and is normally expressed in terms of mass of assimilate per unit biomass per unit time. The amount of assimilate required to maintain a given amount of tissue can be related to the mineral and protein content of the tissue and is a temperature dependent process.

MR can be directly measured by gas exchange techniques. For plant parts that have ceased growth and in which transport processes are absent or much reduced, *e.g.* fully-expanded leaves following a period of darkness, MR equals dark respiration and can be determined with the use of portable gas exchange equipment. However, to determine MR of a whole plant is less straightforward and requires use of whole plant growth chambers and generally involves subsequent destructive measurement to ascertain the biomass. Clearly, except for plants at an early growth stage, this approach is not feasible with oil palm.

The alternative to direct measurement is to estimate MR. Breure (1988) determined MR as a residual term in the equation:

$$GA = MR + GR + DMP \qquad (1)$$

where GA = gross assimilation and DMP = dry matter production, all terms being assessed over a set period, usually one year.

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While DMP can be determined by non-destructive measurements on the biomass and GR calculated from the components of DMP, to estimate GA a model is required, together with climatic inputs.

The alternative is to *model* or calculate MR. GA is then obtained from equation 1. This method is used in the OPSIM model of van Kraalingen (1985) and van Kraalingen *et al.* (1989). OPSIM is an oil palm simulation model based on earlier crop models such as SUCROS (van Keulen *et al*., 1982). The calculation of MR in OPSIM follows the procedures in the earlier related model, BACROS (de Wit *et al*., 1978).

DERIVATION OF MAINTENANCE RESPIRATION COEFFICIENTS

The main organs of the palm, *i.e.* roots, trunk, fronds and bunches are treated separately and the total MR for each is then summed to give the MR per palm or per hectare per year. In the initial treatment, the effects of temperature are ignored and the coefficients are based on a mean of 25°C. The effects of changing the mean temperature are examined separately.

The primary data required to calculate MR are the organ biomass and its protein and mineral contents. Protein content can be assessed from the nitrogen concentration by multiplying by a factor of 6.25. The mineral contents are the sum of P, K, Ca and Mg. The total mineral content may be higher and can be allowed for using an adjustment factor. Comprehensive oil palm dry biomass data, obtained using mainly non-destructive techniques (Corley and Breure, 1981) are now available for a number of sites and ages of palm (*e.g.* Henson and Chai, 1997; 1998; Khalid *et al*., 1999a, b; Henson and Mohd Tayeb, 2003). However, few such studies have included nutrient analysis other than of the leaf laminae. A comprehensive nutrient analysis was undertaken by Ng and Thambou (1967) and Ng *et al*. (1968) and their results are used as a basis for MR calculation where such data are lacking.

Maintenance Respiration of Roots

Ng *et al.* (1968) determined the nitrogen and mineral contents of roots from palms of four different ages (2, 6, 11.5 and 14 years in the field). A regression analysis of their data showed no significant trends with age in protein or mineral contents and hence, the mean values of the calculated coefficients were used. The combined coefficient (*i.e.* protein plus mineral) ($MR_{coefRoots}$; g CH_2O kg^{-1} day^{-1}) was calculated as:

$$(N * 0.036 * 6.25) + (Min * 0.072) \quad (2)$$

where N = mean root nitrogen concentration (g/g) and Min = mean root total mineral concentration (g/g).

From the analytical data of Ng *et al.* (1968) and using the MULCON factor to allow for underestimation of mineral content (see below), the MR of roots (MR_R) in g CH_2O g^{-1} biomass yr^{-1} is given by:

$$\text{total root biomass} * 0.6753 \quad (3)$$

Maintenance Respiration of Trunk

In palms, unlike in dicotyledenous trees, the trunk consists largely of living cells and so might be expected to have a higher MR. As the proportion of standing biomass present as trunk steadily increases during the life of the palm, it was initially considered (Rees and Tinker, 1963) that trunk respiration would impose an increasing burden on the carbon economy as the palm aged, eventually precluding further gain in dry matter. That this does not happen was borne out by the calculations of Squire (1984), who found that the efficiency of conversion of solar radiation to dry matter was constant with age, while Breure (1988) found MR per unit biomass to decrease with age. van Kraalingen (1985) and van Kraalingen *et al.* (1989) suggested that this could be achieved if only the apical portion of the trunk was metabolically active with the remainder having a negligible or low respiration rate. The *active* trunk biomass would be relatively constant with age.

