

PHYSIOLOGICAL ANALYSIS OF AN OIL PALM DENSITY TRIAL ON A PEAT SOIL

IAN E HENSON* and MOHD TAYEB DOLMAT*

ABSTRACT

A detailed physiological analysis was made of an oil palm density x fertilizer experiment established on a deep peat soil near Teluk Intan, Perak. Data on above-ground vegetative dry matter production, leaf area and leaf area development, flowering, bunch dry matter production and bunch composition were collected from the time of first flowering up to the 17th year after planting. Three planting densities (120, 160 and 200 palms ha⁻¹) were combined with 18 factorial fertilizer treatments. From data on leaf area, vegetative, bunch and total dry matter production, it was possible to derive the efficiency of radiant energy conversion to dry matter and the partitioning of dry matter between vegetative and reproductive biomass as well as between oil and non-oil components of dry matter. The influence of planting density on the extent of biomass turnover was assessed. Optimum densities for bunch yield were calculated as a function of age from single palm yield response to density. The proportions of assimilated carbon used for dry matter production, growth respiration and maintenance respiration were also calculated. Maintenance respiration per unit biomass was seen to decrease as a function of increasing palm age and density. The evaluated dry matter production and gross assimilation were compared with outputs from a simulation model.

The results are discussed and compared with those of other studies in the literature.

Keywords: oil palm, planting density, dry matter production, yield, biomass turnover.

Date received: 18 November 2002; **Date approved:** 27 November 2002; **Date revised:** 21 October 2003

INTRODUCTION

Choosing the best planting density for oil palm has always presented a dilemma as the density for maximum yield per unit area changes with the age of the palms. In addition, the optimum density, even when averaged over the life of a planting, may differ with the site, soil, management inputs and planting material. Lower planting densities have generally been used for those sites and soils favouring more vigorous growth while higher densities have been adopted for less productive situations; e.g. 136 palms ha⁻¹ on the more fertile coastal soils and 148 palms ha⁻¹ on the less fertile inland soils. Corley and co-workers (Corley *et al.*, 1972a,b; Corley, 1973) have proposed that excessive competition between

individual palms for resources (light, water, nutrients) impacts mainly on bunch rather than on vegetative production, because the latter receives priority when assimilate supplies are restricted. A consequence of this is that bunch yield, which initially increases with density, after reaching an optimum, is reduced as density increases further. Thus, above the optimum density inter-palm competition becomes excessive, while below the optimum, there is inefficient use of resources. Both cases lead to a reduction in yield.

At present, there is no general method of predicting the best density for individual circumstances comprising the site, planting material, management *etc.* and so density trials continue to be required. Such trials obviously need to be long-term. Further trials become necessary as new planting materials become available, and as oil palm planting expands to encompass previously

* Malaysian Palm Oil Board, P. O. Box 10620, 50720 Kuala Lumpur, Malaysia.
E-mail: henson@mpob.gov.my

unexploited environments. The use of peat soils for planting oil palm is one such example.

For most agronomic experiments, the main purpose is to determine the treatment effects on bunch yield. However, Hardon, Corley and co-workers (Hardon *et al.*, 1969; Corley *et al.*, 1971a,b) argued that a fuller understanding of the total dry matter production (TDMP) of the crop was needed to enable both breeding objectives and agronomic management decisions to become more focused. Their work encouraged the collection of growth data in many trials, though in general such data have not been made full use of despite the demonstration by Squire (1984; 1985) of their utility. Breure (1988a,b) however, used the above approaches to analyse density x fertilizer experiments conducted in Papua New Guinea while Corley and Donough (1992) and Smith *et al.* (1996) undertook a physiological analysis of fan density trials using clones. There appear, however, to be few, if any, similar reports and no in-depth physiological studies concerning trials on peat soils.

The present trial was established by PORIM (Palm Oil Research Institute of Malaysia) in 1985 and

has been monitored continuously since then. Previous reports on the trial (Mohd Tayeb *et al.*, 1995; 1998; 2003) have provided some information on the early vegetative growth and bunch yields. The present work aims to evaluate as completely as possible the effects of density on the physiological and growth parameters, including light interception, dry matter production (DMP), efficiency of radiation use, assimilate partitioning, flowering and yield formation and biomass turnover. *Figure 1* outlines the relationships between the main components and processes that were evaluated. The investigation thus included elements of the *physiological analysis* described by Squire (1985). In addition, the allocation of assimilates for growth and maintenance respiration (Breure, 1988a,b) and gross CO₂ assimilation by the canopy were calculated and the results of the analysis are compared with those obtained using a simple oil palm simulation model (Henson, 1989; 2000).

The data presented mainly represent annual means; shorter-term *cycling* in flowering and bunch production and cycling of bunch components will be examined in subsequent papers.

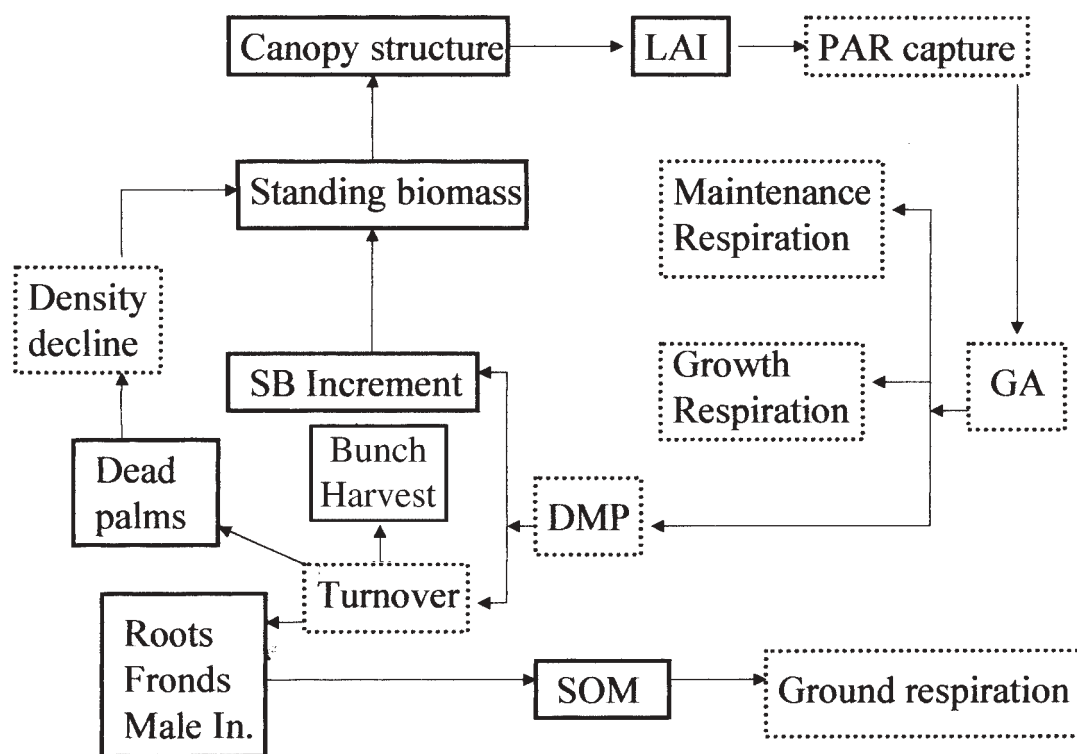


Figure 1. Relationships between calculated, measured and modelled variables. Items in solid rectangles represent material pools, those in dashed rectangles are processes, while lines with arrows indicate connecting links. Key: LAI, leaf area index; PAR, photosynthetically active radiation; GA, gross CO₂ assimilation; DMP, dry matter production; SB, standing biomass; SOM, soil organic matter.

METHODS

Site

The trial occupied 21.45 ha at the PORIM (now MPOB: Malaysian Palm Oil Board) Teluk Intan Research Station, Perak (3.49°N, 101.06°E). The site is flat, receives a moderately high and uniformly distributed rainfall and has a high soil water table (*Appendix 1*). The soil is characterized as a very deep (>3 m) peat (Anderson 3) with a pH of 3.4, a carbon content of 33.6% and an initial bulk density of c. 0.13 g cm⁻³ in the top 15 cm layer. This was increased prior to planting in 1985 to c. 0.23 g cm⁻³ by mechanical compaction (Mohd Tayeb *et al.*, 1995). The site was previously a secondary peat forest.

Rainfall in the area is moderate to high (*Appendix 1*). Between 1990 and 2001, the annual rainfall at the site varied from 1696 to 2404 mm with the driest month being July (95.6 mm) and the wettest, November (287.2 mm). The water table (*Appendix 1*) was high but was lowered following drainage works and its depth subsequently regulated by means of water gates. The depth of the water table has tended to follow the rainfall pattern with the annual mean depth during 1990 to 2001 varying from 51.1 to 96.6 cm, being highest in December (53.6 cm) and lowest in August (94.1 cm).

Experimental Design

The trial was laid out in two replicate blocks each with three planting densities (120, 160 and 200 palms ha⁻¹) comprising the main plots split for fertilizer treatments into 18 sub-plots. (Additional plots receiving different liming treatments were also planted but as these were not fully replicated they were excluded in the present analysis.) Fertilizers were applied on a per palm basis. As there were few significant or only minor effects of fertilizer treatments on fresh fruit bunch (FFB) yield and other parameters (Mohd Tayeb *et al.*, 1995; 1998; 2003), only the effects of density are considered here.

Each sub-plot contained eight central recording palms with eight, 12 or 16 surrounding palms as guards. Subsequently, there were losses of palms due to *Ganoderma* infection (Mohd Tayeb *et al.*, 2003) resulting in changes in the actual densities. These losses were recorded annually and the data used to derive the mean planting density of each plot from which parameters on an area basis were calculated.

The palms (Guthrie DxP material) were planted in August-September 1985 using a hole-in-hole planting method. As mentioned, the land preparation included mechanical compaction to increase the soil bulk density with the aim of improving anchorage of the palms and facilitating movement within the plots.

Vegetative Measurements and Inflorescence Production

Standard procedures described by Corley *et al.* (1971b) and Corley and Breure (1981) were used for recording the above-ground standing biomass, vegetative growth and inflorescence production. Beginning July 1988, the youngest fully-emerged frond (frond 1) was marked and male and female inflorescence production, abortion and emergence of new fronds subsequently recorded at three-monthly intervals. Total frond counts and measurements of frond and trunk dimensions were made annually as described by Hardon *et al.* (1969) and Corley *et al.* (1971b). For completeness, vegetative growth was estimated for the first three years in the field by back extrapolation of growth curves on a per palm basis.

As no root sampling was done during the main period of the experiment, root biomass, production and turnover were estimated using empirical relationships as described. In mid 2002, a systematic set of root auger samples were taken to a depth of 60 cm to determine the standing root biomass. From these and above-ground data, root/shoot ratios were calculated to compare with estimated values.

Bunch Production and Bunch Analysis

Harvesting was carried out twice monthly beginning March 1988 when the first bunches ripened. Bunch numbers and weights were recorded separately for each recording palm. Bunch dry weights were calculated from a regression on fruit/bunch (F/B) ratio as described by Corley *et al.* (1971b). As annual vegetative dry matter production (VDMP) was recorded each July, the annual bunch dry matter production (BDMP) for a year was calculated from bunches harvested over the same period.

From 1992 onwards, random bunch samples were taken for laboratory bunch analysis using standard procedures. Approximately 870 bunches were sampled per density from the main plots over 10 years until 2001. From the analyses oil/bunch (O/B), kernel/bunch (K/B), shell/bunch (S/B), F/B and other parameters were obtained, allowing calculation to be made of palm oil and kernel yields and energy equivalents of bunch dry matter.

Calculations

The procedures used for calculating standing biomass, VDMP and BDMP production and derived parameters were essentially as described by Corley *et al.* (1971b), Corley and Breure (1981) and Squire (1985), but with some modifications.

FronD dry weight and area. The coefficients given by Hardon *et al.* (1969) for deriving the surface area of a frond from leaflet measurements and counts and by Corley *et al.* (1971b) for deriving the total frond dry weight from the cross-sectional area of its petiole have been found for young palms to overestimate both these characteristics (Henson, 1993). Based on the data of Henson (1993), age specific coefficients (*Appendix 2*) were derived to calculate the frond area and dry weight during the first 10 and six years after planting, respectively. Above these ages, the coefficients given by Hardon *et al.* (1969) and Corley *et al.* (1971b) were used.

FronD biomass turnover. The turnover of frond biomass was calculated as the product of the annual number of fronds removed by pruning and the mean dry weight of fronds determined the previous year. The annual number of pruned fronds was calculated from:

number of new fronds emerging per year +
change in total frond number between the start
and end of the year.

The total pruned frond weight obtained was then reduced by 20% to allow for the weight of the frond bases left adhering to the trunk. These probably slowly lose dry weight over time from respiration (Henson and Chang, 2000) and eventually fall off, so adding to the turnover. However, the precise lifetime of cut frond bases varies with individual palms and this was not recorded; hence base abscission was ignored in the study.

Standing root biomass, root turnover and root dry matter production. The standing root biomass was estimated from a linear regression of root on shoot biomass (*Appendix 2*) derived from intensive measurements of palms on inland soils (Henson and Chai, 1997; Khalid *et al.*, 1999a,b).

An estimate of root biomass turnover was obtained from a regression of turnover on standing root biomass derived from the data of Henson and Chai (1997) and Dufrene (1989) (*Appendix 2*). Annual root biomass production was taken as the sum of turnover and annual biomass increment.

Trunk dry matter and dry matter production. The standing trunk dry matter was calculated as described by Corley *et al.* (1971b), but when calculating the dry matter production the increase with age in density of the whole trunk was included in addition to new growth at the apex.

Bunch and male inflorescence standing biomass. The following method was adopted to calculate the standing biomass of developing bunches. A mean development time of 160 days from anthesis to ripening was assumed. An exponential equation was fitted (*Appendix 2*) to a standard dry matter accumulation curve derived from Corley (1986). From the curve, the mean fraction of the final bunch

dry matter present each day over the bunch growth period was found to be 0.4286. The mean annual bunch standing dry weight ($t\ ha^{-1}$) was then calculated as:

$$BDMP * 0.4286 * 160/365$$

where BDMP is $t\ ha^{-1}\ yr^{-1}$.

