

**FACTORS ASSOCIATED WITH THE ALLOCATION OF CARBOHYDRATES
TO BUNCH DRY MATTER PRODUCTION IN OIL PALM
(*Elaeis guineensis* Jacq.)**



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TO BUNCH DRY MATTER PRODUCTION IN OIL PALM
(*Elaeis guineensis* Jacq.)**

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C.C. Oosterlee,
in het openbaar te verdedigen
op dinsdag 10 november 1987
des namiddags te vier uur in de aula
van de landbouwuniversiteit te Wageningen.

STELLINGEN

1. De optimale plantdichtheid voor de trosopbrengst van oliepalm per hectare neemt kort nadat het gemiddelde bladoppervlak niet verder toeneemt weer toe en stabiliseert zich op een waarde die hoger ligt dan ten tijde van het bereiken van het maximale bladoppervlak.

Dit proefschrift

2. Overdadig gebruik van westerse technici voor buitenlandse grootlandbouwbedrijven in ontwikkelingslanden werkt nadelig op de efficiëntie van de lokale staf.

3. Veredeling van ideotypes, als toegepast bij graan veredeling, zal bij oliepalm tot een snellere opbrengstverhoging leiden dan de conventionele veredeling op olieproduktie per palm.

4. Meer onderzoek over de factoren welke de snelheid van bloeiwijze ontwikkeling bij de oliepalm beïnvloeden is van belang voor oogstvoorspellingen.

5. De correlatie tussen eigenschappen van oliepalm zaailingen in het kweekbed en de latere opbrengst is van belang voor de selectie in de kweekbed phase. Selectie op het magnesium gehalte in het blad en op de verhouding bladoppervlak/bladgewicht lijken zinvol.

Dit proefschrift

6. Uitdunnen of snoei van ongeselecteerde palmen in zaadtuinen resulteert in een sterke verhoging van de zaadproduktie per palm. Dit betekent dat, bij een gegeven zaadproduktie, de selectie intensiteit verhoogd kan worden.

Dit proefschrift

7. Toename van de diepte in het bladerdek van overblijvende gewassen zal waarschijnlijk de opbrengst per hectare verhogen.

Dit proefschrift

8. Het is waarschijnlijk dat insekteschade aan het bladerdek op de opbrengst van oliepalm overschat wordt omdat het groene bladoppervlak onderbenut is.

9. De introductie van klonaal oliepalm plantmateriaal maakt het mogelijk seizoenschommelingen in opbrengst te verminderen. Dit voordeel kan belangrijker zijn dan de verhoging van de totale opbrengst.

10. Door het toenemend gebruik van de kokospalm als schaduwboom voor cacao is het nodig de selectie criteria te wijzigen.

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INTRODUCTION

The search for yield increase in oil palm (*Elaeis guineensis* Jacq.) through breeding and cultural practices has been based on field experimentation, but there is scanty information on the underlying factors causing the results obtained. Broekmans (1957) analysed in much detail the factors associated with growth and yield of the oil palm in an attempt to explain the seasonal fluctuations in bunch yield in Nigeria. In the same country, Sparnaaij (1960) analysed the factors associated with the components of bunch yield and attempted to "show how additional useful information can be gained by a more thorough treatment of the yield figures, and by a study of the available growth and flowering data". He argued that this type of analysis would be a better basis for subsequent field experiments than the conventional method, i.e. that based on past results of exploratory trials. More recently, Corley (1976 a,b) reviewed results of basic research carried out on inflorescence development and sex differentiation, and on photosynthesis and productivity. These reports were preceded by the development of methods to estimate, from simple non-destructive measurements, the area of a single leaf (Hardon et al, 1969) and vegetative dry matter production (Corley et al, 1971). By applying their methods a more fundamental approach to oil palm breeding could be formulated (Hardon, 1976).

Dry matter production is formed from assimilates. It is therefore considered to be in particular relevant to explain experimental results, and to formulate a research program, from an analysis of factors associated with the supply of assimilates by the leaf surface (source strength) and those with the allocation of assimilates to oil yield (sink strength of the economic product). Equally important is to apply basic research on oil palm physiology for computer modelling of yield and growth. These models have proved to be a valuable research tool in other crops and might be used, for example, for yield forecasting and for testing the response of yield to a wide range of characters; the latter might assist in the formulation of selection criteria for oil palm breeding. For simulation

models a proper understanding of factors affecting the components of the carbon budget is essential, i.e. gross assimilation and the partitioning of assimilates into those required for maintenance of existing biomass (maintenance respiration) and for the production of the components of dry matter. In addition, when the model is used for yield forecasting, it is necessary to establish the stage in inflorescence development at which the components of yield, i.e. those determining the number and mean weight of the bunches, are affected by the level of assimilates allocated. These developmental stages have not been adequately identified (Corley & Gray, 1976).

An analysis of factors affecting the components of the carbon budget, and the developmental stage at which the determination of yield components occurs are the main objectives of this thesis.

Oil palm is an indeterminate species, which means that the main growing point remains vegetative and the economic yield originates from axillary buds. In most of these species the allocation of assimilates to generative growth has a low priority; this also applies for oil palm (Corley et al, 1971). An increase in bunch dry matter can thus be achieved, in addition to increasing gross photosynthetic production, by reducing assimilate requirements for maintenance respiration and vegetative growth. The latter can be diminished through breeding and selection for high bunch index, i.e. the proportion of total dry matter used for fruit bunches (Hardon et al, 1972). Maintenance respiration may also be reduced by breeding, as shown for rye grass by Wilson (1982) and a number of other crops (C.J.T. Spitters, pers. com.). The latter approach could not be studied because, at the time of the present study, no reliable method was available to determine the amount of maintenance respiration. Factors related to reducing assimilate allocation to vegetative growth and, in particular, to those of increasing the supply of assimilates from the leaf surface will be explored in this thesis.

Gross assimilation depends, first, on the amount of solar radiation absorbed by the canopy. Absorption during the early years from field planting depends on the rate of canopy closure.

Since the production of fruit bunches starts several years before the canopy is closed, a rapid closure is expected to increase early yield. This can be achieved by palms having a rapid crown expansion or by increasing the planting density. Both methods will be studied in the present thesis.

Crop photosynthesis depends further on the health of the leaf surface. In the West New Britain environment where most of the research work for this thesis was done, oil palm leaves show pronounced symptoms of what is believed to be magnesium deficiency; this element is closely related to photosynthesis since magnesium is an essential component of the chlorophyll molecule. Indeed, Peaslee and Moss (1966) established a close relation between magnesium deficiency and photosynthesis in maize. Exploring the relationship between magnesium status of palms and oil yield is one of the objectives of this thesis. In other environments, particularly North Sumatra, interception of radiation may be reduced by incidence of crown disease because the disease appears as bending of unopened spear leaves. The bend is permanent and Breure & Soebagyo (in prep.) showed that crown disease decreases early yield, indicating a relationship between rate of light interception and photosynthetic production.

The second factor which determines the supply of assimilates is the conversion rate of absorbed radiation which in turn depends on the assimilation-light response curve of the leaf surface. This curve is characterized by a region of low light intensity where assimilation rate is proportional to absorbed light leading to a plateau at light saturation which is reached at about 30% of full sunlight (Corley, 1976a). It is thus clear that light is more efficiently utilised when the proportion of leaf surface in the linear portion of curve is maximised, that is when light is evenly distributed over the leaf surface.

On the other hand, it is well documented that there is little genetic variation in the slope of the curve at low light intensities (Björkman, 1981; Ehleringer & Pearcy, 1983). Although the genetic variation in the assimilation rate at light saturation may be considerable (for a review see Spitters & Kramer, 1986), these differences are only partly reflected

in changes in photosynthetic production of the entire leaf surface, mainly because only a minor part of the leaf surface photosynthesises at light saturation; further the response of genetic variation depends strongly on the degree of cloudiness, being strongest under a clear sky (Spitters, 1986). The most important scope for increasing photosynthetic production seems therefore to maximize the light distribution over the leaf surface.

The way in which the absorption and distribution of sunlight might be manipulated to increase photosynthetic production will be analysed in the present thesis.

Regarding internal competition for available assimilates, the sink strength of vegetative growth is of paramount importance. There is considerable evidence that this sink strength becomes weaker when a certain minimum level of vegetative growth is achieved. Above this level additional allocation of assimilates to vegetative growth depends on the demand for bunch production (Corley, 1976a). In this respect, the sink strength of bunches for assimilates differs between the stages of bunch formation, and is strongest from the onset of fruit development, i.e. after pollination (anthesis). The load of developing bunches, termed "fruiting activity" (Broekmans, 1957), is therefore particularly relevant when internal competition for assimilates is at issue. The level of fruiting activity may, similar to other factors associated with the supply of carbohydrate to bunch production, affect the number of inflorescences which reach anthesis (through an effect on the proportion of female inflorescences differentiated, and on that of abortion rate of female inflorescences). The effect of fruiting activity on the components of bunch yield and vegetative growth will be studied through artificial limiting the number of bunches on the palms (different levels of castration), i.e. by means of a manipulative method.

The work reported is based on research carried out when the author was Agronomist-in-charge of Dami Oil Palm Research Station, West New Britain, Papua New Guinea, from March 1971 to March 1977. Subsequently, the author worked as consultant to this research station, during which the various research projects of this thesis were continued under his guidance.

EXPERIMENTAL

Experiment 1. This was a dura x pisifera progeny experiment testing nine ex-Avros pisifera onto four Deli dura. The fifteen progenies are arranged in randomised blocks with five replications and sixteen palms per plot. The trial was planted at Dami at 143 palms per ha in December 1968.

Experiment 2. This was a density x fertilizer experiment planted at Dami in October 1970 with mixed dura x pisifera progenies of the same parentage as that in Experiment 1. Four densities were compared, 56, 110, 148 and 186 palms per ha. The three higher densities were divided into four sub-plots, each corresponding to a different level of fertilizers; these were applied until 1979, whereafter application was stopped. In October 1981 part of the 186 palms per ha density was thinned to identify the stage in inflorescence development at which the components of bunch yield are determined.

Experiment 3. This was a dura x pisifera progeny trial testing 16 pisifera onto a set of four dura palms. The trial was planted at Dami in April 1976, with three replications at 115 and three at 143 palms per ha.

Experiment 4 (without the author's involvement in the implementation of the experiment).

These were two castration trials laid down in commercial plantings in Johore, Malaysia.

Experiment 4a was planted in 1969; inflorescences were removed as soon as palms started to flower, about 1.5 years after planting.

Experiment 4b commenced in a ten-year old planting when palms had been fruiting already for seven years.

ENVIRONMENTAL CONDITIONS AT DAMI

Soils. The soils are andosols (Muller, 1969), derived from recent volcanic deposits with little or no profile development, except for an accumulation of organic matter in the surface horizon which extends to a maximum of about 15 cm. The organic matter is, due to the near absence of clay, of relatively high importance since it represents nearly the only source of exchange sites. Below the sub-surface soils, buried horizons may occur. Drainage of the soils is excellent. The area had been used extensively as gardens prior to clearing of the land from heavy rain forest.

The profile at Dami clearly shows alluvial deposits of mineral and pumicious sands washed by the Ko river which runs through the area.

Climate. Mean daily sunshine varies from 3.9 hours in January to 6.5 in September, with a total of about 2000 hours per year.

Rainfall is about 4000 mm per annum and is well distributed, so that there is usually no water deficit (Waringa, 1985).

General description.

Leaf production increases rapidly during the early years in the field until a peak, after which it declines slowly and appears to stabilise at a rather constant rate when palms are about eleven years old (Table 1).

Table 1. Annual leaf production and number of green crown leaves, for different ages, of dura x pisifera palms planted at Dami.

<u>Age</u> (years after planting)	<u>Leaf</u> <u>production</u>	<u>Number of</u> <u>leaves per</u> <u>palm</u>
1	29.9	-
2	42.3	55
3	36.8	55
4	32.8	55
5	31.8	55
6	27.8	55
7	28.0	50
8	26.9	45
9	24.3	40
10	25.8	40
11	23.3	35
12	22.9	35
13	22.2	35
14	21.5	35

1) Based on Experiment 3 (mean of 115 and 143 palms per ha; years 1 to 4), and Experiment 2 (mean of 110 and 148 palms per ha; years 5 to 14).

2) Based on values reported by Breure, 1985; Corley, 1976; Gray, 1969.

Stem growth, during the early years in the field, involves the formation of a wide stem-base without internodal elongation. From the third year onwards, a by and large fixed increment per year is reached (Fig 1).

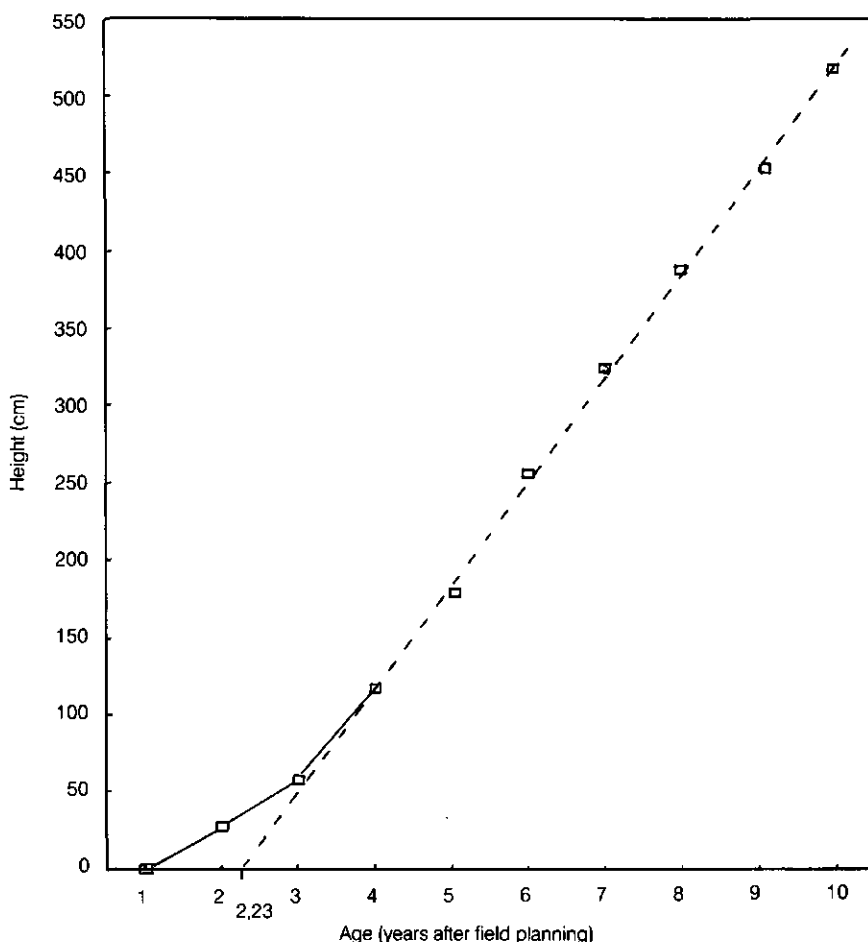
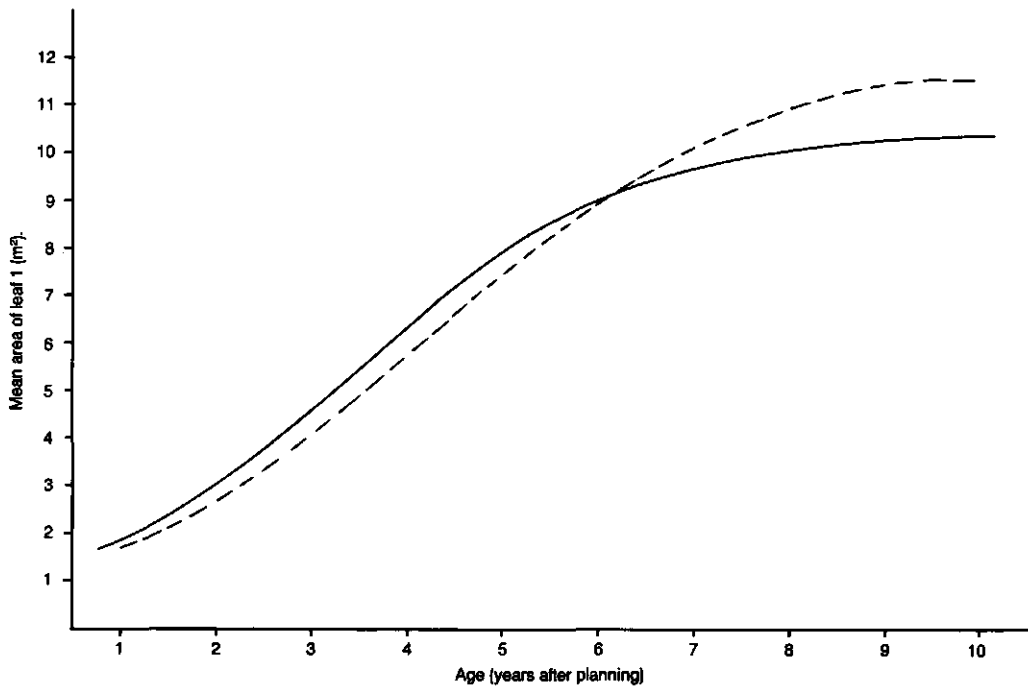


Figure 1. Height to the base of leaf 25 for palms of different ages. Expt. 3.

Mean area of the crown leaves against age fit a logistic growth curve in that there is a rapid initial increase whereafter the leaf area/age gradient levels off and becomes by and large constant when palms are about 9 years old (Breure, 1985). Curves for two dura x pisifera crosses of Experiment 3, bases on leaf area values of the first 10 years from field planting, are given in Figure 2.

Fig. 2 The relationships (fitted logistic growth curves) of leaf area with palm age two progenies 43.210 (----) and 43.514 (—) of Expt 2.



The number of leaves in the crown is controlled by regular pruning rounds to harvest the bunches. Typically, mean number of crown leaves for the first 14 years are as given in Table 1. In palms older than about 15 years, leaves and old leaf bases fall away gradually until the palm reaches it, so-called smooth-stemmed phase, i.e. when all leaf bases except a few near the crown have been lost.

A detailed description of the botany of the oil palm and its development, from nursery seedlings to fully developed palms, has been given in several hand books. The most recent are "Oil Palm Research" edited by Corley, Hardon and Wood (1976), and "The Oil Palm" by Hartley (1977).

The present study deals with oil palm growth, i.e. the green leaf surface, dry matter incorporated in vegetative growth (trunk, leaves and roots) and in generative growth (male inflorescences and fruit bunches).

Non-destructive measurements to estimate the area of a single leaf and the components of above-ground dry matter production have been developed by Hardon et al (1969) and Corley et al (1971), respectively. A detailed description of collecting the necessary records in the field and, from these, to estimate growth parameters has been given by Corley & Breure (1981). More recently, Breure & Powell (1987) have developed an instant method to estimate relative values of these growth parameters.

Leaf measurements. Sampled leaves are cut close to the stem; leaves are sampled by either taking a standard crown leaf (usually leaf 17) or by marking the latest fully expanded leaf; advantages of the latter method include (1) the date of leaf opening is known, and (2) leaves can be measured when convenient (the increase in leaf size after opening is negligible).

The following measurements are assembled:

1. The length of the rachis.
2. The petiole cross-sectional area (to estimate the leaf dry weight).
3. Length x width of three leaflets sampled from each side

of the rachis; these sampled leaflets are the longest undamaged leaflets out of a set of ten leaflets cut immediately under the region 2/5 from the tip of the leaf.

4. The number of leaflets on one side of the rachis, including rudimentary leaflets at the base and fused leaflets at the tip of the leaf.

From measurements mentioned under 3 and 4 the leaf area is estimated.

Rate of leaf production. Leaves are marked at opening, usually at annual intervals. Since every eighth leaf is on the same spiral, the position of the previously marked leaf in relation to the newly marked leaf can be easily obtained from a specially designed diagram (Fig 3)

For example, if marked leaf is now the third leaf down the spiral next to spiral 1, Fig 3 shows that 19 leaves have been produced.

Trunk measurements. Height is measured at annual intervals to a standard point on the base of leaf 25.

Once in the life of a palm only, the trunk diameter is measured at about 1.5 m above ground level (two points on opposite sides of the trunk); old leaf bases are removed to expose a small area of the trunk. From records of height increment and trunk diameter the annual increment in volume is estimated. Density (kg/ltr.) of the trunk depends on the age of the palm and is estimated by applying a formula developed by Corley et al (1971).

Bunches. All fruit bunches are harvested at intervals of 7 to 10 days. A factor of 0.5275 was adopted from Corley (1971) to convert fresh weight to dry weight. In some instances components which determine the oil and kernel extraction were determined following the method of Blaak et al (1963).

No root measurements were done.

Frond Number	Parastichy Number								Number of Fronds produced since marking
	1	2	3	4	5	6	7	8	
	Present position of previously marked leaf 1								
1	1								0
2				1					1
3							1		2
4		1							3
5					1				4
6								1	5
7			1						6
8						1			7
9	2								8
10				2					9
11							2		10
12		2							11
13					2				12
14								2	13
15			2						14
16						2			15
17	3								16
18				3					17
19							3		18
20		3							19
21					3				20
22								3	21
23			3						22
24						3			23
25	4								24
26				4					25
27							4		26
28		4							27
29					4				28
30								4	29
31			4						30
32						4			31
33	5								32
34				5					33
35							5		34
36		5							35
37					5				36
38								5	37
39			5						38
40						5			39
41	6								40
42				6					41
43							6		42
44		6							43
45					6				44
46								6	45
47			6						46
48						6			47

Figure 3. Diagram for determining number of leaves produced in a given period, from the present position of leaf 1 marked at the beginning of the period.

THE INSTANT METHOD OF GROWTH MEASUREMENTS

The conventional method of estimating growth parameters, as described above, takes at least one year because essential variables for estimating vegetative dry matter production, i.e. height increment and rate of leaf production, are measured between annually marked reference points. However, it frequently happens that only long-term records of yield and its components are available and that, in view of the growing interest in including vegetative characteristics in the breeding and selection of oil palm, growth records are urgently required. To meet such instant demand, and also to reduce recording costs, Breure & Powell (1987) developed a method to obtain relative values of growth parameters in one single recording round, as follows:

Remember that a mature rate of increment is reached in the fourth year from planting (Fig 1). From that time, the following linear regression line, based on annual height records of Experiment 3, gave an excellent fit to height at different ages:

$$\text{Height}_t = -150 + 67 t$$

The intercept with the x-axis is reached at $t = 150/67$. Breure & Powell (1987) applied an age correction of two years, so that annual height increment is

$$\frac{\text{Height at year } t}{t-2}$$

Regarding rate of leaf production, it is relevant that leaves remain adhered to the stem until approximately 15 years from planting. Counting the total number of leaf bases on the trunk appears therefore to be an obvious method of determining the leaf production, but the older leaf bases are no longer visible, due to expansion of the trunk during the early years in the field. The corresponding period of production was estimated based on actual number of leaves produced, of progenies of Experiment 3, until September 1986 and those counted on the trunk in the same month (Table 2).

Table 2. Actual number of fronds produced for the first ten years after field planting (FP 86A) and those estimated from a single frond base count at the end of the recording period (FP 86E), together with the corresponding period (months) of concealed leaf bases (PCL). *Dura* x *pisifera* progenies derived from 4 crosses of 14 different *pisifera*, planted at 115 palms per ha (D_1) and 143 palms per ha (D_2). Experiment 3.

<u>Progeny</u>	<u>FP 86A</u>		<u>FP 86E</u>		<u>PCL (months)</u>	
	D_1	D_2	D_1	D_2	D_1	D_2
1	303	296	255	247	15.5	16.2
2	321	307	274	262	15.0	14.7
3	304	301	259	253	14.9	16.0
4	308	301	259	254	16.1	15.9
5	314	308	269	259	14.7	16.2
6	317	306	265	258	16.3	15.6
7	306	307	260	258	15.9	16.4
8	319	311	271	266	15.8	15.0
9	332	318	275	267	17.6	16.2
10	313	305	265	258	15.6	15.6
11	323	314	267	259	17.9	17.7
12	304	301	254	250	16.3	17.2
13	316	307	266	259	16.5	15.8
14	300	296	252	250	15.9	15.7
Mean	313	306	264	257	16.0	16.0

The period during which leaf bases are concealed under the trunk did not differ significantly among progenies derived from each of the 14 *pisifera*, or between densities. Therefore, the mean period of all progenies can be used to correct the frond base count for the number of concealed leaf bases. As this amounts to about one year (actually 16 months), Breure & Powell (1987) estimated the annual leaf production by the formula:

$$\frac{\text{number of visible leaf bases at year } t}{t-1}$$

where t is the number of years after field planting at the moment of the frond base count.

Leaf area and leaf weight are estimated from conventional measurements on leaf 17 and 25. Measurements at a certain age,

however, do not lead to the actual mean values for the entire recording period because leaf weight and leaf area of subsequent spear leaves increase with palm age for at least the first ten years after field planting; data of Bunch Index (BI) and Leaf Area Ratio (LAR) thus obtained should be considered of relative value. Estimates of BI and LAR do give, however, high correlations with actual values (Table 3).

Table 3a. Correlation coefficients ¹⁾ between Actual (A) and Estimated (E) values of Bunch Index (BI) made at six years (82) and ten years (86) after planting. Dura x pisifera progenies derived from crosses of fourteen different pisifera, planted at 115 palms per ha (D₁) and 143 palms per ha (D₂).

<u>Estimated values</u>	<u>Actual values</u>			
	BI 82A-D ₁	BI 82A-D ₂	BI 86A-D ₁	BI 86A-D ₂
BI 82E-D ₁	0.98 ^{xx}			
BI 82E-D ₂		0.90 ^{xx}		
BI 86E-D ₁			0.96 ^{xx}	
BI 86E-D ₂				0.97 ^{xx}

Table 3b. Correlation coefficients ¹⁾ between Actual (A) and Estimated (E) values of Leaf Area Ratio (LAR), based on vegetative dry matter (VDM) and frond dry matter (FDM), made at six years (82) and ten years (86) after planting. Dura x pisifera progenies derived from crosses of fourteen different pisifera, planted at 115 palms per ha (D₁) and 143 palms per ha (D₂).

<u>Estimated values of LAR</u>	<u>Actual Values</u>			
	LAR 82A-D ₁	LAR 82A-D ₂	LAR 86A-D ₁	LAR 86A-D ₂
VDM 82E-D ₁	0.96 ^{xx}			
VDM 82E-D ₂		0.92 ^{xx}		
VDM 86E-D ₁			0.89 ^{xx}	
VDM 86E-D ₂				0.91 ^{xx}
FDM 82E-D ₁	0.91 ^{xx}			
FDM 82E-D ₂		0.81 ^{xx}		
FDM 86E-D ₁			0.88 ^{xx}	
FDM 86E-D ₂				0.80 ^{xx}
FDM 82/86-D ₁			0.93 ^{xx}	
FDM 82/86-D ₂				0.87 ^{xx}

1) Based on mean values of 48 palms per pisifera.

Indeed, screening of progenies on the basis of estimated values of BI is very efficient, as shown in Figure 4.

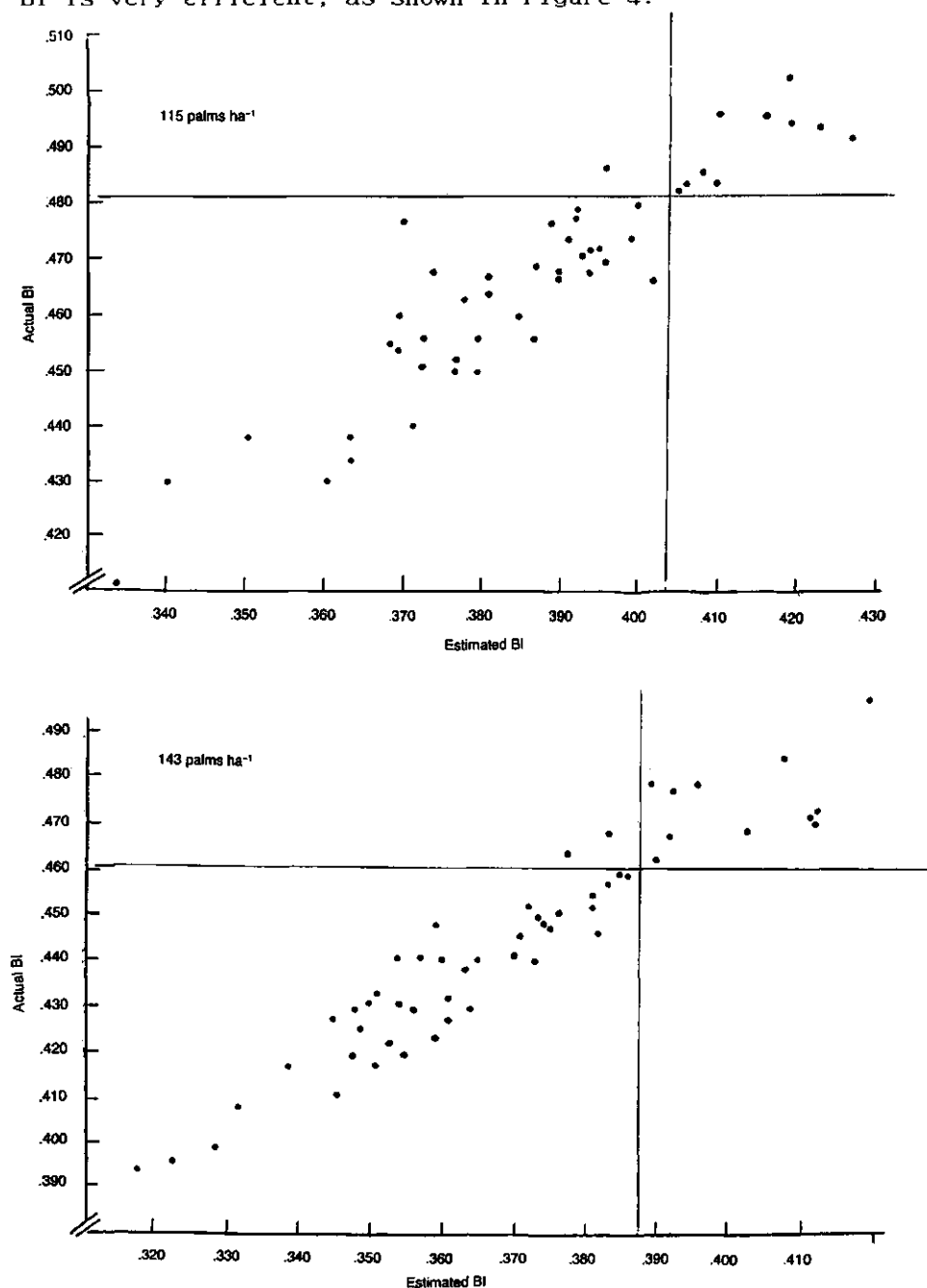


Figure 4. Progeny values of Bunch Index (BI), estimated from growth measurements ten years after planting, and those derived from mean actual values of years 3 to 10 after planting. 56 *dura* x *pisifera* progenies of Expt. 3, at two planting densities.

Here ten dura x pisifera families, screened on the basis of high estimated BI-values, were by and large the same as those selected on actual values (BI 86A).

In respect of parameters describing the logistic growth curve (ER, $t_{0.95}$ and L_m), four leaves should be measured to achieve sufficiently high correlations with actual values, i.e. those based on leaf area measurements for the first ten years from planting (Table 4).