Dufrene (1989) measured trunk CO_2 efflux from an enclosed lower (mature) portion of a trunk from which the leaf bases had been shed. Using this method, he obtained only a low respiratory coefficient of 0.0005 g CH_2O kg^{-1} day^{-1} at 25°C and demonstrated its temperature dependence.

Work at PORIM (now Malaysian Palm Oil Board; MPOB) reviewed by Henson and Chang (2000) confirmed the principle of variation in metabolic activity within the trunk. There appeared to be a vertical gradient, with the respiration rate increasing towards the crown. This needs to be taken account of in a proper modelling of trunk respiration. However, as the higher respiration near the crown must include both growth and maintenance components, and as data on nutrient concentrations at different positions up the trunk are generally not available, the simpler treatment proposed by van Kraalingen (1985) is adopted here. Based on unpublished data of Breure, the active trunk portion near the crown was set at 45 kg for palms with this amount or more, of trunk. For smaller palms with a lesser amount, the whole trunk was deemed to be *active*.

Unlike roots, Ng *et al.*'s (1968) N and mineral data for the trunk show a significant change with palm age. In consequence, the combined MR coefficient calculated for the *active* trunk using equation 2 was significantly negatively correlated with palm age (n=13; R_2=0.86; for palms ranging from two to 15 years in the field). Thus, from this:

$$MR_{coefTrunk(active)}\ (g\ CH_2O\ kg^{-1}\ day^{-1}) = 4.461 - (0.1545 * \text{palm age}) \quad (4)$$

with the mean coefficient for the *active* trunk for two to 15 year old palms = 0.0031 g day^{-1}, indicating that the age-dependence of the coefficients derived using nutrient contents, while significant, did not greatly influence the outcome.

Using the approach, the MR of the trunk (MR_T) is given by:

$$MR_T(g\ CH_2O\ day^{-1}) = \text{active trunk biomass (kg)} * MR_{coefTrunk(active)} + \text{inactive trunk biomass (kg)} * MR_{coefTrunk(inactive)} \quad (5)$$

Maintenance Respiration of Cut Frond Bases

A question is whether or not to include the respiration of the cut frond bases that adhere to the trunk. These bases can comprise a significant proportion of the standing biomass of palms, especially at the *mid-point* of growth (young palms have a low proportion of trunk while palms >17 years shed the bases). The bases have low, but measurable respiration (Henson and Chang, 2000) but their respiration could be due to microbial decomposition rather than the consumption of palm assimilates.