The standing biomass of male inflorescences was calculated from the inflorescence number and their estimated mean dry weight (Ng and Thamboo, 1967).

Bunch components. Contrary to earlier results (Mohd Tayeb *et al.*, 1995), the bunch analyses indicated no significant difference at $P < 0.05$ between densities for oil and kernel contents or F/B but there were significant year effects. Polynomial curves were fitted to the annual data to predict the O/B, K/B, S/B and F/B ratios for each year. The curves were extrapolated for those years that lacked bunch analysis data. The ratios obtained were used to calculate palm oil and kernel yields. The percentage dry weight of bunches was calculated from its relationship to F/B given by Corley *et al.* (1971b). Bunch energy contents were calculated in terms of non-oil equivalent dry matter (Squire, 1985) based on mesocarp oil, kernel and shell contents and standard component energy values (Henson, 1997). Palm kernel oil was assumed to equal 38% by weight of fresh kernels.

Bunch index (BI) and harvest index (HI). Following Corley *et al.* (1971a,b), $BI = BDMP / TDMP$ and $HI = PO + PK / TDMP$ where PO is palm (mesocarp) oil and PK is palm kernel. In many cases, however, only the above-ground DMP has been used to calculate BI or HI. Here, TDMP (*i.e.* including an allowance for roots) was used. When root DMP was excluded, the values of BI and HI were increased by c. 9%.

Optimum palm density. The optimum density (D_{opt}) was calculated using the equation given by Corley (1976):

$$D_{opt} (\text{palms } ha^{-1}) = a / 2b$$

where a is the intercept and b , the slope of the linear regression relating yield per palm to density.

Radiation interception (f) and radiation use efficiency (e). These parameters were calculated as described by Squire (1984; 1985).

Respiration losses and estimation of gross assimilation. Maintenance respiration (MR) and growth respiration (GR) of biomass components were calculated as described by Henson (2000) and Henson (2004), using the procedures and coefficients given by Breure (1988b) and van Kraalingen *et al.* (1989). When calculating the GR of bunches, new

coefficients were derived to allow for variation in bunch lipid content.

The gross assimilation (GA) of palm stands was taken as the sum of TDMP (vegetative plus inflorescence and bunch production) and total respiration (MR plus GR).

Modelling of Dry Matter Production

A simplified version of the OPSIM model of van Kraalingen *et al.* (1989) described by Henson (2000) was used to calculate VDMP, BDMP and GA. Solar radiation was the sole environmental input. The output from the model was compared with the *measured* data.

Meteorological Data

Solar radiation was not recorded at the experimental site and so data from nearby stations of the Malaysian Meteorological Service (MMS) were used. The MMS station closest to the experimental site, at MARDI Hilir Perak (c.10 km), recorded sunshine hours (SH) only while both total short-wave radiation and SH were available from the Sitiawan station some 25 km to the NW. The relationship between mean monthly SH and radiation at Sitiawan was calculated with the Angstrom equation (Jones, 1983) using a substantial long-term dataset (1976 to 1999). The coefficients obtained were then used to derive mean monthly solar radiation from SH at Hilir Perak covering the period 1985 to 2001. These data were input to the simulation model assuming photosynthetically active radiation (PAR) to be 50% of solar radiation.

Statistical Analysis

Analyses of variance of the main effects of density, year and block and their interactions were carried out for each of the variables of interest using a SAS programme (SAS, 1998). Curve fitting was done in Excel spreadsheets.

RESULTS

Canopy Development and Standing Biomass

A measure of canopy development is important as this determines the interception of radiation that in turn largely determines productivity, particularly in the early growth stages. Canopy development is best characterized in terms of the leaf area index (LAI; the ratio between total leaf and ground surface area). In oil palm, LAI depends on mean single frond area, number of fronds per palm and palm density.

Single frond area significantly ($P>0.05$) increased with palm density while frond number per palm decreased with density (*Figures 2a* and *2b*). This resulted in there being no significant difference in mean frond area per palm at the two higher densities (*Figure 2c*) though, averaged over years, the mean frond area per palm was significantly lower ($P>0.05$) at the lowest density of 120 palms ha^{-1} . However, the reduction in leaf area per palm at low density was insufficient to negate the advantage of lower density in terms of increased PAR interception per palm (*Figure 2d*).

As would be expected, on a ground area basis, higher density resulted in increased LAI and

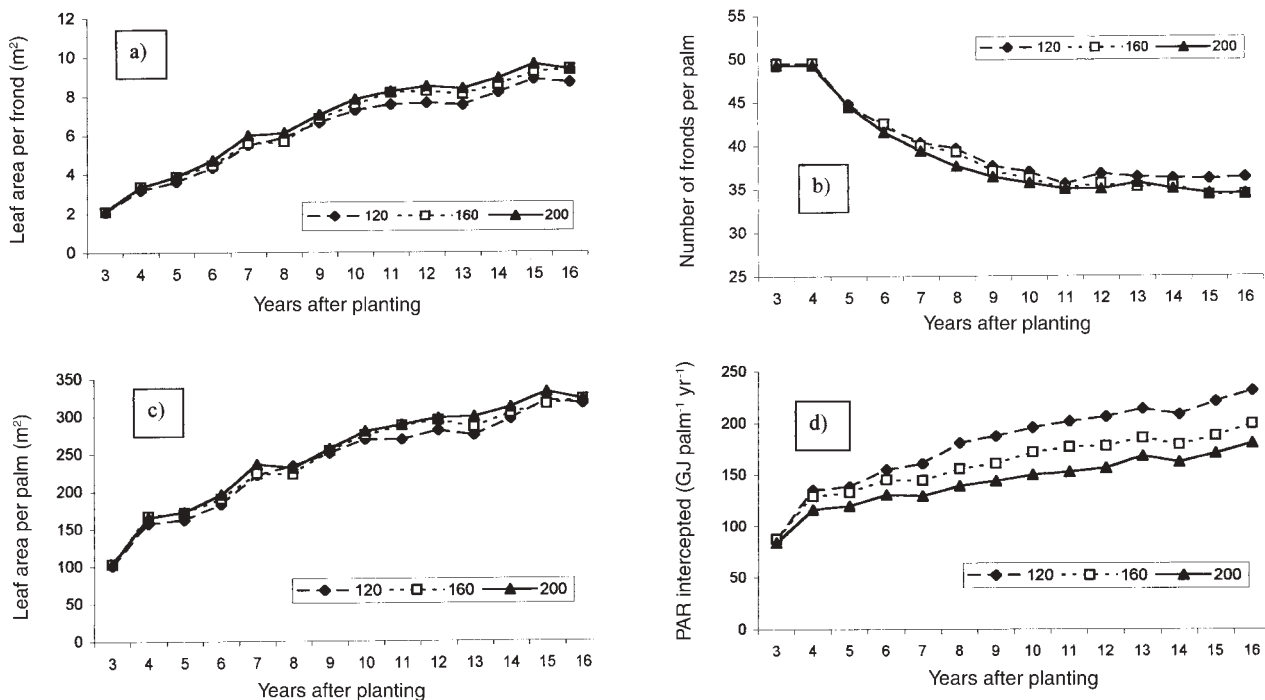


Figure 2. Effects of planting density on a) single frond area, b) total frond number per palm, c) leaf area per palm and d) photosynthetically active radiation (PAR) interception per palm.

interception of PAR (Figures 3a and 3b). The effects of density on both were highly significant ($P < 0.001$).

As found in previous studies (e.g. Rao *et al.*, 1992; Kwan, 1994), the rate of frond emergence (production) was significantly ($P < 0.01$) reduced as density increased. In contrast, single frond dry weight, as assessed from petiole cross-section measurements, was higher at the two higher densities (Figures 4a and 4b). The result of these opposed changes was that the calculated frond dry matter production per palm was not significantly affected by density (Figure 4c).

Crowding generally results in etiolation as reflected in longer frond rachises and greater trunk heights. This was plainly evident in the present experiment (Figures 5a and 5b). An increased rachis length was already apparent by the fourth year when for 200 palms ha^{-1} , it was greater than 4 m and

exceeded the mid distance between palms. Increased rachis length was thus amongst the earliest responses to increased density.

Trunk height also increased substantially with density (Figure 5b) with the mean annual rate of increase showing a significant linear relationship with density, amounting to 1.3 cm yr^{-1} for every additional 10 palms ha^{-1} . While increased rachis length did not necessarily denote increased frond dry weight (Figure 4b), the increase in trunk height represented a greater trunk dry weight, as this was calculated as the product of trunk density and volume and the latter is a function of height.

Changes over time in total standing biomass per hectare and its components (roots, trunk, fronds and developing bunches) are shown for the three planting densities in Figure 6. These results illustrate the increasing proportion of biomass accrued in the

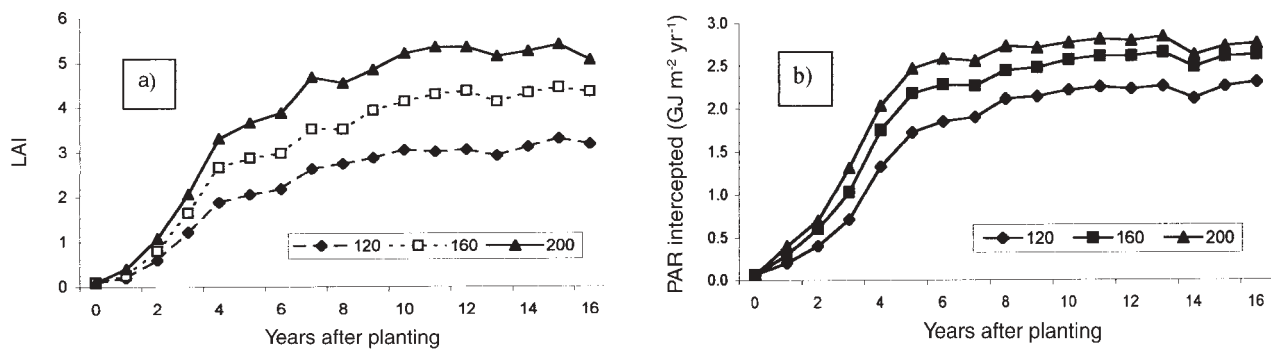


Figure 3. Effects of planting density on a) leaf area index (LAI) and b) interception of photosynthetically active radiation (PAR).

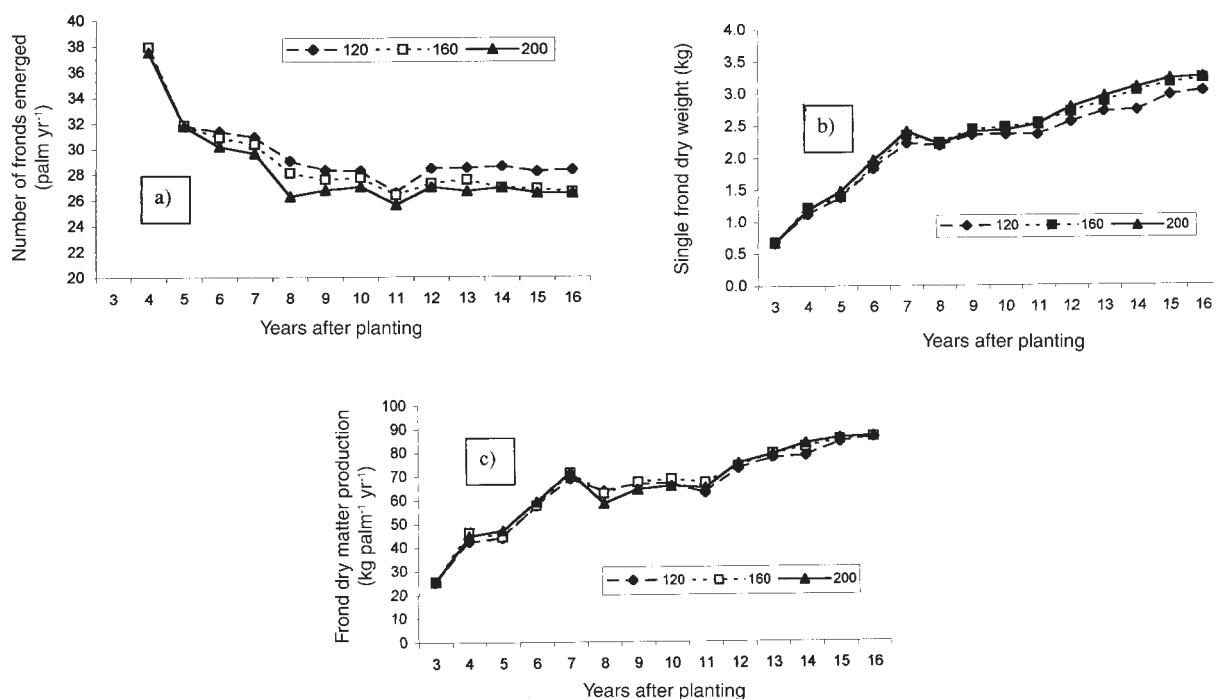


Figure 4. Effects of planting density on a) number of new fronds emerging per year, b) single frond dry weight and c) total frond dry matter production per year.

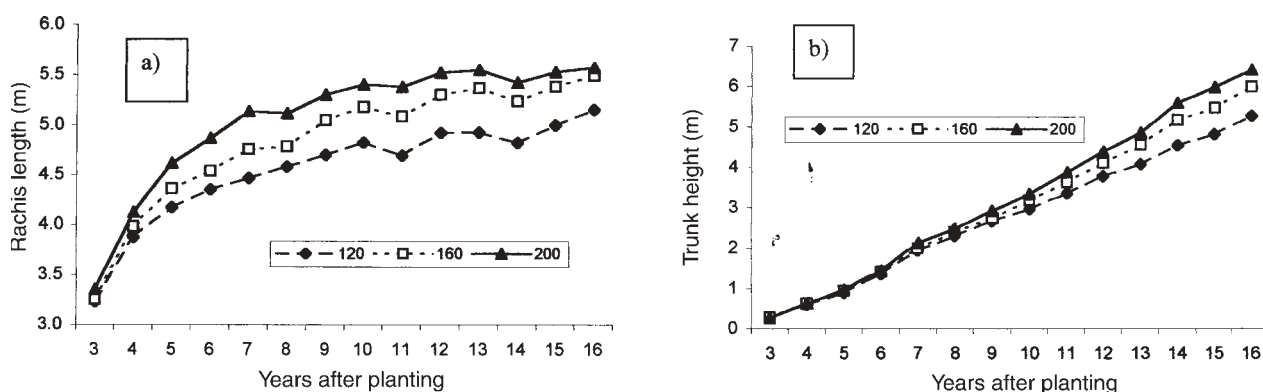


Figure 5. Effects of planting density on a) rachis length and b) trunk height.