Table 4. Correlation coefficients ¹⁾ between Actual (A) and Estimated (E) values of parameters describing crown expansion, based on four sets of leaf measurements. Dura x pisifera progenies derived from crosses of fourteen different pisifera, planted at 115 palms per ha (D_1) and 143 palms per ha (D_2).

Estimated values	Actual values (1,2,3,4,5,6,7,8,9,10) ²⁾					
	$L_m D_1$	$L_m D_2$	$t_{.95} D_1$	$t_{.95} D_2$	ER D_1	ER D_2
L_m E 5,6,9,10- D_1	0.99 ^{xx}					
L_m E 4,5,8,9- D_1	0.99 ^{xx}					
L_m E 5,6,9,10- D_2		0.96 ^{xx}				
L_m E 4,5,8,9- D_2		0.89 ^{xx}				
$t_{.95}$ E 5,6,9,10- D_1			0.91 ^{xx}			
$t_{.95}$ E 4,5,8,9- D_1			0.93 ^{xx}			
$t_{.95}$ E 5,6,9,10- D_2				0.92 ^{xx}		
$t_{.95}$ E 4,5,8,9- D_2				0.93 ^{xx}		
ER E 5,6,9,10- D_1					0.92 ^{xx}	
ER E 4,5,8,9- D_1					0.94 ^{xx}	
ER E 5,6,9,10- D_2						0.89 ^{xx}
ER E 4,5,8,9- D_2						0.88 ^{xx}

1) based on mean of 48 palms per pisifera

2) in brackets age of leaf opening (years after planting).

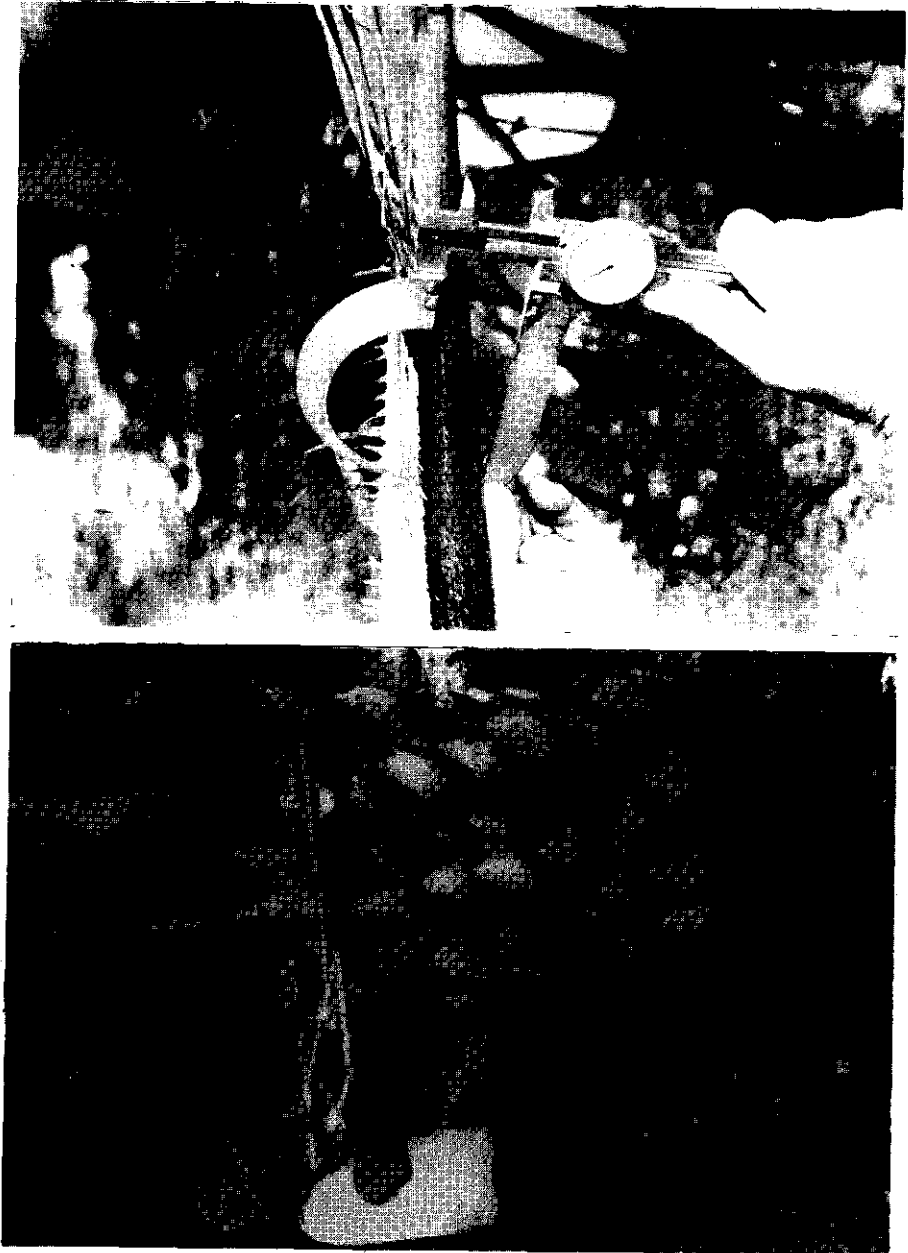
L_m = Maximum leaf area derived from the logistic growth curve (Breure, 1985).

$t_{.95}$ = Time to reach .95 L_m .

ER = The ratio of leaf area at maximum expansion rate and L_m .

A double set of leaf measurements also permits an alternative estimate of LAR based on the ratio leaf area/leaf weight (Table 3).

The method of measuring the trunk diameter and the petiole sectional area is shown on the following photographs (Fig. 5).



CARBOHYDRATES AVAILABLE FOR BUNCH DRY MATTER PRODUCTION.

Breure (in press a) adopted the following model to study the carbon budget of oil palm.

From gross assimilation of the canopy (crop photosynthesis) assimilates are used, firstly, for maintenance of existing biomass (maintenance respiration). An additional loss of weight (through CO_2 and H_2O) occurs when the remaining carbohydrates are converted into structural DM (growth respiration). The growth rate (the total of vegetative and bunch dry matter production) can thus be described by the following general formula:

$$dW/dt = C_f (A - RW),$$

where W = structural biomass (kg DM/ha); C_f = the conversion factor of carbohydrate into structural DM (kg DM/kg CH_2O); A = gross assimilation of the canopy (kg CH_2O /ha/d); R = the amount of maintenance respiration per unit existing DM (kg CH_2O /kg DM/d).

Maintenance respiration is the most difficult variable to establish (for a review of different methods explored see Amthor, 1984). Moreover, calculating maintenance respiration as a constant rate (R) per unit biomass gives unrealistic results, particularly with perennials where no further increase in gross assimilation occurs from the stage of canopy closure, although in the field biomass continues to increase. The model would then predict a proportional decrease in carbohydrate available for structural growth, and, since carbohydrate needed for vegetative dry matter (VDM) are known to have priority over those for bunch DM (Corley et al, 1971), a negligible yield in older plantings would result. This is at odds with yield trends with age observed in commercial plantings (cf Corley & Gray, 1976).

In contrast, the amount of carbohydrate needed for DM production can be fairly accurately estimated from actual DM production when the conversion factors (C_f)-values of carbohydrate required for the production of the main components of structural DM formed (bunches, leaves, trunk, and roots)

are known. These C_f -values are established (Breure, in press a) from the conversion efficiency of their biochemical products (F.W. Penning de Vries, pers. com.; Table 5).

Table 5. Percentage composition and conversion factors (C_f , g DM g⁻¹ CH₂O) of the main components of oil palm.

<u>Percentage composition</u>					
	Conversion factor	Leaves	Trunk	Bunches	Roots
Carbo- hydrates	0.761	75	68	41	71
Protein	0.503	6	4	3	3
Lipids	0.304	5	2	48	2
Lignin	0.435	5	20	4	2
Organic acid	1.017	5	2	2	2
Minerals	10.0	4	4	2	2
C_f		0.696 ¹⁾	0.657	0.436	0.649
1					

1) $(.75/.761+.06/.503+.05/.304+.05/.436+.05/1.017+.04/10.0)$

The fraction $1 - C_f$ gives the fraction carbohydrate (remaining after subtraction of maintenance respiration) lost in growth respiration (Table 6).

To estimate crop photosynthesis, first, potential A for a closed canopy at the latitude of Dami was estimated by applying descriptive equations developed by Goudriaan & van Laar (1978). The required constants were obtained from the literature. These are the parameters of the assimilation-light response curve which is characterized by a region, at low light intensity, where assimilation rate is proportional to light intensity (slope at the origin is ; Ehleringer & Pearcy, 1983), and a region where assimilation rate is no longer dependent on light intensity (assimilation rate at light saturation, A_{max} ; Corley, 1973). To estimate photosynthetically active

radiation (PAR) absorbed by the leaf surface, the following procedure was followed. Since only records of daily hours of bright sunshine were available at Dami, these were first converted to solar radiation (Waringa, 1985). From intercepted radiation 50% is estimated to be photosynthetically active (Szeicz, 1974), of which 8% is approximately reflected by the leaf surface (Monteith, 1972). The method of Goudriaan & van Laar (1978) calculates A for clear and overcast skies; the proportion of canopy photosynthesis under an overcast sky was calculated as 0.47 from tabulated data for incoming PAR at a standard clear sky and an overcast sky (Goudriaan & van Laar, 1978) and actual PAR observed at Dami. This fraction is to be squared (Lantinga, 1985) for the best interpolation of A between clear and overcast sky. Potential A thus amounted to $516 \text{ kg CO}_2 \text{ ha}^{-1} \text{ per day}$ or $128 \text{ ton CH}_2\text{O ha}^{-1} \text{ a}^{-1}$. Gross assimilation for non-closed canopies was corrected for fractional interception of PAR (f):

$$A_{\text{non-closed}} = f \cdot A_{\text{closed}}$$

In turn, f was estimated from recorded values of Leaf area index (L).

This method of estimating gross assimilation assumes first that light is the sole limiting factor for gross assimilation, ignoring other limiting factors such as occasional water deficit and magnesium deficiency (Breure, 1982), and, secondly that there is a linear relationship between light interception and A: this does not take into consideration the effect of distribution of intercepted light on A (Breure, in press a). The relevance of these factors will be reported later.

Finally, in the model adopted by Breure (in press a), maintenance respiration (in terms of assimilate requirements) is estimated from the difference between calculated gross assimilation and carbohydrate needed for DM production. Since, as mentioned, the latter component can be quite accurately estimated by our method, the uncertainty in estimating maintenance respiration depends mainly on that in estimating A.

Based on the above model, the partitioning of gross

assimilation between maintenance and growth respiration and carbohydrate incorporated in structural DM formed was calculated, for two extreme commercial planting densities, 6 to 9 years from planting (Table 6).

Table 6. Gross assimilation ($\text{kg CH}_2\text{O ha}^{-1}\text{d}^{-1}$) and assimilates needed for maintenance and growth respiration, and carbohydrate incorporated in structural dry matter (DM) formed. Two planting densities of experiments 2 and 3 during the period 6 to 9 years from planting. (In brackets requirements as a percentage of gross assimilation).

<u>Density</u> (palms per ha)	<u>Gross</u> <u>assimilation</u>	<u>Carbohydrate needed for</u> <u>structural DM production</u>		<u>Maintenance</u> <u>requirements</u>
		growth respiration	incorporated in structural DM	
110 ¹⁾	308	67	80	161
148 ¹⁾	331	73	92	166
115 ²⁾	315	63	78	174
143 ²⁾	333	72	90	172
Mean	322	68 (21)	86 (27)	168 (52)

1) Experiment 2

2) Experiment 3

Mean weight losses in respiration amounted to 73% (21% for growth respiration and 52% for maintenance respiration). Thus only 27% of gross assimilation was used for structural DM production.

Decreasing the amount of carbohydrate allocated to dry matter (DM) production per palm, through increasing the planting density, reduced carbohydrate for bunch DM, but had little effect on those for vegetative DM (Table 7).

Table 7. Gross assimilation ($\text{kg CH}_2\text{O palm}^{-1}\text{d}^{-1}$) at four densities and its partitioning into carbohydrate needed for growth and for maintenance respiration, compared with mean total biomass (kg palm^{-1}) and its maintenance ($\text{g CH}_2\text{O kg}^{-1}\text{DM d}^{-1}$). Experiment 2 during the period 6 to 9 years from planting.

<u>Density</u> (palms per ha)	<u>Carbohydrate</u> <u>needed for</u>					<u>Daily maintenance</u> <u>respiration</u> <u>per unit biomass</u>
	<u>Gross</u> <u>assimilation</u>	<u>Bunch</u> <u>growth</u>	<u>Vegetative</u> <u>growth</u>	<u>Maintenance</u> <u>respiration</u>	<u>Mean total</u> <u>biomass</u>	
56	3.96	1.01	0.62	2.33	356	6.5
110	2.92	0.74	0.60	1.58	358	4.4
148	2.22	0.55	0.55	1.12	345	3.2
186	1.83	0.37	0.54	0.92	341	2.7

The effect of increasing planting density, on a per ha basis (increase in leaf area index, L), on the main components of DM production is for, the same age group, depicted in Fig 6. This diagram shows the relationship between L and plotted values of carbohydrate ($\text{kg CH}_2\text{O ha}^{-1}\text{d}^{-1}$) incorporated in total DM production, and those in vegetative DM production. The latter fitted a linear regression line ($R^2 = 0.97$), whereas the former relationship was best fitted by a quadratic curve ($R^2 = 0.91$). The distance between these regression curves is the amount of carbohydrate allocated to bunch DM. This amount, which is derived from actually recorded bunch DM production and C_f -values (Table 5), showed an optimum at $L=5.6$. This was estimated by

fitting a quadratic regression through sub-plot values of L and carbohydrate allocated to bunch DM.

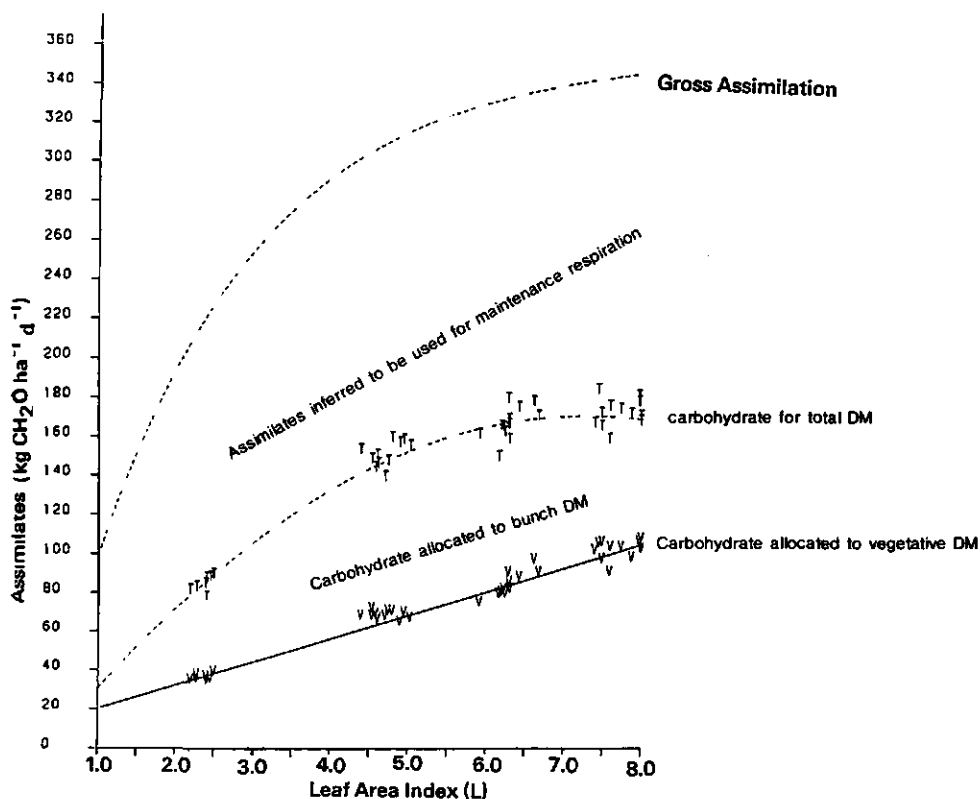


Figure 6. Relation between leaf area index (L) and carbohydrate ($\text{kg CH}_2\text{O ha}^{-1} \text{d}^{-1}$) allocated to vegetative DM (V—V), bunch DM, and total DM (the total of measured vegetative DM and bunch DM, T-----T). Points being sub-plot values of the four planting densities of Experiment 1 from 6 to 9 years from planting.

The relationship between L and Gross assimilation (----) is derived from the formula of Squire (1984). Maintenance respiration is in the adopted model inferred as the difference between Gross assimilation and carbohydrate allocated to total DM production.

These results confirm those reported by Corley (1976a) in that only when a certain threshold value of carbohydrate for vegetative growth is reached, carbohydrate are allocated to bunch dry matter. In other words, when carbohydrate supply is reduced (stress) vegetative growth has priority over that of generative growth.

EFFECT OF CARBOHYDRATE SUPPLY TO BUNCH DRY MATTER ON THE COMPONENTS OF OIL YIELD.

The amount of carbohydrate for bunch DM is contingent on the supply of assimilates from the leaves (the source activity) and/or on internal competition from other sinks, such as the amount of carbohydrate required for maintenance respiration, vegetative growth, and the load of developing bunches on the palm (fruiting activity).

The source can be manipulated, for example, by higher density planting. The resulting increase in the green leaf surface per ha (L), as shown previously, does not lead to a proportional rise in canopy photosynthesis, so that gross assimilation per palm is reduced. This reduction mainly diminishes the amount of carbohydrate allocated to bunch DM, as shown in Table 7.

Fruiting activity can be manipulated by different levels of fruit bunch removal (castration).

Breure et al (in prep.a) studied the effect of planting density on oil yield and its components. The change in these components in response to fruiting activity (castration) was reported by Corley & Breure (in prep.).

The effect of planting density on oil yield and its components

Components of bunch number. It is relevant that in each leaf axil either one male or one female inflorescence is differentiated. In exceptional cases only, all leaf axils bear female inflorescences. Some inflorescences may abort before reaching anthesis, but losses during subsequent bunch development are negligible. In practice, therefore, bunch number is mainly determined by the proportion of leaves with male and aborted inflorescences. During the first five years of flowering, higher density planting decreased the proportion of leaves with female inflorescences as a result of a rise in the proportion of male and aborted inflorescences (Table 8).

Table 8. Female, male and aborted inflorescences, as a percentage of leaves produced, for the first five years of flowering (four planting densities) and for the sixth to tenth year of flowering (110 and 148 palms per ha densities only), together with values of mean leaf area index (L).

<u>Component</u>	<u>Density (palms per ha)</u>			
	56	110	148	186
<u>Years 1 to 5</u>				
Female inflorescences (%)	58.3	56.9	53.5	44.5
Male inflorescences (%)	37.7	36.9	38.4	44.2
Aborted inflorescences (%)	4.0	6.2	8.2	11.6
L	1.8	3.7	5.0	6.2
<u>Years 6 to 10</u>				
Female inflorescences (%)	-	51.4	40.7	-
Male inflorescences (%)	-	44.1	51.7	-
Aborted inflorescences (%)	-	4.9	7.6	-
L	-	4.5	5.8	-

Note: Results were not statistically analysed.

The proportion of aborted inflorescences increased linearly as a function of planting density; the proportion of males, however, only increased by changing the density from 148 to 186 palms per ha, corresponding to a leaf area index (L) of 5.0 and 6.2, respectively. During the 6th to 10th year of flowering, on the other hand, Breure et al (in prep.a) found a response of male inflorescences to changing the density from 110 to 148 palms per ha. This corresponded to a rise in L from 4.5 (110 palms) to 5.8 (148 palms), against 3.7 to 4.9 for these densities in the first period. Thus, during the two periods, the proportion of male inflorescences responded at approximately the same level of interpalm competition (in terms of L). This level appears to be higher than that at which abortion responded. It is therefore concluded that abortion is more sensitive to interpalm competition (amount of available carbohydrate per palm) than sex differentiation.

Bunch weight components. Breure et al (in prep.a) studied these components at different ages of the palms, corresponding to different methods of pollen application, being assisted pollination (year 5 after planting) and insect pollination (years 12 and 13). Results are presented in Table 9.

Table 9. Effect of interpalm competition (expressed by the planting density and the leaf area index) on the components of bunch weight (expressed as a percentage of 56 palms per ha), together with the Probability (P-tail) values for significance of pairs of density treatments. Years 12 and 13 after planting (insect pollination), and Year 5 (assisted pollination).

Components	Density (palms per ha).							
	Low (L)			High (H)			L/H ³⁾	
	56	110	P	148	186	P	P	
<u>Years 12 & 13</u>	real	%		%	%			
(insect pollination)								
Bunch weight (kg)	23.4	91	x	80	74	N.S.	xxx	
Stalk weight (g)	1869	85	xx	71	64	N.S.	xxx	
Spikelet weight (g)	16.3	91	xx	84	80	N.S.	xxx	
Frame weight (g)	5310	87	xxx	75	68	xx	xxx	
Spikelet number	212	98	N.S.	92	87	xx	xxx	
Flowers/spikelet	15.1	99	N.S.	91	87	N.S.	xxx	
Fruit set (%)	49.0	104	N.S.	109	117	N.S.	x	
Fruit to bunch (%)	62.5	107	x	107	111	N.S.	x	
Fruit weight (g)	8.8	99	N.S.	99	98	N.S.	N.S.	
Number of bunches analysed	321	408		328	172			
Leaf area index	1.90	3.71		4.80	5.81			
<u>Year 5</u>								
(assisted pollination)								
Bunch weight (kg)	16.7	94		84	83			
Stalk weight (g)	1324	89		77	75			
Spikelet number	132.2	100		99	99			
Flowers/spikelet	12.1	100		95	95			
Fruit set (%)	60.0	96		96	100			
Fruit weight (g)	15.0	97		97	94			
Number of bunches analysed	210	351		409	470			
Leaf area index	1.65	3.38		4.72	5.94			

1) x if $0.01 < P < 0.05$

xx if $0.001 < P < 0.01$

xxx if $P < 0.001$

2) Not statistically analysed.

3) Mean of 56 and 110 against 148 and 186 palms ha⁻¹.

Both sets of records show that stalk weight responded by and large linearly to planting density, but spikelet number and, to a greater extent, flowers per spikelet mainly decreased at the higher density level. Fruit weight tended to be slightly decreased by higher density planting. However, fruit set remained unchanged by increasing the planting density in the first period, but clearly improved in the second period.

Breure et al (in prep.a) studied the sensitivity of response of components to higher density planting as follows. They tested, first, the contrasts in the two lower (56 and 110) and the two higher (148 and 186) planting density levels, and, secondly, the contrasts of the mean of the lower against the mean of the two higher densities. Levels of significance (P-tail) for these tests are given in the upper part of Table 9.

Frame weight (empty spikelets and stalk) mainly decreased in response to a transition from 56 to 110 palms ha^{-1} .

Spikelet number and flowers per spikelet, in contrast, showed the highest response in the top range of the density treatments, but the response was only significant for spikelet number. When the mean values of the lower and of the higher densities were compared, however, the decrease in these components was very highly significant.

Fruit set clearly increased with planting density, but again the response was only significant when the means of the lower and higher densities are compared.

Of paramount importance for oil and kernel extraction is the significant increase in fruit to bunch; the latter mainly responded in the lower density level.

Thus similar to bunch number components, those which contribute to bunch weight also showed differences in sensitivity to planting density. Again, components determined at an advanced stage in inflorescence development (the weight of the frame) are more sensitive to planting density than those which are determined at an earlier developmental stage (number of flowers per inflorescence).

Bunch composition. Under assisted pollination (year 5), we clearly see no effect of planting density on bunch composition,

but for bunches analysed when pollinator insects were fully established (years 14 to 16), nearly all components determining oil and kernel extraction can be significantly described as a linear function of the planting densities (Table 10).

Table 10. Effect of planting densities on bunch composition for Years 14 to 16 after planting (insect pollination) and Year 5 (assisted pollination).

<u>Component</u>	<u>Density (palms per ha)</u>				linear component.
	56	110	148	186	
<u>Years 14 to 16</u> (insect pollination)					
Mesocarp/Fruit (%)	75.4	74.3	74.1	73.6	x
Oil/Mesocarp (%)	52.0	52.3	52.8	52.7	xx
Fruit/Bunch (%)	67.4	69.6	70.5	70.9	xxx
Kernel/Fruit (%)	7.8	8.5	8.8	8.9	xx
Shell/Fruit (%)	16.9	17.2	17.2	17.5	
Single Fruit wt.(g)	12.3	12.4	12.6	12.5	
Oil/Bunch (%)	26.4	27.1	27.7	27.5	xx
Fruit set (%)	66.3	68.3	70.0	69.2	x
Number of bunches analysed	426	608	629	345	
<u>Year 5</u> (assisted pollination)					
Mesocarp/Fruit (%)	-	80.7	80.8	80.4	
Oil/mesocarp (%)	-	48.6	48.8	48.1	
Fruit/Bunch (%)	-	68.2	68.0	69.5	
Kernel/Fruit (%)	-	8.2	8.1	8.4	
Shell/Fruit (%)	-	11.3	11.0	11.4	
Single Fruit wt (g)	-	12.0	12.1	12.0	
Oil/Bunch (%)	-	26.7	26.8	26.9	
Number of bunches analysed		197	253	315	

Table 10 shows, as in the previous set of bunches analysed under insect pollination (Table 9), a rise of fruit set in response to planting density with an absence of response of fruit weight. Again, fruit to bunch increased as a function of planting density.

To study which component contributed to the rise in fruit to bunch, Breure et al (in prep.) employed a multiplicative model. This revealed that fruit set was the main contributor. The interest, from an economical point of view, is mainly in the oil extraction rate of the bunch, which increased with planting density (Table 10). Again, a multiplicative model was employed to study the relative importance of the components of oil to bunch (mesocarp to fruit, oil content of the mesocarp, and fruit to bunch). This showed that fruit to bunch was mainly responsible for the rise in oil extraction, the origin of which, as demonstrated before, is mainly the fruit set. Breure et al (in prep.) suggested that the positive response of fruit set might be due to improved efficiency of pollinator insect with closer planting.

Breure et al (in prep.) evaluated the gain in optimal density by comparing the optimal density for yield of kernel and oil (based on estimated extraction rates of Table 9) with the optimum density for fresh fruit bunches only. Optima were compared for the cumulative yield during the period 12 to 16 years from planting (Table 11).

Table 11. Comparison of estimated optimum density (palms per ha) for yield of kernel and oil, and for yield of fresh fruit bunches, based on linear regression equations fitted through values of four planting densities, during the period 12 to 16 years after planting (5 years).

Optimal density (palms per ha) ¹⁾.

Kernel and oil	Bunches
131 (.99) ²⁾	126 (.99)

1) Estimated as $a/2b$, in which a = intercept and b = slope of the fitted regression lines.

2) In brackets coefficient of determination of the two regression lines.

This table shows that optimal density for the economic product was 5 palms ha^{-1} higher than that based on yield of fresh fruit bunches (131 against 126 palms ha^{-1} for fresh fruit bunches).

The effect of different levels of fruiting activity
on oil yield and its components

Corley & Breure (in prep.) quantified the effect of fruiting activity on the components of bunch yield by removal of zero, 50%, 75%, and 100% of the female inflorescences produced (different levels of castration). Inflorescence removal commenced as soon as the palms started to flower, about 1½ years from planting; treatments continued for 5 years.

Logically, the removal of potential bunches decreased yield significantly. However, there was considerable compensation in that the proportional yield decrease was less than the reduction of removed inflorescences (Table 12).

Table 12. Effect of disbudding on yield of fruit, bunch number per year and mean bunch weight during years 2 to 5 after fruiting started, and oil content of bunches in year 5. Experiment 4.

Treatment	Yield of fruit kg/palm/ /year	Bunch number /palm /year	Mean bunch weight kg	Oil/ bunch %
1 No disbudding	154.6	20.5	7.6	25.2
2 50% disbudding	122.5	11.9	10.3	25.5
3 75% disbudding	84.2	6.6	12.7	25.6
Standard error	2.8	0.3	0.2	0.7

Treatment 4, complete disbudding, gave no yield during this period.

Concerning the effect of castration on the main components, it is evident that bunch number was less reduced than the level of inflorescence removal, indicating that the number of female inflorescences must have increased on the disbudded palms (Table 12). All components associated with bunch number were affected, i.e. the rate of leaf production, abortion, male inflorescences and bunch failure (Table 13).

Table 13. Effect of disbudding on components of bunch number for 4 years after fruiting started. Experiment 4.

Treatment	New leaves /palm /year	<u>Inflorencesces/palm/year</u>			Sex Ratio %
		Aborted	Male	Female	
1 No disbudding	31.8	2.7	8.1	21.1	72
2 50% disbudding	32.6	1.6	7.1	23.8	77
3 75% disbudding	33.2	1.4	5.1	26.6	84
4 100% disbudding	34.9	1.3	3.0	30.6	91
Standard error	0.3	0.2	0.4	0.4	-

Note: The mean number of bunches per year which failed to develop after anthesis, ranged from 0.74 (no disbudding) to 0.14 (75% disbudding).

The compensation effect on bunch yield was strongest on the components determining the weight of the bunches, though (Table 14).

Table 14. Effect of disbudding on components of mean bunch weight for years 4 and 5 after fruiting started. Experiment 4.

Treatment	Spikelet number /bunch	Flowers per spikelet	Fruit set %	Mean fruit weight (g)	Empty bunch weight (kg)
1 No disbudding	105	11.0	44.0	15.1	3.6
2 50% disbudding	114	13.0	45.9	15.8	5.2
3 75% disbudding	120	13.9	47.8	16.3	6.2
Standard error	2	0.3	1.6	0.4	0.2

Treatment 4, complete disbudding, yielded no bunches during this period.

This Table shows that the response of number of flowers per spikelets to castration was strongest; while spikelet number

and mean individual fruit weight showed a weaker response. The weight of the empty bunch (stalk plus spikelets) increased by and large in proportion to the increase of bunch weight. There was a slight trend towards increased fruit set in the disbudded palms, but the difference was, in contrast with the response of the other bunch weight components, not significant.

Components determining the number of bunches produced did not respond linearly to the level of fruit removal. Abortion rate decreased from 8.5% in treatment 1 to 4.9% in treatment 2, but showed an insignificant further decrease in treatments 3 and 4. Thus a 20% decrease in fruiting activity was sufficient to cause the maximum observed change in abortion rate. Male flower production, on the other hand, was little different in treatments 1 and 2, but showed marked reductions in treatments 3 and 4. It appears, therefore, that inflorescence abortion and sex differentiation have different threshold values of response to fruiting activity.

DESCRIPTION OF INFLORESCENCE DEVELOPMENT

Inflorescence primordia from a sample of felled palms in the 186 palms per ha density of Expt. 2 were examined by light microscopy at the Department of Tropical Crops Husbandry, Wageningen University (Staritsky & Breure, 1985). Results, as reported by Breure & Menendez (in prep a), will be given in the following section.

Subsequently, van Heel, Breure & Menendez (1987) described in much detail the development of inflorescences from initiation until anthesis, using scanning electron microscopy. A brief summary will follow, in which the photos are referred to by the numbers of their paper.