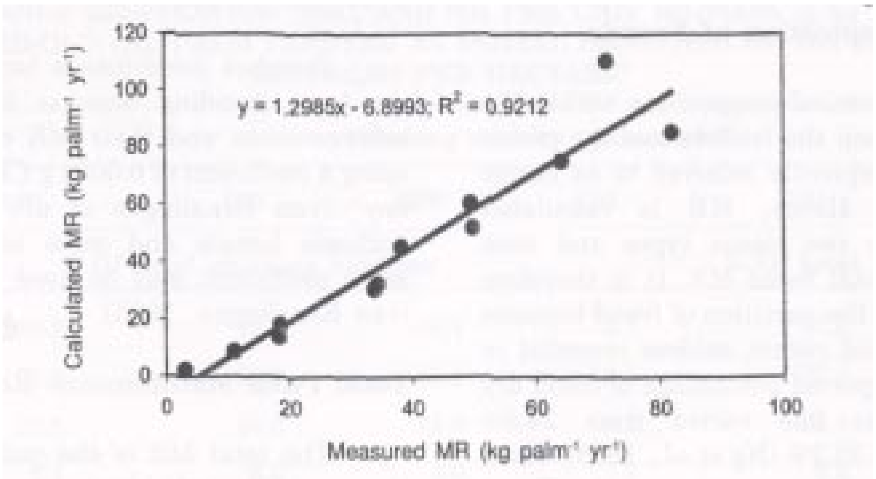

Figure 1. Relationship between maintenance respiration (MR) of the inactive *portion of the trunk calculated using a coefficient 17% of that of the* active *part and MR derived using a directly measured coefficient. Data are for palms aged three to 15 years from planting.*

van Kraalingen (1985) and van Kraalingen *et al.* (1989) proposed that the MR coefficient of the *inactive* trunk portion be set at 6% of that of the active portion based on the assumption that the roots consume only 6% of total assimilates. However, this value is likely to be an underestimate (Dufrene, 1989; Lamade and Setiyo, 1996; Henson and Chai, 1997; Henson and Chang, 2000) and a higher value of 17% is proposed. Using this value for the palms sampled by Ng *et al.* (1968) resulted in estimates of *inactive* trunk MR that closely matched those calculated using the trunk respiratory coefficient determined by Dufrene (1989) (*Figure 1*). Although the latter coefficient was determined only at a single age, agreement was still good,

Calculations were performed to check the possible contribution of bases to total MR. The MR of bases was calculated using the same coefficients as for the inactive trunk on the basis that the respiration of tissue plugs taken from bases was similar to or less than that of mature trunk samples (Henson and Chang, 2000). The results from two studies given in *Table 1* show that despite forming a substantial part of the standing biomass, the bases contributed less than 6% to total MR, and hence, their contribution can be disregarded without

TABLE 1. COMPARISON BETWEEN MAINTENANCE RESPIRATION (MR) OF CUT FROND BASES AND THAT OF THE TRUNK PROPER AND ITS CONTRIBUTION TO TOTAL MAINTENANCE RESPIRATION OF THE STAND USING BIOMASS MEASUREMENTS FROM TWO STUDIES

Palm part	Study 1*		Study 2**	
	Biomass (t ha^{-1})	MR (t ha^{-1} yr^{-1})	Biomass (t ha^{-1})	MR (t ha^{-1} yr^{-1})
Roots	12.7	8.6	16.0	10.1
Trunk	18.7	7.2	41.1	13.4
Frond bases	12.3	2.3	17.6	3.3
Fronds	18.7	21.9	23.9	38.7
Total	62.4	40.0	98.6	65.5
Frond bases as % of total	19.7	5.8	17.8	5.0

Sources: *Henson (unpublished); 10 year-old palms; coefficients calculated using leaf lamina nutrient data obtained *in situ* and nutrient data of other palm parts taken from Ng *et al*. (1968). **Khalid *et al.* (1999a, b; 2000); 23-year-old palms with bases still retained; coefficients calculated from biomass and tissue nutrient concentrations reported by the authors. The biomasses of spear leaves, *cabbage* and inflorescences were also determined but were small and for comparative purposes were excluded.

appreciably affecting the estimate of total MR of the stand.

Maintenance Respiration of Fronds

Tissue biochemical composition within the frond differs between the leaflets and the rachis plus petiole (subsequently referred to as rachis for convenience). Hence, MR is calculated separately for the two tissue types and then summed to give total frond MR. It is therefore necessary to know the partition of frond biomass between leaflets and rachis, seldom recorded in most trials. The reported percentage of frond dry weight in leaflets has varied from 24.8% (Dufrene, 1989) to 32.2% (Ng *et al*., 1968). From Ng *et al.*'s data, there was no significant variation in this with palm age, neither was there any significant variation in the leaflet or rachis MR coefficients with age based on their nutrient composition. The coefficients can thus be calculated directly using equation 2.