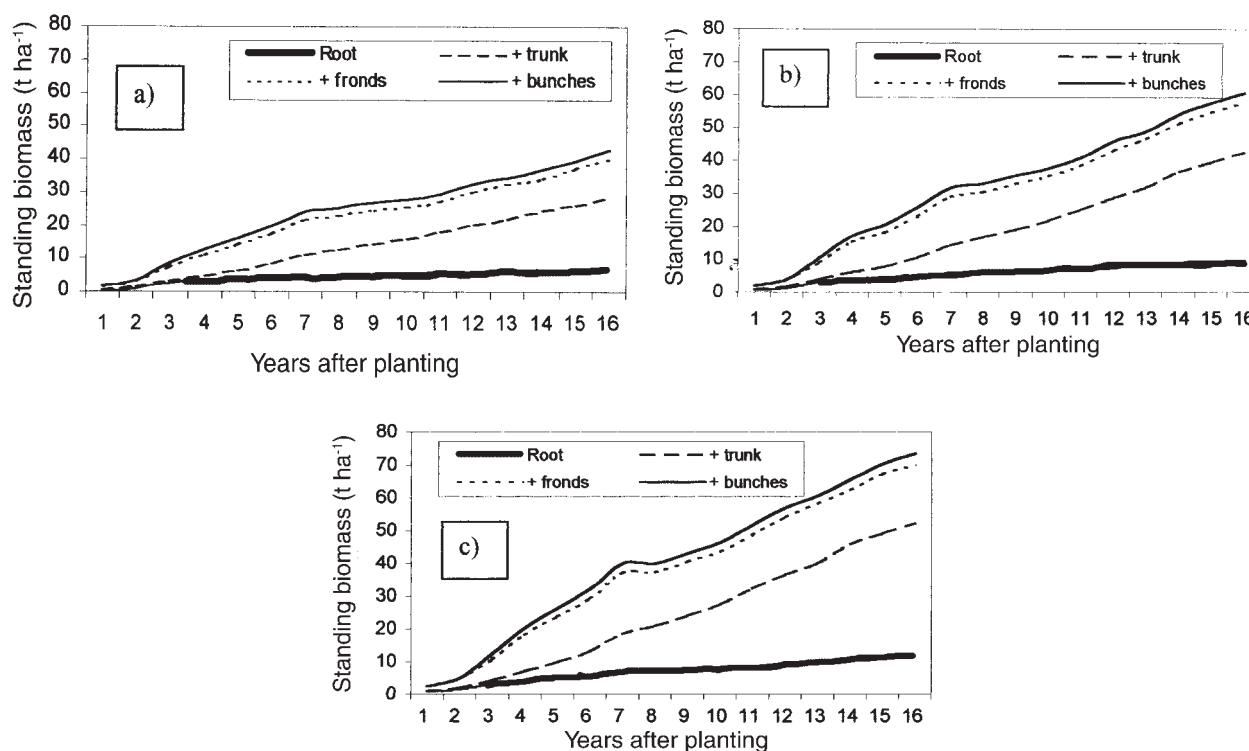


Figure 6. Components of standing biomass (roots, trunk, fronds, bunches) at a) 120, b) 160 and c) 200 palms ha^{-1} . All three densities are plotted on same vertical scale to emphasize differences in total biomass.

trunk and to a lesser extent in the roots, while the frond component, after an initial phase of increase, remained fairly constant. Trunk dry matter as a proportion of the total standing biomass increased from 10.3% at year 3 to over 56% at year 16 and also increased slightly with density, averaging 38.6%, 39.5% and 40.6% for 120, 160 and 200 palms ha^{-1} respectively. Bunch standing biomass, in as far as it could be estimated, was only a minor component (averaging c. 6.5% of the total).

One component of the standing biomass not quantified was the mass of old frond bases adhering to the trunk. These bases fall off after a time but as no counts were made nor samples taken it was not possible to assess the changes in the quantity present. When assessing MR from the standing biomass, an estimation of pruned frond bases was not considered

necessary, as the respiration rate of the bases is low (Henson and Chang, 2000) and most likely microbial in origin.

Biomass Production

The DMP of non-bunch biomass (vegetative biomass and male inflorescences) is outlined for the three densities in Figure 7. Mean values for VDMP are given in Table 1. Fronds constituted by far the largest component of VDMP (Figure 7).

The rate of increase in non-bunch DMP with age was far from smooth, peaking in the seventh and, to a lesser extent, in the 14th year (Figure 7). The first peak was evident for both trunk and fronds while the second was only found for the trunk. The peaks were most pronounced at the higher densities.

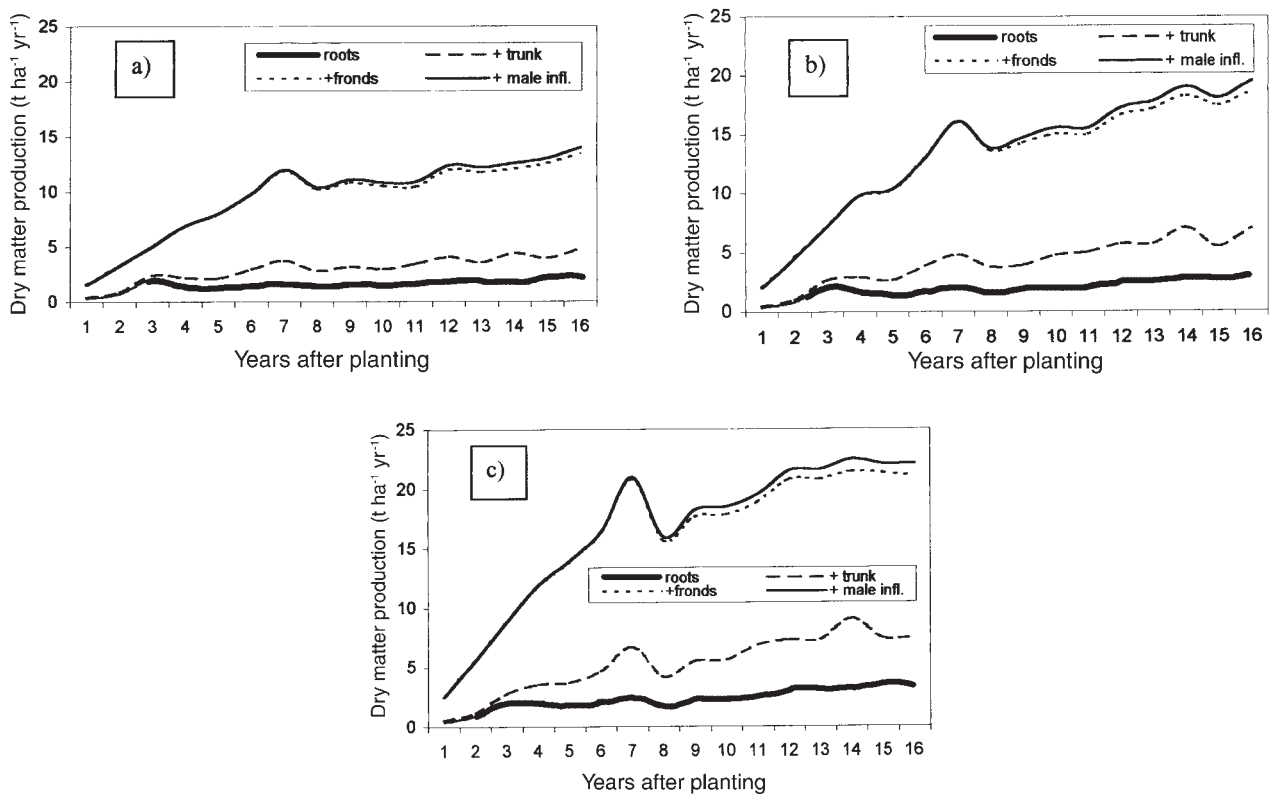


Figure 7. Components of non-bunch (roots, trunk, fronds, male inflorescence) biomass production at initial planting densities of a) 120, b) 160 and c) 200 palms ha⁻¹. All three densities are plotted on same vertical scale to emphasize differences in biomass production.

TABLE 1. EFFECTS OF DENSITY ON MEAN ANNUAL PRODUCTIVITY PER PALM (kg). ALL VALUES ARE AVERAGED OVER 13 YEARS (1989 to 2001). DATA GIVEN ARE FOR VEGETATIVE DRY MATTER PRODUCTION (VDMP), BUNCH DRY MATTER PRODUCTION (BDMP), TOTAL DRY MATTER PRODUCTION (TDMP), PALM (MESOCARP) OIL PRODUCTION (POP) AND PALM KERNEL PRODUCTION (PKP). TDMP INCLUDES AN ESTIMATE FOR MALE INFLORESCENCE BIOMASS. P INDICATES THE OVERALL LEVEL OF SIGNIFICANCE OF THE DENSITY EFFECTS; DATA WITH THE SAME SUPERScript ARE NOT SIGNIFICANTLY DIFFERENT AT P<0.05

Measurement	Initial planting density (palms ha ⁻¹)			P
	120	160	200	
VDMP	96.4 ^a	101.0 ^b	102.4 ^b	<0.01
BDMP	93.4 ^a	85.9 ^b	77.9 ^c	<0.001
TDMP	192.5 ^a	189.9 ^{a,b}	183.4 ^b	<0.001
POP	39.35 ^a	36.05 ^b	32.8 ^c	<0.001
PKP	10.74 ^a	9.87 ^b	9.00 ^c	<0.001

Annual variation in incident or in intercepted radiation (Figure 3b) did not explain these peaks.

While VDMP on a per palm basis significantly increased with density, BDMP per palm showed the expected decline (Table 1). The increase in VDMP with density contrast with results of other studies (Corley, 1973; Kwan, 1994) that showed either no effect or the opposite trend.

The decline in BDMP per palm was greater than the increase in VDMP so there was a significant fall with density in TDMP per palm (Table 1). However, despite the decrease per palm in BDMP with increased density, there was an increase in production per hectare (Figure 8).

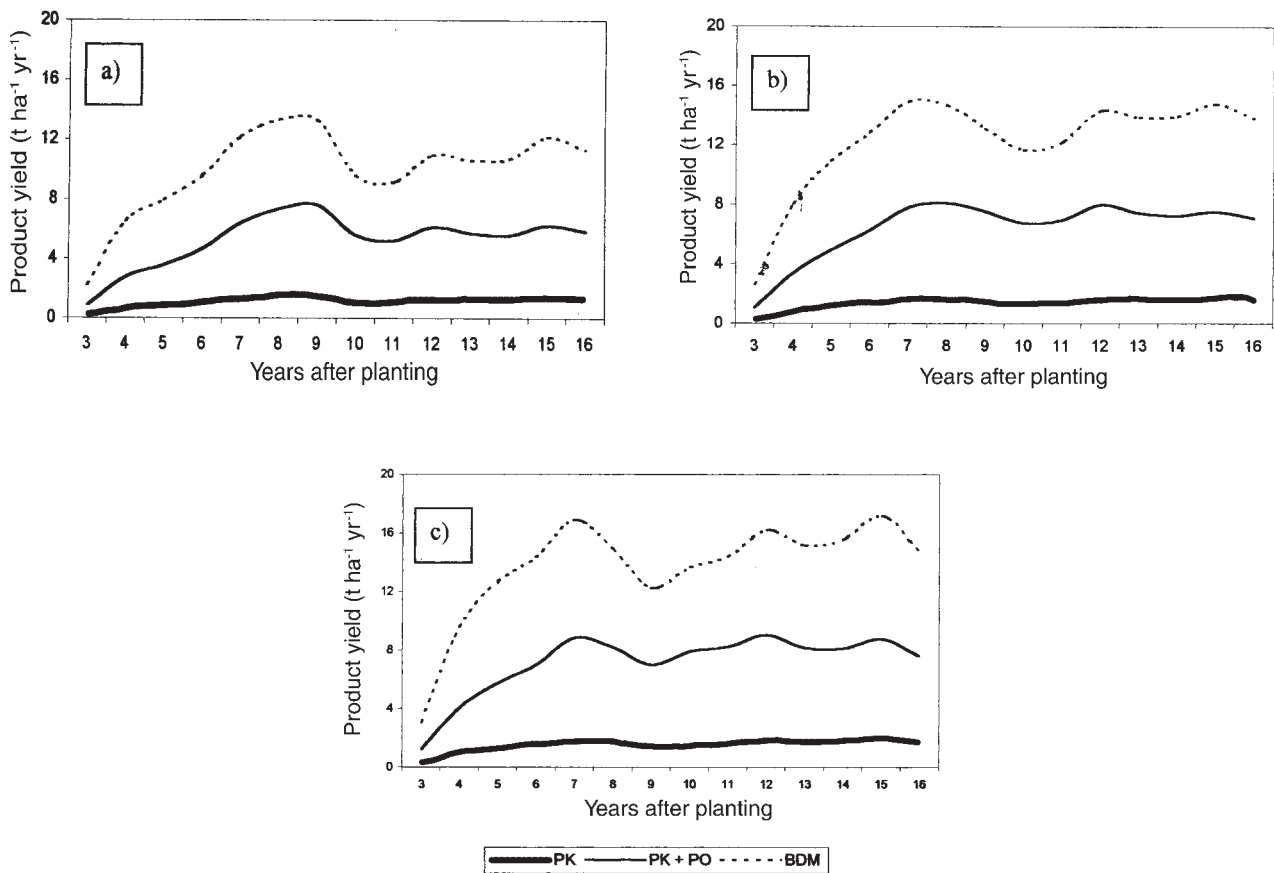


Figure 8. Yield components (palm oil and palm kernel) of harvested bunches from palms at a) 120, b) 160 and c) 200 palms ha⁻¹ initial planting density.