At a very young stage the inflorescence is an elliptic primordium which is surrounded by two spathes. First, two lateral bracts develop, followed by the anterior and posterior bracts (photo 1). Subsequently more bracts are spaced out on the primary apex; this marks the starting point of the formation of the parastichies of bracts (photos 2 to 4). At this stage male and female inflorescences do not differ, neither in the form of the bracts nor in the phyllotaxis.

When development progresses, secondary, flowering axes originate in the axils of the bracts of the primary, central, axis of the inflorescence primordium (photo 8); these develop either into male or female spikelets (rachillae). There is a pronounced basipetal sequence in the origin and further development of the spikelet primordia, i.e. their development starts somewhat below the apex of the primary axis and continues downwards (photos 9 to 10). Since the development of the spikelet primordia begins when that of the acropetal of the primary axis is incomplete, spikelets also originate and further develop in an acropetal sequence which is, however, less pronounced.

Similar to the sequence of initiation of the primary axis, the two lateral bracts on the spikelets develop first (photo 11), and, again, the anterior and posterior bracts lag behind. When the spikelet primordia are larger and less subject to pressure, the remaining bract parastichies are laid down and further develop acropetally. The distal part of a female

spikelet remains sterile, and develops into a spine. The number of bracts and of their parastichies is much greater in male than in female spikelets (photo 12, 13, and 25). The difference in the number of early bracts arising on the base of the spikelet primordia is the first available morphological sign of sex definition.

Flowers arise in the axils of each bract. Developmentally they are all bisexual, but in male spikelets numerous solitary male flowers occur, whereas on female spikelets a triad of flowers arises in the axil of each bract. Each such triad normally consists of a functional female in the centre of two non-functional male flowers. The composition of the triads on a developmental basis is shown on the diagram of the paper. It is idealised only in that the young male companion flowers in reality are located on a slightly higher level of cross-section. The ramification scheme, depicted in the paper, shows the condensed axes in their theoretical position. It can be seen that the development begins with the separation of a bracteole I from the triad primordium (photo 15). The greater part of the primordium develops into the male flower 1. Development continues in the axil of bracteole I giving the reduced secondary axis of the triad (photo 17). From this axis bracteole II, and male flower 2 originate opposite bracteole I (photo 18). Similarly, in the axil of bracteole II the third reduced axis develops, from which bracteole III arises opposite bracteole II, and ending in the female flower (photo 19). Thus there is a succession of three reduced alternating axes, each producing a bracteole and a terminal flower (photos 20 and 21). The result is a cincinnus. In contrast, on a male spikelet a solitary male flower and its bracteole are formed which correspond in position and time with female flower 1 and its bracteole I of the triad in a female spikelet (photo 27). Thus, the development of the flowers on the male spikelet corresponds to the initial development on the female spikelet, but its further development is arrested.

The carpels originate free from each other as semi-globular primordia along the slope of the apex of the flower. They become slightly horseshoe-shaped. Later, when growing upwards, they are contiguous with their lateral faces (photo 22). Their

lateral parts overach the apex, on which one ovule primordium develops axillary to each carpel (photo 22). Lateron, the young carpels are elevated by a common zonal growth at the base, especially on the outside. Through this "fusion" the proximal part of the gynoecium which encloses the ovules is formed.

STAGES IN INFLORESCENCE DEVELOPMENT AT WHICH
CARBOHYDRATE SUPPLY AFFECTS COMPONENTS OF BUNCH YIELD.

Bunch yield depends on the number of bunches and their mean weight. Each of these have a number of sub-components which, at a specific stage in inflorescence development, all respond to the amount of carbohydrate available for the development of inflorescence primordia.

Bunch number is mainly determined by the number of female inflorescences reaching anthesis as losses during bunch development (bunch failure) are negligible (Corley, 1976 b). As mentioned before, bunch number mainly depends on the number of female inflorescences differentiated (sex ratio) and on the abortion rate.

Bunch weight components can be divided into those of the total weight of fruit and those of the weight of the frame (stalk and empty spikelets). Total fruit weight is the product of spikelet number, flower number per spikelet, fruit set (the proportion of flowers which develop into fruit) and the mean weight of individual fruits.

In order to identify the critical developmental stages at which these yield components are determined, Breure & Menendez (in prep. a & b) employed a sudden thinning intervention on part of the 186 palms per ha density of Experiment 2. Thinning took place at the moment of an unusually high fruiting activity, which further enhanced the differences in components of bunch yield between the thinned and unthinned group. The resulting gain in bunch yield of the thinned group subsequently resulted in a relative increase of fruiting activity. This initial gain in fruiting activity must have been sudden and shortlived due to a two-fold reaction to thinning: (1) a reduction in abortions and (2) an accelerated inflorescence development. This sudden demand for carbohydrate, as a result of enhanced fruiting activity, temporarily counteracted the advantage in carbohydrate supply due to thinning.

The first response of a certain component to thinning, in terms of ordinal leaf (L-) number, is inferred as being the critical developmental stage at which the component is

determined. The corresponding scale in inflorescence development was derived by dissecting (a sample of) felled palms (Staritsky & Breure, 1985). The same leaf numbering was followed to record subsequently the sex ratio and abortion rate, and components of bunch weight of the thinned and unthinned group of palms; pairs of two sequential L-numbers are pooled in the analysis. These numbers are given on the x-axis (only the L-number of the youngest leaf is given) and correspond, from left to right, to increasing age of the inflorescences at the moment of thinning (see Figures 8, 9, 10, and 11). A significant (unpaired, two-sided t-test or Fishers's exact two-sided χ^2 -test) change at the oldest developmental stage is indicative of the stage at which the component is determined.

Inflorescence development

Inflorescences grow slowly during the period shortly after leaf opening but in older leaves, at about L +6, a more rapid expansion is observed (Figure 7).

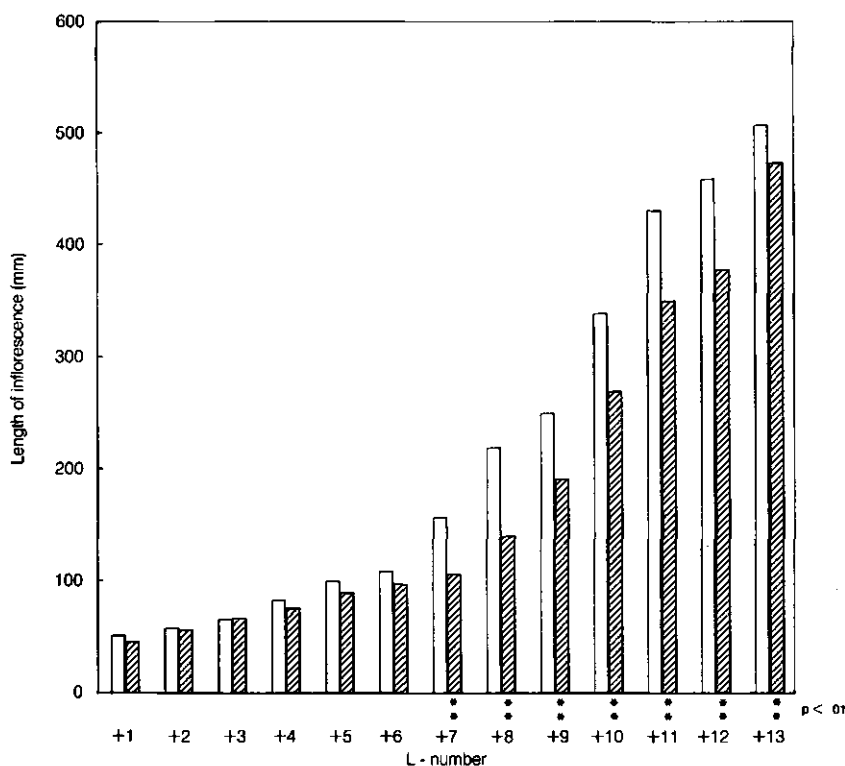


Figure 7. Length of male  and female  inflorescences in leaf axil (L-) number +1 to +13.

Rapid expansion starts about one L-number earlier in females than in males, when males are also larger. The advantage in length of the female over the male inflorescences is highly significant ($P = 0.001$) at L +7 and from that number onwards.

Development of inflorescences was described by Breure & Menendez (in prep. a). Dissection of felled palms revealed that the mean values of L-numbers (with standard deviation in brackets) were for (1) the initiation of the first bract subtending the spikelets, (2) spikelet initiation, and (3) initiation of the first bract subtending the spikelets, L - 18 (1.9), L -4 (1.2), L -2 (1.7), respectively. Anthesis was found at L +17 (1.3).

Bunch number components

Rate of leaf production. Breure & Menendez (in prep.c) reported that the first response of leaf production to thinning was 3 months after thinning (Fig 8), corresponding approximately to the onset of rapid expansion of the leaves (Broekmans, 1957). The response at this stage can only be shortlived and a permanent rise in leaf production must be accompanied by an increase in leaf initiation. Because leaf production became consistently in favour of the thinned palms 6 months after thinning, albeit the response was not consistently significant, it is concluded that leaf initiation responded partly 3 months after the start of leaf expansion. The full response, however, was found for leaves opening after October 1983, i.e. two years after thinning. These leaves, correspond to those younger than about L -48; this leaf number is consistent with the approximate stage of leaf initiation reported by Henry (1955).

Stage of inflorescence abortion. Abortion was significantly higher in the unthinned than in the thinned palms for all leaves younger than L +7/+8 (Fig 9).

This stage, which corresponds with the start of rapid expansion of the inflorescences (Fig 7), must therefore be critical for floral abortion. The observation that these two stages coincide, about 10 leaves before anthesis, is consistent with other

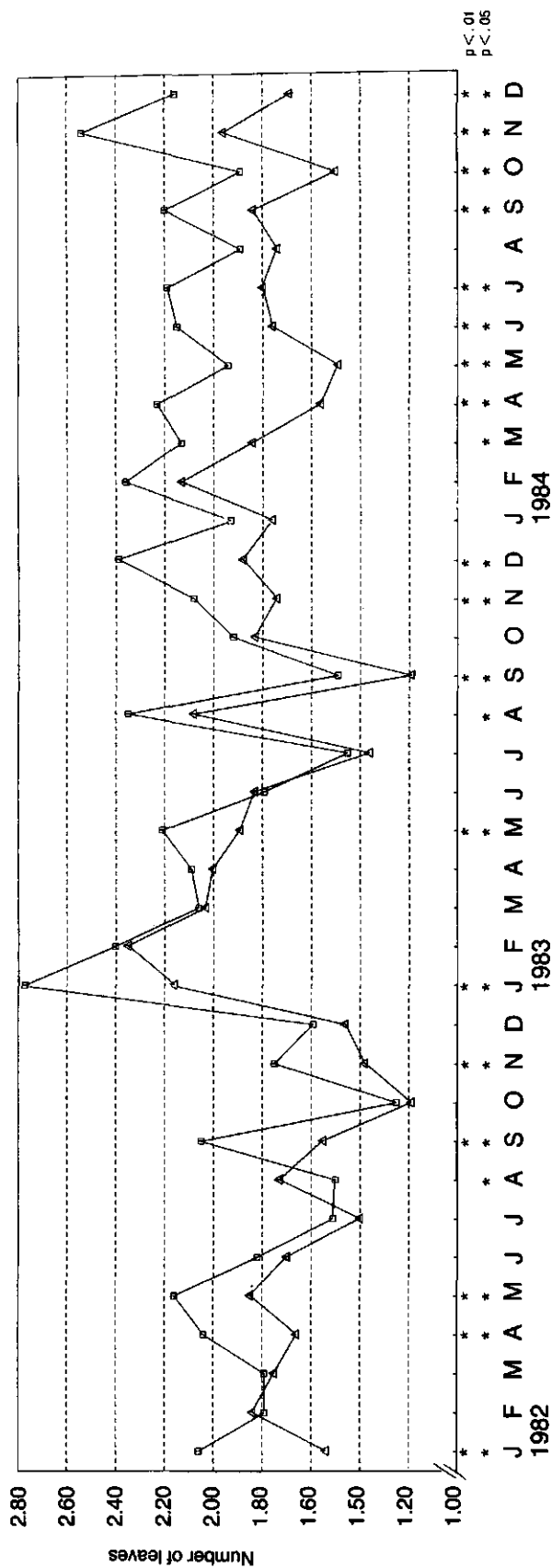


Figure 8. Monthly leaf production of thinned □ and unthinned △ palms from January 1982 to December 1984.

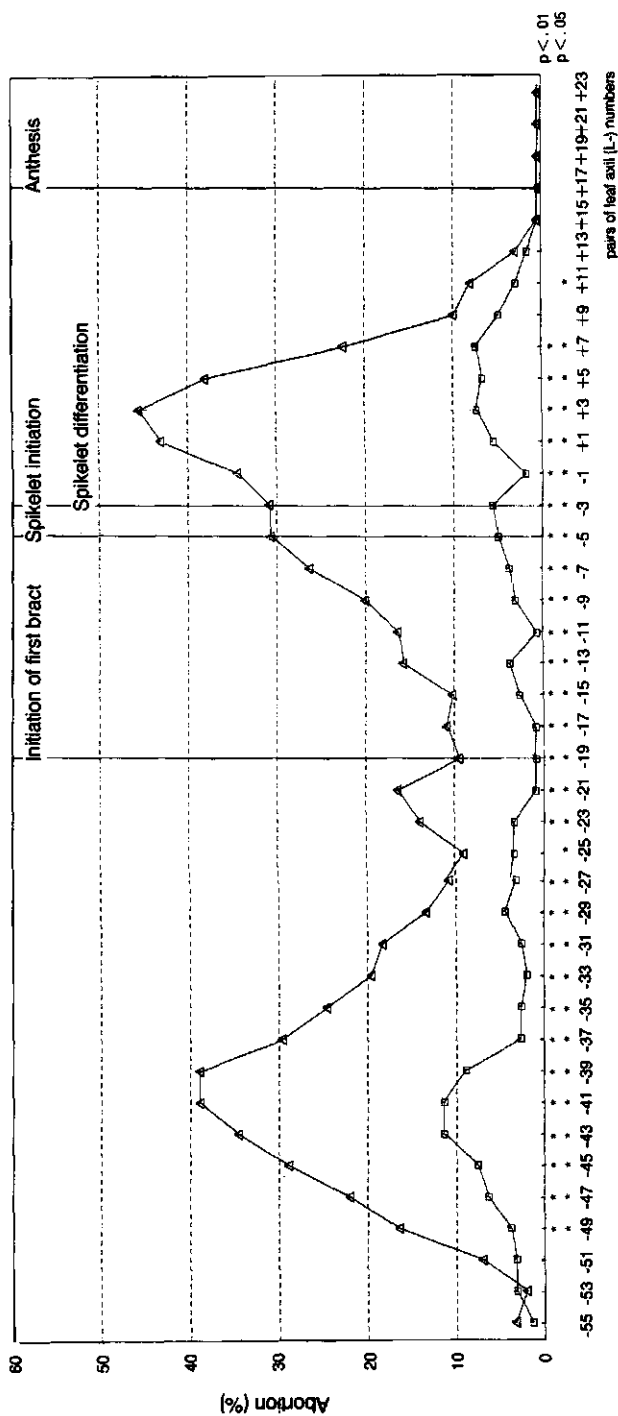


Figure 9. Abortion (%), plotted against two sequential leaf axil (L-) numbers, for thinned (\square) and unthinned (\triangle) palms.

reports (Henry, 1960; Broekmans, 1957; Corley, 1976)

Sex of aborted inflorescences. Because of the relatively low abortion rate of the thinned palms, this group can be regarded as a reference against which the change in sex ratio of the unthinned (high abortion) reflects the extent of preferential abortion of either males or females (Table 15).

Table 15. Number of aborted inflorescences of eighty thinned (T) and eighty unthinned palms (UT) palms for leaf (L-) numbers +9 to +6, together with the sex ratio-values of T and UT palms.

<u>L-number</u>	<u>Aborted inflorescences</u>			<u>Sex ratio</u>	
	T	UT	Difference	T	UT
+9	3	10	-7	0.29	0.33
+8	8	14	-6	0.33	0.29
+7	3	21	-18	0.36	0.19
+6	5	28	-23	0.39	0.21
+5	5	32	-27	0.31	0.13
+4	5	35	-30	0.17	0.22
+3	6	37	-31	0.16	0.09
+2	5	32	-27	0.08	0.10
+1	3	36	-33	0.10	0.18
0	1	26	-25	0.23	0.30
-1	1	28	-27	0.37	0.37
-2	4	23	-19	0.45	0.42
-3	4	25	-21	0.59	0.47
-4	2	21	-19	0.59	0.58
-5	5	27	-22	0.53	0.49
-6	3	24	-21	0.31	0.34
Mean	3.9	26.2	22.3	0.33	0.29

The right column of this table shows that abortion by and large did not change the sex ratio of the surviving inflorescences (with averages of .33 and .29), except for L +5, L+6 and L+7 where a much lower sex ratio was obtained for the unthinned

(.18) than for the thinned (.35) group. Thus, in this range of leaves, aborted inflorescences in the unthinned group must have been mainly females. Note that L +5, +6, +7 were the very first leaves at which abortion of the unthinned palms strongly increased (Table 15). Further, that in these leaves female inflorescences became larger, and rapid expansion started in a younger leaf, than males (Fig 7). Because the base of leaves at that age is still tightly connected with its neighbouring leaf, female inflorescences would be more compressed during their expansion than males. Following the hypothesis of Broekmans (1957), the higher pressure on expanding females would render these more prone to abortion than males. This may explain why, at the onset of a causative shortage of carbohydrate, we find preferential abortion of females.

The observation that the disadvantage in survival of females is bound to this period only, is thus not consistent with results reported by Corley (1976). His results appear to indicate that preferential abortion of female inflorescences may occur for at least 6 months.

Stage of sex differentiation. The increase in sex ratio at L -10/-11 is inferred as the developmental stage at which the sex of the inflorescences is determined (Fig 10).

It corresponds to a developmental stage about 6 to 7 leaves prior to spikelet initiation. Van Heel, Breure & Menendez (1987) suggested, based on their study of inflorescence development, a similar stage for sex differentiation to L -10/-11. Moreover, these L-numbers coincide with those at which the number of flowers per spikelet is determined (see 11b), which is the key morphological characteristic to differentiate the sexes.

Bunch weight components

Figure 11 a-g depicts bunch weight components, for the thinned and unthinned group, against increasing age of the inflorescences at the moment of thinning (paired L-numbers).

Number of spikelets per inflorescence (11a). The oldest developmental stage at which spikelet number increased was

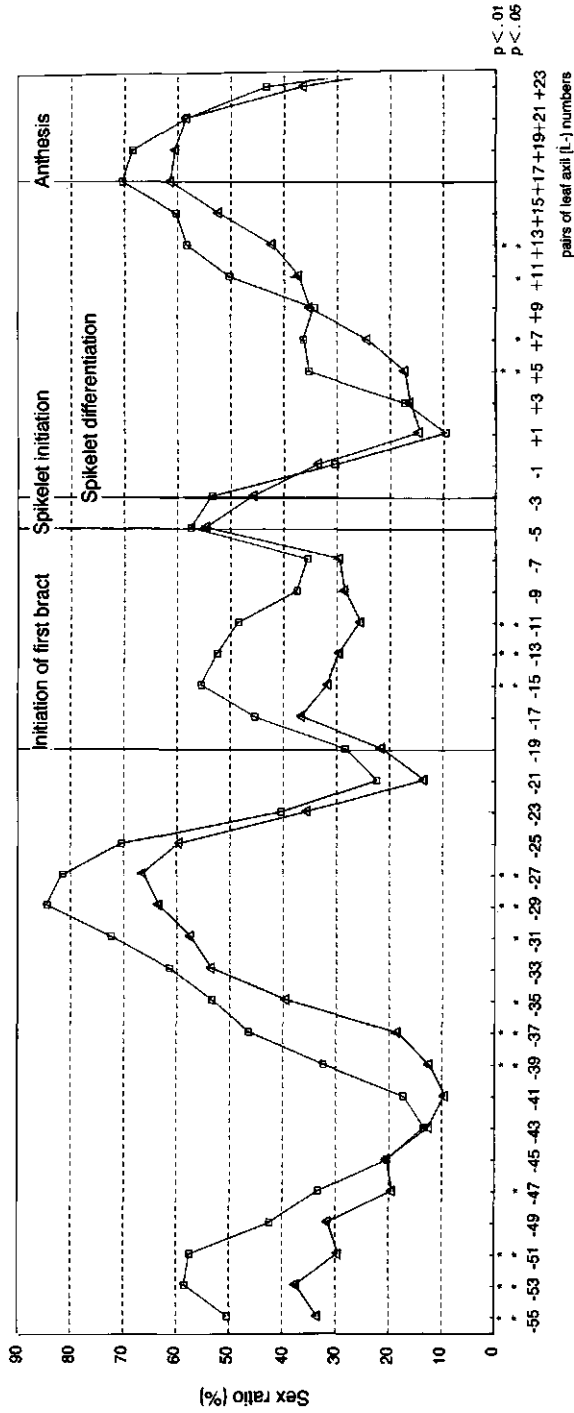


Figure 10. Sex ratio (%), plotted against two sequential leaf axil (L-) numbers, for thinned (\square) and unthinned (\triangle) palms.

between L +7 to +10. Since van Heel et al (1987) showed that the primary axis, from which the spikelets arise, already ceases to be meristematic at about the central spear stage (L 0), this increment must be an artefact. It is assumed to be due to preferential abortion of those inflorescences in the unthinned palms having the greater number of spikelets per inflorescence. Breure & Menendez (in prep. b) therefore concluded that the following candidate, the increase at L +0/-1, must be the actual stage at which spikelet number is determined.

Flowers per spikelet (11b). As shown in our dissection study, spikelet differentiation is completed a few leaves after spikelet initiation. The stage at which the number of flowers per spikelet is determined is thus closely associated with the sequential development of spikelets.

A slight increase in flowers per spikelet of the thinned group starts at L +1/+2; with a second increment at L -8/-9. The latter looks a reasonable stage from a developmental point of view (van Heel et al, 1987). They showed (photo 10) that the development of spikelet primordia begins somewhere below the apex of the primary axis and progresses downwards (in basipetal sequence). At this time the primary axis has completed the greater part of its development, so that the space for most of the spikelets must already be fixed. Additional spikelets arise, to a lesser extent, thereafter (in acropetal sequence), following the meristematic development of the primary axis. It is only on these new spikelets that the number of flowers can still be increased by thinning. This may explain the minor rise in flowers per spikelet starting at L +1/+2, with a major increment at L -8/-9. It is concluded that L -8/-9 is the main stage at which flowers per spikelet is determined, a few leaves prior to spikelet initiation.

Fertile fruit set (11c). This must be determined at anthesis, but the actual response was confounded with an apparent negative response of efficiency of insect pollination to thinning (Breure et al, in prep.).

Single fruit weight (11d). The gain in single fruit weight was fully effectuated on inflorescences which had just passed anthesis. The weight of fruits in the expansion stage was, up to 6 leaves after anthesis, only slightly increased by thinning.

The effect of thinning disappeared as soon as the number of flowers per spikelets was increased, presumably due to a compensation effect, as already suggested by Broekmans (1957).

Frame weight and its components (11e-g). The gain due to thinning was effectuated in three steps: (1) between L +14 and +7, (2) L 0 to -13, and finally in leaves younger than L -14. This observation can be explained from the morphological development of the inflorescence primordia (van Heel et al, 1987) in that the observed increases correspond, in order of decreasing age, to the stage of rapid expansion of inflorescences (Fig 9), to the stage of completion of meristematic development of the primary axis, and to the stage at which flowers per spikelet is determined.

The response of frame weight to thinning was very pronounced, as already observed earlier (Table 7). Further, frame weight was found to respond strongly to fruiting activity (Table 14). Therefore, the disappearance of the advantage of the thinned palms, around L +4/+3, provides convincing evidence of the occurrence of an enhanced fruiting activity on the thinned palms about 3 to 5 months after thinning.

In conclusion, the developmental stages at which the components of bunch yield are determined could be unravelled based on information from different sources. First, the approximate stages were derived from the detailed description of morphological development of inflorescences (van Heel et al, 1987). Second, they were inferred from an empirical study (sudden increase in light intensity on a group of palms). Finally, the apparent sudden increase in fruiting activity of the thinned palms, within 5 months after thinning, strengthened our results. For example, enhanced fruiting activity may explain why the difference in spikelet number disappeared between L -8 to -12 (Fig 11a); further, why the

number of flowers per spikelet was quite similar in the two groups between L -18 to -21 (Fig 11b), and why the difference in sex ratio was negligible between L -17 to -23 (Fig 10).

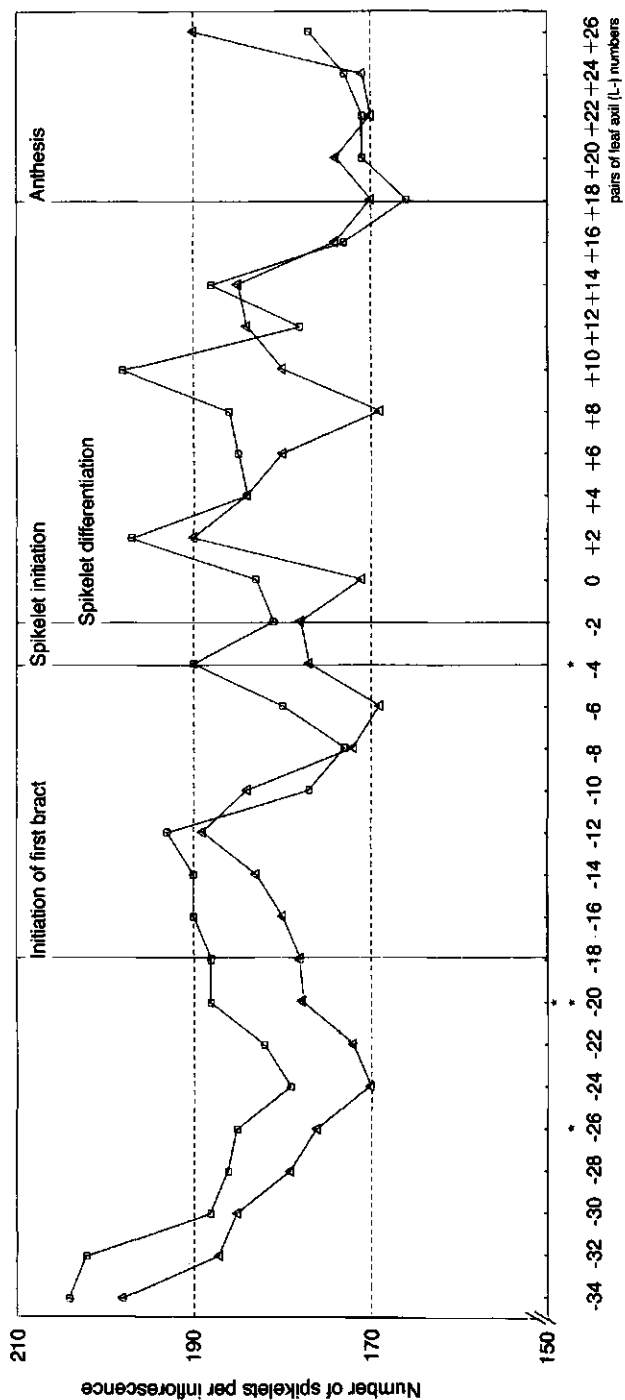


Figure 11a. Number of spikelets per inflorescence, plotted against two sequential leaf axil (L-) numbers, for thinned (\square) and unthinned (\triangle) palms.

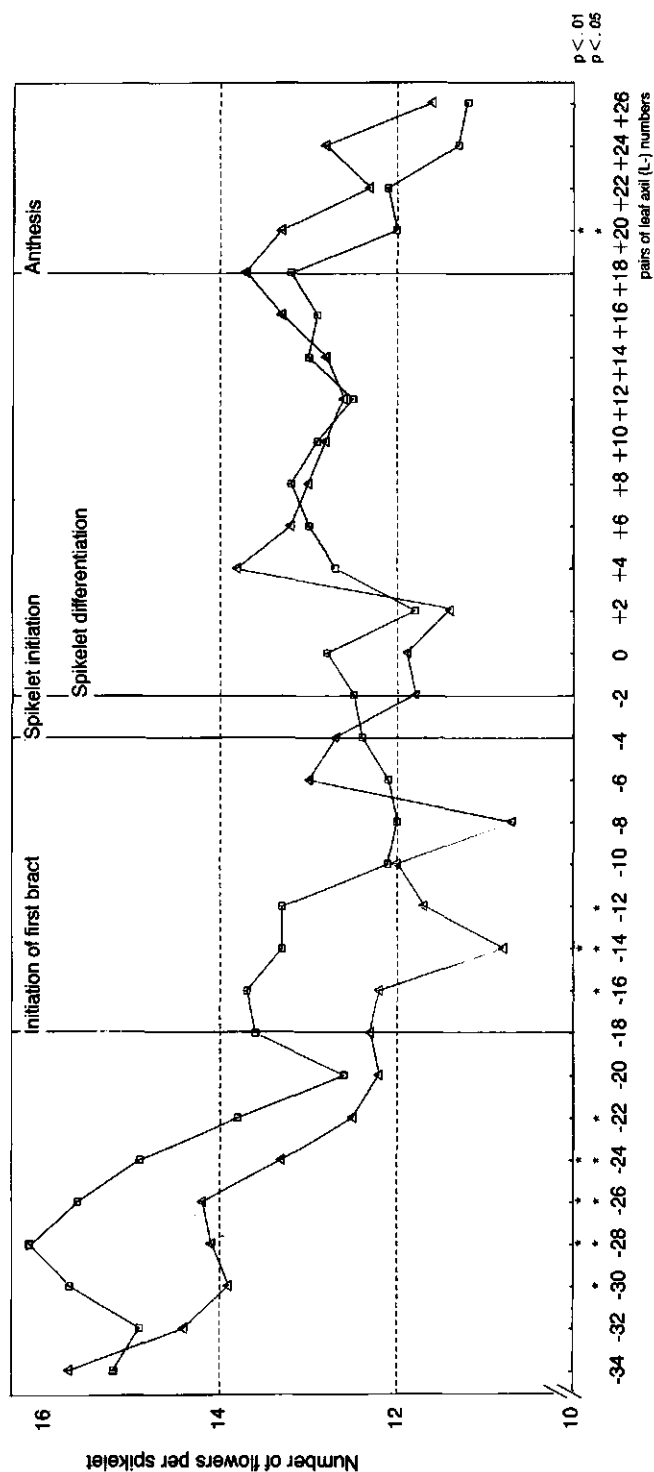


Figure 11b. Number of flowers per spikelet, plotted against two sequential leaf axil (L-) numbers, for thinned (□) and unthinned (△) palms.