Thus, the MR of the fronds (MR_F) is given by:

$$MR_F \text{ (g } CH_2O \text{ day}^{-1}) = \text{leaflet biomass (kg)} * MR_{coefLeaflets} + \text{rachis/petiole biomass (kg)} * MR_{coefRachis} \quad (6)$$

Maintenance Respiration of Developing Inflorescences and Fruit Bunches

There is normally little data on the mean standing dry weight of inflorescences and fruit bunches on the palm though the latter can be estimated based on bunch harvest data (Henson and Mohd Tayeb, 2003). Khalid *et al.* (2000) found that inflorescence dry matter accounted for less than 1% of the total standing dry matter of 23-year-old palms.

Bunches constitute a larger proportion of the total standing biomass than pre-anthesis inflorescences and their MR can be calculated using a coefficient of 0.0022 g CH_2O g^{-1} dry weight day^{-1} (van Kraalingen *et al*., 1989). For pre-anthesis female and male inflorescences, the same coefficient may be used as for the rachis (van Kraalingen, 1985).

Total Palm Maintenance Respiration

The total MR of the palm is obtained as the sum of the individual organ values. Thus, the relative proportions of the main palm parts will influence the total palm MR. This fact probably accounts for the decline in MR per unit of whole palm biomass with age and density (Breure, 1988), as the proportion of less active tissues such as the trunk increases with both of these factors while that of the more active tissues, such as the fronds, decreases (*Tables 2a* and *2b*).

Examples of Oil Palm Maintenance Respiration Coefficients

MR coefficients based on nutrient composition obtained in four studies, are presented in *Table 3*. In study 4, nutrient data were only available for leaflet laminae. Fronds showed the most variation in nutrient concentration and hence, in the MR coefficients that were obtained.

TABLE 2a. CONTRIBUTION OF PLANT PARTS TO TOTAL STANDING BIOMASS AND MAINTENANCE RESPIRATION (MR), AND MR PER UNIT BIOMASS (g kg^{-1} day^{-1}) FOR OIL PALM AT THREE AGES*

Palm part	Age of palms (years in field)					
	4	10	16	4	10	16
	% Of total standing biomass			% Of total MR		
Roots	23.8	18.0	16.1	13.7	13.9	17.9
Trunk	13.2	41.4	55.1	15.9	26.6	20.7
Fronds	52.6	34.5	24.0	63.3	53.9	55.0
Bunches	10.4	6.1	4.8	7.1	5.6	6.4
	Total standing biomass (t ha^{-1})			Total MR (t ha^{-1} yr^{-1})		
Whole palm	21.1	47.0	73.6	24.7	41.0	44.5
MR per unit biomass (g CH_2O kg^{-1} day^{-1})			–	3.21	2.39	1.66

Notes: *Data are from Henson and Mohd Tayeb (2003) for an initial planting density of 200 palms ha^{-1}. The lower % contribution to the total MR by the trunk at 16 years despite higher % contribution to total biomass was due to the lower MR coefficient with age.

TABLE 2b. CONTRIBUTION OF PLANT PARTS TO TOTAL STANDING BIOMASS AND TO MAINTENANCE RESPIRATION (MR), AND MR PER UNIT BIOMASS (g kg^{-1} day^{-1}) FOR 16-YEAR-OLD OIL PALM PLANTED AT INITIAL DENSITIES OF 120, 160 AND 200 PALMS PER HECTARE*

Palm part	Planting density (palms ha^{-1})					
	120	160	200	120	160	200
	% Of total standing biomass			% Of total MR		
Roots	16.2	16.1	16.1	16.7	17.6	17.9
Trunk	51.1	53.9	55.1	19.5	20.4	20.7
Fronds	26.5	24.8	24.0	56.2	55.5	55.0
Bunches	6.1	5.2	4.8	7.5	6.6	6.4
	Total standing biomass (t ha^{-1})			Total MR (t ha^{-1} yr^{-1})		
Whole palm	41.8	60.4	73.6	27.4	37.5	44.5
MR per unit biomass (g CH_2O kg^{-1} day^{-1})				1.79	1.70	1.66

Note: *Data are from Henson and Mohd Tayeb (2003).