Optimum Palm Density for Bunch Production

Palm density declined during the course of the experiment as a result of losses from *Ganoderma*. For the 200 palms ha⁻¹ plots, the density declined to 157 palms ha⁻¹ by the 17th year, a drop of over 21%. The densities of 160 and 120 palms ha⁻¹ were each reduced over the same period by about 16%. The total yields per palm at the initial densities of 160 and 200 ha⁻¹ were on average reduced by 8% and 16.6% respectively compared to yields at the lowest density.

There was a significant linear relationship between mean BDMP/palm (Y) over 14 years of bunch harvest and the mean density (D) over this period, where:

$$Y \text{ (kg palm}^{-1} \text{ yr}^{-1}\text{)} = 119.38 - 0.2216 * D \text{ (palms ha}^{-1}\text{); (R}^2\text{=0.999).}$$

From this, the optimum density (D_{opt}) was calculated to be 269 palms ha⁻¹ and the mean theoretical yield was 16.08 t BDMP ha⁻¹. This was only 3% higher than the mean *potential* yield calculated for 200 palms ha⁻¹ (*i.e.* without losses) and 11% higher than the yield actually achieved following palm losses.

Optimum densities were also calculated separately for individual years and for cumulative yields obtained as each year passed [the *current* and *agronomic* optima as defined by Donough and Kwan (1991)]. Not all the individual years gave significant regressions but for those which did the optimum density initially declined but then increased again around the 14th year followed by a later decline (Table 2). The mean optimum density was 274 palms ha⁻¹. The agronomic optimum density showed a more uniform trend (Figure 9), stabilizing from the ninth year at a mean of 235 palms ha⁻¹.

TABLE 2. OPTIMUM PLANTING DENSITIES FOR BUNCH DRY MATTER PRODUCTION (BDMP) PER HECTARE AT DIFFERENT YEARS AFTER PLANTING. RESULTS ARE PRESENTED ONLY FOR THOSE YEARS WHEN A SIGNIFICANT LINEAR RELATIONSHIP EXISTED BETWEEN BDMP PER PALM AND DENSITY. THE SENSITIVITY OF BDMP PER PALM TO DENSITY IS ALSO INDICATED BY THE BDMP AT THE LOWEST DENSITY EXPRESSED AS A PERCENTAGE OF THAT AT THE HIGHEST DENSITY

Palm age (yr)	Optimal density (palms ha ⁻¹)	BDMP at optimal density (t ha ⁻¹ yr ⁻¹)	R ²	BDMP at minimum density as % at maximum
4	411	13.0	0.97	88.7
7	300	19.2	0.99	83.5
8	178	14.9	1.00	66.8
9	140	13.3	0.99	55.0
10	314	15.9	0.95	86.0
13	313	18.6	0.90	86.8
14	378	22.2	0.94	90.1
15	306	21.1	0.93	88.8
16	213	15.4	0.99	82.7
17	187	13.7	0.99	79.5
4-17	269	16.1	0.99	83.1

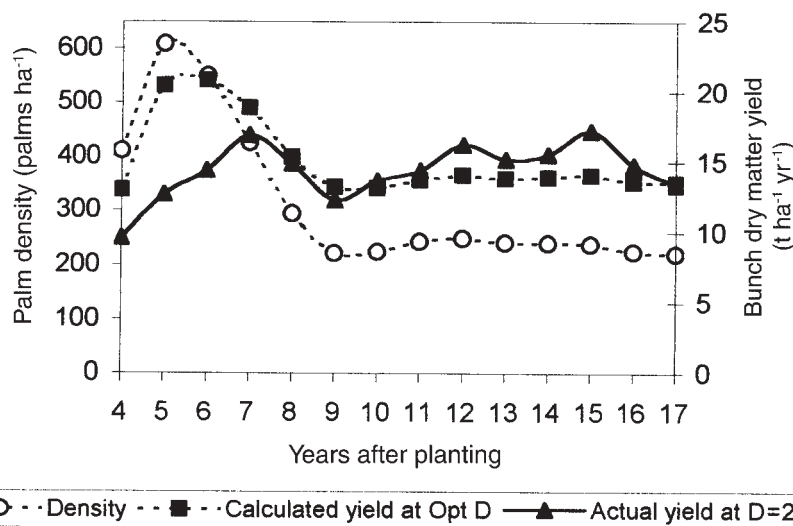


Figure 9. Changes with palm age in the agronomic optimum planting density and in yield of bunch dry matter calculated for the optimum densities. For comparison, yields obtained in the 200 palms ha⁻¹ treatment are also shown. Optimum densities were calculated as described in the text from linear equations fitted to cumulative bunch dry matter production per palm.

Yield Components

Although annual FFB yields and yield components (bunch number and mean bunch weight) have been reported previously (Mohd Tayeb *et al.*, 1995; 1998; 2003), it may be useful to summarize the main findings here. Table 3 shows that bunch number was the main determinant of FFB yield as there was no significant effect of density on mean bunch weight. Mean bunch numbers were about 8%

lower than the recorded female inflorescence numbers, which can be explained by some inflorescences failing to develop into mature bunches either due to bunch rot or to subsequent palm death.

As is normally the case, mean bunch number declined with palm age while the mean bunch weight increased (Henson and Mohd Tayeb, 2004). The decrease in bunch number was a direct consequence of the decline in female inflorescence production, which is detailed in the next section.

TABLE 3. EFFECTS OF DENSITY ON THE MEAN ANNUAL NUMBER PER PALM OF NEWLY EMERGED FRONDS (FrdE), FEMALE INFLORESCENCES (FI), MALE INFLORESCENCES (MI), ABORTED INFLORESCENCES (AbI) AND HARVESTED BUNCHES (B). ALSO GIVEN IS THE MEAN SINGLE BUNCH FRESH WEIGHT (BFW). ALL VALUES ARE AVERAGED OVER 13 YEARS (1989 to 2001). *P* INDICATES THE OVERALL LEVEL OF SIGNIFICANCE OF THE DENSITY EFFECTS; DATA WITH SAME SUPERScript ARE NOT SIGNIFICANTLY DIFFERENT AT $P < 0.05$

Measurement	Initial planting density (palms ha ⁻¹)			<i>P</i>
	120	160	200	
FrdE	29.71 ^a	28.93 ^{ab}	28.34 ^b	<0.05
FI	23.60 ^a	22.13 ^{ab}	21.09 ^b	<0.05
MI	4.89 ^a	5.40 ^b	5.49 ^b	<0.05
AbI	1.05 ^a	1.28 ^{ab}	1.53 ^b	<0.05
B	21.59 ^a	20.40 ^b	19.21 ^c	<0.001
BFW (kg)	9.42 ^a	9.32 ^a	9.09 ^a	ns

In agreement with other trials, there were increases with density in O/B, K/B and F/B ratios (Mohd Tayeb *et al.*, 2003), but in the analysis adopted here, the density differences did not reach statistical significance. The differences with density in the yields of PO and PK (Table 1; Figure 8) were thus mainly a reflection of the differences in bunch yield rather than in bunch composition.

FronD Emergence, Inflorescence Production and Inflorescence Abortion

As the bunch yield of oil palm depends on the weight and number of bunches and bunch number in turn depends on the number of female and hermaphrodite inflorescences initiated which survive to set fruit, it becomes important to quantify these aspects of development as well as biomass production itself. The number of female inflorescences produced is a function of both the sex ratio and the number of nodes initiated. (The latter cannot be observed directly but is inferred from the number of emerging fronds)

As already shown (Figure 4a), frond emergence was reduced with density, limiting the maximum possible mean inflorescence number produced from the fourth to the 16th year to 28.3 and 29.7 palm⁻¹ for the 200 and 120 palms ha⁻¹ densities respectively (Table 3). A very high ratio of female to male inflorescences was produced at all densities such that females reaching anthesis occupied 75% (200 palms ha⁻¹) to 80% (120 palms ha⁻¹) of all the nodes while males and aborted inflorescences accounted for only 16% to 19% and 3.6% to 5.5% of nodes respectively. While the female inflorescence numbers decreased with density, the male and aborted numbers increased (Table 3).

Both node initiation (assessed from frond emergence; Figure 4a) and female inflorescence production (Figure 10) declined substantially with palm age. Excluding the effect of the decline in frond production, the decline in female inflorescence production arose mainly from a decrease in the sex ratio as inflorescence abortion occurred to only a minor extent and showed little consistent trend with age (Figure 10).

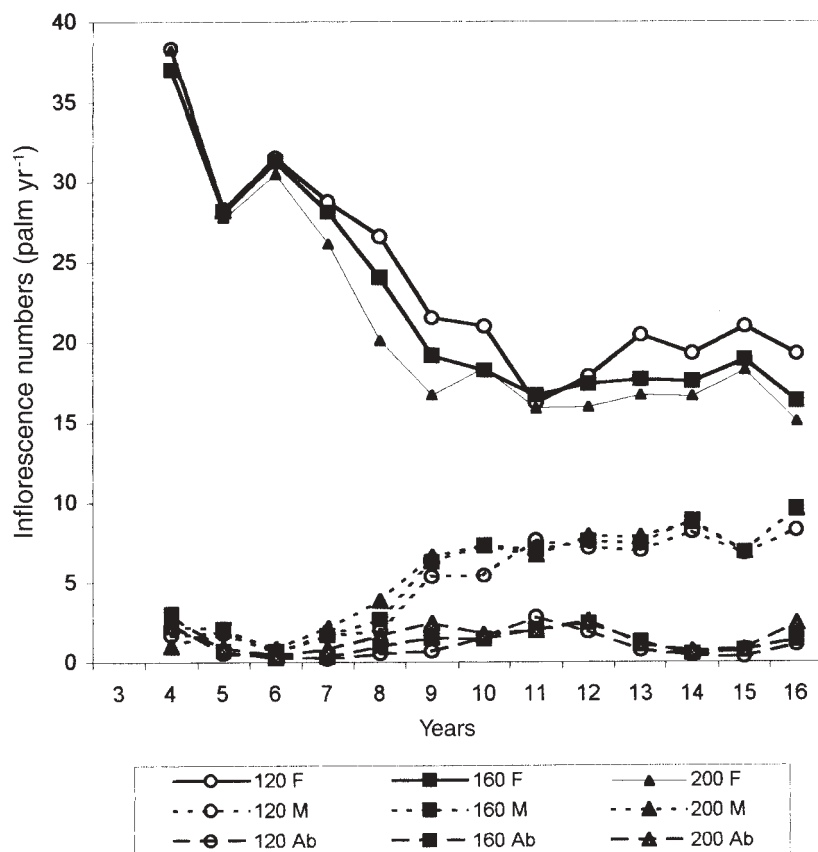


Figure 10. Changes with age in numbers per palm of female inflorescences (F), male inflorescences (M) and aborted inflorescences (Ab) for initial planting densities of 120, 160 and 200 palms ha⁻¹.

Radiation Interception, Light Use Efficiency and Partitioning of Assimilates

In the *summary* model of Montieth (1972; 1977) crop yield (Y) = $S * f * e * P$ where S = incoming radiation ($MJ m^{-2} yr^{-1}$), f = fractional interception of radiation, e = radiation use efficiency ($g MJ^{-1}$) and P represents the fraction of dry matter partitioned into harvested biomass. For oil palm P can be expressed in terms of BI or HI. The values of f and e may be calculated using total short wave (solar) radiation or PAR; the latter is used here.

The value of f_{PAR} increased significantly with planting density (Table 4) as would be expected from the increased LAI at higher density. In addition, however, the efficiencies of radiation use, e and e^* (the latter based on non-oil equivalent dry matter production; Squire, 1985), also increased significantly with density in contrast to observations by Breure (1988a). When the dependence of VDMP and BDMP on f_{PAR} , e and e^* was examined, it was found that increases in VDMP were more highly positively correlated with f_{PAR} than with e or e^* , while increases in BDMP were most closely correlated with increases in e and e^* (Table 5).

As shown earlier (Figure 2), PAR interception per palm declined significantly with density. Both VDMP

and BDMP per palm were significantly correlated with the amount of intercepted PAR with R^2 values of 0.52 and 0.64, respectively ($n=39$; $P>0.001$). BI and HI both decreased significantly with increased density (Table 4).

Biomass Turnover

Only a proportion of the biomass produced annually is retained by the palm to augment its existing biomass. The rest is lost either in natural turnover processes or as a result of frond pruning and harvesting of bunches. Biomass turnover can also occur due to death of palms from disease and other causes. The major turnover not involving whole palm death, quantified on a per palm basis, is shown in Table 6.