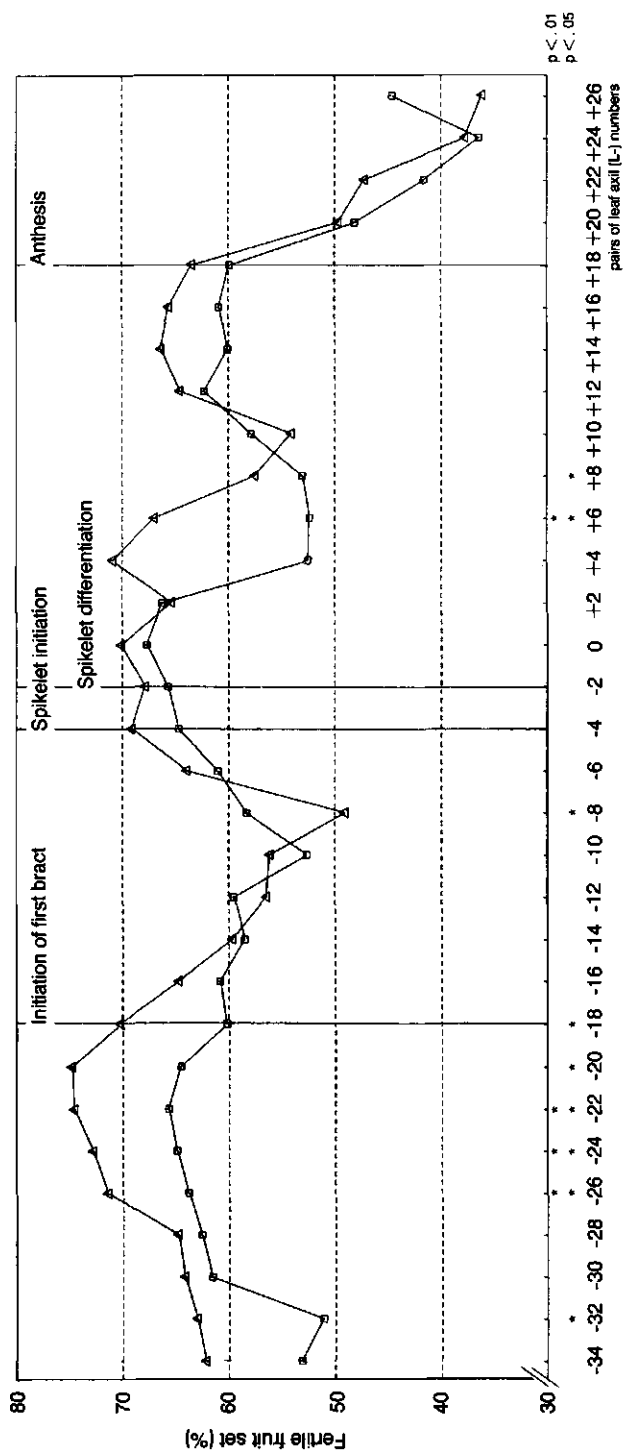


Figure 11c. Fertile fruit set (%), plotted against two sequential leaf axil (L-) numbers, for thinned (O-O) and unthinned (Δ-Δ) palms.

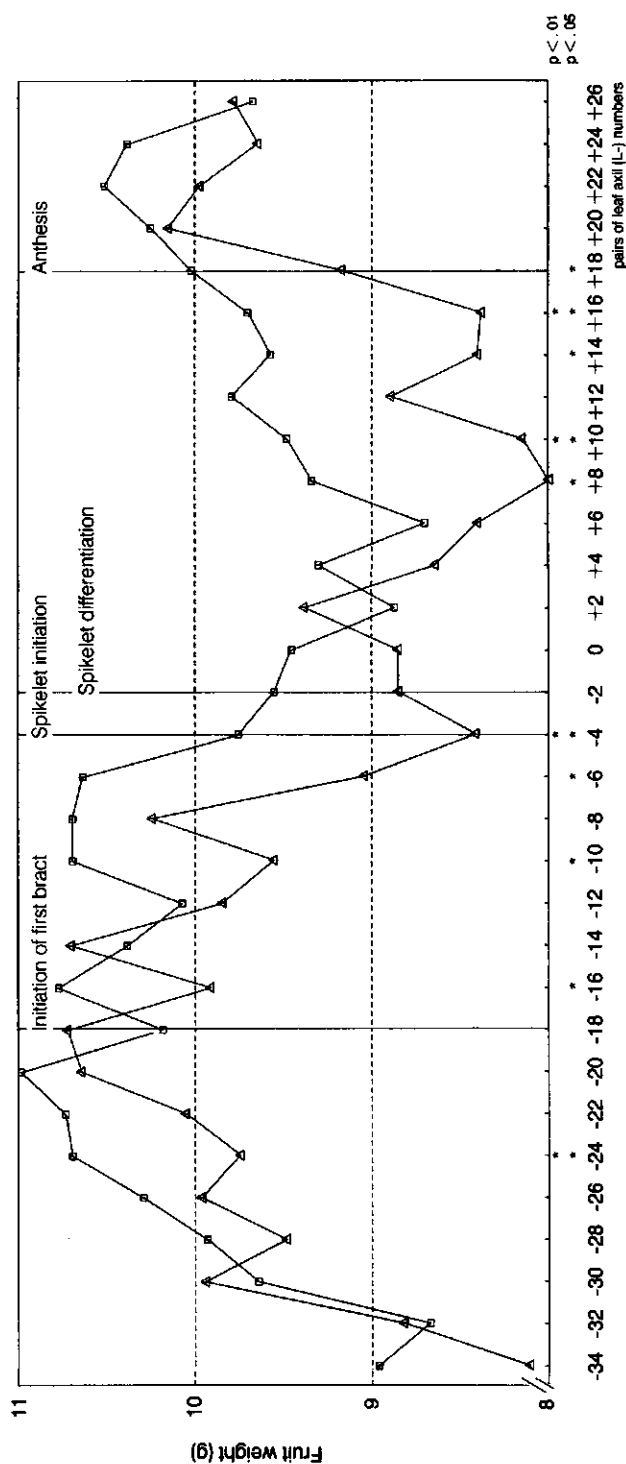


Figure 11d. Weight of individual fruits (g), plotted against two sequential leaf axil (L-) numbers, for thinned (\circ - \circ) and unthinned (Δ - Δ) palms.

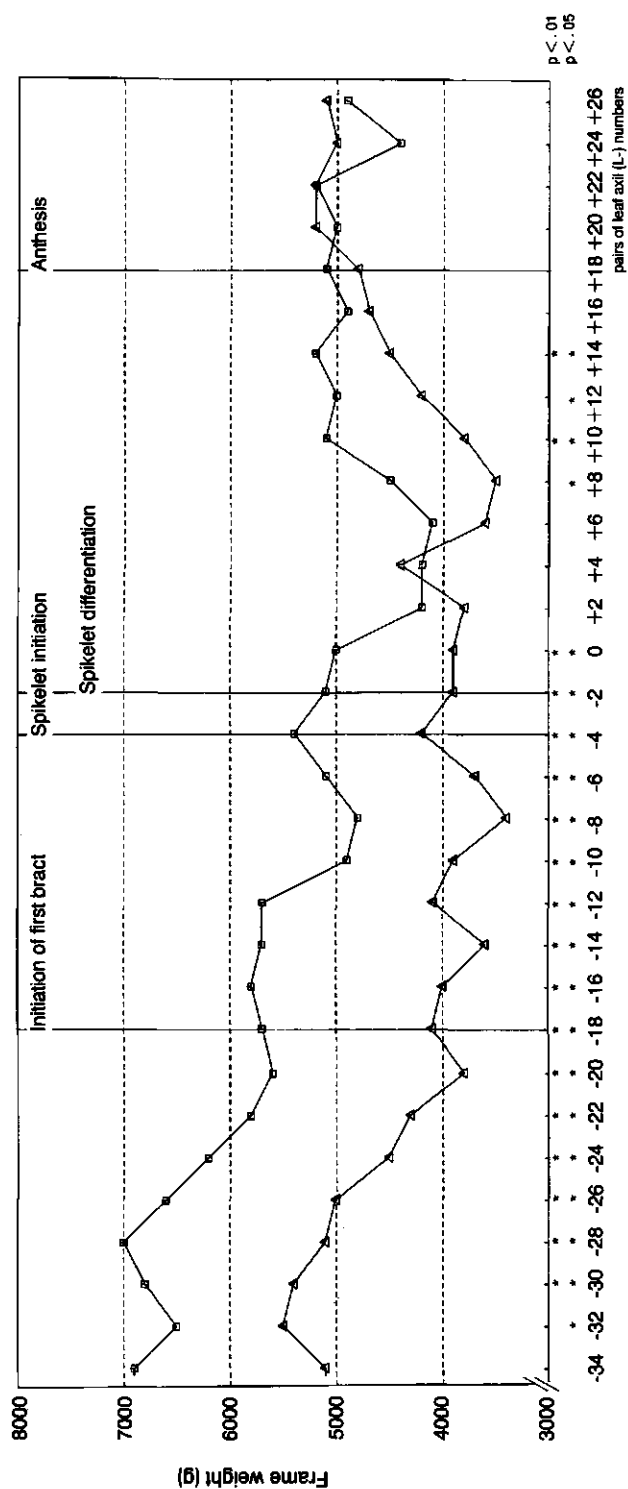


Figure 11e. Frame weight (g), plotted against two sequential leaf axil (L-) numbers, for thinned (\square) and unthinned (\triangle) palms.

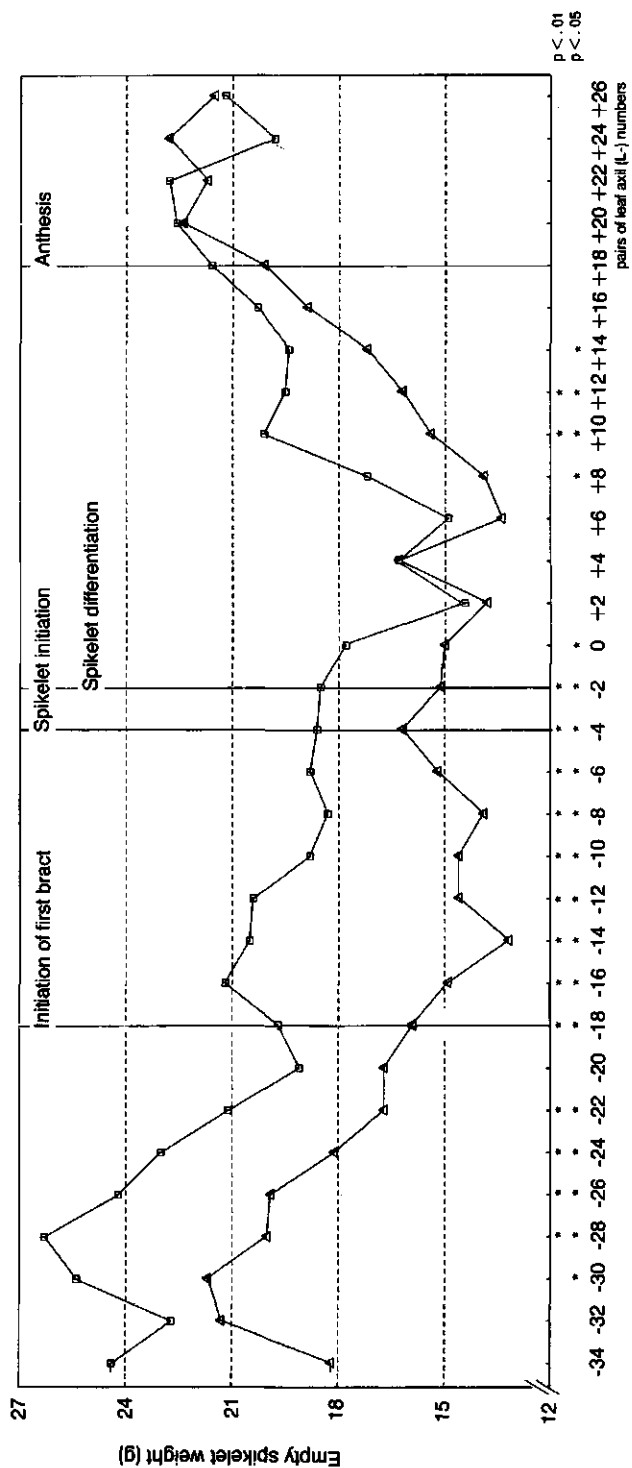


Figure 11f. Mean weight per empty spikelet (g), plotted against two sequential leaf axil (L-) numbers, for thinned (□) and unthinned (△) palms.

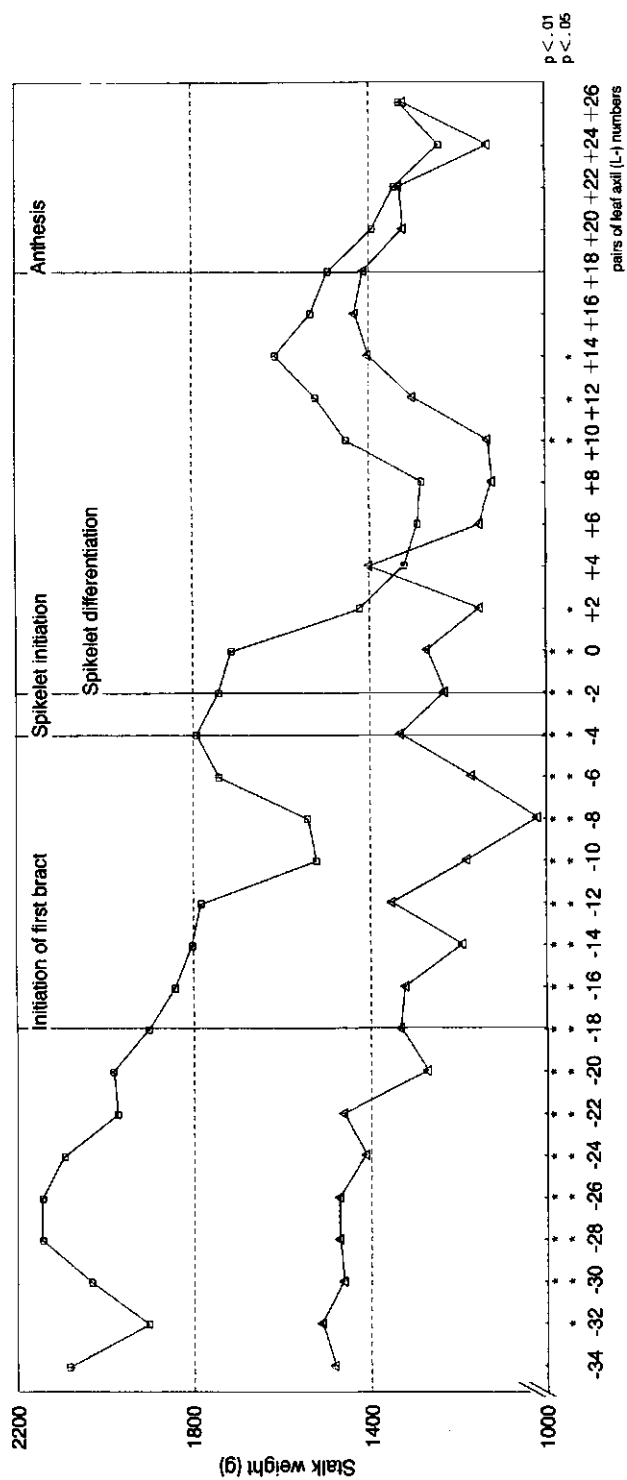


Figure 11g. Stalk weight (g), plotted against two sequential leaf axil (L-) numbers, for thinned (□) and unthinned (Δ) palms.

$p < .01$
 $p < .05$

THE EFFECT OF INTERCEPTION AND DISTRIBUTION OF LIGHT ON THE COMPONENTS OF DRY MATTER PRODUCTION

Gross photosynthetic production depends primarily on the solar radiation absorbed by the canopy, which is directly related to leaf area index (L), i.e. the green leaf surface per unit ground area. To derive the light interception from L requires establishing the extinction coefficient (k), defined by Squire (1984) for oil palm as

$$k = \frac{-\ln(1-f)}{L-a}$$

where f is the light interception, and a is a constant.

Breure (in press b) measured interception of PAR on palms of the four densities of Expt 3 in the 14th year from planting. He confirmed this general equation in that it has an intercept on the L-axis. However, the extinction coefficient obtained was smaller than reported by Squire (0.32 against 0.47 found by Squire); both regression equations are depicted in Fig 12.

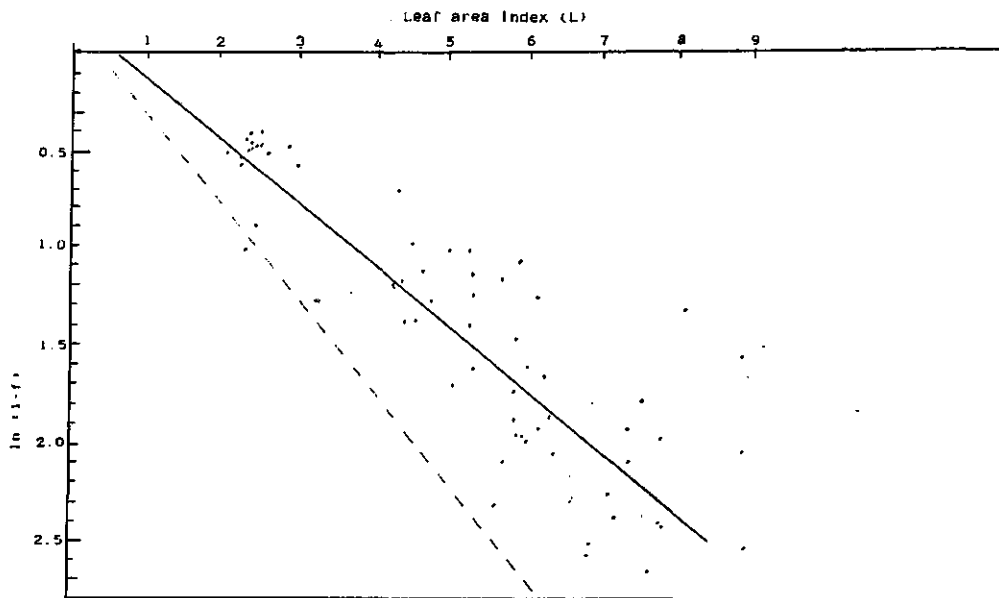


Figure 12. Relationship between interception of PAR (f) and leaf area index (L) based on sub-plot values of Experiment 1, 14 years from planting. The relationship of Squire (1984b) is also presented (dotted line).

Figure 12. Relationship between interception of PAR (f) and leaf area index (L) based on sub-plot values of Experiment 2, 14 years from planting. The relationship of Squire (1984) is also presented (dotted line).

W. Gerritsma (pers. com., 1987) repeated Breure's measurements on the same palms of Expt 3, in the 16th year after planting; he found a nearly identical k-value (0.33). He further showed that the intercept of the regression line is not significantly different from zero (origin).

Note that the equation of Squire is based on pooled data assembled for different ages. It is, however, evident that shortly after the crown size has stabilized at a mature level (about ten years from field planting), transmission of light usually increases sharply, in particular at high planting densities. This change in light interception at mature crown size suggests that k-values differ with the age of the palms. Breure (in press b) established therefore the trend in k with age by measuring interception of PAR and L in plantings of different ages in West New Britain and North Sumatra. Because the actual regression lines per age group could not be established, because the range of L-values within one planting was too small, k-values were derived from the equation:

$$k = \frac{-\ln(1-f)}{L}$$

L

i.e. without an intercept at the L-axis (as mentioned, W. Gerritsma, pers. com., showed that this is justified). The k-values thus obtained showed a marked peak shortly after crown expansion was completed, i.e. year 9-11 (0.45) and year 10-13 (0.38), respectively, and indeed shows a marked decline thereafter (Table 16).

Table 16. Values of extinction coefficients (k) in oil palm plantings of different ages in West New Britain (Breure, in press b) and North Sumatra (T. Moeliono, pers. com.).

<u>Age</u> (years)	<u>New Britain</u>	<u>Age</u> (years)	<u>Sumatra</u>
6-8	0.37	5-8	0.35
9-11	0.45	10-13	0.38
13-14	0.36	11-14	0.33

The annual k-values, between years 6 to 14 (as shown later

in Table 17), differed significantly ($P < 0.01$). It should be noted that Corley (1976a) found a similar k-value for ten year-old palms (0.44) to that presented in Table 17, but he did not report on k-values of other ages.

Measured light transmissions were quite similar to those estimated from the formula of Squire for palms younger than 11 years, but for older palms transmission was intermediate between those estimated by the two different equations (Table 17).

Table 17. Extinction coefficients (k) and leaf area index values (L) established in commercial plantings in West New Britain between 6 and 14 years after planting, together with measured transmission of PAR (1-f) and estimated values derived from Figure 12 and the formula presented by Squire (1984).

Age (years)	L	k	s.e.	<u>Transmission of PAR (1-f)</u>		
				<u>measured</u>	<u>estimated</u>	
					Fig 12	Squire
6	4.52	0.438	0.0282	0.15	0.29	0.14
7	5.45	0.341	0.0277	0.17	0.21	0.09
8	5.16	0.355	0.0254	0.16	0.23	0.10
9	5.51	0.465	0.0225	0.08	0.21	0.09
10	5.65	0.401	0.0207	0.11	0.20	0.08
11	5.97	0.439	0.0278	0.07	0.18	0.07
12	-	-	-	-		
13	4.97	0.348	0.0248	0.18	0.25	0.11
14	5.30	0.359	0.0312	0.16	0.22	0.10

Note: s.d of k-values is 0.375 with 53 d.f.

Example of testing whether k-values of year 9 and 10 are significant:

$$t = \frac{0.465 - 0.355}{\sqrt{0.0225^2 + 0.0254^2}} = 3.2417 \text{ (53 d.f.)}, \text{ which is significant.}$$

These two equations (Squire, 1984; Breure, in press b) were applied accordingly to estimate light interception from measured L-values.

Results of the 110, 148, and 186 palms per ha densities for different ages (Fig 13) show that, during the stage of canopy closure, light interception increases steadily to a peak, reached earlier, at a higher value, as the planting density increased.

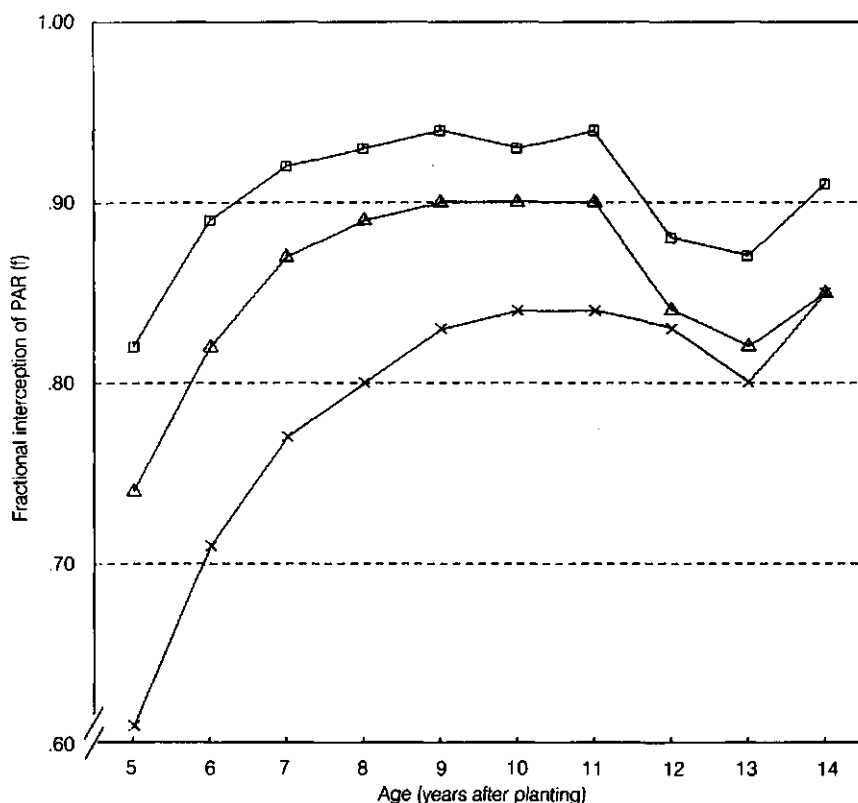


Figure 13. Fractional interception of PAR (f) as a function of palm age (years after planting). x—x, 110 palms ha⁻¹; Δ—Δ, 148 palms ha⁻¹; ◻—◻, 186 palms ha⁻¹. Years 5 to 11 based on Squire (1984). Years 12 to 14 based on Breure (in press b).

At about year 11 interception declines, and shortly thereafter appears to stabilize at a lower level. The decline confirms the visual observation and is probably brought about by an increase in gaps of the canopy coupled to differences in height

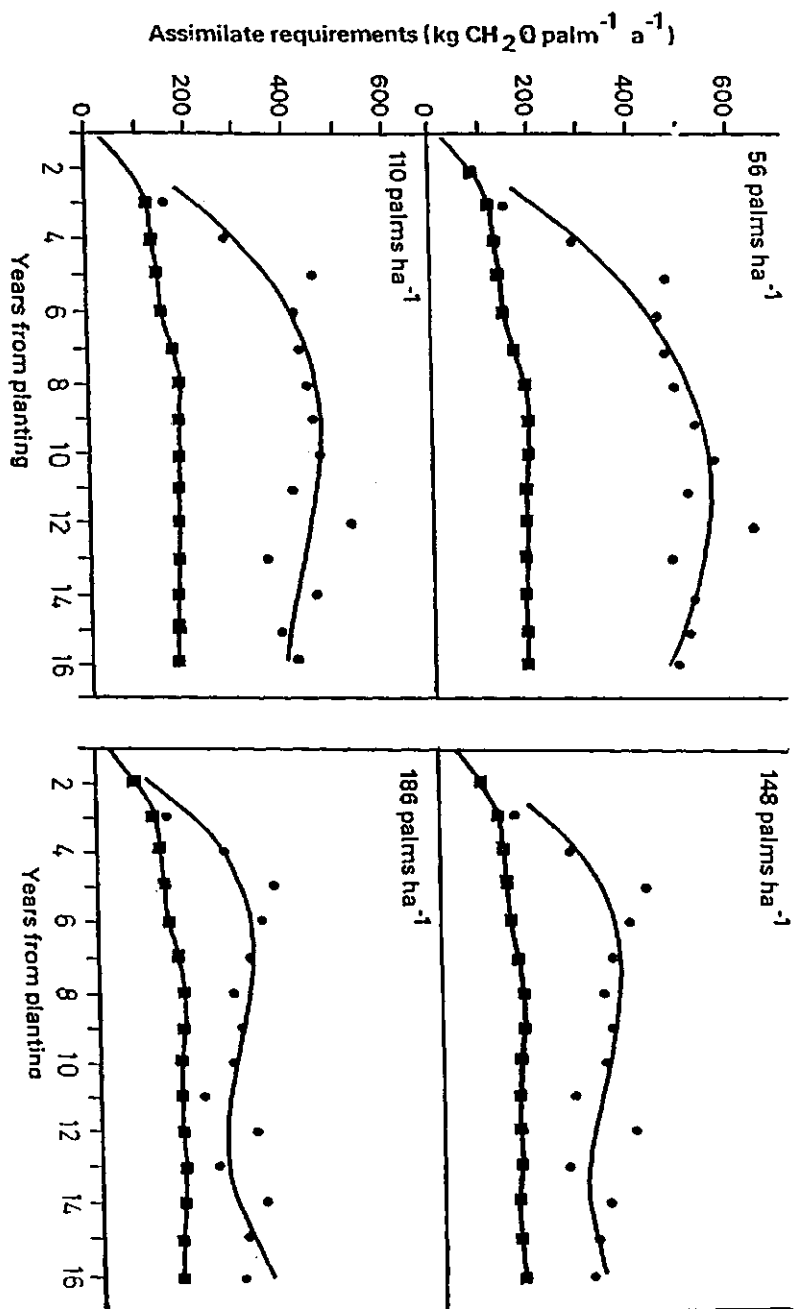


Figure 14. Carbohydrate requirements for total (TDM_c) growth, plotted as a function of palm age (in years) for the planting densities of Experiment 2 (VDM_c for the third and fourth years adopted from Experiment 3, and^c for the fifteenth and sixteenth years estimated as the mean of the three preceding years).

between the palms (increase in depth of the canopy).

The second factor which determines the supply of assimilates is the conversion rate of absorbed radiation which in turn depends on the assimilation-light response curve of the leaf surface. This curve, as mentioned before, is characterized by a region at low light intensity where assimilation rate is proportional to absorbed light, leading to a plateau at light saturation which is reached at about 30% of full sunlight (Corley, 1976a). Light is thus more efficiently utilised when evenly distributed over the leaf surface. It seems reasonable to assume that light distribution is inversely proportional to light interception. The decrease in light interception from year 11 onwards (Fig 13.) is, for example, accompanied by a strong increase in the vigour of the ground vegetation (to be considered as the lowest layer of the intercepting green leaf surface); this increase in vigour was particularly pronounced in the higher densities.

TDM_C and VDM_C (carbohydrates for total and vegetative DM) were established from measured dry matter production and conversion factors derived from those presented in Table 5. VDM_C continued to increase at all densities, until about 8 years from planting, and thereafter remained more or less constant while TDM_C increased initially to a peak, reached earlier at lower values as the planting density increased (Fig 14). The fitted curves are based on cubic regression equations with coefficients of determination (R^2) varying from 0.81 to 0.94. The peaks occurred at 132, 117, 92 and 87 months from planting, corresponding to maxima of 568, 474, 385 and 325 kg CH_2O palm⁻¹a⁻¹ or 31.7, 52.3, 57.1 and 60.4 t CH_2O per ha per year, at the 56, 110, 148 and 186 palms ha⁻¹ density levels, respectively. Initial production of carbohydrates per ha can be largely explained from the fractional light absorption (Fig 13), since, similar to TDM_C , canopy closure (maximum light interception) occurs earlier and reaches a higher maximum as a function of planting density. The subsequent decline in TDM_C can either be caused by a reduction in gross photosynthetic production or by an increase in maintenance respiration losses. These losses are stabilized when the crown approaches its maximum size (Table 18) and their contribution to the decline

depends thus on the planting density.

Table 18. Carbohydrate ($\text{kg CH}_2\text{O ha}^{-1}\text{d}^{-1}$) needed for total dry matter (DM) production and maintenance respiration, together with maintenance respiration per unit biomass ($\text{g CH}_2\text{O kg}^{-1}\text{DM d}^{-1}$). Mean values for the 115 and 143 palms per ha densities of Experiment 2.

<u>Age</u> (years after planting)	<u>Gross</u> <u>assimilation</u>	<u>Carbohydrate requirements</u> for		<u>Daily</u> <u>maintenance</u> per unit <u>biomass</u>
		Growth	Maintenance	
3	243	107	136	7.1
4	287	134	153	5.6
5	311	155	156	4.1
6	325	149	176	4.4
7	327	145	182	4.1
8	326	168	158	3.4
9	323	146	177	3.7

In the two higher densities (148 and 186) leaf size still increases at a rapid rate after the canopy is practically closed (Fig 15).