The maintenance requirement of the major organs was in the order: leaflets>active trunk>rachis>roots=bunches>inactive trunk.

Effects of Temperature on Maintenance Respiration

MR is temperature sensitive and expected to double for every 10°C increase in tissue temperature (Q_{10} = 2). However, observed relationships often deviate from this (*e.g.* Jones, 1983). Dufrene (1989) observed a linear increase in the respiration rate of a mature oil palm trunk over the temperature range of 25°C to 33°C (*Figure 2*). Based on the calculated MR at 25°C and 35°C, Q_{10} = 1.83; not too dissimilar from the expected value of two.

Henson (2000) examined the effect of temperature variation associated with radiation levels on oil palm MR and bunch yield. The effects were small, chiefly because there were only small variations (<2°C) in the mean canopy air temperature between the conditions compared. Using a simple simulation model, it can nevertheless be demonstrated that increased MR resulting from increasing temperature can lead to a reduction in bunch yield (*Table 4*). In

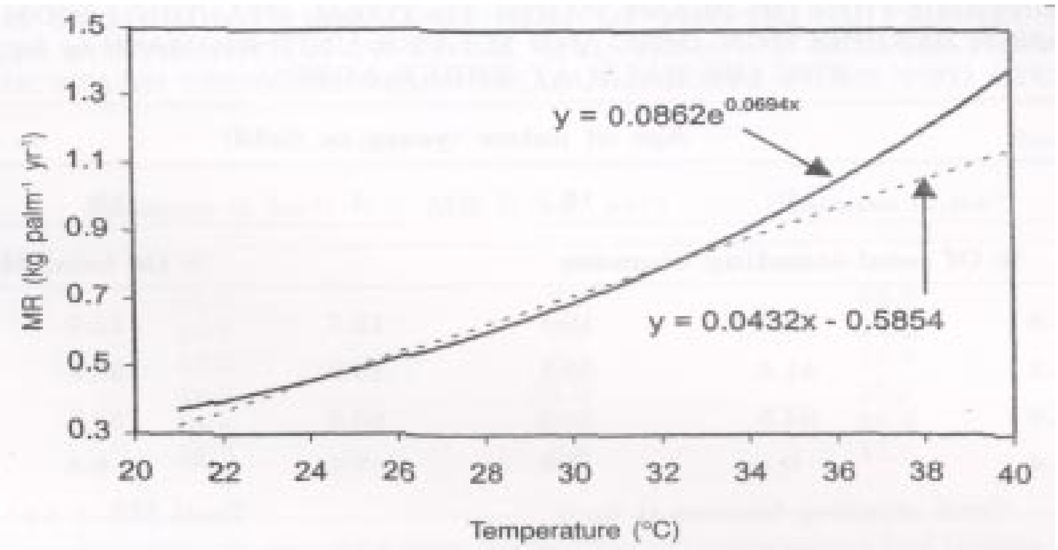

Figure 2. A comparison of the temperature response of maintenance respiration (MR) of the mature trunk using a linear vs. *exponential equation. Curves are based on the data of Dufrene (1989) and are extrapolated beyond the measured temperature range of 25°C to 33°C. A base temperature of 19°C used with the exponential equation gave the closest approximation within the measured temperature range to the linear regression.*

TABLE 3. EXAMPLES OF MAINTENANCE RESPIRATION COEFFICIENTS (g CH_2O g^{-1} day^{-1}) CALCULATED FROM TISSUE NUTRIENT CONCENTRATIONS MEASURED IN FOUR STUDIES

	Ng *et al.* (1968)	Dufrene (1989)	Khalid *et al.* (1999a, b; 2000)	Henson and Mohd Tayeb (2003)
Age of palms (yr)	3 to 15	13	23	3 to 13
		MR coefficient (gCH_2O g^{-1} day^{-1})		
Roots	0.0017	0.0022	0.0017	na
Trunk (active portion)	0.0031	nd	0.0031	na
Leaf laminae	0.0057	0.0083	0.0077	0.0077
Rachis/petiole	0.0022	0.0020*	0.0028	na

Notes: na = not available (no nutrient data).
* Mean of separate determinations for rachis and petiole.

this model, the effects of temperature on other processes are disregarded and, in particular, fixed values of gross assimilation and vegetative dry matter production are assumed. It is likely that these parameters would also vary with temperature, although whether this would lead to a moderation of the effects of increased MR with temperature is uncertain. There is presently little information on temperature responses, which may become of increasing importance with the onset of global warming or as a consequence of severe *El Niño* events.