Estimated root turnover increased with planting density though root turnover as a proportion of root biomass production decreased. Density did not affect frond turnover nor total vegetative biomass turnover per palm. Turnover of biomass in the form of male inflorescences (assumed to equal production) was increased by density (reflecting the greater number of male inflorescences per palm at high density; see above) while lower bunch production per palm at higher density resulted in a significant reduction of

TABLE 4. EFFECTS OF DENSITY ON FRACTIONAL INTERCEPTION OF PAR (f_{PAR}), RADIATION USE EFFICIENCY (e), RADIATION USE EFFICIENCY ADJUSTED FOR NON-OIL EQUIVALENT BIOMASS PRODUCTION (e^*), PARTITIONING OF DRY MATTER TO BUNCHES (BUNCH INDEX; BI) AND TO MESOCARP OIL PLUS KERNEL (HARVEST INDEX; HI). ALL VALUES ARE AVERAGED OVER 13 YEARS (1989 to 2001). P INDICATES THE OVERALL LEVEL OF SIGNIFICANCE OF EFFECTS OF DENSITY; DATA WITH SAME SUPERScript ARE NOT SIGNIFICANTLY DIFFERENT AT $P<0.05$

Measurement	unit	Initial planting density (palms ha ⁻¹)			P
		120	160	200	
f_{PAR}	MJ/MJ	0.67 ^a	0.79 ^b	0.86 ^c	<0.001
e	g/MJ PAR	1.05 ^a	1.17 ^b	1.26 ^c	<0.001
e^*	g/MJ PAR	1.30 ^a	1.43 ^b	1.52 ^c	<0.001
BI	g/g	0.49 ^a	0.46 ^b	0.43 ^c	<0.001
HI	g/g	0.26 ^a	0.24 ^b	0.23 ^c	<0.001

TABLE 5. CORRELATION COEFFICIENTS (R^2) FROM LINEAR REGRESSIONS OF MEAN ANNUAL VEGETATIVE DRY MATTER PRODUCTION (VDMP), BUNCH DRY MATTER PRODUCTION (BDMP) AND TOTAL DRY MATTER PRODUCTION (TDMP) (all t ha⁻¹ yr⁻¹) ON MEAN ANNUAL RADIATION USE EFFICIENCY (e) AND RADIATION USE EFFICIENCY ADJUSTED FOR NON-OIL EQUIVALENT BIOMASS PRODUCTION (e^*). ALL R^2 VALUES WERE SIGNIFICANT AT $P<0.001$

	R^2		
	VDMP	BDMP	TDMP
f_{PAR}	0.78	0.69	0.83
e	0.70	0.75	0.77
e^*	0.64	0.81	0.75

TABLE 6. BIOMASS TURNOVER (kg palm⁻¹ yr⁻¹) AT THREE PLANTING DENSITIES. DATA ARE THE MEANS FOR THE FOURTH TO 16th YEAR AFTER PLANTING. BIOMASS TURNOVER DUE TO DEATH OF WHOLE PALMS AND ABSCISING BRACETS AND FROND BASES IS NOT INCLUDED. FIGURES IN BRACKETS ARE TURNOVER AS PERCENTAGES OF THE BIOMASS PRODUCTION. FOR PRIMARY DATA, P INDICATES THE OVERALL LEVEL OF SIGNIFICANCE OF EFFECTS OF DENSITY; VALUES WITH SAME SUPERScript ARE NOT SIGNIFICANTLY DIFFERENT AT $P<0.05$

	Initial planting density			P
	120	160	200	
Roots	9.80 ^a (72.5)	10.27 ^b (71.7)	10.54 ^c (70.7)	0.001
Trunk	0	0	0	-
Fronds	50.28 ^a (75.0)	51.59 ^a (75.3)	51.17 ^a (75.2)	ns
Total VDM	60.08 ^a (62.3)	61.86 ^a (61.3)	61.71 ^a (60.3)	ns
Bunches	93.37 ^a (100)	85.94 ^b (100)	77.9 ^c (100)	0.001
Male inflorescences	2.68 ^a (100)	2.95 ^a (100)	3.09 ^b (100)	0.05
TDM	156.1 ^a (81.1)	150.8 ^b (79.4)	142.7 ^c (77.8)	0.001

turnover in this form. Overall, between 78% and 81% of the biomass produced was *lost* as turnover, mostly as fronds and bunches. The lower percentage of turnover at high planting density was likely to have been partly a consequence of the higher proportion of biomass present as trunk biomass, for which no turnover was assumed.

Yearly changes in turnover of biomass per hectare, excluding bunches, are shown in *Figures 11* and *12*. These data again demonstrate the dominant contribution of fronds to the recycling of biomass. *Figure 12* shows that the amount of biomass recycled in the form of dead palms resulting from *Ganoderma* infection was small by comparison with the loss by pruned fronds.

Maintenance Respiration

MR is normally the largest component of total respiration. It was calculated from the product of standing biomass and respiratory coefficients. *Figure 13* shows that the largest contribution to MR was by the fronds, followed by trunks, roots and bunches. Total MR increased steeply at all densities up to year seven, after which it largely stabilized. This was a

consequence of the relatively constant standing frond and *active* trunk biomass present from that time, combined with a reduction in trunk MR coefficients with palm age (Henson, 2004).

Breure (1988b) found that MR per unit biomass declined as palm age and density increased. The present analysis revealed the same trends (*Figure 14*). MR per unit biomass underwent a marked decline from the sixth year onwards. From years three to six, MR per unit biomass *increased* with density while from year nine, the reverse was observed. This resulted in a highly significant ($P>0.001$) year x density interaction.

MR constituted 57% to 61% of total respiration and 38% to 40% of calculated gross assimilation, both proportions significantly increasing with density.

Growth Respiration

GR is a function of the quantity and composition of new biomass. Changes over time are shown in *Figure 15*. Bunches were by far the major source of GR due both to their large contribution to total biomass production and to the high energy required for oil formation.

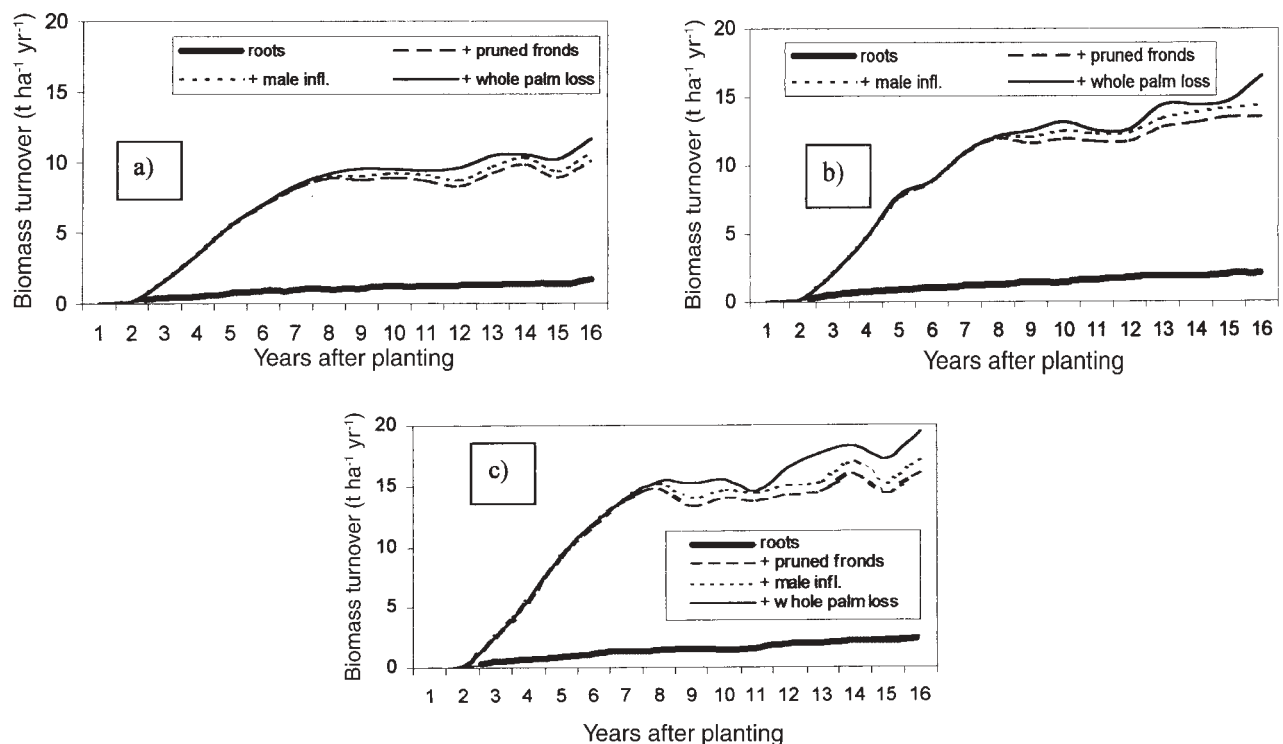


Figure 11. Components of biomass turnover excluding bunches (roots, fronds, male inflorescences, diseased palms) at a) 120, b) 160 and c) 200 palms ha⁻¹. All three densities are plotted on same vertical scale to emphasize the differences in biomass turnover.

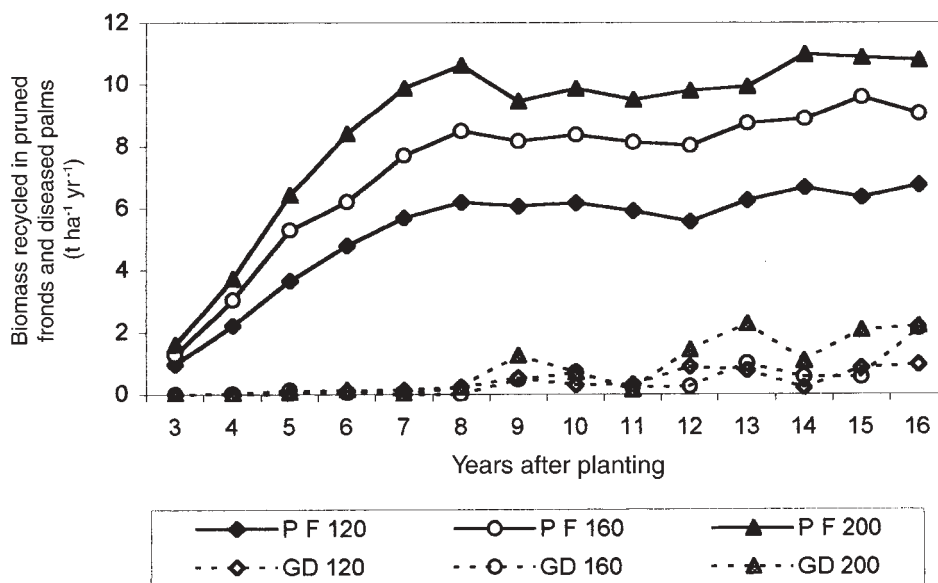


Figure 12. Comparison of biomass turnover per hectare in the form of pruned fronds (PF) in comparison to turnover due to whole palm death as a result of Ganoderma infection (GD) for palms planted at initial densities of 120, 160 and 200 palm ha⁻¹

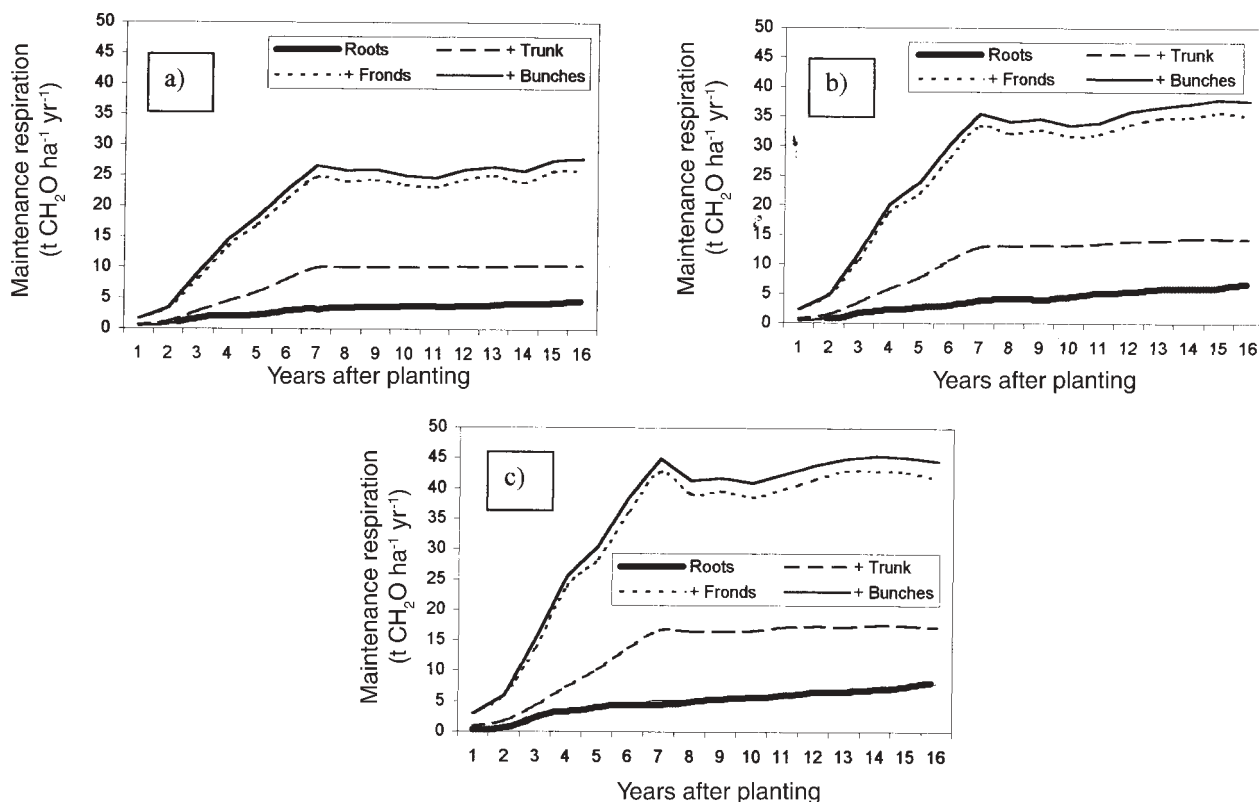


Figure 13. Maintenance respiration of biomass components at initial planting densities of a) 120, b) 160 and c) 200 palms per ha⁻¹.

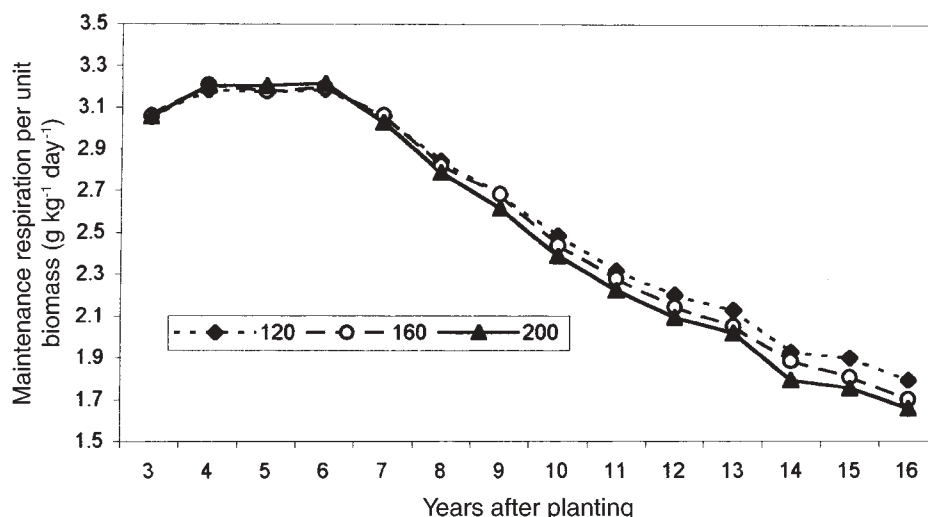


Figure 14. Changes in maintenance respiration per unit biomass for palms planted at three initial planting densities.