The dominant cause of the decline in TDM_c at these densities might therefore be the increase in maintenance respiration losses. These losses are apparently not compensated by an increase in photosynthetic production. This seems logical because the relationship between L and light transmission is by and large asymptotic (Fig 13) , which means that, for relatively high L-values an increase in L results in a lower proportional increase in light interception. Moreover, our results suggest that after canopy closure, intercepted radiation becomes less evenly distributed over the foliage due to excessive interception by the top layer of the canopy, thus decreasing photosynthetic production per unit green leaf. In contrast, the decline in TDM_c at the lower densities (56 and

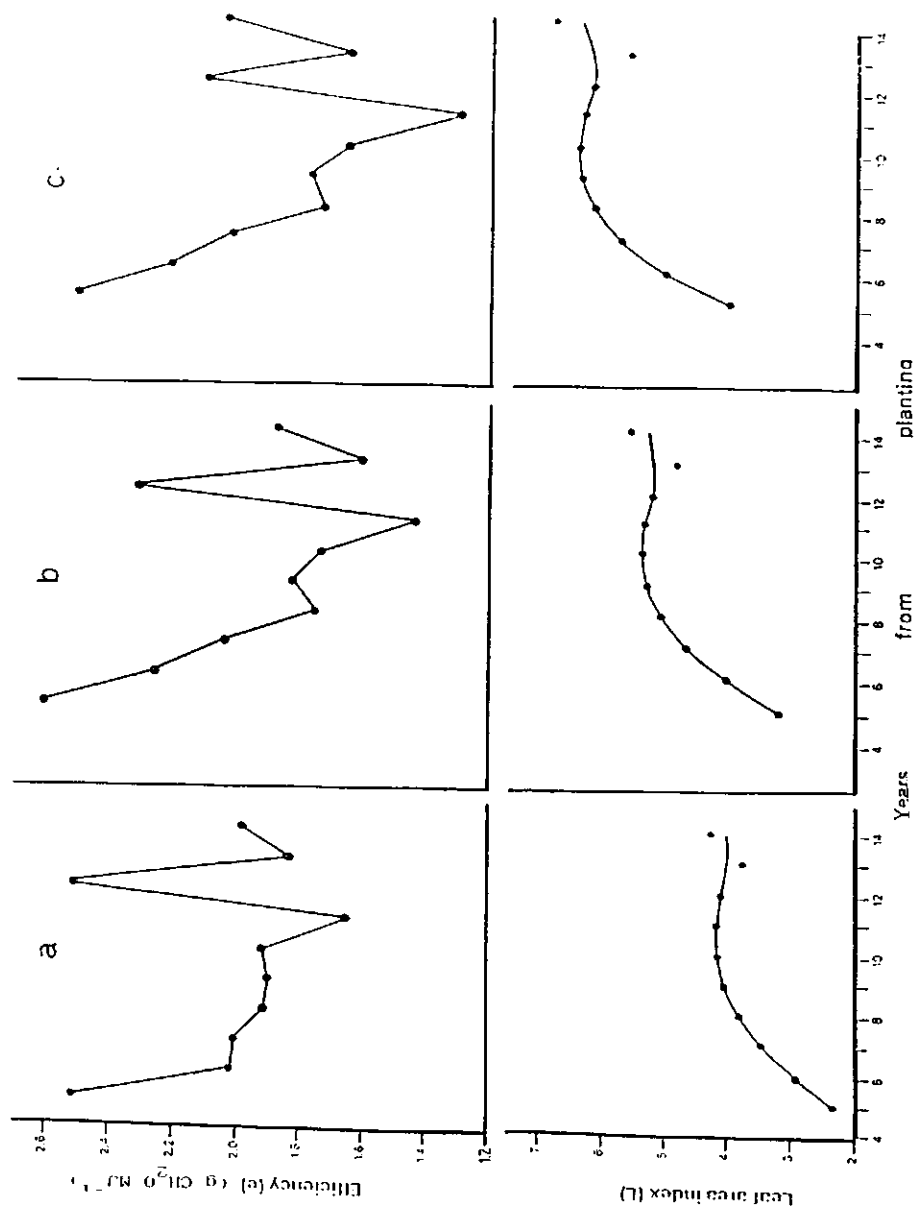


Figure 15. Teh efficiency (e), expressed in g CH₂O MJ⁻¹, of conversion of PAR to carbohydrates for above-ground dry matter production and leaf area index (L), plotted as functions of age at 110 palm ha⁻¹ (a) 148 palms ha⁻¹ (b) and 186 palms ha⁻¹ (c).

110) and also the continuing decline at the higher densities, took place at a time when any increase in maintenance respiration would have stopped and must be due to a reduction in gross photosynthetic production. There are two factors which must be responsible for the decline when maintenance respiration has stabilised: first a reduction in light interception, and, second, a decrease in efficiency to convert intercepted radiation into assimilates.

Therefore, the efficiency (e) of conversion of intercepted PAR to assimilates required for TDM_c for the three higher densities was established (Fig 15). The initial decrease in e is assumed, as mentioned before, to be due to an increase in requirements for maintenance respiration. The lower minima at the two higher densities might be due to poor light distribution (high k -values). The subsequent increase in e may be explained from the improved light distribution associated with the inferred reduction in light interception (Fig 13). In the higher densities the increase in e apparently more than compensated for the reduction in light interception, as TDM_c tended to increase. On the other hand, at the lower densities, the increase in e appears to be insufficient to compensate for reduced light interception as TDM_c continued to decline.

Thus the hypothesis is put forwards that trends in TDM_c at mature crown size are governed by differences in response of gross photosynthetic production to changes in interception and distribution of sunlight. At lower densities the reduction in light interception is specially important, while at the higher planting densities the beneficial effect of improved light distribution becomes more dominant.

Clearly, these differences in response of reduced light interception between planting densities is strongly reflected in trends of Y_c (carbohydrates for bunch dry matter production) with age since the allocation of carbohydrates to fruit bunches depends on the surplus of assimilates when those for maintenance respiration and VDM_c have been met. The result is an increase in optimal density for current yield from the 13th year onwards, following the usual decline with age during the previous period. A similar, but less pronounced, dip in optimal density, shortly after completion of crown expansion, can be obtained from long-

term yield data of a density experiment reported by Prevot & Duchesne (1955) and Ramachandran et al (1972).

Table 19. Estimated optimum densities for bunch yield, at different ages (years after planting), based on linear regression equations fitted through yield per palm at different densities. Density experiments at Papua New Guinea²⁾, Ivory Coast³⁾ and Malaysia⁴⁾.

Optimum density (palms per ha)¹⁾

<u>Age</u> (years after planting).	<u>Papua New</u> <u>Guinea</u>	<u>Ivory Coast</u>	<u>Malaysia</u>
3 & 4	320		
5 & 6	193		
7 & 8	127	-	146
9 & 10	<u>118</u>	164	127
11 & 12	<u>112</u>	131	<u>116</u>
13 & 14	131	140	128
15 & 16	126	<u>118</u>	131
17 & 18	-	<u>115</u>	128
19 & 20	-	145	
21	-	142	-

1) Estimated as $a/2b$, where a = intercept and b = slope of the fitted regression lines.

2) based on 110, 148, and 186 palms per ha densities (Breure, in press b).

3) based on 100, 123, and 156 palms per ha (Prevot & Duchesne, 1955).

4) based on 96, 114, 138, 158, and 183 palms per ha (Ramachandran et al, 1973).

Note: throughs in optimal densities are underlined.

The suggestion by Corley (1976c) that optimal density remains constant after the crown size reaches its maximum does therefore not hold for palms grown in the environment of this study. Further, the suggestion by Corley et al (1973) that optimal density for current yield can be estimated from the mean area of the crown leaves does not appear to apply for plantings with mature crown size. A further implication of the observed trends in optimal density for current yield is seen in the interpretation of results of thinning experiments in commercial plantings. Such experiments are usually laid down at the time of minimum light penetration (8 to 10 years

from planting) and the quick response to thinning at that time (Anon 1985) might be misleading when results are extrapolated for long term policy on thinning and even optimal planting density.

The above analysis of possible factors responsible for the trend in Y_c provides a basis for suggesting that yield per ha might be improved by increasing TDM_c and reducing VDM_c . The latter can be diminished through breeding and selection for high bunch index (Corley et al, 1971; Hardon et al, 1972; Breure & Corley, 1983; Breure, 1986), while the period during which it increases can be reduced, and a lower mature value obtained, by selection for so-called rapid expansion rate ideotypes, i.e. palms with rapid increase in mean leaf area and a reduced expansion time (cf Breure, 1985). Apart from a reduction in VDM_c these ideotypes show increased initial TDM_c due to speed of ground coverage, combined with a decrease in leaf maintenance requirements due to reduced leaf size, as explained later. A reduction of losses due to leaf maintenance respiration may further be possible through breeding as shown for rye grass by Wilson (1982). There seems to be little scope for breeding for favourable parameters of the assimilation-light response curve for gross photosynthetic production because there is considerable evidence that there is little genetic variation in the slope of the curve at lower intensities in C_3 crops (Björkman, 1981; Ehleringer & Pearcy, 1983), but Corley et al (1973) reported significant differences between oil palm progenies in the nursery, though. Secondly, although the genetic variation in assimilation rate at light saturation may be considerable these differences would only be partly reflected in changes in photosynthetic production of the entire leaf surface (Spitters, 1986). On the other hand, our results suggest that there might be considerable possibilities in increasing gross photosynthetic production through measures which improve the light distribution over the leaf surface. This means that, for a given leaf area index (L), light penetration should be improved. This might, for example, be achieved through increasing the canopy depth by planting a mixture of clonal palms with distinct differences in height increment.

SELECTION FOR RATE OF CROWN EXPANSION

Maximum light interception per ha is reached when the canopy is practically closed. Since fruit bunch production starts, at commercial planting densities, prior to canopy closure, the initial amount of carbohydrates available for bunch DM (Y_c) is contingent upon the speed of canopy closure. Following the stage of canopy closure, on the other hand, additional crown expansion increases the requirements of carbohydrates for vegetative growth (VDM_c) and maintenance respiration without a further increase in gross assimilation. The end result will be a reduction in the the proportion of total DM used for fruit bunches (Bunch Index). Ideally, palms should therefore combine rapid crown expansion with a short expansion time.

Breure (1985) termed such palms Rapid Expansion Rate ideotypes (RER). With respect to the supply of assimilates from the total leaf surface (source of assimilates) and the partitioning between bunch DM and vegetative DM production (available sinks of assimilates), RER ideotypes are expected to show the following characteristics in comparison with Slow Expansion Rate (SER) ideotypes.

First, an increase in source of assimilates prior to canopy closure, as a result of a more rapid crown expansion, should lead to a higher initial amount of carbohydrates for total DM production (TDM_c). Secondly, when the canopy is closed, RER ideotypes will have a lower sink size of vegetative growth (smaller final leaf size) and hence a higher proportion of assimilates available for bunch DM (Y_c). Thirdly, the combination of a relatively high initial area of the youngest fully expanded leaf (LA) and a lower sink strength of vegetative growth will result in RER palms having a high initial Leaf Area Ratio (LAR), the ratio of new total leaf area produced to VDM. Since RER palms stabilize at a lower LA level, LAR will subsequently decrease with age; the decrease in LAR is not expected for SER palms.

Breure (1985) tested the expected differences in rate of crown expansion and their effect on carbohydrate requirements and on trends in LAR with age on palms of two extreme, but

Table 20. Amount of carbohydrates ($\text{kg CH}_2\text{O palm}^{-1} \text{ a}^{-1}$), for different ages (years after planting), required for fruit bunches (Y_C), above-ground vegetative growth (VDM_C) and total dry matter production (TDM_C) of palms selected for slow (SER) and rapid (RER) leaf expansion. Experiment 2 (110 and 148 palms per ha) and Experiment 3 (115 and 143 palms per ha).

<u>Expt. 2</u>									
<u>110 palms ha^{-1}</u>									
Age	SER 1)			RER 2)			RER minus SER		
	Y_C	VDM_C	TDM_C	Y_C	VDM_C	TDM_C	Y_C	VDM_C	TDM_C
5-6	281	154	435	330	153	483	+49	-1	-1
6-7	261	183	444	284	174	458	+23	-9	-9
7-8	275	201	476	270	182	452	-5	-19	-19
8-9	275	196	471	286	179	465	+11	-17	-17
9-10	272	208	480	268	198	466	-4	-10	-10
10-11	215	195	410	231	185	416	+16	-10	-10
Total	2071	1282	3353	2153	1214	3367	+82	-68	-68
<u>148 palms ha^{-1}</u>									
Age	SER 1)			RER 2)			RER minus SER		
	Y_C	VDM_C	TDM_C	Y_C	VDM_C	TDM_C	Y_C	VDM_C	TDM_C
4-5	291	141	432	323	147	470	+32	+6	+6
5-6	236	147	383	272	142	414	+36	-5	-5
6-7	185	173	358	204	158	362	+19	-15	-15
7-8	165	186	351	183	170	353	+18	-16	-16
8-9	185	180	365	181	172	353	-4	-8	-8
9-10	165	186	351	190	185	375	+25	-1	-1
10-11	117	182	299	124	173	297	+7	-9	-9
Total	1344	1195	2539	1477	1147	2624	+133	-48	-48

Table 20 continued.
Expt 3

115 palms ha⁻¹

Age	SER 3)			RER 4)			RER minus SER	
	Y _C	VDM _C	TDM _C	Y _C	VDM _C	TDM _C	Y _C	VDM _C
3-4	202	125	327	215	136	351	+13	+11 ^x
4-5	262	127	389	264	134	398	+2	+7 ^x
5-6	219	169	388	250	164	414	+31 ^x	-5
6-7	202	165	367	223	162	385	+21 ^x	-3
7-8	261	166	427	291	160	451	+30 ^x	-6 ^x
8-9	163	184	347	172	167	339	+9	-17 ^x
9-10	274	199	473	263	189	452	-11	-10
Total	1583	1135	2718	1678	1112	2790	+95	-23

143 palms ha⁻¹

Age	SER 3)			RER 4)			RER minus SER	
	Y _C	VDM _C	TDM _C	Y _C	VDM _C	TDM _C	Y _C	VDM _C
3-4	196	132	328	211	136	347	+15	+4 ^x
4-5	250	123	373	267	131	398	+17	+8 ^x
5-6	204	170	374	222	167	389	+18	-3 ^x
6-7	191	166	357	195	156	351	+4	-10 ^x
7-8	224	162	386	239	154	393	+15	-8 ^x
8-9	127	178	305	126	164	290	-1	-14 ^x
9-10	210	191	401	197	174	371	-13	-17 ^x
Total	1402	1122	2524	1457	1082	2539	+55	-40

x = p .05

xx = p .01

- 1) Mean of palms sampled for the two lowest ER-values in each main plot
- 2) Mean of palms sampled for the two highest ER-values in each main plot
- 3) Mean of palms sampled for the lowest ER-values in each of 56 progenies.
- 4) Means of palms sampled for the highest ER-values in each of 56 progenies.

commercially used planting densities.

As a first step, an index for the trend in crown expansion was developed. LA against age was found to be best fitted by a logistic growth curve with maximum LA (L_m) and the time required to reach $0.95 L_m$ ($t_{0.95}$) as characteristic parameters. From this fitted curve the trend in crown expansion is conveniently described by the ratio of LA at maximum expansion rate (year 4 was adopted) and LA at its final size (L_m); this ratio is referred to as Leaf Expansion Ratio (ER). ER-values were established for individual palms of two planting densities of experiments 2 and 3, and groups of palms were sampled with high (RER) and low ER-values (SER). For both RER and SER palms mean values of Y_c , VDM_c , and TDM_c were determined for different palm ages (Table 20).

As expected, cumulative requirements for vegetative growth (VDM_c) are higher in SER than in RER palms, mainly because the latter group stabilised at lower values. Because TDM_c was higher in the RER palms, selection for RER ideotypes resulted in a rise in carbohydrate allocated to bunch DM (Y_c). The advantage in Y_c of RER palms over SER palms is mainly bound to the period of during which the canopy closes, as expected on theoretical grounds.

Table 21 presents the LA and LAR values for the same groups of palms.

Table 21. Mean leaf area (LA) values (m^2) and leaf area ratio (LAR) values for different ages of palms selected for slow (SER) and rapid (RER) expansion. Experiments 2 and 3.

Age (years)	Experiment 2				Experiment 3			
	SER		RER		SER		RER	
	LA	LAR	LA	LAR	LA	LAR	LA	LAR
1					1.89		1.87	
2					3.84		4.18	
3					5.29		5.91	
4	5.64		6.50		5.86	2.05	6.52	2.14
5	7.18	2.11	8.09	2.26	7.72	2.16	8.90	2.36
6	8.83	2.16	9.10	2.24	8.12	2.08	8.55	2.29
7	9.69	2.14	9.16	2.13	9.51	2.06	9.06	2.12
8	10.38	2.06	9.44	1.97	10.38	2.15	9.26	2.09
9	11.33	1.96	10.26	1.85	13.64	2.41	10.89	2.20
10		1.98		1.79	13.48	2.36	11.61	2.15
11		1.96		1.79				

This Table clearly illustrates the characteristic differences in trends of LA between RER and SER palms in respect of increase in LA and its finale size. Differences in trends of LA with age are reflected in those of LAR in that RER palms showed a more downward trend than SER palms.

MAGNESIUM-STATUS AND DRY MATTER PRODUCTION

Peaslee & Moss (1966) found that rates of photosynthesis in maize leaves were closely related to magnesium (Mg-) concentrations in the leaves. W. Gerritsma (pers. com., 1987) confirmed this relationship for oil palm in West New Britain, where magnesium deficiency is very pronounced.

Most typical of magnesium deficiency symptoms in oil palm is the strong shading effect of one leaflet lying over another; the shaded portion of the lower leaflet, particularly when in proximity to the upper one, is dark green (Fig 16).

Breure (1982) scored incidence of magnesium deficiency on the oil palm leaf surface, applying a score from 0 (severe symptoms) to 5 (absence of symptoms). He found the mean score per progeny, in Expts 1 and 3, to be strongly correlated with leaf-Mg levels ($r = 0.92^{xx}$ in Expt 1 and $r = 0.82^{xx}$ in Expt 3).

Progeny differences in magnesium status are highly significant in both experiments (Breure, 1982); these results are consistent with those obtained in other crops (Epstein, 1965). Progeny leaf-Mg levels and oil yield are highly correlated ($r = +0.65^{xx}$ in Expt 1 and $r = +0.71^{xx}$ in Expt 3), but there is an absence of such relationship with vegetative growth ($r = -0.17$ in Expt 1 and $r = +0.23$ in Expt 3). The finding that leaf-Mg level is closely correlated with oil yield but not with vegetative growth is not surprising since vegetative growth has a higher priority for carbohydrates than economic yield.

Attempts to correct the severe magnesium deficiency in the West New Britain environment through soil application of magnesium containing fertilizers proved to be unsuccessful, both in respect of yield and leaf-Mg levels (Breure, 1977; Breure, 1982; Breure & Rosenquist, 1977); this indicates that magnesium absorption, by the oil palm roots, in the young volcanic soils in West New Britain is obstructed. The possibility of breeding for magnesium status, in order to increase oil yield per ha, was therefore explored. It was established, from Breure's data (1982 and 1985), that the correlation between mid-parental values of magnesium levels and those of their offspring of Expt 3 was highly significant ($r = 0.71^{xx}$); this correlation coefficient equals the heritability

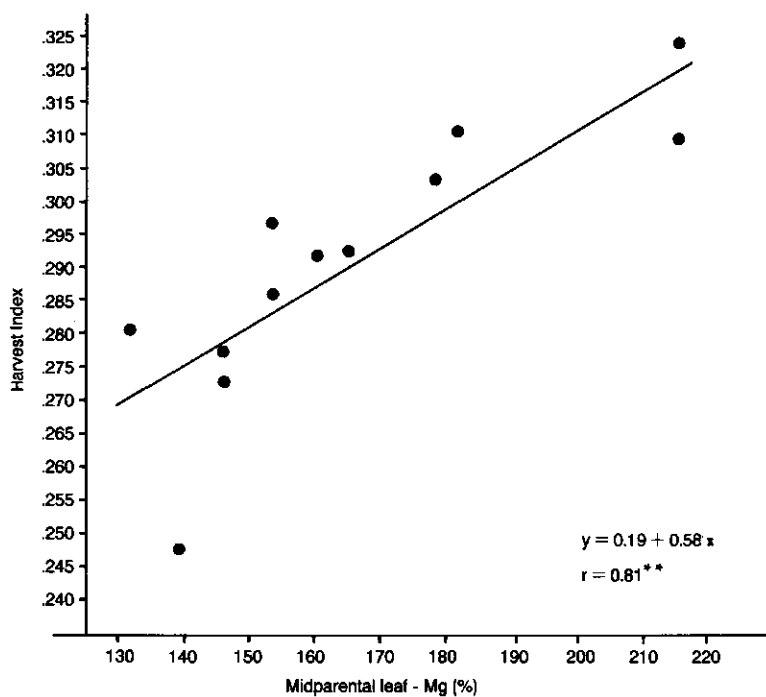
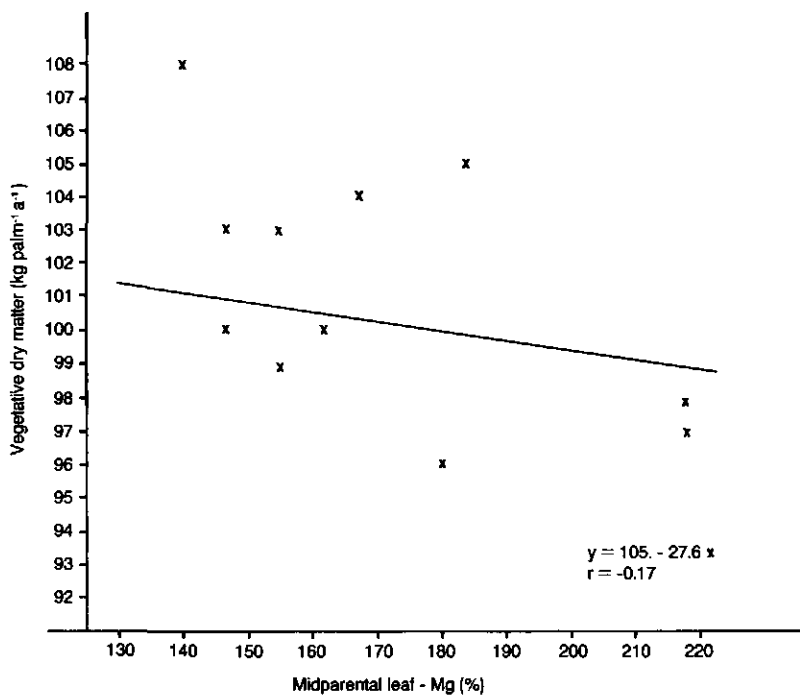


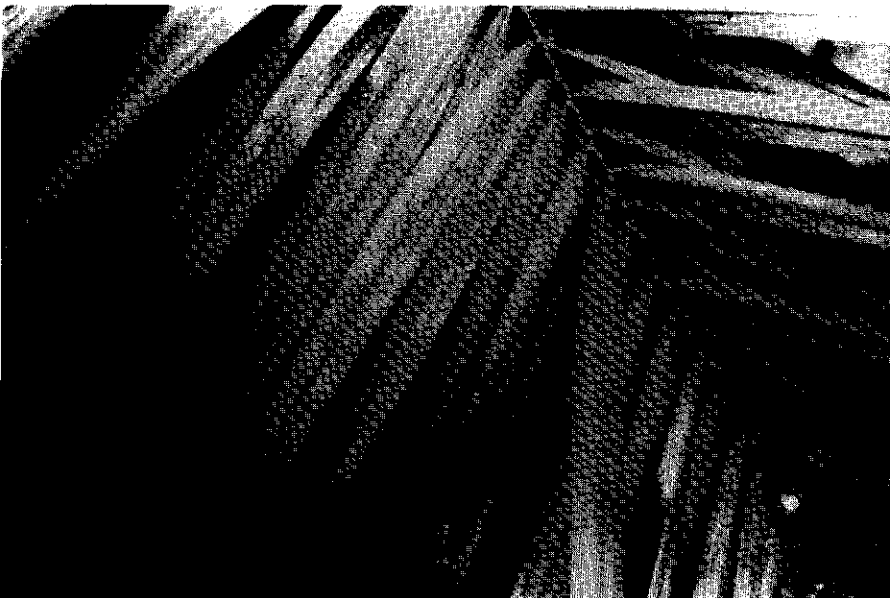
Figure 17. Relationship between midparental values of magnesium content in leaf 17 and vegetative dry matter production (\bar{x}) and Harvest Index (based on kernel and oil) (\bar{x}) of their dura x pisifera offspring. Twelve pisifera crossed each onto a set of four dura palms (Expt 3)

in standard units (Frey & Horner, 1957). The high heritability of magnesium status could be confirmed in other progeny experiments at Dami (Breure et al, 1982), and are consistent with heritability values reported by Tan & Rajaratnam (1978).

Breure (1986) tested the feasibility of indirect selection for magnesium status of both parents on yield and BI of their offspring by employing a step-wise multiple regression analysis in which parental values of leaf-Mg were included as a secondary variable (in addition to LAR and Sex ratio). Breure's analysis showed that 80% of the variance for bunch yield of the offspring is exclusively accounted for by leaf-Mg levels of both the dura and pisifera parents. He further showed, that leaf-Mg of the pisifera parent explained 66% of the variance of the BI of the offspring.

The benefit of selection for magnesium status is demonstrated in Fig 17, where the relationships between mid-parental leaf-Mg levels of Expt 3 and both Harvest Index (oil + kernel yield to total dry matter produced) and vegetative DM production are depicted. Figure 17 shows a very good relationship between mid-parental Leaf-Mg levels and Harvest Index, but a complete absence of a relationship with vegetative growth.

Selection for high leaf-Mg level is therefore of paramount importance when magnesium deficiency is at issue.



CONCLUSIONS

Fruit bunch yield appears to have a low priority in the carbon budget. Minimum requirements for maintenance respiration and vegetative growth are met first. It is only at a certain threshold carbohydrate level of the palm that bunch production starts; above this critical amount, additional carbohydrate is almost exclusively allocated to economic yield. Therefore measures which increase the supply of carbohydrate from the leaf surface (source activity) and those which reduce requirements for maintenance respiration and vegetative growth, directly benefit yield of oil.

Source of carbohydrate

At the moment of field planting, the green leaf surface, and thus photosynthetic production, is still insufficient to reach the required threshold carbohydrate level for the start of bunch production. Some measures to reduce this immature period, i.e. during which carbohydrate is exclusively allocated to maintenance respiration and vegetative growth, have been explored in the present study.

Selection for speed of leaf expansion, i.e. for so-called Rapid Expansion Rate (RER) ideotypes, appears to be one of the most promising methods. Considerable differences are found in trends of crown expansion. The quickest way to explore this variability seems through clonal propagation. Ortets (the seedling palm from which tissue is collected with a view of the production of clonal plants) with a wide range of parameters describing the expansion of the crown (ER and $t_{0.95}$ should be tested. Apart from testing whether selection for trends in crown expansion is feasible, such trials should serve to confirm the benefits of selection for RER ideotypes.

Another method of improving speed of ground coverage appears to be selection for tolerance to crown disease (Breure & Soebagyo, in prep.). Logically, photosynthetic production per unit ground area, and thus early yield, can also be increased by maintaining a healthy green leaf surface; this is particularly relevant prior to canopy closure when the leaf surface is still fully exposed to sunlight. In the environment

of the present study, magnesium deficiency is very pronounced; and selection for high leaf-Mg levels appears to be an efficient way to increase yield (Breure et al, 1982; Breure et al, 1987); moreover, several trials have shown that application of magnesium containing fertilizers is unsuccessful (Breure & Rosenquist, 1977; Breure, 1982). Recently, it has been shown that differences in leaf-Mg levels between progenies can already be detected in the nursery, and screening of progenies for magnesium status at the nursery stage appears to be feasible. This means that a higher number of progenies must be observed in the nursery than actually required for field planting. A suitable crossing scheme should be adopted to establish breeding values for leaf-Mg level in the nursery, with two important advantages: first, only crosses derived from palms with high breeding values would be selected for field planting, and, second, elite mother palms can be selected for further breeding. More research is required to test the efficiency of nursery selection on the basis of leaf-Mg.

Another way to increase the supply of carbohydrate per unit leaf surface may be selection for increased photosynthetic production at light saturation. There are clear indications of pronounced differences between progenies (W. Gerritsma, pers. com., 1987); and the recently developed carbon dioxide portable gas analysers appear to be suitable for routine measurements in the nursery. The relationship between measured gross assimilation rate in the nursery and yield potential should be studied, for example, on crosses with known yield performance.

Equally promising seems selection for reduced leaf maintenance respiration. Recently, Irving and Silsbury (1986) tested three different methods of measuring maintenance respiration and one of them, the so-called "dark decay method", looks of considerable interest for application in oil palm nurseries.

The present study showed that measures which improve light distribution over the leaf surface would increase photosynthetic production and thus oil yield, following the stage at which the canopy is closed. The most critical period seems to be shortly after canopy closure, when there is an excessive interception by the top layer of the canopy.

Further selection for canopy structure looks promising. This can be evaluated by determining the extinction coefficient (k). Ideally, ideotypes should be developed with leaves in a horizontal plane prior to canopy closure (high k -values) and erect leaves when the canopy is closed (low k -values). The former will lead to increased light interception, while low values will improve light distribution (C.J.T. Spitters, pers. com., 1987).

The occurrence of periods of poor light distribution, at the end of crown expansion, appears to lead to a dip in optimal density for current yield. An important implication is that optimal density is apparently higher than that derived by the conventional method, i.e. based on yield data assembled during the period of crown expansion (9 or 10 years from field planting), as suggested by Corley (1976c).

Excessive interpalm competition might also be diminished by selection for reduced period of leaf expansion. As mentioned earlier, this should be combined with rapid crown expansion; both objectives can be achieved by selection for so-called RER ideotypes.

Sink activity

In view of the low priority of carbohydrate allocated to bunch dry matter, reduction of competitive sinks must directly benefit yield.

The most important progress can probably be achieved by reducing leaf maintenance respiration; as mentioned, direct measurements appear possible to screen progenies in the nursery.

Selection for a more favourable distribution of carbohydrate between vegetative and generative growth (high BI) is another promising method to increase yield per ha. There appears to be not much scope for direct selection for BI. Therefore, selection should concentrate on secondary characters having a higher heritability than BI. Such characters are leaf Mg-level and increased proportion of photosynthetic tissue to total vegetative growth, i.e. selection for high leaf area ratio (LAR). This is not surprising because both characters increase photosynthetic tissue without affecting requirements for vegetative growth.

On the other hand, the potential sink size of bunch production should be fully exploited. Adequate pollination is clearly the most obvious method. Great progress has been made through the introduction of pollinator insects; however, research is justified to reduce presently observed seasonal fluctuations in efficiency. These may be confounded with seasonal differences in fruiting activity (Breure & Corley, in prep.); this can only be properly studied by comparing fruit set, under insect pollination, at different levels of fruit bunch removal (castration).

Results of the castration trial described in this study clearly demonstrate that if the sink size for bunch production is reduced, vegetative growth will be increased. Therefore, castration of early inflorescences, a standard practice in many countries, should be kept to a minimum; this particularly applies to environments which are favourable for vegetative growth.

Carbohydrate supply and components of yield

The detailed description of inflorescence development (van Heel et al, 1987) provided a sound basis for predicting the approximate stage at which most of the components of bunch yield are determined. By using this description as a basis, the stage of determination of most of the yield components could be identified. The hypothesis is put forward that developmental stages do not change very much between environments; differences in time-lag between determination of components and anthesis probably depend mainly on speed of inflorescence development.