ALTERNATIVE FORMULATIONS

Mineral Content Coefficient

van Kraalingen (1985) used a scaling factor (MULCON) when calculating that part of the MR coefficient based on mineral content, on the basis that not all minerals would be accounted for by conventional analysis. Silica is often present in relatively high concentrations in oil palm leaflets and to a lesser extent in trunks and other parts. A recent analysis (Khalid *et al.*,

TABLE 4. SIMULATED EFFECTS OF TEMPERATURE ON MAINTENANCE RESPIRATION (MR), TOTAL DRY MATTER PRODUCTION AND BUNCH YIELDS*

Mean daily canopy temperature (°C)	MR	Total respiration	Total respiration as % gross assimilation	Total dry matter production	Bunch dry matter production
	$t\ CH_2O\ ha^{-1}\ yr^{-1}$			$t\ ha^{-1}\ yr^{-1}$	
22	44.2	66.5	62.7	39.5	19.7
23	45.1	67.0	63.3	39.0	19.2
24	45.9	67.6	63.8	38.4	18.7
25	46.8	68.1	64.3	37.9	18.1
26	47.6	68.7	64.8	37.3	17.6
27	48.5	69.2	65.3	36.8	17.1
28	49.3	69.7	65.8	36.3	16.5
29	50.1	70.3	66.3	35.7	16.0
30	51.0	70.8	66.8	35.2	15.4
31	51.8	71.4	67.3	34.6	14.9
32	52.7	71.9	67.8	34.1	14.4

Notes: *Data were calculated using the following constants: standing biomass = 53.4 t ha^{-1}; gross assimilation rate = 106 t ha^{-1} yr^{-1}; vegetative dry matter production = 19.75 t ha^{-1} yr^{-1}. A linear response to temperature based on the data of Dufrene (1989; *Figure 2*) was assumed. Calculations used data from a coastal stand of oil palm aged 10 years from planting which experienced a mean canopy air temperature of 25.5ºC and gave a bunch dry matter production of 18.3 t ha^{-1} yr^{-1} (Henson, 2000).

2000) showed silica to contribute an additional 15% (rachis), 34% (trunk), 46% (roots) and 66% (leaflets) to total organ mineral content (P + K + Ca + Mg). However, the content of minerals other than P, K, Ca, Mg and SiO_2 is likely to be small and doubling the coefficient for all palm parts as done by van Kraalingen (1985) would seem rather excessive. However, the factor may be usefully applied with roots in which mineral contents are often underestimated due to losses during extraction from soil.

Maintenance Respiration of Leaflets

A refinement for leaflets included in the OPSIM model (van Kraalingen, 1985) involves the assumption that leaflet MR requirements during daylight are met by excess ATP production rather than consumption of assimilate. Daily MR of leaflets is thus reduced by the factor: DLE/24, where DLE is the effective day length (approximately 11 hr for Malaysia). However, Penning de Vries *et al.* (1989) considered that this would only operate for the upper leaves at high light intensities. The threshold intensity at which MR is satisfied by ATP excess does not appear to have been determined and further work is needed to verify this mechanism.

Metabolic Component

In the BACROS model, an additional provision is made in the calculation of MR for general metabolic activity. This metabolic component is formulated as a given percentage of gross photosynthesis. A value of between 10% and 20% has been suggested (Penning de Vries *et al*., 1989) and 16% is used in the OPSIM model (van Kraalingen *et al*., 1989) where this additional term is given by:

$$0.16 * GA/SB \qquad (7)$$

where GA is the gross assimilation rate (kg $palm^{-1}$ day^{-1}) and SB the standing palm biomass (kg).