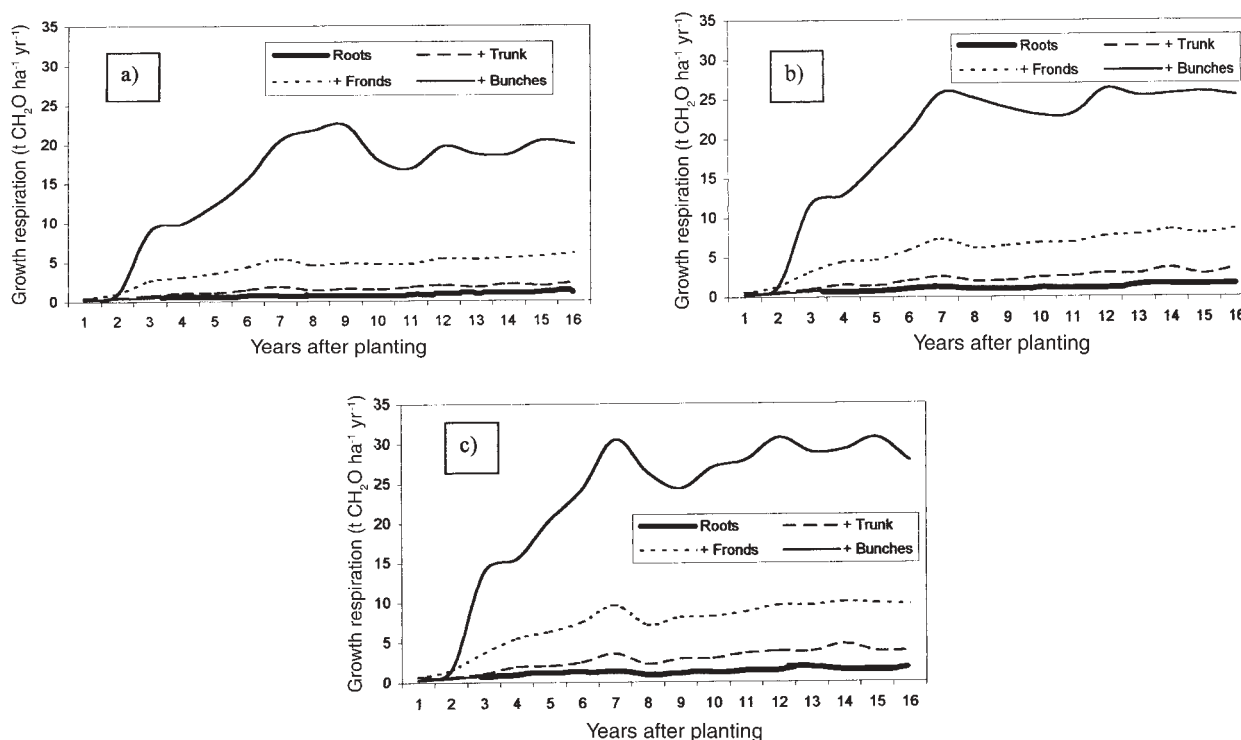


Figure 15. Growth respiration of biomass components at initial planting densities of a) 120, b) 160 and c) 200 palms ha⁻¹.

Gross Assimilation and Allocation of Assimilates

Changes in GA, derived as the sum of TDMP, MR and GR, are shown together with those components in Figure 16. GA was greatest at year 15 on the 200 palms ha⁻¹ plots, where it exceeded 115 t CH₂O ha⁻¹ yr⁻¹, the equivalent of 168 t ha⁻¹ yr⁻¹ CO₂ uptake. By contrast, the equivalent uptakes by the low and medium density plantings were 106 and 142 t ha⁻¹ yr⁻¹ CO₂, respectively.

Of GA, respiration (MR+GR) accounted for around 66% (Figure 17), leaving 34% incorporated into biomass. A significantly higher fraction of respiratory loss was observed for the 200 palms ha⁻¹ than for the other densities, and there was a significant effect of year and a significant year x density interaction.

As density increased, proportionately more assimilates were allocated to VDMP and less to BDMP as reflected in reduced values of BI (Table 4).

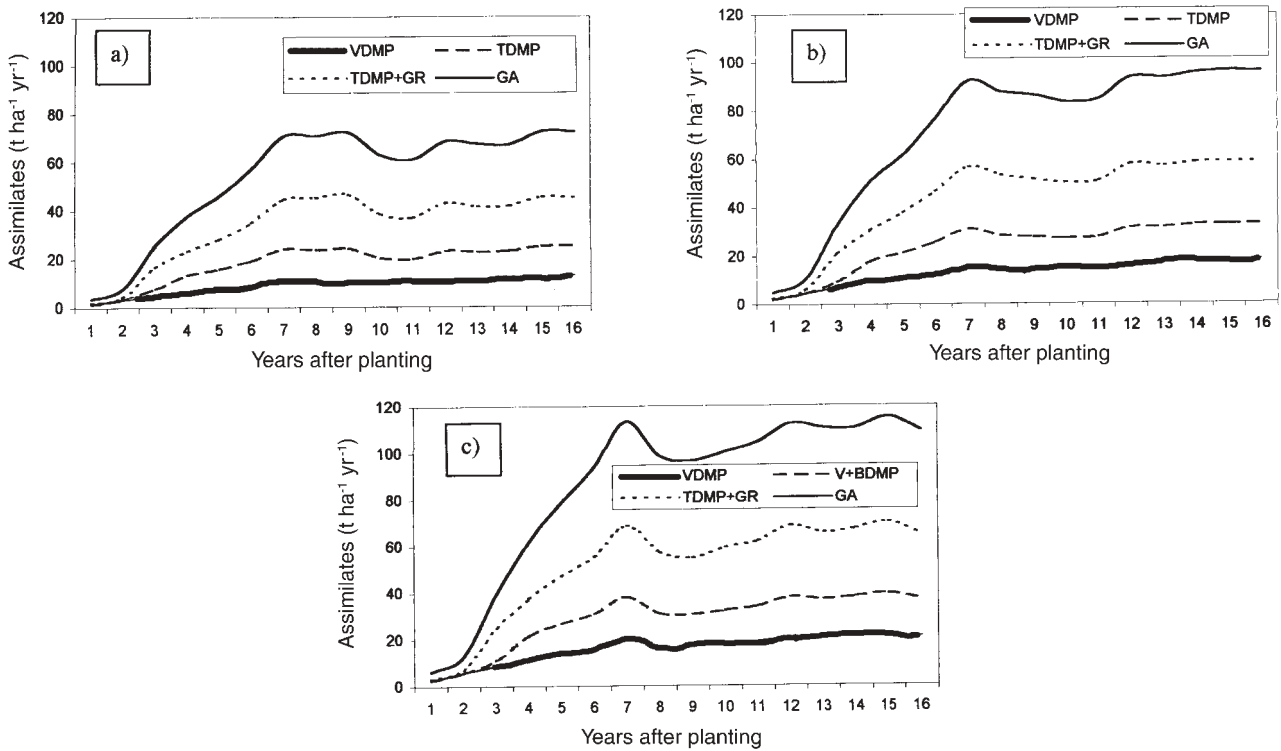


Figure 16. Allocation of gross assimilates between production of vegetative dry matter, bunch dry matter, growth respiration and maintenance respiration, at initial planting densities of a) 120, b) 160 and c) 200 palms ha⁻¹.

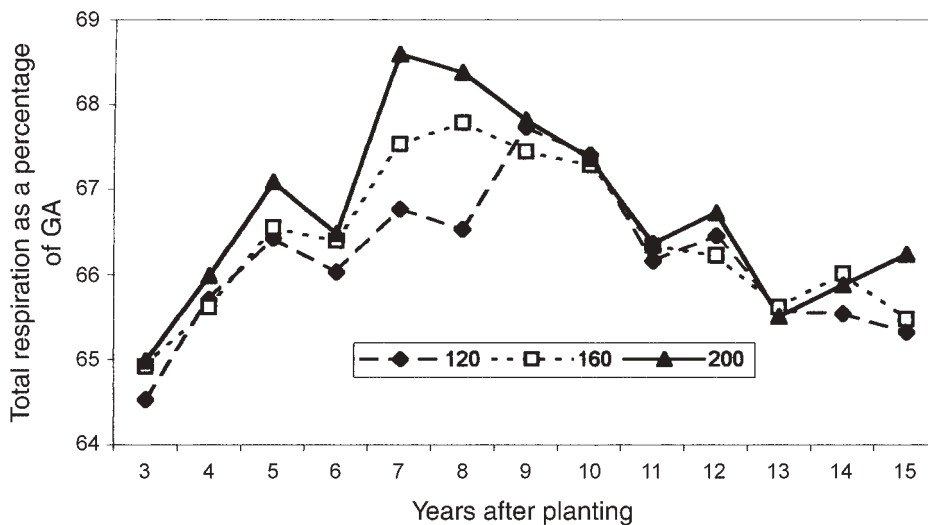


Figure 17. Changes with age in the proportion of gross assimilate used in respiration by palms at initial planting densities of 120, 160 and 200 palms ha⁻¹.

Simulation Modelling of Gross Assimilation and Dry Matter Production

A simple mechanistic model of DMP, based on that of van Kraalingen *et al.* (1989), was used to simulate the measured data. The model did not provide a truly independent test of the data in that certain parameter values used in the model were derived from the experiment. Nevertheless, it was a step towards formulating a less dependent version and was useful for identifying critical inputs.

Figure 18 provides an example of the values over time for the modelled and measured VDMP, TDMP and GA. Agreement for VDMP was close since this was calculated in the model using a regression on mean frond dry weight derived in the trial (*Appendix 2*). The agreement for TDMP was less good though acceptable, while for GA there was some discrepancy between the modeled and measured values in the early years of production. Plots of modeled versus measured data are shown in *Figures 19a* and *19b*.

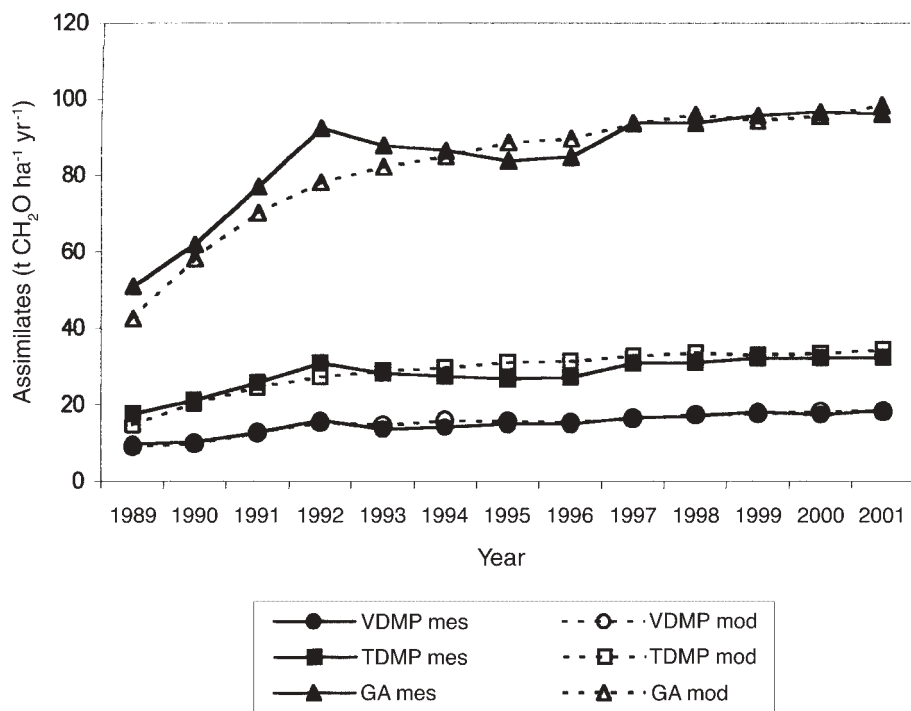


Figure 18. Comparison of measured (mes) and modelled (mod) vegetative dry matter production (VDMP), total dry matter production (TDMP) and gross assimilation (GA) for palms planted at 160 palms ha⁻¹. The simulation model was run using a fixed AMAX of 19 μmol m⁻² s⁻¹.

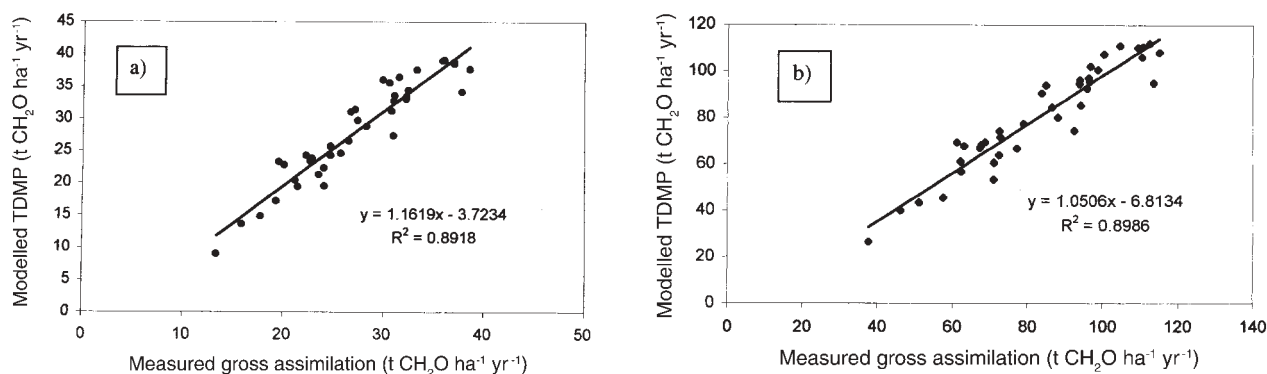


Figure 19. (a) Modelled versus measured annual total dry matter production (TDMP) and (b) modelled versus measured annual gross assimilation (GA) for the three planting densities from 1989 to 2001. The simulation model was run using a fixed AMAX of 19 μmol m⁻² s⁻¹.