Our study indicates that a change in carbohydrate status is more critical for those components which are determined in an advanced stage of inflorescence development; these components are, for example, frame weight and floral abortion. On the other hand, sex ratio and flowers per inflorescence, determined at an earlier developmental stage, appear to be more tolerant to changes in the supply of carbohydrate. The strong increase in number of flowers per inflorescence due to decreasing planting density is of considerable interest for seed production. Thinning or heavy pruning of palms

surrounding selected seed parents may increase seed production per palm by 15% with two important advantages: first, the same output of seed can be obtained from a reduced number of palm which permits the discarding of a number of lower grade seed palms and, secondly, height increment will be reduced which increases the productive life of a seed garden.

Although this study of the effect of carbohydrate supply on components of bunch yield may contribute to further improvement of the first attempt at a computer simulation of oil palm growth and yield (van Kraalingen, Breure and Spitters, in prep.), the most important conclusion of the present thesis is that there is apparently great scope for ideotype selection in oil palm.

SUMMARY

This thesis reports on the factors relevant to the allocation of assimilates to oil palm bunch dry matter (DM) production, based on an extensive set of growth and yield records from experiments in Papua New Guinea and Malaysia.

Basically, assimilates from gross assimilation of the canopy are first used for maintenance of existing biomass (maintenance respiration). The remaining assimilates are converted into structural DM production. Carbohydrate requirements for components of DM production are derived from conversion factors based on the biochemical composition of the DM. Maintenance respiration is estimated as the difference between gross photosynthetic production, derived from the assimilation light response curve of individual leaves, and the amount of carbohydrate required for DM production. About 50% of total gross assimilation is lost in maintenance respiration; losses appear to be more related to growth rate than to the amount of existing biomass.

The allocation of assimilates to bunch DM production has a low priority in the carbon budget. Thus bunch production starts when certain minimum requirements of assimilates for maintenance respiration and vegetative growth have been met; above this critical value additional assimilates are virtually all utilized for economic yield. This implies that yield will benefit greatly from measures which increase photosynthetic production. Further, that yield will respond strongly to a reduction in internal competition, in terms of assimilates, from vegetative growth and maintenance respiration.

This thesis shows that the efficiency of converting intercepted radiation into carbohydrates for dry matter production decreased with the expansion of the crown leaves, which might be linked to the resulting increase in maintenance respiration losses. These losses were apparently not compensated by an increase in photosynthetic production. The efficiency increased again when crown expansion was complete, which appears to be due to improved light distribution consequent on an observed increment in light penetration. These effects of changing levels of interception and distribution of sunlight

on efficiency were more pronounced as the planting density increased, and resulted in marked differences in yield trends with age between densities. The end result was a decrease in optimum density for current yield until 12 to 13 years from planting, followed by a strong increase. It is concluded that optimal density for cumulative yield might be increased by measures which optimize the balance between light interception by and distribution of light over the foliage. The response of improved light distribution would be enhanced by selection for net assimilation rate of the leaves.

Palms differ considerably in rate of leaf expansion. As expected, this is reflected in total DM production per palm, which to a great extent benefits bunch yield.

DM production per palm was also increased through reducing the incidence of deficiency of magnesium, an essential component of the chlorophyll molecule; again, the benefit is mainly obtained in oil yield. Selection for high magnesium status is feasible and appears to be an efficient way to increase oil yield.

Increasing bunch yield, at a certain level of DM production, implies reducing requirements for vegetative growth (increase of the Bunch Index). Ideally, a reduction in vegetative DM production should be restricted to non-photosynthesizing tissue. This aim can be achieved by selection for high leaf area ratio (LAR), defined for this crop as the ratio of new leaf area produced to new dry matter used for vegetative growth. Another method might be to reduce the period of crown expansion subsequent to canopy closure; from this stage onwards, no further increase in gross assimilation occurs but additional crown expansion continues to increase requirements for vegetative growth and maintenance respiration. Therefore, speed of crown expansion should be combined with a reduction in crown expansion time. These two objectives can be achieved by selection for so-called rapid expansion (RER) ideotypes, i.e. a high ratio of leaf area at maximum expansion rate and a relatively low final size.

The observation that palms selected on the basis of increased light interception and reduced vegetative requirements do indeed have higher BI, indicates that selection for ideotypes

(defined as biological models which are expected to perform or behave in a predictable manner within a defined environment), is feasible. This finding justifies exploring other methods which, through manipulation of the carbon budget, would increase assimilates available for bunch dry matter production. Selection for increased photosynthetic production at light saturation, and also for reduction of leaf maintenance requirements, may be rewarding. Screening of progenies in the nursery on the basis of increased photosynthetic production of the leaf surface and for reduced maintenance respiration, as well as for leaf-Mg level and LAR, may be possible.

To permit large scale testing of the response of yield to ideotype selection, a method to improve the conventional time-consuming method of growth recording is proposed. The main finding is that rate of leaf production, which is the key for an instant method of growth recording, can be obtained by counting the leaf bases on the trunk. The proposed, so-called "one-shot" method of growth recording, in particular, resulted in an efficient selection of progenies on the basis of BI.

In addition to vegetative growth and maintenance respiration, the development of bunches competes with inflorescence primordia for carbohydrates. Fruiting activity also, to a certain extent, competes with vegetative growth. Thus if the potential sink size for fruit bunch production is not fully utilized, palms tend to produce excessive vegetative growth. A direct implication is that adequate pollination is essential, as could be demonstrated by comparing vegetative growth of similar planting material under poor and adequate assisted pollination.

The supply of carbohydrate affects all the components which determine the number of bunches (sex ratio, abortion, and leaf production) and those which determine their mean weight. The latter can be divided into the frame (stalk and empty spikelets) and the fruit (the product of spikelet number, flower number per spikelet, fruit set and the mean weight of individual fruits). The number of flowers per spikelet and sex are both determined just prior to spikelet initiation. For floral abortion the critical stage is at the onset of rapid expansion of the inflorescences, about 10 leaves prior to

anthesis. It was also at this stage that the first response of frame weight to carbohydrate supply was observed. The weight of the frame is further affected at two earlier developmental stages: first, when the central axis ceases to be meristematic and, second, just prior to spikelet initiation. The latter stage, which is about two years before harvest, is thus the most important stage in inflorescence development in that here key components of bunch yield are affected by the supply of carbohydrate.

An analysis of components of oil yield at different spacings (varying levels of carbohydrate supply) showed that components which are determined at an advanced stage in inflorescence development (floral abortion and stalk weight) are more sensitive to changes in carbohydrate supply than those determined at an earlier developmental stage (sex ratio and number of flowers per spikelet). These findings are supported by an analysis of response of yield components to different levels of fruit bunch removal (disbudding). Moreover, in respect of abortion, it appears that initial response to shortage of carbohydrate mainly decreases the number of female inflorescences; if this shortage is prolonged both sexes abort.

Insect pollination, which replaced the method of assisted pollination in the course of this study, appears to have increased optimal planting density by at least 5 palms per ha. This finding is derived from a measured increase in extraction of oil and kernels in response to planting density, and from a decrease in vegetative growth due to, as mentioned earlier, an increase in sink strength of the fruits.

SAMENVATTING

In dit proefschrift staat centraal dat de opbrengst van een gewas de resultante is van de hoeveelheid koolhydraten die in het fotosyntheseproces wordt gevormd en het deel hiervan dat ten goede komt aan de economisch gewenste plantendelen. Op een gewasfysiologische wijze beoogt dit proefschrift de factoren te bepalen die in de oliepalm de omvang van de koolhydratenstroom naar de vruchttrossen verbeteren.

Daartoe zijn gedurende 15 jaar gedetailleerde groei en opbrengstgegevens verzameld in experimenten met oliepalm in Papua Nieuw Guinea en Maleisië. Het betreft onder andere metingen die leiden tot een schatting van het fotosynthetiserende bladoppervlak en van de vegetatieve drogestofproductie. Daarnaast wordt de wijze waarop de groei op niet-destructieve wijze werd gemeten uiteengezet.

Het proefschrift introduceert een eenvoudig model waarmee de omvang en de verdeling van de assimilatenstroom van het gewas wordt beschreven. Het uitgangspunt is dat een gedeelte van de assimilaten, gevormd in het fotosynthese proces, wordt gebruikt voor het onderhoud van de aanwezige biomassa (onderhoudsrespiratie). De resterende assimilaten worden omgezet in (structureel) plantmateriaal. Deze hoeveelheid, met inbegrip van het gedeelte dat als groeirespiratie verloren gaat, wordt afgeleid uit de chemische samenstelling van het eindprodukt.

Onderhoudsrespiratie is volgens het model het verschil tussen berekende totale gewasfotosynthese en de hoeveelheid fotosynthesesuikers die nodig is voor de vorming van de gemeten hoeveelheid structureel plantmateriaal. Het blijkt dat ongeveer 50% van de totale gewasfotosynthese ten deel valt aan onderhoudsrespiratie; deze hoeveelheid houdt meer verband met de groeisnelheid van de palm dan met de hoeveelheid biomassa die onderhouden moet worden. Deze studie maakt aannemelijk dat vooral het onderhoud van het bladoppervlak van de palm daaraan debet is.

Het proefschrift toont aan dat van de assimilaten voor drogestofproductie, alleen de overschotten aan de vruchttrossen toegewezen worden. Zo begint de assimilatenstroom naar de

trossen pas op gang te komen als aan een bepaalde minimum behoefte voor onderhoudsrespiratie en vegetatieve groei is voldaan. Boven deze kritieke drempelwaarde komt de assimilatenstroom echter vrijwel geheel ten goede aan de trosproduktie. Dit houdt in dat wanneer dit minimum niveau bereikt is, de trosproduktie vooral afhankelijk is van maatregelen die leiden tot verdere verhoging van de gewasfotosynthese. Aldus hangt trosopbrengst sterk af van de fotosynthesesnelheid alsmede van het behoefteniveau van onderhoudsrespiratie en vegetatieve groei.

Het proefschrift richt zich vervolgens op de omzetting van het door de bladeren onderschepte licht in assimilaten die beschikbaar komen voor drogestofproduktie. De efficiëntie waarmee dit gebeurt neemt af met de toename van het bladoppervlak, hetgeen verband zou kunnen houden met de extra onderhoudsrespiratie die deze toename vergt. De kosten van onderhoud van het extra blad worden kennelijk onvoldoende gecompenseerd door een toename van gewasfotosynthese welke met de vergroting van het bladoppervlak gepaard gaat. Oudere palmen, daarentegen, laten na verloop van tijd een verhoogde efficiëntie zien. Dit lijkt een gevolg te zijn van een progressieve verbetering van de lichtverdeling over het bladoppervlak met leeftijd. Deze veronderstelling is gebaseerd op de gemeten afname van lichtonderschepping van het bladerdek. De mate waarin de veranderingen van lichtonderschepping en lichtverdeling in het bladerdek optreden, zijn meer uitgesproken naarmate de plantdichtheid toeneemt, hetgeen zich manifesteerde in duidelijke verschillen in het verloop van de opbrengst tussen de plantdichtheden als functie van de leeftijd van de palm. Het eindresultaat was een aanvankelijke afname in optimale plantdichtheid tot 12 à 13 jaar na het planten, gevolgd door een sterke toename van de optimale dichtheid in oudere palmen.

De conclusie van het proefschrift is, derhalve, dat de plantdichtheid welke de hoogste cumulatieve opbrengst geeft over de totale produktieperiode verhoogd zou kunnen worden door het juiste evenwicht te vinden tussen opvang en verdeling van het licht. Dit zou, bijvoorbeeld, bereikt kunnen worden

door de verschillen in lengtegroei van de stam tussen palmen in een aanplant te verhogen, waardoor meer diepte in het bladerdek wordt verkregen. Het effect daarvan op gewasfotosynthese zal waarschijnlijk nog geprononceerder zijn als daarnaast nog wordt veredeld op de fotosynthese snelheid van individuele bladeren.

De studie laat zien dat palmen verschillen in magnesium status en dat drogestofproduktie en vooral opbrengst, verband houden met het magnesiumgehalte. Dit is niet verwonderlijk, want magnesium is een essentieel bestanddeel van het chlorofylmolecuul dat een rol speelt in de fotosynthese. Het selecteren op verhoging van het magnesiumgehalte is goed mogelijk en blijkt een doeltreffende methode te zijn om de opbrengst te verhogen.

Verhoging van de trosopbrengst, bij een gegeven assimilaten toewijzing aan de totale droge stof, betekent een vermindering van de vegetatieve groei (verhoging van de zogenaamde "trosindex"). Om aan de voorwaarde van het op peil houden van de assimilatenvoorziening te voldoen, moet de afname van de vegetatieve groei zoveel mogelijk beperkt blijven tot het niet-fotosynthetiserende gedeelte van de palm. In de terminologie van dit proefschrift betekent dit een verhoging van de "leaf area ratio" (LAR), een parameter die voor dit gewas wordt gedefiniëerd als de verhouding van het nieuw gevormde bladoppervlak tot het nieuw gevormde vegetatief materiaal. Dit is vooral van belang in een nog niet gesloten, jonge aanplant, waar verhoging van het bladoppervlak leidt tot verhoging van de lichtopvang.

Behalve door selectie op LAR, kan verbetering van lichtopvang- onder minimale toename of stilstand van vegetatieve groei- worden verwezenlijkt door de periode van kroonexpansie te bekorten (snelle sluiting van het gewas) en de uiteindelijke bladgrootte zelf geringer te laten zijn (reductie van het niet-fotosynthetiserende gedeelte van het blad). Na de sluiting van het bladerdek heeft de gewasfotosynthese namelijk zijn maximale capaciteit bereikt. Elke toename van het bladoppervlak daarna leidt tot een nadelige verhoging van de

assimilatenbehoefte voor onderhoudsrespiratie en vegetatieve groei, hetgeen ten koste gaat van de tros opbrengst. Dus, na gewassluiting moeten de kroonbladeren zo min mogelijk uitgroeien. Kortom, men moet een type palm ontwikkelen waarvoor geldt dat de optimale plantdichtheid voor cumulatieve opbrengst zo snel mogelijk na het tijdstip van aanplanten is bereikt; anderzijds, moet een opbrengstafname, welke gewoonlijk optreedt na gewassluiting, zoveel mogelijk beperkt blijven. Het proefschrift toont aan dat die tweevoudige wens verwezenlijkt kan worden door selectie voor een zogenaamde "Rapid Expansion Rate" (RER) ideotype. Een dergelijk type boom is gekarakteriseerd door een snelle toename van het bladoppervlak dat echter op een relatief lage waarde uitkomt. Het proefschrift heeft kunnen aantonen dat palmen die geselecteerd zijn op verhoogde lichtopname- onder minimale toename van vegetatieve groei- inderdaad een verhoging van de trosindex vertonen. Daarmee bewijst het proefschrift dat selectie voor een bepaald ideotype (omschrijving van een ideaal gewastype ten aanzien van biologische kenmerken) realiseerbaar is; met andere woorden, doeltreffende manipulatie op het vlak van gewasfotosynthese en van de verdeling van de assimilatenstroom binnen de plant werkt opbrengst verhogend. De meest belovende eigenschappen voor verdere selectie zijn verhoging van bladfotosynthese en verlaging van de onderhoudsrespiratie, tezamen met een hoger magnesiumgehalte van het blad.

Er zijn echter een groot aantal proeven nodig om de eigenschappen van een bepaald ideotype te toetsen. Ten einde het aantal waarnemingen te reduceren en daarbij de mogelijkheid openlatend om in een gevorderd stadium van de proeven nog op vegetatieve groei te selecteren, bepleit dit proefschrift een verkorte, zogenaamde "one-shot" methode van groeiwaarnemingen. Basaal hierbij is dat bladproduktie, over een bepaalde periode, zich betrouwbaar laat schatten door het tellen van het aantal afgesnoeide en niet-afgesnoeide bladeren. De "one-shot" methode is met name betrouwbaar voor de bepaling van de trosindex, die in dit proefschrift beschouwd wordt als de belangrijkste eigenschap om op te selecteren.

Behalve vegetatieve groei en onderhoudsrespiratie, oefenen

zich ontwikkelende trossen een zekere zuigkracht uit op de assimilatenstroom binnen de palm. Dit wordt "fruiting activity" genoemd. De zich ontwikkelende trossen wedijveren met vegetatieve groei om de aangevoerde assimilaten. Wanneer de zuigkracht van de trossen niet op een bepaalde sterkte wordt gehouden, worden assimilaten gebruikt voor extra vegetatieve groei in plaats van trosproductie. Vanuit een economisch gezichtspunt is het dus belangrijk trossen met een goede vruchtzetting te krijgen door maatregelen die leiden tot efficiënte bestuiving. Dit betekent dat de insekten populatie voor de bestuiving op zo'n hoog mogelijk peil moet blijven.

Vrijwel alle componenten die tot de economische opbrengst van de palm bijdragen reageren, in meerdere of mindere mate, op de hoeveelheid beschikbare koolhydraten. Dit proefschrift gaat het effect na van de assimilatenvoorziening op die componenten, welke het aantal trossen bepalen. Deze componenten zijn het percentage van de gedifferentieerde bloeiwijzen dat vrouwelijk is (en zo hoog mogelijk moet zijn) en het percentage van de bladoksels met geaborteerde bloeiwijzen (waarvoor een zo laag mogelijke waarde wordt nagestreefd). Daarnaast zijn er componenten die bijdragen tot het gewicht van de trossen. Naast het frame van de bloeiwijze hangt dit af van het gewicht van de vruchten, welke op hun beurt weer bepaald worden door het aantal aartjes, het aantal bloempjes per aartje, de vruchtzetting en het gemiddeld gewicht van de vrucht. Allereerst beschrijft het proefschrift in welke stadium van de ontwikkeling van de bloeiwijze de componenten aangelegd worden. Daarbij werd gebruik gemaakt van een aanplant met hoge plantdichtheid waarin de lichthoeveelheid door middel van uitdunnen werd verhoogd. Daarnaast werden de ontwikkelingsstadia van de bloeiwijze aan de hand van genummerde bladeren geregistreerd (door ontleding van de gevelde palmen). Het stadium waarop deze ingreep aanslaat (in termen van verhoogd aantal en/of gewicht der componenten) is kritisch voor het stadium waarop een component bepaald wordt, aldus de operationele definitie gebruikt in dit proefschrift. Het bleek dat het aantal bloempjes per aartje en het geslacht van de bloeiwijze beide in ongeveer hetzelfde stadium vastliggen. Dit is enige bladeren voor het zichtbaar worden van de eerst aartjes. Abortie van bloeiwijze

grijpt aan op het moment dat de bloeiwijze het stadium van snelle groei bereikt heeft (ongeveer tien bladeren voor de bloei). Dit is tevens het eerste stadium in de ontwikkeling dat het frame reageert op dunning. Deze opbrengstcomponent blijkt verder afhankelijk te zijn van de mate van meristematische activiteit ter hoogte van de apex in de hoofdas van de bloeiwijze (tweede stadium); daarvoor reageert het frame, in het derde stadium, in samenhang met het aantal bloempjes per bloeiwijze.

De dissertatie handelt tenslotte over het gevolg van toename van de plantdichtheid (verdeling van totale gewasfotosynthese over een groter aantal palmen) op de eerder genoemde opbrengstcomponenten. De analyse toonde aan dat die componenten, welke in een later stadium in de ontwikkeling van de bloeiwijze vastliggen - te weten het frame en abortie van bloeiwijzen - meer gevoelig zijn voor de assimilatenvoorziening dan die welke in een vroeger stadium vastliggen, met name het aantal bloemetjes per bloeiwijze en het geslacht. Dit resultaat werd bevestigd in een castratie proef (manipulatie van fruiting activity). Variatie in de assimilatenvoorziening lijkt niet alleen door te werken op de mate van abortie maar ook op die van het geslacht van de geaborteerde bloeiwijze. Bij het reduceren van de toevoer van assimilaten aborteren in eerste instantie alleen vrouwelijke bloeiwijzen, maar bij een meer acuut tekort aborteren ook de manlijke bloeiwijzen.

Het gebruik van insecten voor de bestuiving, dat in de loop van het onderzoek de methode van kunstmatige bestuiving verving, bleek een verhoging van de optimale plantdichtheid tot gevolg te hebben van tenminste vijf palmen per ha. Deze nieuwe waarde werd afgeleid uit een verhoging van het percentage olie en palmpitten per tros, en een vermindering van de vegetatieve groei als gevolg van de eerder genoemde vergroting van de zuigkracht van de trossen voor assimilaten, dientengevolge waarvan de lichtconcurrentie tussen de palmen afneemt. Er is nog ruimte voor verdere verhoging van de optimale plantdichtheid; wellicht komt als volgende factor veredeling op verhoging van de trosindex in aanmerking, zoals een nader onderzoek, buiten het kader van dit proefschrift, zal aantonen.

REFERENCES

- AMTHOR, J.S. (1984). The role of maintenance respiration in plant growth. Plant, Cell and Environment, **7**, 561-569.
- BJÖRKMAN, O. (1981). Responses to different quantum densities. Encyclopedia of Plant Physiology New Series, Springer-Verlag, Berlin **12A**, 57-107.
- BLAAK, G., SPARNAAIJ, L.D. & MENENDEZ, T. (1963). Breeding and inheritance of the oil palm. Part II. Methods of bunch quality analysis. Jl W. Afr. Inst. Oil Palm Res., **4**, 145-155.
- BREURE, C.J., (1977). Preliminary results from an oil palm density x fertilizer experiment on young volcanic soils in West New Britain. In D.A. Earp & W. Newall (Eds.), International developments in oil palm (pp 192-207). Kuala Lumpur, Incorporated Society of Planters.
- BREURE, C.J. (1982). Factors affecting yield and growth of oil palm tenera in West New Britain. Oléagineux, **37**, 213-227.
- BREURE, C.J. (1985). Relevant factors associated with crown expansion in oil palm (Elaeis guineensis Jacq.), Euphytica, **34**: 161-175.
- BREURE, C.J. (1986). Parent selection for yield and bunch index in the oil palm in West New Britain, Euphytica, **35**: 65-72.
- BREURE, C.J. (in press a) The effect of palm age and planting density on the partitioning of assimilates in oil palm (Elaeis guineensis Jacq.).
- BREURE, C.J. (in press b). the effect of different planting densities on yield trends in oil palm.
- BREURE, C.J., & CORLEY, R.H.V. (1983). Selection of oil palms for high density planting. Euphytica, **32**, 177-186.
- BREURE, C.J., & CORLEY, R.H.V. Fruiting activity and yield of oil palm. II. Observations in an untreated population, submitted.
- BREURE, C.J., KONIMOR, J., & ROSENQUIST, E.A.R. (1982). Oil Palm selection and seed production at Dami Oil Palm Research Station, Papua New Guinea. Oil Palm News, **26**, 6-22.
- BREURE, C.J. & MENENDEZ, T. The determination of the components of bunch yield in the development of inflorescences in oil palm (Elaeis guineensis Jacq.). I Bunch number components, submitted a.
- BREURE, C.J. & MENENDEZ, T. The determination of the components of bunch yield in the development of inflorescences in oil palm (Elaeis guineensis Jacq.). II. Bunch weight components, submitted b.

BREURE, C.J. & MENENDEZ, T. The timing of the response of rate of leaf production to light competition in oil palm, submitted c.

BREURE, C.J., MENENDEZ, T., & POWELL, M.S. The effect of planting density on the components of bunch yield in oil palm (Elaeis guineensis Jacq.), submitted.

BREURE, C.J. & POWELL, M.S. (1987, June). The one-shot method of establishing growth parameters in oil palm. Paper presented at the 1987 International Oil Palm Conference, Kuala Lumpur, Malaysia.

BREURE, C.J. & ROSENQUIST, E.A.R. (1977). An Oil Palm fertilizer experiment on volcanic soils in Papua New Guinea. Oléagineux, 32, 301-310.

BREURE, C.J., ROSENQUIST, E.A.R., KONIMOR, J., & POWELL, M.S. (1987). Oil Palm Introductions to Papua New Guinea and the Formulation of Selection Methods at Dami Oil Palm Research Station. Worksp. Proc. Palm Oil Res. Inst. Malaysia, 10, 189-197.

BREURE, C.J. & SOEBAGYO, F.X. The influence of genetic composition, nutrition and location on crown disease of oil palm (Elaeis guineensis Jacq.) and the effect of the disease on growth and yield, submitted.

CORLEY, R.H.V. (1973). Effect of planting density on growth and yield of the Oil Palm. Expl. Agric., 9, 169-180.

CORLEY, R.H.V. (1976a). Photosynthesis and Productivity. In R.H.V. Corley, J.J. Hardon & B.J. Wood (Eds.), Oil Palm Research (pp 273-283), Amsterdam, Elsevier.

CORLEY, R.H.V. (1976b). Inflorescence abortion and sex differentiation. In R.H.V. Corley, J.J. Hardon & B.J. Wood (Eds.), Oil Palm Research (pp 37-55), Amsterdam, Elsevier.

CORLEY, R.H.V. (1976c). Planting Density. In R.H.V. Corley, J.J. Hardon & B.J. Wood (Eds.), Oil Palm Research (pp 273-283), Amsterdam, Elsevier.

CORLEY, R.H.V. & BREURE, C.J. (1981). Measurements in oil palm experiments (Internal Report), London, Unilever Plantation Group, 35pp.

CORLEY, R.H.V. & BREURE, C.J. Fruiting activity and yield of oil palm. I. Experiments with fruit removal, submitted.

CORLEY, R.H.V. & GRAY, B.S. (1976). Yield and yield components. In R.H.V. Corley, J.J. Hardon & B.S. Wood (Eds.), Oil Palm Research (pp 77-89). Amsterdam, Elsevier.

CORLEY, R.H.V., HARDON, J.J. & OOI, S.C. (1973). Some evidence for genetically controlled variation in photosynthetic rate of oil palm seedlings. Euphytica, 22, 48-55.

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

EHLERINGER, J., & PEARCY, R.W. (1983). Variation in quantum yield for CO₂-uptake among C₃ and C₄ plants. Plant Physiol., 73, 555-559.

EPSTEIN, E. (1972). Mineral nutrition of plants: Principles and Perspectives (pp 412). New York, Wiley.

FREY, K.J. & HORNER, T. (1957). Heritability in standard units. Agron. J., 49, 59-62.

GRAY, B.S. (1969). A study of the influence of genetic, agronomic and environmental factors on the growth, flowering and bunch production of the oil palm on the West Coast of Malaysia. Ph.D. Thesis, University of Aberdeen, 947 pp.

GOUDRIAAN, J., & VAN LAAR, H.H. (1978). Calculation of daily total of the gross CO₂ assimilation of leaf canopies. Neth. J. of Agric. Sci., 26, 373-382.

HARDON, J.J. (1976). Oil Palm Breeding. In R.H.V. Corley, J.J. Hardon & B.S. Wood (Eds.), Oil Palm Research (pp 89-107), Amsterdam, Elsevier.

HARDON, J.J., CORLEY, R.H.V. & OOI, S.C. (1972). Analysis of growth of the oil palm. II. Estimation of genetic variances of growth parameters and yield of fruit bunches. Euphytica, 21, 257-264.

HARDON, J.J., WILLIAMS, C.N. & WATSON, I. (1969). Leaf area and yield in the oil palm in Malaysia. Expl. Agric., 5, 25-52.

HEEL, van W.A., BREURE, C.J. & MENENDEZ, T. (1987). The early development of inflorescences and flowers of the oil palm (Elaeis guineensis Jacq.) seen through the scanning electron microscope. Blumea, 32, 67-78.

HENRY, P. (1960). Recherches cytologiques sur l'appareil floral et la grain vez Elaeis guineensis et Cocos nucifera. I. La formation de l'appareil floral. Rev. gén. Bot., 68, 111-132.

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

KRAALINGEN, van D.W.G., BREURE, C.J. & SPITTERS, C.J.T. Simulation of oil palm growth and yield, submitted.

LANTINGA, E.A. (1985). Productivity of grasslands under continuous and rational grazing (pp 61). Thesis, University of Wageningen.

MONTEITH, J.L. (1973). principles of environmental physics (pp 241). Edward Arnold, London.

MULLER, A. (1969). Volcanic ash soils. Tropical Abstracts 24, 353-358.

PEASLEE, D.E. & MOSS, D.N. (1966). Photosynthesis in K- and Mg- deficient maize (Zea mays L.) leaves. Soil Sci. Soc. Amer. Proc. 30, 220-223.

PREVOT, P. & DUCHESNE, J. (1955). Densités de plantation pour le palmier à huile. Oléagineux, 10, 117-122.

RAMACHANDRAN, P., NARAYANAN, R. & KNECHT, J.C.X. (1973). A planting distance experiment on dura palms. In R.L. Wastie & D.A. Earp (Eds.), Advances in oil palm cultivation (pp 72-87). Kuala Lumpur, Incorporated Society of Planters.

SPARNAAIJ, L.D. (1960). The analysis of bunch production in the oil palm. J.W. Afric. Inst. Oil Palm Res., 2, 244-264.

SQUIRE, G.R. (1984). Light interception, productivity and yield of oil palm. Palm Oil Res. Inst. (pp 73), Malaysia unpublished manuscript.

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

SPITTERS, C.J.T. & KRAMERS, Th. (1986). Differences between spring wheat cultivars in early growth. Euphytica, 35, (in press).

STARITSKY G. & BREURE, C.J. (1985). The morphogenesis of the inflorescence of the oil palm in relation to yield components. Acta Bot. Neerl., 34, 437-438.

SZEICZ, G. (1974). Solar radiation for plant growth. J. Appl. Ecol., 11, 617-636.

TAN, G.Y. & RAJARATNAM, J.A. (1978). Genetic variability of leaf nutrient concentrations in oil palm. Crop Science, 18, 548-550.

WARINGA, N.A. (1985). Soil moisture and climate in the West New Britain Area". Agricultural University, Wageningen. Unpublished manuscript.

WILSON, D.R. (1982). Response to selection for dark respiration of mature leaves in Lolium perenne L. and its effect on growth of young plants. Ann. Bot., 49, 313-320.

Factors affecting yield and growth of oil palm *tenera* in West New Britain

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Summary. - In a $D \times P$ progeny trial, testing nine *pisifera*, progenies differed significantly in yield, growth parameters and leaf nutrient levels. Yield during the fourth to the sixth year of production was negatively correlated with vegetative growth ($r = -0.51^*$) and height ($r = -0.58^*$) while these parameters were less correlated with early yield. Progeny oil yields were positively correlated with leaf Mg-levels ($r = +0.70^{**}$). In a density \times fertiliser experiment, comparing 110, 148, 186 palms per hectare, each with four fertiliser levels (split-plot), density and fertiliser affected yield and most growth parameters significantly. Increasing light competition reduced yield response to fertilisers, but except for leaf area, did not affect growth response. Effects of N, K, P, Mg, Mn and S were studied in a quarter replicate of a $4^2 \times 2^4$ design. Potassium chloride increased yield. Potash increased kernel-to-fruit at the expense of mesocarp. High negative correlations were found between leaf Cl-levels and oil-to-wet mesocarp ratio. Intensity of pollination differed between the experiments. Improving pollination increased yield and reduced growth. VDM has a high plasticity and seems, partly, replaceable by fruit dry matter through adequate pollination. The combination of less light-competitive progenies with high Mg-levels and adequate pollination without ablation could increase yield.

In Papua New Guinea, oil palm cultivation started on a commercial scale in 1968. By 1976, about 12 000 ha were planted.

The first oil palm trials were laid down with the objective to study responses to fertilisers, to establish optimal spacing and to test *pisifera* male parents. Apart from yield, detailed records were collected for growth and other characters to gain a deeper understanding of oil palm physiology in this new environment.