This factor was not applied by Dufrene (1989) and is yet a further area of uncertainty in the modelling of MR.

Effect of Including Additional Factors

The effect on total MR of including the MULCON factor and excluding leaflet MR in the light was evaluated using data for 17-year-old stands of oil palm planted at three densities. The net effect was to increase total MR per ha by around 8% to 9%.

DIRECT MEASUREMENT OF MAINTENANCE RESPIRATION

Unlike growth respiration, which is tightly coupled to dry matter formation, MR varies in efficiency and there may be scope for selecting progenies that have low MR per unit biomass. This appears to have been possible in ryegrass (Wilson and Jones, 1982).

Direct measurement of MR usually requires measurement of the whole plant gas exchange. This is only practicable for small plants that can easily be enclosed in suitable chambers. Any measurements on oil palm may therefore have to be confined to young plants.

Amthor (1984) reviewed the various methods used to determine MR and noted their limitations. Irving and Silsbury (1987) compared three techniques using a number of annual crop plants. These were:

- dark decay method. The plants are placed in continuous darkness and the rate of CO_2 efflux determined. The asymptotic value reached following decay of the efflux is used to calculate MR (see below).

- dynamic method. The plants are subjected to daily changes in radiation level and the CO_2 efflux in the following dark period related to the net CO_2 uptake in the preceding photoperiod. When the later becomes zero, MR is indicated by the dark CO_2 efflux rate.

- zero growth rate method. The CO_2 uptake is plotted as a function of the growth rate and MR is equated to the CO_2 efflux when the growth rate becomes zero.

The authors concluded that the dark decay method provided the best estimate of MR and was also the simplest and least demanding technique. For this method, MR is obtained from:

$$MR = (2 * Nm)/W \quad (8)$$

where Nm = integrated half-day rate of CO_2 efflux after a prolonged dark period and W = CO_2 equivalent of the plant dry weight.

In all these methods, it is necessary to determine the plant dry weight (or its equivalent in terms of CO_2). This means that the methods are destructive and their use as a selection tool for oil palm would only be appropriate with highly homogeneous families or clones.

For tissues in which growth is complete, the rate of dark respiration can be used as a measure of MR, provided transport has ceased. This approach is theoretically applicable in the case of mature, fully expanded leaf laminae of oil palm assuming a sufficient period in darkness. As shown in *Table 3*, leaflets have the highest calculated MR coefficients and fronds contribute the most to total palm MR (*Table 2*).

Rates of oil palm leaflet dark respiration were determined from light-response curves by Henson (1991a, b) using a portable gas exchange system. Values ranged from 0.032 to 0.057 g CH_2O g^{-1} dry weight day^{-1}. These rates are 3.8 to 6.8 times the highest values calculated in *Table 3*. This suggests that transport may have been an important factor contributing to the respiratory activity. In addition, however, leaf temperatures of nearly 35ºC were recorded during the measurements and these would account for a doubling of the MR rates over those based on a nominal mean air temperature of 25°C.

CONCLUSION

From the above, it is evident that there are major uncertainties in the estimation of MR. It is recognized that the modelling of MR has a less firm theoretical basis than the modelling of GR (Amthor, 1984). Direct measurement of MR is likewise problematic and unlikely ever to be practicable with large trees such as mature oil palm. An alternative approach needing further study is to conduct whole canopy gas exchange measurements using micrometeorological methods. These should enable both GA and total respiration to be assessed and, together with measurements of dry matter production, should enable MR to be estimated as a residual term.

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REFERENCES

AMTHOR, J S (1984). The role of maintenance respiration in plant growth. *Plant, Cell and Environment, 7*: 561-569.

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.

CORLEY, R H V and BREURE, C J (1981). Measurements in oil palm experiments. *Internal Report*. Unilever Plantations Group, London. 21 pp.