The modelled results were obtained using a constant value for the maximum leaf photosynthetic rate (AMAX), which is an important determinant of model output. It was possible to calculate the *best* values of AMAX needed for the model to correctly predict FFB yield. These varied with year and density and are shown in Figure 20. These data indicate that a higher AMAX was needed at lower density and in younger palms to achieve the measured bunch production. As the palms aged, the AMAX values required declined and showed less difference with density.

DISCUSSION

Yield Response to Planting Density

When the trial was initiated, it was envisaged that the planting densities chosen would span the density giving the highest bunch yield. It was not anticipated that a planting density of 200 palms ha⁻¹ would produce the highest yield per hectare at the site and that a higher density could give even higher production. Gurmit *et al.* (1986) considered 160 palms ha⁻¹ to be the best density for deep peat soil. On

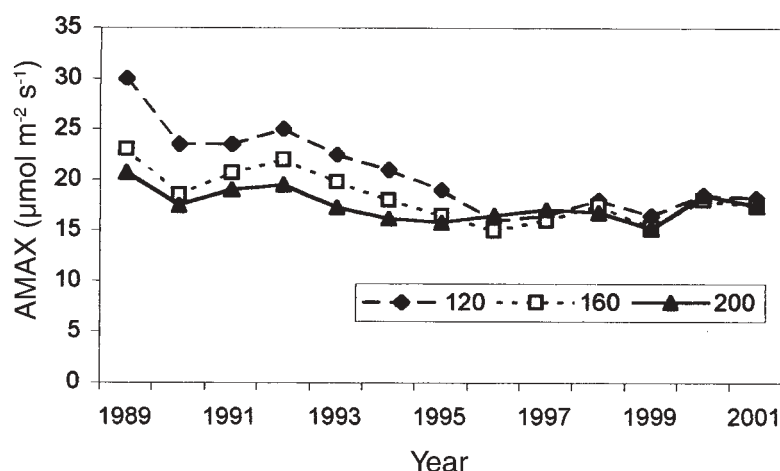


Figure 20. Computed values of maximum photosynthetic rate (AMAX) required to correctly predict fresh fruit bunch (FFB) yield with the simulation model for palms at the three planting densities.

mineral soils, yields per hectare for palms above seven or so years have been found to decline once densities exceed 150 to 180 palms ha⁻¹ (Corley, 1973; Breure, 1988a; 2003; Rao *et al.*, 1992) and reducing standard densities by thinning can lead to increases in yield (Menendez, 1988; Nazeeb *et al.*, 1990).

The optimum density for bunch yield indicated in the present experiment exceeded 200 palms ha⁻¹ and may have been as high as 240 palms ha⁻¹, even in the 17th year. Although not the case for all the years, the response in terms of yield per palm to density was generally highly significant despite the densities tested being limited to three. Nevertheless, calculation of the *agronomic optimum* as defined by Donough and Kwan (1991) is considered more useful as this gives a better indication of the density resulting in the highest yields long-term.

Several previous studies (Gurmit *et al.*, 1986; Nazeeb *et al.*, 1990; Donough and Kwan, 1991; Kwan, 1994) have also indicated that the standard densities of 130 to 148 palms ha⁻¹ may be too low for optimum yield in certain environments, especially on peat and high organic matter soils. This has been attributed to the poorer vegetative growth on such soils. Thus, the mean VDMP and TDMP per palm for the 120 and 160 palm ha⁻¹ densities 10 years after planting were 63% and 61% respectively of those for the same age palms planted at 136 palms ha⁻¹ on a coastal mineral soil (see Table 4.2 of Henson and Chang, 2000).

Part of the explanation for maximum yield at the highest density in the present experiment was that the actual densities were reduced progressively due to palm losses from *Ganoderma* infection. In the densest treatment, density declined from 200 palms ha⁻¹ at planting to 157 palms ha⁻¹ by the 16th year; a drop of over 21%. The initial density treatments of 160 and 120 ha⁻¹ were each reduced over the same period by about 16%. Although the total yields per

palm at the initial densities of 160 and 200 ha⁻¹ were reduced by 8% and 15% respectively, compared to the lowest density, the increased number of palms per hectare more than compensated for the reductions in yield per palm.

The optimum density in terms of product yields (*i.e.* oil and kernel) will not differ here from the optimum density for bunch yield as, despite earlier indications to the contrary, there were not found to be any significant differences in bunch composition between densities. It is probable, however, that such differences might occur with higher density plantings.

Effects of Palm Leaning

Another factor favouring tolerance to high density in the present experiment was leaning of palms due to weak anchorage in the low bulk density peat soil. Palm leaning is a common problem on such soils and is considered to reduce yield. Attempts were made to quantify the leaning. The extent and frequency of leaning, monitored yearly on two plots of each density, were similar across densities. The dip in yield after the seventh year (Figure 8) could have been at least partly due to this factor.

Leaning and subsequent toppling result in a change in canopy distribution and hence in inter-palm competition for light. Interception of radiation plays an important role in influencing crop productivity (Squire, 1985), particularly in the early growth stages. Radiation interception, though largely a function of leaf area, is also dependent on the distribution and orientation of the foliar elements. Here, the interception of PAR (f_{PAR}) was calculated using the formula of Squire (1985). The underlying model assumes a random distribution of leaf area which is not expected to be the case with oil palm and is likely to be least accurate in the

absence of a closed canopy, as for young palms and low planting densities. Its use would be further compromised by the uneven canopy distribution developing over the years due to palm leaning, as discussed.

While yield could be reduced temporarily due, e.g. to root damage and/or shading by nearby upright palms, it might also serve to *open up* the canopy, giving a better light distribution. Leaning palms usually revert to an upright growth habit but the crown becomes laterally displaced from its original position. It should also be noted that leaning effectively reduces palm height and the resulting increased heterogeneity in height may be favourable for yield (van Kraalingen, 1985). (It also facilitates harvesting.) The fact that crown distribution may no longer be uniform however, means that simple models of radiation interception such as used here are likely to be inadequate. However, to employ more elaborate approaches requires detailed data on changes in the canopy distribution over the years that were not available. Such data should be collected in future experiments to enable a more accurate assessment to be made.

Vegetative Dry Matter Production

The overflow hypothesis (Corley *et al.*, 1971a,b) states that assimilate requirements for VDMP on a per palm basis are relatively constant and take priority over BDMP. While there are exceptions (Corley and Tinker, 2003), this is broadly true and density trials have provided some of the best

examples of the concept (Corley, 1973). As density increases, the assimilates captured per palm decrease. This decrease mainly impacts on bunch production. A point is reached when the fall in bunch yield per palm overrides the yield increase per unit area, hence the existence of an optimum density for yield.

In assessing VDMP, root DMP is usually ignored. To our knowledge, there have been no direct measurements of the effect of planting density on root growth. This remains an important gap to be filled. It was assumed in the present analysis that root growth was proportional to shoot growth. Results from several sites in West Malaysia (Henson and Chai, 1997; Khalid *et al.*, 1999a,b) support this contention and permitted the estimation of standing root biomass on the basis of a highly significant correlation for inland soils (*Appendix 2*). To check the root estimates, a test sampling of root standing biomass was conducted in the present trial in its 17th year. However, it was not possible to sample depths below 60 cm due to the lack of soil coherence and the height of the water table. Allowance had, therefore, to be made for the root biomass likely to be present below this depth and a regression procedure was adopted. These new standing biomass estimates were higher, but close (within c. 17%) to those previously estimated for the 16th year (*Table 7*). Again, so far as we are aware, there have been no previous data published on root growth in peat soil and more work is required to confirm these results.

TABLE 7. ESTIMATES OF STANDING ROOT BIOMASS AT THE THREE PLANTING DENSITIES

Density (palms ha ⁻¹)	Root biomass (kg palm ⁻¹)		
	A. Estimated from regression equation using shoot data for the 16 th year	B. Calculated from auger samples taken in 17 th year	A as a percentage of B
120	67.4	77.9	86.5
160	72.3	79.5	90.9
200	75.4	94.6	79.7
Mean	71.7	84.0	85.4

As commonly observed, trunk height was strongly affected by density. Using the standard method to calculate trunk biomass, the height increase with density leads, in the absence of any marked change in diameter, to a corresponding increase in trunk biomass. Whether this is indeed so should, however, be questioned. Firstly, other studies have indicated a reduction with planting density in trunk diameter (Rao *et al.*, 1992; Kwan, 1994; Henson *et al.*, 2003). Secondly, the assumption that trunk tissue density is independent of planting density may not be correct. While more measurements are needed, a preliminary study (Henson *et al.*, 2003) has shown differences in tissue density at different planting densities. The results, however, did not change the conclusion that trunk biomass per palm increased with planting density.

Rachis length likewise increases with density. While in previous studies (Breure, 1982; Rao *et al.*, 1992; Kwan, 1994), this has not been associated with a significant increase in petiole cross-section (and

Inflorescence and Bunch Production

Changes in inflorescence and bunch numbers per palm in response to density were in accord with previous findings (*e.g.* Rao *et al.*, 1992). Thus, female inflorescence and bunch numbers were reduced with density while the number of male inflorescences and abortions increased. Bunch weight was not significantly affected. It is noteworthy that the decline in female inflorescence and hence bunch number per palm with age was mainly due to a change in sex ratio rather than to increased abortion, although the decline in frond production also contributed.

Sensitivity of Growth Processes to Density

As noted by others (Breure, 1982; Rao *et al.*, 1992), growth in rachis length was amongst the most sensitive of the growth processes to density change, being evident by the fourth year after planting.

TABLE 8. PERCENTAGES OF TOTAL VEGETATIVE DRY MATTER PARTITIONED TO ROOTS, TRUNK AND FRONDS AT THE THREE PLANTING DENSITIES. DATA ARE AVERAGED FOR YEARS 4 TO 16. THERE WAS NO OVERALL TREND WITH PALM AGE

Component	Density (palms ha ⁻¹)		
	120	160	200
Roots	14.1	14.2	14.6
Trunk	16.2	17.5	18.6
FronDs	69.7	68.4	66.8

hence in single frond dry weight), such an increase was observed here. It could be assumed that this is a compensatory response to the reduced rate of frond emergence at higher densities. However, the causes of the latter remain obscure. The net effect was to stabilize total frond dry matter production, a major component of VDMP, across the densities.

On average, VDMP increased with planting density in this trial. This is at variance both with the assumption of little or no effect of density on VDMP and observations of the reverse trend (Breure, 1988a,b; Kwan, 1994). Underlying this increase may be the contribution from increased trunk and the compensatory effect of single frond dry weight *vis-à-vis* the decline in frond production. The trunk contributed the largest positive change to the distribution of dry matter between the main vegetative organs with density (Table 8).

Differences in BI were also evident at this time (Table 9). Smith *et al.* (1996) have suggested that rachis length could serve as an useful early indicator of the optimum planting density for different progenies or clones.

Effects of Density on Maintenance Respiration

Respiratory activity required for the *maintenance* of biomass (strictly, all processes other than growth) constitutes the single largest drain on assimilates. Breure (1988b) noted that MR per unit biomass declined with both age and density. In the present experiment, this occurred as a consequence of differences in the relative proportions of the different tissues. Table 10 provides an example of this, showing that the proportions of less active tissues such as the trunk increased with density while those of more

TABLE 9. RELATIVE SENSITIVITY OF GROWTH AND DEVELOPMENT PROCESSES OF SINGLE PALMS TO PLANTING DENSITY

Process/measurement	Direction of response to increased density	Year after planting when differences first noted
Rachis length	+	4
Bunch index	-	4
Fronde emergence rate	-	6
Bunch dry matter production	-	6
Bunch number	-	7
Female inflorescence number	-	7
Male inflorescence number	+	7
Single frond dry weight	+	10
Single frond area	+	10
Trunk height	+	10
Vegetative DMP	+	10

active tissues such as the fronds, decreased. Also, the proportion of the trunk that is *inactive* and so has a low respiration rate, increases with the trunk biomass and hence with density. Additionally, MR per unit biomass of fronds may be lower in dense canopies if a greater proportion of the fronds are subjected to lower light intensities, since leaflet *dark* respiration as a fraction of photosynthesis declines with radiation (Henson, 1991). Similar considerations account for the decrease in MR per unit biomass with age (Henson, 2004).

Effects of Density on Light Use Efficiency

It has been observed in several trials, though not all, that *e* increases with planting density and with LAI (Squire, 1984; Squire and Corley, 1987; Corley

and Donough, 1991). Such an increase was observed in the present trial (Table 4). Squire and Corley (1987) suggested that the increased *e* could be due to a change in the balance between photosynthesis and respiration. In the present trial, however, oil production increased with density and while bunch respiration as a fraction of total stand respiration decreased with density (data not presented), the proportion of gross assimilates respired increased with density (Figure 7).

Corley and Tinker (2003) suggested that canopy photosynthesis may have been underestimated for high density canopies with high LAIs. It is possible that photosynthesis in dense canopies could be higher than expected either because a higher humidity (which favours photosynthesis) is maintained, both above and within such canopies,

TABLE 10. 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	Initial 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
Fronde	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 ₂ O kg ⁻¹ day ⁻¹)			-	1.79	1.70	1.66

or because a change in canopy architecture gives a more erect frond arrangement and improves light distribution, as suggested by Breure (1988a).

The reason for higher mean e values at higher densities lies in the relationship assumed between LAI and f_{PAR} . This is partly illustrated in Figure 21 which confirms a trend previously shown by some of the data analysed by Squire (1984). The positive curvilinear relationship between TDMP and radiation interception represents directly the tendency for e to increase with TDMP. (Hence, treatments producing the greatest total biomass will also have the highest e .) This in turn is an outcome of the saturation-type relationship between f_{PAR} and LAI (Squire, 1984) which is a consequence of the light interception model. Thus, to verify the conclusions regarding e and density, it would be best to measure light interception directly using radiation sensors. Such measurements have been made (Squire, 1984; Corley and Donough, 1992) but more are required.

CONCLUSION

Further work

It will be necessary to check if the estimates of e and MR in relation to increasing density are correct by more careful measurements of f and of DMP including roots. If this is the case then the cause(s)

of increasing e need to be further investigated. An increase in e could arise from increased photosynthesis or reduced respiration, most likely, MR. Thus, the following should be done in a long-term density trial:

- measure changes in f directly using light sensors;
- measure VPD above and within the canopies;
- measure photosynthesis rates within the canopies; and
- measure root as well as shoot DMP.