Preliminary results of two trials were reported by Breure [1977] and Breure and Rosenquist [1977]. Since publishing these papers, the trials have been studied in more detail and over a longer period. It also proved possible to evaluate the effect of pollination as a separate factor.

By combined results of a factorial fertiliser experiment, a density \times fertiliser trial, and a $D \times P$ progeny trial, the effects of genetic constitution, fertilisers, spacing and the standards of assisted pollination on yield and growth of commercial *tenera* materials were studied.

MATERIALS AND METHODS

Details of experiments.

Experiment 1. An exploratory fertiliser experiment, testing N (urea), K (muriate of potash) at four levels, and P (disodium phosphate), Mg (magnesium chloride), Mn (manganese chloride), and S (sulphur) at two levels in a quarter replicate of a $4^2 \times 2^4$ factorial design was set up at Bebere Estate in 1968 at 9 m triangular spacing. A detailed description has been given by Breure and Rosenquist [1977].

Experiment 2. This is a *dura* \times *pisifera* progeny trial testing nine ex-Avros *pisifera* with four selected *Deli dura*. The fifteen progenies are arranged in randomised blocks with five replications and sixteen palms per plot. The trial was set up at Dami O.P.R.S. (1) in 1968 in a 9 m triangular spacing.

Experiment 3. This density \times fertiliser experiment tests 110, 148, and 186 palms per hectare density treatments in main plots and four levels of a mixture of muriate of potash plus kieserite in sub-plots. Treatments are arranged in randomised blocks with four replications with main plots of about 0.8 ha. The trial was set up at Dami O.P.R.S. in 1970, at triangular spacing. Full details have been given by Breure [1977].

In all trials ablation was carried out at monthly intervals during the first year of flowering, followed by assisted pollination during the entire recording period.

Recording.

The number and weight of fresh fruit bunches were recorded for individual palms at each harvesting round. Some bunches were analysed for bunch composition following the method of Blaak, Sparnaay and Menendez [1963]. Samples of Leaf 17 were taken from all palms, bulked per plot, and analysed at Banting O.P.R.S.

Growth parameters were estimated from non destructive measurements following a system developed by Hardon, Williams and Watson [1969] and Corley, Hardon and Tan [1971]. In Experiment 2 growth parameters were calculated per palm, while in Experiments 1 and 3 plot means of growth records were used.

Growth parameters were abbreviated in the text as follows:

VDM = vegetative dry matter production,
BI = bunch index,
CGR = crop growth rate,
LAR = leaf area ratio,
NAR = net assimilation rate.

Symptoms of magnesium deficiency were obtained by visual scoring of each palm using a score from 0 (severe symptoms) to 5 (absence of symptoms). Results of this scoring were averaged per plot.

Environmental conditions of experimental sites.

The soils are andosols [Muller, 1969], derived from recent volcanic deposits with little or no profile development, except for an accumulation of organic matter in the surface horizon which extends to a maximum of about 15 cm. This organic matter is, due to the near

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absence of clay, of relatively high importance since it represents nearly the only source of exchange sites. Below the sub-surface soils, buried horizons may occur. Drainage of the soils is excellent. The area had been used extensively as gardens prior to clearing of the land from heavy rain forest.

The profile of soils at Bebere Estate is more uniform than at Dami where the soils clearly show alluvial deposits of mineral and pumiceous sands washed by the Ko river which runs through the area. Soils at Bebere Estate are also richer in exchangeable K and Mg and show a higher percentage base saturation throughout the profile.

Rainfall and sunshine data of Dami O.P.R.S. are presented in Table I.

TABLE I. — Mean monthly rainfall and sunshine data Dami O.P.R.S. for 1970-1980
(Pluviosité moyenne mensuelle, et ensoleillement, à Dami en 1970-1980)

Months (Mois)	Rainfall (Pluviosité) (mm)	Raindays (Nomb. jours de pluie)	Sunshine (Ensoleillement) (h/day-h/jour)
J.	709	24	3.9
F.	653	23	3.9
M.	520	26	4.1
A.	360	21	5.1
M.	264	18	5.7
J.	128	17	6.0
J.	179	16	5.8
A.	170	15	6.2
S.	195	13	6.5
O.	179	16	6.0
N.	249	19	5.9
D.	365	21	4.7
Annual (Année)	3 971	229	5.3

TABLE II. — Progeny means for bunch yield and some growth parameters, (Experiment 2), planted 1968
(Moyennes des descendance pour la production des régimes et certains paramètres de croissance -
Expérience n° 2 - plantation 1968)

Progeny (Descendance) code	Weight (1) (Poids) (kg/palm -/arbre)	Height (Taille) 1976 (cm)	Mean annual height increment (Croissance moyenne annuelle en hauteur) (cm) (2)	Leaf area (Surface foliaire) (m ²) (2)	Rachis length (Long- ueur) (cm) (2)	VDM (MSV) (kg/palm/yr) (kg/arbre/an) (2)	BI (IR) (2)	CGR (TCC) (t/ha/yr) (t/ha/an) (2)	LAR (RSF) (2)	NAR (TAN) (gm/dm ² /week) (g/dm ² /semaine) (2)
51	196	415	80	9.62	579	107.4	0.503	31.1	2.34	0.099
52	187	402	77	9.24	554	111.2	0.488	31.4	2.20	0.102
53	185	412	80	9.44	584	112.0	0.492	31.4	2.14	0.102
54	183	430	84	9.17	580	102.6	0.496	29.8	2.30	0.098
55	174	405	78	9.31	587	123.8	0.437	31.4	1.98	0.102
56	176	468	90	9.30	554	122.2	0.427	30.7	2.05	0.099
57	153	469	89	9.53	581	123.3	0.386	29.4	2.12	0.096
58	183	447	84	9.70	586	128.4	0.434	32.4	1.98	0.107
59	157	476	92	9.86	609	135.8	0.379	31.1	2.06	0.094
60	186	427	83	9.02	568	119.2	0.454	31.6	2.08	0.107
61	184	413	80	9.65	602	132.1	0.435	33.5	1.96	0.106
62	187	426	80	9.93	592	120.4	0.461	32.1	2.27	0.099
64	165	375	73	9.18	543	109.8	0.454	28.5	2.20	0.097
65	178	417	81	9.42	601	126.1	0.432	32.3	1.94	0.105
66	176	422	83	9.13	579	113.5	0.462	30.5	2.15	0.104
Mean (Moyenne)	177	428	83	9.43	580	119.6	0.448	31.1	2.12	0.101
LSD (p.p.d.s.)										
5 %	12.2	22	5.2	0.46	19	6.8	0.044	1.2	0.09	0.007
1 %	16.0	28	6.8	0.61	25	9.0	0.088	1.6	0.12	0.010

(1) First five years of production (5 premières années de production).

(2) Mean of 1974, 1975 and 1976 (Moyennes de 1974, 1975 et 1976).

Rainfall is well distributed over the year (Table I). About 45 p. 100 of the rain falls between 2.00 and 6.00 p.m. Temperature does not fluctuate much, but monthly variation in the number of hours of bright sunshine is quite pronounced. Except for 1972, no moisture deficit as assessed by the method proposed by Surre [1968] was recorded. However, he assumes 200 mm of available soil water. This reserve is most likely less on the shallow soils overlying pumice as found at Dami.

Soils and climate in the experimental area are described in greater detail by Breure [1978].

RESULTS

Effects of genetic constitution.

Statistically significant differences between progenies were found for yield and all growth parameters studied. Progeny yields and relevant growth parameters are given in Table II. Yield differences are small compared with West African progeny trials [Sparnaay, 1980]. Coefficients of correlation between progeny yields of the first to third year of production (pre-competition yield) and growth parameters measured in the sixth to eighth year after planting are shown in Table III. In addition, correlations between progeny yields of the fourth to sixth year (more mature yield) and growth parameters measured in the mentioned period are also shown. It appears that correlations are more negative when leaf area, height, and VDM are compared with more mature yields. This indicates that with increasing light competition, the more « vigorous » progenies show a relatively higher yield reduction. By using the « Z » transformation of correlation coefficients, it appears that differences between correlations of leaf area and VDM for the early and later period are highly significant. Sparnaay [1969] found a similar effect in a spacing trial in Nigeria where each experimental block was planted

TABLE III. — Correlations between yield and growth parameters for progeny means (a) and a single palm sample consisting of 2 palms per plot (b) (Experiment 2)
(Corrélation entre les paramètres de production et de croissance pour les moyennes des descendance -a- et un seul échantillon de palmier composé de 2 arbres/parcelle -b- Expérience n° 2)

Years (Années)	Yield (Production)		
	a) genetic effect (effet génétique)	b) environmental effect (effet de l'environnement)	
	1-3	4-6	1-5
Leaf area (Surface foliaire)	+ 0.13	- 0.30	+ 0.31**
Height (hauteur)	- 0.30	- 0.51*	- 0.08
VDM (MSV)	- 0.17	- 0.58*	- 0.03

with a different progeny. He found, at the widest spacing, the same order of production per palm for pre-competition yields and mature yields, but at the closest spacing the order of production appeared to be practically reversed. The latter result was thought to be due to differences between progenies in characters associated with interpalm competition for light. For individual palms a small but significant positive correlation was found between yield and leaf area (Table III). A similar relationship was reported by Hardon *et al.* [1969] and Van der Vossen [1974].

Crop growth rate (CGR) is, generally, in oil palm more or less equally divided into dry matter incorporated in vegetative (VDM) and generative growth or bunch dry matter (Y). Corley *et al.* [1971] found a highly positive correlation between progeny values of CGR and Y ($r = + 0.92^{***}$) but no correlation between CGR and VDM ($r = - 0.06$). Interpalm competition for light, during the period when records of their experiment were collected, was similar to the 1974-1976 period of Experiment 2. Unlike the Malaysian results reported by Corley, however, during the 1974-1976 period positive correlations were found in Experiment 2 between both CGR and Y ($r = + 0.44$), and CGR and VDM ($r = + 0.53^{**}$). This implies that increasing CGR of the Dami progenies favours yield of bunches and vegetative growth to the same extent.

Statistically significant progeny differences were found in Experiment 2 for concentrations of N, P, Mg, Ca, Mn, and B in Leaf 17, but not for leaf K-levels. A high positive correlation was found between progeny leaf Mg-levels and estimated yield of oil as given in Table IV ($r = + 0.70^{**}$). Symptoms of Mg deficiency are very widespread in the New Britain environment. A scoring of Mg-deficiency symptoms, carried out in three successive years prior to leaf sampling in 1973, appeared to be strongly correlated with leaf Mg-levels ($r = + 0.92^{***}$). In a more recent $D \times P$ progeny trial at Dami, the same positive correlation ($r = 0.70^{**}$), was found between estimated progeny oil yield for the first three years of production and leaf Mg levels (Table IV).

TABLE IV. — Progeny means for magnesium status and yield of oil in $2 D \times P$ progeny trials
(Moyennes des descendance pour la nutrition en Mg et le rendement en huile dans 2 essais comparatifs d'hybrides $D \times P$)

Exp. 2 (1982)			$D \times P$ Exp. (1976) (1)		
Progeny (Descendance) code	% Mg in leaf 17 (dans la feuille 17) (1973)	Yield of oil for the first 5 years (Rendement en huile des 5 premières années) (t/ha/year/-an) (2)	Progeny (Descendance) code	% Mg in leaf 17 (dans la feuille 17) (1980)	Yield of oil for the first 3 years (Rendement en huile des 3 premières années) (t/ha/year/-an) (3)
51	0.212	6.76	42.112	0.178	5.65
52	0.222	6.72	205	0.175	5.73
53	0.222	6.12	207	0.200	6.27
54	0.242	6.73	307	0.175	5.23
55	0.226	6.18	316	0.190	5.95
56	0.204	6.30	503	0.178	5.14
57	0.210	5.63			
58	0.192	6.21	43.202	0.170	5.01
59	0.186	6.00	207	0.180	4.75
60	0.218	7.26	210	0.163	4.24
61	0.220	6.61	302	0.183	5.36
62	0.244	6.90	510	0.168	4.62
64	0.162	5.37	514	0.142	4.56
65	0.248	6.37			
66	0.244	6.75	19/16	0.210	5.42
			19/26	0.182	5.44
Means (Moyennes)	0.217	6.39			
LSD (p.p.d.s.) 5 %	0.024			0.009	
1 %	0.031			0.012	
Correlation coefficient Mg-status and oil yield (Coefficient de corrélation nutrition Mg/rendement en huile)		+ 0.70**			0.70**

(1) Hellingsman, 1980.
(2) Based on bunch analysis results 1976 (basé sur les résultats d'analyses de régimes 1976).
(3) Based on bunch analysis results 1979 and 1981 (basé sur les résultats d'analyses de régimes 1979 et 1981).

Effect of spacing.

In Experiment 3, already in the second year of production, a highly significant reduction in yield per palm was found due to higher density planting. Data on yield per palm for the first to fourth and the fifth to the eighth year of production are given in Table V. For these two periods, the optimal density is estimated [Corley, 1976b] as being 178 palms per hectare for the first to the fourth year and 115 palms per hectare for the fifth to the eighth year of production. The annual bunch yield per hectare in the first eighth years of production are given for the three densities in Table VI, together with the estimated optimal density for current yield. In the same table results are compared with those of a spacing experiment planted with similar (though not identical) $D \times P$ planting material on the Selangor series soil, one of the highest producing areas in Malaysia. The results (Table VI) show that interpalms competition has developed at an earlier stage and more intensely in the New Britain environment than in Selangor. In both environments, yields per hectare are similar for the 110 palms per hectare treatment, but at higher densities substantially lower yields per hectare are found in West New Britain than in Selangor. From the fifth year of production onwards, it appears that in New Britain the highest yield per hectare is obtained at the lowest density, but in the Selangor experiment this lowest density continued to show the lowest yield per hectare up to the eighth year of production.

Corley, Hew, Tam and Low [1973] arrived at the conclusion that mean leaf area can be used to estimate current optimal density with the following equation based, mainly, on results of spacing trials in Malaysia :

$$D(\text{opt./acre}) = \frac{2242}{(\text{mean leaf area})^2} + 36.7$$

Using this equation, optimal densities based on mean leaf area values in the third to the seventh year of production, are given in Table VI. Compared with optimal density values estimated from actual yield, it appears that, at any mean leaf area, a much lower optimal density is found in the New Britain environment than in Malaysia.

The annual results of the effect of planting density on growth in the fifth to the tenth year after planting are given in Table VII. Higher density clearly appears to have an « etiolation » effect, since higher density increased leaf length significantly from the fifth year after planting while, at a later stage, a density effect on height increment was recorded. For the period seven to nine years after field planting, during which a significant density effect on height increment was recorded, the extra height increment caused by an increase of one palm per hectare appears to be 0.16 cm.

Leaf production and VDM are significantly reduced by higher density from the start of recording. From the eighth year onwards, higher density tended to reduce leaf area. This effect of density on leaf area became significant in the tenth year after planting. Bunch Index (BI) was markedly reduced by higher density.

Leaf nutrient levels were not influenced by density, except for a highly significant increase in leaf Mg-levels due to higher density of planting in samples collected six and seven years after planting. There appeared to be no effect of density on bunch composition.

Effect of fertilisers.

The effect of fertilisers on yield is given in Table V. In Experiment 1, a small, but significant response of cumulative yield in the first five years of production to muriate of potash was found. This could have been due, however, to the chlorine rather than the potash [Breure and Rosen-

TABLE V. — Annual yield data of Experiment 1 for the first five years of production
(Données annuelles de production de l'Expérience n° 1 pour les 5 premières années de production)

Fertiliser (Engrais)	Urea (Urée)				Muriate of potash (Chlorure de potassium)				LDS (p.p.d.s.)		Magnesium chloride (Chlorure de Mg)		Manganese chloride (Chlorure de Mn)		Sulphur dust (Soufre pulvéulent)		Disodium phosphate (disodique)		Mean (Moyenne)		LDS (p.p.d.s.)	
Level (Niveau) Yield (Production) (kg/palm/yr) (kg/arbre/an)	0	1	2	3	0	1	2	3	5 %	1 %	0	1	0	1	0	1	0	1			5 %	1 %
	136	136	141	136	131	133	143**	143**	5	7	136	139	138	137	136	138	137	137	137			NS

Annual yield data of Experiment 3 for the first to fourth year and the fifth to eighth year of production
(Données annuelles de production de l'Expérience n° 3 de la 1^{re} à la 4^e année et de la 5^e à la 8^e année de production)

Fertiliser level (Engrais-niveau)	Yield (Rendement)							
	Year (Années) 1-4 (kg/palm/yr./arbre/an) Palms (Arbres)/ha				Year (Années) 5-8 (kg/palm/yr./arbre/an) Palms (Arbres)/ha			
	110	148	186	Mean (Moyenne)	110	148	186	Mean (Moyenne)
0	171	172	140	161	228	157	91	159
1	202	177	143	174	225	147	89	154
2	216	178	142	179	228	142	83	151
3	208	181	147	179	233	153	83	156
Mean (Moyenne)	199	177***	143***	173	229	150***	87***	155
Density LSD (Densité p.p.d.s.) (5 %)	—	6	—	—	—	17	—	—
Fertiliser LSD (Engrais p.p.d.s.) (5 %)	—	—	—	6	—	—	—	NS

TABLE VI. — Effects of density on annual and cumulative yield for the first eight years of production in West Britain and Selangor (1)
(Effets de la densité sur la production annuelle, et cumulée pour les 8 premières années en Nouvelle-Bretagne occidentale et au Selangor) (1)

Location (<i>Lieu</i>)	Density (palms/ha) (arbres /ha)	Year (<i>Année</i>) :								Cumulative yield
		1	2	3	4	5	6	7	8	(<i>Production cumulée</i>)
Yield (<i>Rendement</i>) (tonnes FFB/ha) (2)										
Selangor	110	10.28	24.91	25.25	28.20	25.58	26.17	24.41	27.10	191.9
	148	14.43	30.10	29.16	32.32	29.06	28.22	26.93	30.29	220.5
	186	18.73	32.10	29.33	30.52	26.66	25.85	25.95	25.52	214.6
Current optimum density (<i>Densité opti- male actuelle</i>) (palms-arbres/ha)			218	178	162	156	146	158	143	168
West New Britain (3) (<i>Nouvelle-Bretagne occidentale</i>)	110	8.83	26.01	29.21	27.92	24.50	24.11	27.80	24.47	193.0
	148	12.08	31.39	34.11	28.50	22.59	22.35	24.40	17.65	193.1
	186	14.36	36.01	30.77	25.77	17.89	17.66	17.82	10.10	170.2
Current optimum density based on yield/palm (palms/ha) (<i>Densité opti- male actuelle basée sur le rende- ment/arbre - arbres/ha</i>)			261	158	139	121	121	116	104	134
Current optimum density based on leaf area (palms/ha) (4) (<i>Densité optimale actuelle basée sur la surface foliaire - arbres/ha</i>)				210	175	163	157	152	—	—

(1) Tam, 1980. — (2) Densities giving highest yield are in italics (Les densités qui donnent les meilleurs rendements sont en italique).
(3) Plot with fertilizer application (avec apport d'engrais). — (4) Corley et al., 1973.

TABLE VII. — Effect of plant density on growth (Effet de la densité de plantation sur la croissance)

Parameter (Paramètre)	Plant density (palms/ha) (Densité-arbres/ha)			LSD (p.p.d.s.) 5 %	Years from field planting (Années depuis la plantation)	Parameter (Paramètre)	Plant density (palms/ha) (Densité-arbres/ha)			LSD (p.p.d.s.) 5 %
	110	148	186				110	148	186	
VDM (MSV) (kg/palm/yr) (kg/arbre/an)	107.1	102.2*	102.2*	3.3	5	Height increment from	74	72	73	NS
	103.2	98.7*	97.9*	4.2	6	base leaf 25 (Croissance	78	77	73	NS
	117.9	112.5*	110.3**	4.0	7	en hauteur de la base de	78	77	90*	8
	127.8	119.8*	116.1**	6.2	8	la feuille 25)	76	80	82	NS
	125.6	120.0	122.7	NS	9	(cm/yr/palm) (cm/an/arbre)	78	87**	96***	6
CGR (TCC) (t/ha/yr) (t/ha/an)	27.2	34.4***	37.6***	1.3	5	Leaf production	32.0	31.3*	30.6**	0.7
	25.6	31.2***	34.2***	1.3	6	(Emission foliaire)	28.1	27.0	26.1***	0.5
	25.7	29.6***	32.2***	1.2	7		28.0	27.2**	25.5***	0.8
	26.9	28.9**	29.9***	1.2	8		27.3	25.8**	24.3***	1.0
	27.1	30.0**	31.6***	1.4	9		24.9	23.4*	23.4*	0.9
BI (IR)	0.564	0.555	0.494***	0.014	5	Height base leaf 25	157	157	157	NS
	0.554	0.531*	0.467***	0.017	6	(Hauteur base feuille 25)	235	234	240	NS
	0.493	0.437***	0.363***	0.017	7	(cm)	313	311	330	NS
	0.476	0.383***	0.279***	0.037	8		389	391	411	NS
	0.488	0.406***	0.278***	0.033	9		467	475	508*	NS
LAR (RSF)	2.02	2.07	2.05	NS	5	Leaf length leaf 17	453	466*	473*	12
	2.19	2.24	2.17	NS	6	(Longueur de la feuille 17)	509	531**	549***	14
	2.08	2.16	2.01*	0.07	7	(cm)	508	525**	543***	8
	1.97	2.02	1.87*	0.10	8		535	558***	586***	10
	1.97	1.87*	1.79**	0.10	9		601	635***	660***	5
Leaf area leaf 17 (Surface foliaire feuille 17) (m²)	5.90	5.96	6.08	NS	5	Frond weight leaf 17	2.51	2.45	2.49	NS
	7.52	7.63	7.60	NS	6	(Poids de la feuille 17)	2.82	2.82	2.90	NS
	8.58	8.63	8.68	NS	7	(kg)	3.31	3.26	3.33	NS
	8.92	9.08	8.69	NS	8		3.81	3.71	3.82	NS
	9.49	9.57	9.02	NS	9		4.18	4.11	4.16	NS
	10.10	9.49*	9.10	0.58	10		4.24	4.22	4.34	NS

TABLE VIII. — Effects of fertilisers on fruit composition and Cl-levels in leaf 17 (Experiment 1)
(Effets des engrais sur la composition du fruit et les teneurs en Cl dans la feuille 17 - Expérience n° 1)

Fertiliser level (Engrais-niveau)	No. of analysis (Nomb. d'analyses)	Kernel to fruit (Amande/fruit) (p. 100)	Mesocarp to fruit (Pulpe/fruit) (p. 100)	Oil-to-wet mesocarp (Huile/pulpe fraîche)	P. 100 Cl in leaf 17 (Cl in leaf 17)
N 0	251	8.7	81.1	49.4	0.449
1	227	8.6	80.0	48.4	0.510**
2	230	8.5	80.8	48.4	0.513**
3	225	8.8	80.0	48.6	0.472
K 0	198	7.8	81.7	49.5	0.338
1	209	8.7**	81.0	48.9	0.502**
2	268	9.3**	79.1**	48.2	0.545**
3	258	8.8**	80.3**	48.3	0.559**
LSD (p.p.d.s.) (5 %)		0.6	1.4	NS	0.044
Mg 0	467	8.5	80.7	49.3	0.425
1	466	8.8	80.2	48.1**	0.548**
Mn 0	434	8.5	80.3	48.5	0.470
1	449	8.7	80.6	48.9	0.498
S 0	436	8.4	80.5	49.0	0.483
1	497	8.8	80.4	48.5	0.489
P 0	464	8.7	80.2	48.7	0.484
1	469	8.5	80.7	48.7	0.488
LSD (p.p.d.s.) (5 %)		NS	NS	0.8	0.031

Note : Correlation coefficient between oil-to-wet mesocarp and percentage Cl = - 0.84**. Experiment 1 planted 1968, analysed 1976.
(Coefficient de corrélation entre huile/pulpe fraîche et p. 100 Cl = - 0.84** - Expérience n° 1 plantée en 1968, analysée en 1976).

quist, 1977]. In Experiment 3, response of yield to fertilisers was reduced with increasing interpalms competition for light. Yield was only increased by fertilisers in the 110 palms per hectare density in the first four years of production.

The effect of different fertilisers on fruit composition is given in Table VIII. It appears that muriate of potash significantly increased kernel-to-fruit at the expense of mesocarp. As clearly shown in Table X, both chlorine-containing fertilisers, KCl and MgCl, reduced oil-to-wet mesocarp ratio. Table X shows that oil-to-wet mesocarp was also reduced through increasing fertiliser levels in Experiment 3. Because of the indicated association with chlorine (Tables VIII, IX and X) leaf Cl-levels and correlations between leaf Cl-levels and oil-to-wet mesocarp were also considered. The high and significant negative correlations found between leaf Cl-levels and oil-to-wet mesocarp suggest that the increase in Cl-levels due to some fertiliser

TABLE IX. — Effect of muriate of potash and magnesium chloride on oil-to-wet mesocarp (Experiment 1)
(Effet du chlorure de potassium et du chlorure de magnésium sur le rapport huile/pulpe fraîche - Expérience 1)

Level (Niveau)	K0	K1	K2	K3
Mg 0	50.7 (0.190)	48.9 (0.456)	48.3 (0.520)	48.4 (0.534)
Mg 1	48.5 (0.486)	48.6 (0.548)	47.7 (0.579)	47.8 (0.584)

Note : Correlation coefficient between oil-to-wet mesocarp and percentage Cl = - 0.98***. Figures within brackets indicate percentage Cl in leaf 17 (Coefficient de corrélation entre huile/pulpe fraîche et p. 100 de Cl = - 0.98***; les chiffres entre parenthèses donnent le p. 100 de Cl de la feuille 17).

TABLE X. — Effects of fertiliser rates on fruit composition and Cl-levels in leaf 17 (Experiment 3)
(Effets des doses d'engrais sur la composition du fruit et les teneurs en Cl de la feuille 17 - Expérience n° 3)

Fertiliser level (Engrais-niveau)	No. of analysis (Nomb. d'analyses)	Kernel to fruit (Amande/fruit) (p. 100)	Mesocarp to fruit (Pulpe/fruit) (p. 100)	Oil-to-wet mesocarp (Huile/pulpe fraîche)	P. 100 Cl in leaf 17 (Cl dans feuille 17)
0	208	6.9	82.2	49.0	0.180
1	189	8.3	80.7	48.6	0.465***
2	178	9.1	80.0	48.2	0.549***
3	196	8.7	79.8	48.1	0.594***
Standard deviation (Ecart-type)		2.0	4.3	4.5	

Note : Correlation coefficient between oil-to-wet mesocarp and percentage Cl = - 0.96*. Experiment 3, planted 1970 (analysed 1975) (Coefficient de corrélation entre huile/pulpe fraîche et p. 100 de Cl = - 0.96* - Expérience n° 3, plantée en 1970, analysée en 1975).

treatments could be responsible for the observed reduction in oil-to-wet mesocarp. No clear effect of fertilisers on percentage shell or oil-to-dry mesocarp was found.

In Experiment 1, no response of growth parameters to fertilisers was found except for a small, but significant, increase in leaf area and leaf production due to sulphur and magnesium chloride. On the other hand, results of the effect of fertilisers on growth in Experiment 3, which are given in Table XI, show a very highly significant response of VDM to fertilisers due to an increase in both leaf production and leaf weight (see page 220). In the period eight to ten years after planting fertilisers increased mean leaf area for this period from 9.18 to 9.84 m² at the lowest density with an absence of response of leaf area to fertilisers at the higher densities. During the period of high light competition, the interaction between density and fertilisers was significantly negative. The effects of fertilisers on bunch dry matter (Y), vegetative growth (VDM) and bunch index (BI) are given in Table XII for the period eight to nine years after planting. It appears that even under conditions of high light competition, VDM is increased by fertiliser with the same proportion at all densities. Due to a complete absence of response of yield (Y) to fertilisers, BI was reduced by fertiliser application during this period.

The effect of fertilisers on leaf nutrient levels has been described in greater detail by Breure [1977] and Breure and Rosenquist [1977].

Effect of standards of assisted pollination.

In the West New Britain environment, the bunch survival rate depends primarily on standards of assisted pollination. Recently, Syed [1979] found that poor natural pollination in some environments is due to the absence of a suitable insect pollinator. For various reasons, standards of assisted pollination had been quite different in the three experiments during the recording period considered in this paper.

In Experiment 1, standards were poor until early 1976. In Experiment 2 pollination was extremely poor for the greater part of the first year of flowering after ablation, but had been good in the following years, while in Experiment 3 excellent standards of assisted pollination were achieved, initially with conventional puffers but for the greater part of the recording period with the so-called PNG-pollen blowers which were developed at Dami O.P.R.S.

Yield and growth data of commercial *tenera* in the three experiments are compared in Table XIII. Although the data do not permit a statistical analysis, Table XIII clearly indicates that poor pollination is associated with low yield. Comparing fruit set data of Experiment 2 and 3, there appears to be a marked increase in fruit set when the

TABLE XII. — Effects of fertilisers and density on dry matter (kg/palm/yr) incorporated in fruit bunches (Y) and vegetative growth (VDM) together with bunch index (BI) during the eighth and ninth years after planting (Effets des engrais et de la densité sur la matière sèche — kg/arbre/an — dans les régimes — Y —, et la croissance végétative — MSV — ainsi que l'indice de régimes — IR — pendant la 8^e et la 9^e année)

Fertiliser level (Doses d'engrais)	110 palms (arbres)/ha			148 palms (arbres)/ha			186 palms (arbres)/ha		
	Y	VDM (MSV)	BI (IR)	Y	VDM (MSV)	BI (IR)	Y	VDM (MSV)	BI (IR)
0	116	117	0.499	83	114	0.420	47	113	0.294
1	117	128	0.477	78	123	0.386	49	117	0.294
2	120	130	0.480	75	128	0.367	44	125	0.260
3	120	133	0.473	80	116	0.407	45	122	0.267

TABLE XIII. — Effect of different standards of assisted pollination on bunch yield and growth (Effet de diverses qualités de pollinisation assistée sur le rendement en régimes et la croissance)

Pollination standards (Qualité)	Exp.	Fruit set (1) (Fertilité fruit) (%)	Yield (2) (Rendement) (kg FFB/ palm/yr) (/arbre/an)	Height increment (Croissance en hauteur) A (3) B (4)		VDM (MSV) (kg/palm/yr-/arbre/an) A (3) B (4)		Leaf area expansion (leaf 17) (Augmentation de la surface foliaire-feuille 17) (m ²)		
Poor (Mauvaise)	1		126.5	94	—	125.7	—	8.03 (74)	10.42 (86)	10.71 (98) 11.42 (132)
Initially poor (Mauvaise au début)	2	46.6	171.7	90	86	121.4	135.0	7.96 (70)	10.08 (82)	10.45 (94) 11.22 (138)
Excellent with pollen blower (Excellente avec poudreuse)	3 (5)	57.4	178.7	79	78	108.0	121.6	7.63 (68)	8.63 (80)	9.08 (92) 9.49 (116)

(1) Based on ± 500 bunches (Basée sur ± 500 régimes).

(2) First four years of production (4 premières années de production).

(3) During sixth and seventh years after planting (Au cours des 6^e et 7^e années de la plantation).