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

HENSON, I E (1991a). Adaptation to light environment by leaves of oil palm (*Elaeis guineensis*). *PORIM Bulletin No. 22*: 1-8.

HENSON, I E (1991b). Age-related changes in stomatal and photosynthetic characteristics of leaves of oil palm (*Elaeis guineensis* Jacq.). *Elaeis*, *3*: 336-348.

HENSON, I E (2000). Modelling the effects of 'haze' on oil palm productivity and yield. *J. Oil Palm Research Vol. 12 No. 1*: 123-134.

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*: 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. *J. Oil Palm Research Vol. 10 No. 1*: 35-51.

HENSON, I E and CHANG, K C (2000). Chapter 4. Oil palm productivity and its component processes. *Advances in Oil Palm Research.* Vol. 1. p. 97-145.

HENSON, I E and MOHD TAYEB, D (2003). Physiological analysis of an oil palm density trial on a peat soil. *J. Oil Palm Research Vol. 15 No. 2*: 1-27.

IRVING, D E and SILSBURY, J H (1987). A comparison of the rate of maintenance respiration in some crop legumes and tobacco determined by three methods. *Annals of Botany, 59*: 257-264.

JONES, H G (1983). *Plants and Microclimate*. Cambridge University Press, Cambridge. 323 pp.

KHALID, H; ZIN, Z Z and ANDERSON, J M (1999a). Quantification of oil palm biomass and nutrient value in a mature plantation. I. Above-ground biomass. *J. Oil Palm Research Vol. 11 No. 1*: 23-32.

KHALID, H; ZIN, Z Z and ANDERSON, J M (1999b). Quantification of oil palm biomass and nutrient value in a mature plantation. II. Below-ground biomass. *J. Oil Palm Research Vol. 11 No. 1*: 63-71.

KHALID, H; ZIN, Z Z and ANDERSON, J M (2000). Decomposition processes and nutrient release patterns of oil palm residues. *J. Oil Palm Research Vol. 12 No. 1*: 46-63.

LAMADE, E and SETIYO, I E (1996). Test of Dufrene's production model on two contrasting families of oil palms in North Sumatra. *Proc. of the 1996 PORIM International Palm Oil Congress - Agriculture Conference*. PORIM, Bangi. p. 427-435.

NG, S K and THAMBOO, S (1967). Nutrient contents of oil palms in Malaya. I. Nutrients required for reproduction: fruit bunches and male inflorescence. *The Malaysian Agricultural Journal, 46*: 3-45.

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; JANSEN, D M; TEN BERGE, H F M and BAKEMA, A (1989). *Simulation of Ecophysiological Processes of Growth in Several Annual Crops.* Pudoc, Wageningen. 270 pp.

REES, A R and TINKER P B H (1963). Dry matter production and nutrient content of plantation oil palms in Nigeria. I. Growth and dry matter production. *Plant and Soil, 19*: 19-32.

SQUIRE, G R (1984). *Light interception, productivity and yield of oil palm. Occasional Report*. PORIM, Bangi. 45 pp.

van KEULEN, H; PENNING de VRIES, F W T and DREES, E M (1982). A summary model for crop growth. *Simulation of Plant Growth and Crop Production*. Simulation Monographs, Pudoc, Wageningen. p. 87-94.

van KRAALINGEN, D W G (1985). Simulation of oil palm growth and yield. Doctoral thesis, 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.

WILSON, D R and JONES, J G (1982). Effect of selection for dark respiration rate of mature leaves on crop yields of *Lolium perenne* cv. S23. *Annals of Botany*, *49*: 313-320.

WIT, C T; de GOUDRIAAN, J; LAAR VAN, H; PENNING de VRIES, F W T; RABBINGE, R; KEULEN VAN, K; LOUWERSE, W; SIBMA, L and JONGE de, C (1978). *Simulation of Assimilation, Respiration and Transpiration of Crops*. Simulation Monographs, Pudoc, Wageningen. 141 pp.