Also:

- new trials on peat soils should include planting densities higher than 200 palms ha^{-1} and probably up to 300 palms ha^{-1} would be worthwhile;
- to increase the precision of optimum density estimates, trials should include more than three and preferably at least five initial densities. The alternative is to use a fan design but this may pose practical difficulties on peat soils due to the layout of drains and estate roads; and
- the incidence of palm losses and palm leaning should be carefully recorded with mapping of the canopy throughout the life of the experiment. More elaborate radiation interception models can then be applied to the data.

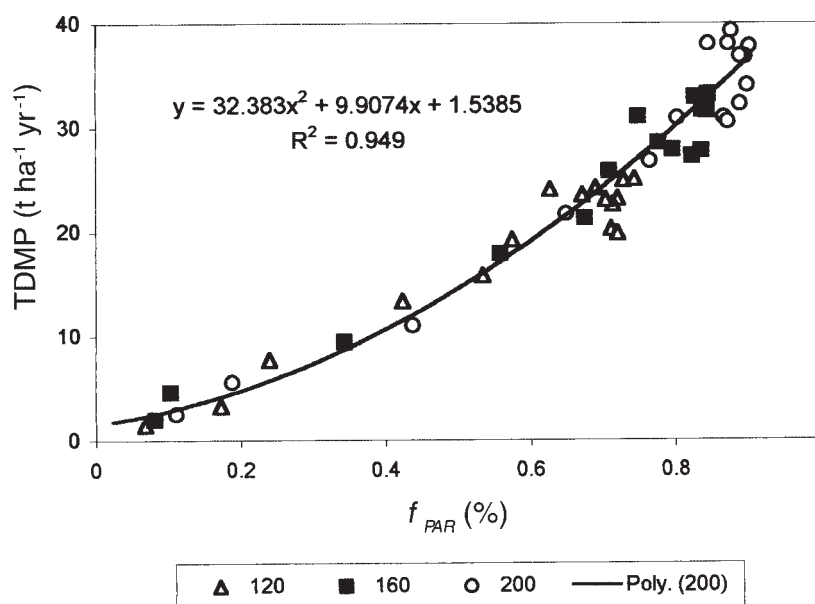


Figure 21. The relationship between total dry matter production (TDMP; $t\ ha^{-1}\ yr^{-1}$) and the fractional interception of photosynthetically active radiation (PAR) (f_{PAR}) at initial densities planting densities of 120, 160 and 200 palms ha^{-1} .

ACKNOWLEDGEMENTS

We thank Mr Mazli Eswa for excellent supervision of the experiment, collection and compilation of the field data, Mr K C Chang for his critical comments on the manuscript, Mr Ahmad Tarmizi Mohd for help with statistical analysis and Mr Azhar Ishak of the Malaysian Meteorological Service for providing climatic data.

REFERENCES

- BREURE, C J (1982). Factors affecting yield and growth of oil palm *tenera* in West New Britain. *Oleagineaux*, 37: 213-227.
- BREURE, C J (1988a). The effect of different planting densities on yield of oil palm. *Experimental Agriculture*, 24: 37-52.
- BREURE, C J (1988b). The effect of palm age and planting density on the partitioning of assimilates in oil palm (*Elaeis guineensis*). *Experimental Agriculture*, 24: 53-66.
- BREURE, C J (2003). The search for yield of oil palm - basic principles. *The Oil Palm. Management for Large and Sustainable Yields* (Fairhurst, T and Hardter, R eds.). Potash & Phosphate Institute / Potash Institute of Canada and International Potash Institute. p. 59-98.
- CORLEY, R H V (1973). Effects of plant density on growth and yield of oil palm. *Experimental Agriculture*, 9: 169-180.
- CORLEY, R H V (1976). Planting density. Chapter 18. *Oil Palm Research* (Corley, R H V; Hardon, J J and Wood, B J eds.). Elsevier, Amsterdam. p. 273-283.
- CORLEY, R H V (1986). Oil palm. *CRC Handbook of Fruit set and Development* (Monselise, S P ed). CRC Press, Boca Raton, Florida. p. 253-259.
- CORLEY, R H V and BREURE, C J (1981). Measurements in oil palm experiments. Internal Report. Unilever Plantations Group, London. 21 pp.
- CORLEY, R H V and DONOUGH, C R (1992). Potential yield of oil palm clones – the importance of planting density. *Proc. of Workshop on Yield Potential in the Oil Palm*. International Society for Oil Palm Breeders/Palm Oil Research Institute of Malaysia. p. 58-70.
- CORLEY, R H V and TINKER, P B (2003). Chapter 4. *The Oil Palm*. 4th edition. Blackwell Science, Oxford, UK. In press.
- CORLEY, R H V; GRAY, B S and NG, S K (1971a). Productivity of the oil palm (*Elaeis guineensis*) in Malaysia. *Experimental Agriculture*, 7: 129-136.
- CORLEY, R H V; HARDON, J J and TAN, G Y (1971b). Analysis of growth of the oil palm (*Elaeis guineensis* Jacq.). I. Estimation of growth parameters and application in breeding. *Euphytica*, 20: 307-315.
- DONOUGH, C R and KWAN, B (1991). Oil palm planting density: results from trials in Sabah and the possible options. *The Planter*, 67: 483-508.
- DUFRENE, E (1989). *Photosynthese, consommation en eau et modelisation de la production chez le palmier a huile* (*Elaeis guineensis* Jacq.). Doctoral thesis. Universite de Paris-Sud Centre d'Orsay. 154 pp.
- GURMIT, S; TAN, Y P; RAJAH PADMAN, C V and LEE, F W (1986). Experiences on the cultivation and management of oil palms on deep peat in United Plantations Berhad. *Proc. of the 2nd International Soil Management Workshop on Classification, Characterisation and Utilisation of Peat Land* (Eswaran; Abu Talib; Panichapong and Chitchumnong eds.). p. 177-193.
- 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 (1989). Modelling gas exchange, yield and conversion efficiency. Paper presented at Workshop on Productivity of Oil Palm. PORIM, Bangi. 27 May 1989.
- HENSON, I E (1991). Adaptation to light environment by leaves of oil palm (*Elaeis guineensis*). *PORIM Bulletin No. 22*:1-8.
- HENSON, I E (1993). Assessing frond dry matter production and leaf area development in young oil palms. *Proc. of 1991 PORIM Palm Oil Development Conference – Module 1 (Agriculture)*. PORIM, Bangi. p. 473-478.
- HENSON, I E (1997). Analysis of oil palm productivity. I. The estimation of seasonal trends in bunch dry matter production. *Elaeis*, 9: 69-77.
- 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 (2004). Estimating maintenance respiration of oil palm. *Oil Palm Bulletin*. In press.
- 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 CHANG, K C (2000). Oil palm productivity and its component processes. Chapter 4. *Advances in Oil Palm Research*. Vol. 1. p. 97-145.

HENSON, I E and MOHD TAYEB, D (2004). Seasonal variation in yield and developmental processes in an oil palm density trial on a peat soil. II. Bunch weight components. *J. Oil Palm Research*. In press.

HENSON, I E; MOHD HANIFF HARUN; MAZLI ESWA and MOHD TAYEB, D (2003). Estimating density and biomass of oil palm trunks. *Proc. of the PIPOC 2003 International Palm Oil Congress - Agriculture Conference*. MPOB, Bangi. p. 975-984.

JONES, H G (1983). *Plants and Microclimate*. Cambridge University Press, Cambridge, UK. 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. 2*:63-71.

KWAN, B K W (1994). The effect of planting density on the first fifteen years of growth and yield of oil palm in Sabah. *Technical Bulletin No. 11*. Department of Agriculture, Sabah. 26 pp.

MENENDEZ, T (1988). The results of thinning oil palm in West New Britain. *Proc. of the 1987 International Oil Palm/Palm Oil Conference - Agriculture Conference*. PORIM, Bangi. p. 410-418.

MOHD TAYEB, D; HAMDAN, A B and ZULKIFLI, H (1995). Novel agronomic innovations in the exploitation of peat for oil palm. *Proc. of the 1993 PORIM International Palm Oil Congress: Update and Vision – Agriculture Conference*. PORIM, Bangi. p. 360-372.

MOHD TAYEB, D; HAMDAN, A B; AHMAD TARMIZI, M and ROSLAN, A (1998). Recent progress on research and development on peat for oil palm. *Proc. of the 1996 Seminar on Prospects of Oil Palm Planting on Peat in Sarawak: The Golden Opportunity*. PORIM, Bangi. p. 71-89.

MOHD TAYEB, D; JUSOH, L; HASNOL, O and AHMAD TARMIZI, M (2003). High oil palm planting density on deep peat. *Proc. of the Seminar on Elevating the National Oil Palm Productivity and Recent Progress in the Management of Peat and Ganoderma*. MPOB, Bangi. p. 133-141.

MONTEITH, J L (1972). Solar radiation and productivity in tropical ecosystems. *J. Applied Ecology*, 9: 747-766.

MONTEITH, J L (1977). Climate and the efficiency of crop production in Great Britain. *Phil. Trans. Roy. Soc.*, 281: 277-294.

NAZEEB, M; LOONG, S G; GOH, K H and WOOD, B J (1990). Trials on planting oil palms at high initial density with later thinning. *Proc. of the 1989 PORIM International Palm Oil Development Conference – Agriculture Conference*. PORIM, Bangi. p. 199-214.

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.

RAO, V; RAJANAIDU, N; KUSHAIRI, A and JALANI, B S (1992). Density effects in the oil palm. *Proc. of Workshop on Yield Potential in the Oil Palm*. International Society for Oil Palm Breeders/PORIM, Bangi. p. 71-79.

SAS INSTITUTE, INC. (1998). SAS/STAT user's guide: Release 6.03 ed. SAS Institute, Cary, N.C.

SMITH, G; DONOUGH, C R and CORLEY, R H V (1996). Relationships between oil palm clone phenotype and optimal planting density. *Proc. of the 1996 PORIM International Palm Oil Congress - Agriculture Conference*. PORIM, Bangi. p. 76-86.

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

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

SQUIRE, G R and CORLEY, R H V (1987). Oil palm. *Tree Crop Physiology*. Elsevier, Amsterdam. p. 141-167.

VAN KRAALINGEN, D W G (1985). Simulation of oil palm growth and yield. Thesis, Wageningen Agricultural University. 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.

Trial Details

Soil: series: peat
 depth: >3 m
 pH: 3.4

Design: 3 x 18 split-plot with density as main plots and fertilizer treatment in factorial combination as sub-plots; two replicate blocks.

Planting material: Guthrie C9677 DxP.

Densities: 120, 160 and 200 palms ha⁻¹; equi-triangular planting.

Year planted: August-September 1985

Plot size: 16 to 24 palms per plot with eight central recording palms per plot.

Recording schedule:

Vegetative measurements: annually from July 1988

Flower census: quarterly from July 1988

FFB harvest: bimonthly from March 1988

Bunch analysis: monthly from January 1992

Leaf nutrient analysis: annually from September 1987

Fertilizer sub-plot treatments (relative levels):

Plot	N	P	K
1	0	0	1
2	0	0	2
3	0	0	3
4	0	1	1
5	0	1	2
6	0	1	3
7	0	2	1
8	0	2	2
9	0	2	3
10	1	0	1
11	1	0	2
12	1	0	3
13	1	1	1
14	1	1	2
15	1	1	3
16	1	2	1
17	1	2	2
18	1	2	3

Rainfall and water table depth:

a) monthly means: 1990 to 2001

Month	Rainfall (mm)	Water table depth (cm)
Jan	158.6	54.4
Feb	164.8	62.0
Mar	163.0	69.0
Apr	174.3	68.8
May	139.5	70.2
Jun	103.8	75.6
Jul	95.6	88.5
Aug	127.9	94.1
Sep	166.7	91.7
Oct	196.1	74.6
Nov	287.2	55.6
Dec	242.1	53.6

b) annual means: 1990 to 2001

Year	Rainfall (mm)	Water table depth (cm)
1990	1858	75.2
1991	2353	78.0
1992	1769	96.6
1993	1696	64.2
1994	2034	63.3
1995	2404	51.1
1996	2274	59.8
1997	2223	77.2
1998	1833	77.5
1999	2065	66.8
2000	1903	70.2
2001	1823	78.1

Appendix 2**Equations used to estimate growth parameters**

True leaf area (LA_t) from nominal leaf area (LA_n) for palms 10 years or less in field:

$$LA_t \text{ (m}^2\text{)} = 0.13 + \beta * LA_n \text{ (m}^2\text{)}$$

where:

$$\beta = 0.2049 + 0.0319 * \text{palm age (years)}$$

FronD dry weight (FDW) from petiole cross-section (PCS) area for palms six years or less in field:

$$\text{FDW (kg)} = \alpha + \beta * \text{PCS (cm}^2\text{)}$$

where:

$$\alpha = -0.0076 + 0.0394 * \text{palm age (years)}$$

and:

$$\beta = 0.0284 + 0.0101 * \text{palm age (years)}$$

Standing root biomass (RB) from standing shoot biomass (SB):

$$\text{RB (kg palm}^{-1}\text{)} = 13.505 + 0.1667 * \text{SB (kg palm}^{-1}\text{)} \text{ R}^2=0.98; \text{ n}=11$$

Root turnover (RT) from standing root biomass (RB)

$$\text{RT (kg palm}^{-1}\text{yr}^{-1}\text{)} = -0.0704 + 0.2391 * \text{RB (kg palm}^{-1}\text{)} \text{ R}^2=0.67; \text{ n}=7$$

Standard bunch growth curve:

$$\text{Fraction of final bunch dry weight} = 12.917e^{0.0128 * \text{DAA}}$$

where DAA = days after anthesis and bunch growth occurs over 160 days.

Equation used in dry matter production model.

Vegetative dry matter production (VDMP) from single frond dry weight (FDW):

$$\text{VDMP (kg palm}^{-1}\text{ yr}^{-1}\text{)} = 12.739 + 36.412 * \text{FDW (kg)} \text{ R}^2=0.95; \text{ n}=39$$