(4) During eighth years after planting (Au cours de la 8^e année de la plantation).

(5) Plots with fertilisers at 148 palms per hectare (Parcelles avec engrais, de 148 arbres/ha).

Note : Figures within brackets indicate months from field planting (Les chiffres entre parenthèses indiquent le nombre de mois depuis la plantation).

TABLE XI. — Effect of fertiliser rate on growth (Effet des doses d'engrais sur la croissance)

Parameter (Paramètre)	Fertiliser rate (Engrais-doses)				LSD (p.p.d.s.) (5 %)	Years from field planting (Années depuis la plantation)	Parameter (Paramètre)	Fertiliser rate (Engrais doses)				LSD (p.p.d.s.) (5 %)
	0	1	2	3				0	1	2	3	
VDM (MSV) (kg/palm/yr)	99.1 93.9 103.8 113.1 115.9	105.1** 101.2*** 116.6*** 122.3** 122.9***	107.9*** 103.9*** 118.5*** 127.1*** 127.6***	104.5*** 100.8*** 115.3*** 122.5** 124.7***	3.1 1.8 5.2 5.5 2.5	5 6 7 8 9	Height increment from base leaf 25 (Croissance en hauteur de la base de la feuille 25) (cm/yr/palm-cm/an/arbre)	70 76 76 77 83	75 81 84 80 89	74 81 83 82 89	74 79 83 79 87	NS NS NS NS NS
CGR (TCC) (t/ha/ant)	30.8 28.4 27.6 27.6 28.7	33.4*** 30.4*** 29.4*** 28.9*** 29.4	34.2*** 31.6*** 30.0*** 28.9*** 30.4	33.9*** 30.8*** 29.5*** 28.8*** 29.8	1.3 0.9 1.0 0.9 NS	5 6 7 8 9	Height base leaf 25 (Taille de la base de la feuille 25) (cm)	150 226 303 379 463	159 240 324* 404* 493*	162 243 325* 407* 492*	157 236 320 398 484	NS NS NS NS NS
BI (IR)	0.528 0.515 0.450 0.401 0.406	0.538 0.513 0.421 0.382 0.388	0.537 0.519 0.423 0.355* 0.383	0.548* 0.521 0.429 0.379 0.385	0.015 NS NS 0.029 NS	5 6 7 8 9	Leaf production (Emission foliaire)	31.0 26.6 25.7 24.9 23.6	31.7 27.4* 27.8* 26.2 24.2	31.5 27.3* 27.2* 26.4 24.0	31.0 26.9 26.9* 25.8 23.9	NS NS NS NS NS
LAR (RSF)	2.14 2.29 2.15 1.98 1.93	2.03** 2.15*** 2.07* 1.95 1.84	1.99** 2.16*** 2.04* 1.92 1.83	2.03** 2.19*** 2.07* 1.95 1.82	0.05 0.06 0.08 NS NS	5 6 7 8 9 10	Leaf length leaf 17 (Longueur de la feuille 17) (cm)	461 526 519 555 631 602	466 534 525 562 634 612	465 530 533 561 632 616*	464 531 525 561 630 606	NS NS NS NS NS 12
Leaf area leaf 17 (Surface foliaire feuille 17) (m ²)	6.05 7.56 8.61 8.67 9.25 9.57	6.00 7.47 8.47 8.91 9.24 9.46	5.97 7.62 8.74 8.96 9.52 9.66	6.00 7.68 8.72 9.04 9.43 9.58	NS NS NS NS NS NS	5 6 7 8 9 10	Fron weight leaf 17 (Poids de la feuille 17) (kg)	2.43 2.73 3.16 4.01 4.06	2.45 2.86 3.28 4.01 4.23*	2.55 2.94* 3.41** 4.11** 4.38***	2.49 2.86 3.34* 4.19*** 4.29*** 4.40***	NS 0.17 0.14 0.08 0.08 0.17

intensive 'pollination method with the pollen blower is used. Poor pollination in the short period after ablation (Experiment 2) seems to cause similar vegetative growth (VDM) as when standards are poor during a substantially longer period (Experiment 1). Intensive pollination from the start (Experiment 3) appears to induce a markedly lower growth rate. The large differences between palms of Experiment 2 and Experiment 3 (two adjacent plantings of the same commercial $D \times P$ material) in height increment, VDM and leaf area expansion up to 8 years after planting indicates a long residual effect of standards of assisted pollination on growth.

Similar values of growth parameters were found in Experiment 1 (Bebere) and Experiment 2 (Dami) which indicate that the observed differences in growth characters between Experiment 1 and Experiment 3 cannot be attributed to environmental factors.

DISCUSSION

High values of estimated heritability were found for most of the growth parameters studied in progeny trials at Dami (Breure, unpublished). The observed differences between progeny growth parameters of Experiment 2 (Table II) are therefore likely, for the greater part, to be of genetic origin. Except for height of the *pisifera* male parents, no growth parameters were determined for the parents of Experiment 2 [Tam, 1980]. For height the genetic origin is clearly indicated, since a high and significant positive *pisifera* male parent-offspring correlation was found ($r = +0.79^*$). On the other hand, there is strong evidence that genetic differences in the number of rotten bunches are associated with the differences of growth parameters in Experiment 2. Even with good pollination, highly significant differences between progenies of Experiment 2 were found for the number of rotten bunches per palm (range 16 p. 100-35 p. 100 of the total bunches produced). A highly significant positive correlation exists between the number of rotten bunches and VDM of progenies in Experiment 2 ($r = +0.82^{***}$). Corley [1976a] found, in an ablation trial, a similar relationship between different proportion of inflorescence removal and VDM which suggests that, in the same fashion, the different proportion of rotten bunches in Experiment 2 could have, partly, caused progeny differences in VDM. The latter hypothesis is borne out by the fact that a much higher positive correlation was found between the number of rotten bunches and diameter of the stem (a parameter associated with vegetative development) laid down in the third year of production ($r = +0.75^{**}$) than between rotten bunches and stem diameter laid down prior to bunch production ($r = +0.33$ n.s.).

The effect of spacing appears to be more intense at Dami than reported from spacing trials in other oil palm areas. Hartley [1977] mentions that, in West African experiments, effect of density on yield per palm was not evident over a wide range of planting densities until nine years after planting. Table VI shows a more acute competition between palms at Dami than in Malaysia, an environment more favourable for oil palm cultivation than West Africa. Sparnaay [1969], comparing yield progression with age of one progeny in fertile and infertile plots, found an initially higher yield per palm in the fertile plots, but from the seventh year of production onwards yield in the infertile plots was higher than in the fertile plots. He

suggested that, in particular, high sex ratio progenies may show the above effect. The strong effect of planting density on yield at Dami could therefore be attributed to the high sex ratio of the planting material together with the high fertility of the young volcanic soils. In addition, competition for water in periods of only a few days without rain might occur in the Dami environment with shallow soils overlying pumice and dry, strong, winds during the drier part of the year. The Selangor coast palm roots can often reach subsoil water while only a few roots penetrate the pumice layers in the Dami soils. The possible role of water deficit in explaining partly the lower optimal density in New Britain should be further investigated. Annual values of current optimum density given in Table VI can be used to estimate the density giving the highest yield over the full life of the planting. Leaf area appears to reach its maximum about ten years after field planting in Dami; thus interpalms competition for light can be assumed constant from the eighth year of production onwards. It is therefore likely that future optimal density for current yield will continue to be more or less identical to the optimal density for the seventh to eighth year of production

$$\text{density} = \left(\frac{116 + 104}{2} \right) = 110 \text{ palms/ha}$$

Assuming an economic life of twenty years (seventeen years of production), the density giving the highest yield can thus be estimated from the optimum density for cumulative yield over the first eight years of production (Table VI) and the current optimal density for the seventh to eighth year of production, which gives an optimum

$$\text{density of } \frac{(8 \times 134) + (9 \times 110)}{17} = 121 \text{ palms per}$$

hectare against 158 palms per hectare suggested by Corley *et al.* [1973] for a wide range of conditions. The strong response of yield per palm to thinning in New Britain (in two experiments, planted at 143 palms per hectare already in the second and third year after thinning one-third of the palms, a similar yield per hectare was found in the thinned plantings as in the original stand) supports the suggested low optimal density.

In progeny trials where progenies are selected of high yield potential, in particular, a lower than 143 palms per hectare density should be adopted, since the ranking of progeny yields per palm seems to be quickly affected by the relative vigour of the progenies (Table III). The strong effect of light competition on yield further implies that special attention should be given to select progenies which are more tolerant to light competition.

It is indicated that VDM has a high plasticity in the New Britain environment. This is, in the first place concluded from the fact that a positive correlation exists between Crop Growth Rate (CGR) of progenies and both bunch yield and vegetative dry matter. Further, a significant effect of density on VDM was found in the range of practical planting densities as early as five years after planting. Corley [1973] reported a relative constancy of VDM over a wide range of planting densities but, although not statistically significant, the magnitude of VDM response to density was similar [Corley, 1980]. Van der Vossen [1974] concluded from leaf length and stem height data that VDM under West African conditions was strongly affected by the annual water stress in the palms.

The high plasticity of VDM is further indicated by the relatively low value of estimated heritability found for

VDM in the Dami trial (Breure, unpublished). A high plasticity of VDM implies that a desirable reduction in VDM of palms in the favourable environment of New Britain would seem feasible. Corley [1976a] suggested that « some minimum level of vegetative growth must be achieved, varying with palm age, progeny and soil fertility, before dry matter is diverted to fruit production, but if fruit production is prevented or restricted, then more dry matter may be incorporated in vegetative tissue ». This is clearly borne out by data given in Table XIII. Better standards of assisted pollination at the early stage of flowering (Experiment 3) seem to increase fruit production at the expense of VDM. On the other hand, if fruit production is restricted at the early stage through poor pollination (Experiments 1 and 2) then an excessive amount of VDM seems to be produced. Reduction of VDM through intensive pollination is therefore indicated. The apparent strong residual effect of standards of assisted pollination on VDM suggests that ablation may, in the same fashion, induce a similar excessive production of vegetative dry matter for a considerable period. Corley [1976a] suggested to start assisted pollination without a period of ablation in the West Britain environment. His suggestion is clearly borne out by results as presented in Table XIII.

Apart from the effect of restricting fruit production on VDM, under good standards of pollination, fertiliser application can also cause an excessive production of VDM without an accompanying increase in bunch yield (Table XII). Fertilisers are, under these conditions of high light competition, only used to produce VDM above a required minimum level which increases interpalp competition for light.

For the first five years of production, fertilisers increased bunch weight by 12 p. 100 in the 148 palms per hectare treatment of Experiment 3, but only a 4 p. 100 response of bunch weight to fertilisers was obtained in Experiment 1 (poor pollination). This difference in response of bunch weight between the two experiments is probably due to different pollination standards. More clearly response of yield to fertilisers is restricted by the degree of interpalp competition for light. From the fifth year of production onwards, no response of yield was found in any of the densities studied (for the 5th to the 8th year of production, fertiliser application even appears to reduce yield in the two highest densities). The increase of leaf area (a parameter associated with interpalp competition of light) due to fertiliser, at the lowest density, starting eight years after planting, may explain the sudden absence of response of yield to fertilisers in this lowest density from the fifth year of production.

Tan and Rajaratnam [1978], studying the genetic variation of leaf nutrient concentrations in 20 $D \times P$ crosses, found a similarly wide range of nutrient levels in leaf 17 as obtained in Experiment 2. They found a high value of narrow sense heritability for Mg-levels but, unlike results of Experiment 2, no correlation between Mg-levels and yield. This is not surprising since the leaf Mg-levels in their experiment (range 0.248-0.365) were much higher than in Experiment 2 (range 0.162-0.248). The high correlations obtained in New Britain between leaf Mg-levels and oil yield, together with indications that Mg-levels may be highly heritable, justifies selection for high Mg in

the leaves. Similar to Experiment 2, highly significant progeny differences for leaf Mg-levels were found in a $D \times D$ progeny trial used as a source of mother trees (Breure, unpublished). Work to establish heritability values for leaf nutrient concentrations in the Dami trials is in progress. Van Weering [1972] reported that in a $D \times P$ trial laid down in liparitic soils in Sumatra, higher oil-to-wet mesocarp corresponds with high leaf Mg-levels (range 0.20-0.28) as was found in Experiment 2. Further Ochs and Ollagnier [1977] found a strong positive effect of kieserite application on oil to bunch ratio at similar high levels of muriate of potash as applied in Experiment 2. This was mainly due to an effect on oil to mesocarp percentage. They reported a positive correlation between plot values for oil to bunch ratio and leaf Mg-levels ($r = +0.464$). The possible role of Mg in oil synthesis of oil palm had been reported by Venema [1962].

Table VIII shows a strong evidence that fertilisers which increase leaf Cl-levels depress oil extraction rates.

The depressive effect of chlorine on oil-to-wet mesocarp was also reported by Biessen [1965] and Green [1976]. It is likely that the Cl-ion may only promote water uptake by the mesocarp, since no correlation between Cl-levels and oil-to-dry mesocarp was found. In Experiment 3 no effect of fertilisers on percentage fruit-to-bunch was found. Assuming a similar absence of response of fruit-to-bunch to fertilisers in Experiment 1, it appears that muriate of potash had reduced oil extraction rates by 5 p. 100 in Experiment 1. Wood [1978] reported that muriate of potash decreased oil extraction rates in *dura* and *tenera* material. Although he did not give leaf analysis data, results of Table VIII indicate that this reduction in oil content might also have been associated with increased leaf Cl-levels due to the application of muriate of potash. Recent results of a source of potash trial laid down in New Britain, showed that, apart from muriate of potash (Table VIII), bunch ash and potassium sulphate also significantly increased kernel-to-fruit at the expense of mesocarp. It is not evident, however, whether the increase in kernel-to-fruit is due to potassium. The three potash sources all increased leaf Cl-levels significantly while leaf K-levels were slightly reduced. The correlation coefficients between leaf Cl-levels and kernel-to-fruit in this experiment were significantly positive (r between kernel-to-fruit and Cl-levels in leaf 1, leaf 9, and leaf 17 respectively $+0.94^{**}$, $+0.89^*$, and $+0.84^*$). Genty [1981] found similar, significant, correlations between leaf Cl-levels and kernel-to-fruit in a fertilizer experiment in Colombia. In a coconut fertilizer experiment in Sumatra, Rosenquist [1980] reported a strong increase in copra content of the nuts (a fruit component comparable to kernel in oil palm) due to muriate of potash. Hartley [1977] has pointed out that in selection work increasing the kernel at the expense of mesocarp could be considered as an advantage. Further, with modern planting material, increasing the size of the nuts might improve factory efficiency.

The increase in fruit set due to intensive pollination (Table XIII) is of considerable interest in view of the recent introduction of pollinator insects in Papua New Guinea. Syed [1981] found insect pollination to be superior to any standards of assisted pollination currently achieved, and Table XIII indicates the magnitude of response in fruit set which might be expected after pollinator insects will have established.

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REFERENCES

- [1] BIESSEN J. VAN (1969). — (Personal communication). Foliar Analysis Laboratory, Colworth House, Bedford.
- [2] BLAAK G., SPARNAAY L. D. and MENENDEZ T. (1963). — Breeding and inheritance of the oil palm. Part II: Methods of bunch quality. *Jl W. Afr. Inst. Oil Palm Res.*, 4, 145-155.
- [3] BREURE C. J. (1977). — Preliminary results from an oil palm density x fertiliser trial on young volcanic soils in West New Britain. In: *International Developments in Oil Palm* (ed. D. A. Earp and W. Newall), p. 192-207. Kuala Lumpur: Incorporated Society of Planters.
- [4] BREURE C. J. (1978). — Research report Dami Oil Palm Research Station 1971-1977, Vol. I and II, 215 pp.
- [5] BREURE C. J. and ROSENQUIST E. A. (1977). — An oil palm fertiliser experiment on volcanic soils in New Guinea. In: *International Developments in Oil Palm* (ed. D. A. Earp and W. Newall), p. 327-342. Kuala Lumpur: Incorporated Society of Planters.
- [6] CORLEY R. H. V. (1976a). — Photosynthesis and productivity. In: *Oil Palm Research* (ed. R. H. V. Corley, J. J. Hardon and B. J. Wood), p. 55-76. Amsterdam: Elsevier.
- [7] CORLEY R. H. V. (1976b). — Planting density. In: *Oil Palm Research* (ed. R. H. V. Corley, J. J. Hardon and B. J. Wood), p. 273-284. Amsterdam: Elsevier.
- [8] CORLEY R. H. V. (1980). — (Private communication). Harrisons and Crosfield Oil Palm Research Station, Banting, Selangor, Malaysia.
- [9] CORLEY R. H. V., HARDON J. J. and TAN G. Y. (1971). — Analysis of growth of the oil palm (*Elaeis guineensis* Jacq.). I. Estimation of growth parameters and application in breeding. *Euphytica*, 20, 307-315.
- [10] CORLEY R. H. V., HEW C. K., TAM T. K. and LO K. K. (1973). — Optimal spacing for oil palms. In: *Advances in Oil Palm Cultivation* (ed. R. L. Wastie and D. A. Earp), p. 52-69. Kuala Lumpur: Incorporated Society of Planters.
- [11] GENTY P. (1981). — (Personal communication). Institut de Recherches pour les Huiles et Oléagineux, Indupalma S.A., Bucaramanga (Colombie).
- [12] GREEN A. H. (1976). — Field experiments as a guide to fertiliser practice. In: *Oil Palm Research* (ed. R. H. V. Corley, J. J. Hardon and B. J. Wood), p. 235-261. Amsterdam: Elsevier.
- [13] HARDON J. J., WILLIAMS C. N. and WATSON I. (1969). — Leaf area and yield in the oil palm in Malaysia. *Expl. Agric.*, 5, 25-52.
- [14] HARTLEY C. W. S. (1977). — *The Oil Palm*, 806 p., London: Longman.
- [15] HELLINGMAN C. (1980). — (Personal communication). Dami Oil Palm Research Station.
- [16] MULLER A. (1969). — Volcanic ash soils. *Tropical Abstracts*, 24, 353-358.
- [17] OCHS R., OLLAGNIER M. (1977). — The effect of fertilizers on the yield and composition of lipids in some tropical crops. Proceedings of the 13th IPI-Colloquium of the International Potash Institute, York, p. 269-293.
- [18] ROSENQUIST E. A. (1980). — A coconut fertiliser trial on the podsol soils of North Sumatra. *Oléagineux*, 35, N° 5, p. 241-246.
- [19] SPARNAAY L. D. (1969). — Oil Palm. In: *Outlines of Perennial Crop Breeding in the Tropics* (Misc. Papers), (ed. F. P. Ferwerda & F. Wit), p. 339-387. Agric. Univ. Wageningen (Netherlands).
- [20] SPARNAAY L. D. (1980). — (Personal communication). Institute of Horticultural Plant Breeding, Wageningen (Netherlands).
- [21] SYED R. A. (1979). — Studies on oil palm pollination by insects. *Bull. Ent. Res.*, 69, p. 213-224.
- [22] SYED R. A. (1981). — (Personal communication). Commonwealth Institute of Biological Control.
- [23] SURRE C. (1968). — Les besoins en eau du palmier à huile. Calcul du bilan de l'eau et des applications pratiques. *Oléagineux*, 23, p. 165-167.
- [24] TAM T. K. (1980). — (Personal communication). Harrisons and Crosfield Oil Palm Research Station, Banting, Selangor, Malaysia.
- [25] TAN G. Y. and RAJARATNAM J. A. (1978). — Genetic variability of leaf nutrient concentration in Oil Palm. *Crop Science*, 18, p. 548-550.
- [26] VENEMA K. C. W. (1962). — Some notes regarding the function of the sulphate-anion in the metabolism of oil producing plants, especially oil palms. *Potash Trop. Agr.*, 5, (4).
- [27] VOSSEN (VAN DER) H. A. M. (1974). — Towards more efficient selection for oil yield in the oil palm (*Elaeis guineensis* Jacquin) Ph. D. Thesis, University of Wageningen, Netherlands, p. 107.
- [28] WEERING (VAN) J. J. (1972). — Differences in leaf composition between *dura* and *tenera* palms. *Oil Palm News*, 13, p. 6-8.
- [29] WOOD B. J. (1978). — Research in relation to natural resources-oil palm. *Planter, Kuala Lumpur*, 54, p. 414-442.

RÉSUMÉ

Les facteurs influant sur la production et la croissance des palmiers à huile *tenera* en Nouvelle-Bretagne occidentale.

C. J. BREURE, *Oléagineux*, 1982, 37, N° 5, p. 213-227.

Dans un essai comparatif d'hybrides D x P, étudiant 9 *pisifera*, des différences significatives ont été observées entre les descendance pour la production, les paramètres de croissance et les niveaux d'éléments nutritifs de la feuille. Le rendement de la 4^e à la 5^e année de production est en corrélation négative avec la croissance végétative ($r = -0,51^*$), et en hauteur ($r = -0,58^*$), tandis que ces paramètres sont en moins bonne corrélation avec la production précoce. Les rendements en huile des descendance sont en corrélation positive avec la teneur en Mg de la feuille ($r = 0,70^{**}$). Dans des expériences densité x fertilisation, comparant 110, 148 et 186 arbres/ha chacune à 4 niveaux de fertilisation (parcelle subdivisée), la densité et la fumure ont eu un effet significatif sur la production et la plupart des paramètres de croissance. L'accroissement de la compétition pour la lumière a réduit la réponse de la production aux engrais mais, à l'exception de la surface foliaire, n'a pas eu d'effet sur la réponse de la croissance. Les effets de N, K, P, Mg, Mn et S ont été étudiés dans un dispositif incomplet $4^2 \times 2^4$. Le chlorure de potassium a augmenté la production. La potasse a augmenté le rapport palmiste-fruit aux dépens du mésocarpe. Des corrélations hautement négatives ont été trouvées entre les teneurs en Cl des feuilles et le rapport huile/mésocarpe frais. L'intensité de la pollinisation a varié selon les expériences. L'amélioration de la pollinisation augmente la production et réduit la croissance. La matière sèche végétative (MSV) a une forte plasticité et semble remplaçable en partie par la matière sèche du fruit à la suite d'une pollinisation adéquate. La combinaison de descendance moins compétitives pour la lumière avec des teneurs élevées en Mg, et une pollinisation suffisante sans castration, pourrait augmenter la production.

RESUMEN

Los factores que influyen en la producción y el crecimiento de las palmas africanas *tenera* en Nueva Bretaña occidental.

C. J. BREURE, *Oléagineux*, 1982, 37, N° 5, p. 213-227.

En una prueba comparativa de híbridos D x P que estudiaba 9 *pisifera*, se observó diferencias significativas entre las descendencias para la producción, los parámetros de crecimiento y los niveles de elementos nutritivos de la hoja. El rendimiento del 4° al 5° año de producción muestra una correlación negativa con el crecimiento vegetativo ($r = -0,51^*$) y la altura ($r = -0,58^*$), mientras que estos parámetros tienen una correlación un poco menos favorable con la producción precoz. Los rendimientos de aceite de las descendencias muestran una correlación positiva con el contenido de Mg de la hoja ($r = +0,70^{**}$). En experiencias de densidad x fertilización que comparan 110, 148 y 186 árboles/ha, cada una con 4 niveles de fertilización (parcela subdividida), la densidad y la fertilización han tenido un efecto significativo en la producción y en la mayoría de los parámetros de crecimiento. El aumento de la competencia por la luz ha reducido la respuesta de la producción a los fertilizantes, pero con excepción de la superficie foliar, no ha surtido efecto en la respuesta del crecimiento. Se estudió los efectos de N, K, P, Mg, Mn y S en un dispositivo incompleto $4^2 \times 2^4$. El cloruro potásico aumentó la producción. La potasa aumentó la relación palmiste-fruto a expensas del mesocarpo. Se encontraron correlaciones altamente negativas entre los contenidos de Cl de las hojas y la relación aceite: mesocarpo fresco. La intensidad de la polinización ha variado según los experimentos. La mejora de la polinización aumenta la producción y reduce el crecimiento. La materia seca vegetativa (MSV) tiene una alta plasticidad y parece sustituible en parte por la materia seca del fruto como consecuencia de una polinización adecuada. La combinación de descendencia menos competitiva por la luz con altos contenidos de Mg, y una polinización suficiente sin castración, podría aumentar la producción.

RELEVANT FACTORS ASSOCIATED WITH CROWN EXPANSION IN OIL PALM (*ELAEIS GUINEENSIS* JACQ.)

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Elaeis guineensis, oil palm, crown expansion, leaf area, dry matter production.

SUMMARY

Trends in crown expansion, the area of the youngest fully expanded leaf (LA) against age were studied in two oil palm progeny trials, and one density \times fertilizer experiment, the latter comparing 110, 148, and 186 palms per ha each with four fertilizer levels. LA against age was best fitted by a logistic growth curve with maximum LA (L_m) and the time required to reach 0.95 L_m ($t_{0.95}$) as characteristic parameters. Progenies significantly differed in L_m and $t_{0.95}$. Increasing planting density significantly decreased L_m and $t_{0.95}$, while fertilizers increased L_m and $t_{0.95}$ only at the lowest density. Population means of the experiments markedly differed in L_m and $t_{0.95}$ values. Based on the, so called, Leaf Expansion Ratio (ER), being the ratio of LA at maximum expansion rate and LA at its final size, individual palms were selected for a rapid increase in LA, but a relatively low final size. The first characteristic means selection for rapid ground coverage, which resulted in palms with a higher Total Dry Matter Production (TDM) prior to canopy closure. The second characteristic appeared to lead to selection for high Bunch Index (the proportion of TDM used for fruit bunch production), indicating that L_m is a measure for the relative sink strength of leaves for assimilates. Selection for high ER values appeared feasible and this would increase yield during the economic life of a planting. The practical aspects of using ER values as a new selection criterion in oil palm breeding were discussed.

INTRODUCTION

The development of model plants or ideotypes, to be regarded as biological models which are expected to perform or behave in a predictable manner within a defined environment, was suggested as an additional basis of breeding programs by DONALD (1968). As yet this approach has not been followed in oil palm breeding programs.

Competition between oil palms (*Elaeis guineensis* JACQ) grown in the favorable environment of South East Asia and the Pacific Region is mainly for light. Interpalm competition increases with increasing planting density and also through the expansion of the crown during the early years in the field. Leaf Area Index (LAI), the total leaf area per unit ground area, is, in this environment, the most suitable index to describe the level of interpalm competition (CORLEY, 1976). In oil palm, LAI can be calculated as the product of the number of leaves per palm, their mean area, and the number

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of palms per unit ground area. In commercial oil palm plantings, dependent on age, a rather fixed number of 40 to 50 green fronds are retained in the crown through regular pruning rounds for harvesting the fruit bunches. Typically, the final area of successive leaves (LA) continues to increase until palms are approximately eight years old (HARDON et al., 1969). At normal planting densities, the oil palm canopy is closed before LA has reached its final level. Contrary to annual crops, the production of fruit bunches starts several years before complete canopy closure. Since closure of the oil palm canopy implies maximum light interception, resulting in maximum Crop Growth Rate (CGR), high early yields per unit area are contingent upon obtaining a high LAI as soon as possible after field planting. This can be achieved by palm ideotypes with a more rapid crown expansion and by higher density planting. Following the stage of complete canopy closure, additional crown expansion increases the level of interpalm competition (increase in LAI) without affecting CGR. In this respect it is relevant to note that oil palm is an indeterminate species, which means that the main growing point remains vegetative and the economic yield originates from axillary buds. A characteristic of several of such species is that when the flow of photosynthates per plant is reduced, through increasing the level of interplant competition for light, there may occur, at extreme levels of light competition, a monopolization of this flow by vegetative growth at the expense of economic yield (DE WIT et al., 1979). This also applies for oil palm where increasing LAI will, at a certain level, result in a decrease of the Bunch Index (BI), which is the proportion of the total above ground dry matter production (TDM) used for bunch dry matter (Y). Increasing LAI at early years through high density planting will therefore result in a proportional decrease in BI when LA reaches its final size. It looks logical to eliminate this reduction in BI by thinning a high density planting when interpalm competition becomes intense, but studies of CORLEY et al. (1973) proved that this approach is not feasible. A more effective way is to select palms with high BI for a given LAI; for such palms Y is relatively less reduced by prolonged crown expansion, as could be shown by BREURE & CORLEY (1983). An alternative, studied in this paper, is to plant palms with rapid crown expansion combined with a reduced expansion time. This ideotype is referred to as Rapid Expansion Rate ideotype (RER). With respect to the supply of assimilates from the total leaf surface (source of assimilates) and the partitioning between Y and VDM (available sinks of assimilates), RER ideotypes are expected to show the following characteristics in comparison with Slow Expansion Rate (SER) ideotypes.

Firstly, an increase in source of assimilates prior to canopy closure, as a result of a more rapid crown expansion, should lead to a higher initial TDM. Secondly, when the canopy is closed, RER ideotypes will have a lower sink size of vegetative growth (smaller final LA) and hence a higher proportion of the source of assimilates available for Y. This more favorable partitioning of the source between the competitive sinks will result in a higher BI. Thirdly, the combination of a relatively high initial area of the youngest fully expanded leaf (LA) and a lower sink strength of vegetative growth (VDM) will result in RER palms having a high initial Leaf Area Ratio (LAR), the ratio of the new total leaf area produced to VDM. Since RER palms stabilize at a lower LA level LAR will subsequently decrease with age.

Oil palm spacing experiments have been described by several authors (BEIRNAERT & VANDERWEYEN, 1940; PREVOT & DUCHESNE, 1955; SLY & CHAPAS, 1973; MARIJNEN,

1963; CORLEY et al., 1973; CORLEY, 1973; BREURE, 1977, 1982). Concerning trends in crown expansion and their relation with dry matter production no published work is known to the author.

From two oil palm progeny trials and one density \times fertilizer experiment (established at Dami Oil Palm Research Station, West New Britain, Papua New Guinea) bunch yield and detailed growth rate data were collected for several successive years. In the present paper, outcomes from these three experiments are used to compare RER and SER ideotypes for their relevant growth parameters (BI, LAR etc.). The objective is further to study the effect of genotype, planting density and fertilizers on trends of LA expansion. Extensive LA data of the three experiments are further used for a critical examination of earlier published work which was based on a more restricted set of LA measurements (CORLEY, 1973; CORLEY & MOK, 1973; CORLEY et al., 1973; HARDON et al., 1969; GRAY, 1969; CORLEY & GRAY, 1976).

MATERIALS AND METHODS

The experiments described in this paper were all planted at Dami. Details of the environmental conditions of the experimental sites have been given by BREURE (1982). Planting material is of the tenera fruit form, which is a monofactorial hybrid between dura female parents and pisifera male parents. A description of these fruit forms and the origin of the parents of F_1 palms of these experiments has been given by BREURE et al (1982).

Experiment one. This was a dura \times pisifera progeny trial testing nine pisifera each with four dura. The 15 progenies were arranged in randomized blocks with five replications and 16 palms per plot. The trial was planted at 143 palms per ha in 1968.

Experiment two. This was also a dura \times pisifera progeny trial testing 14 pisifera each with four dura in plots of 16 palms. The experiment was planted in 1976 with three replications planted at 115 palms per ha and three replications at 143 palms per ha.

Experiment three. This density \times fertilizer experiment was planted in October 1970. Three densities were 110, 148 and 186 palms per ha. Each plot was divided into four sub-plots for four different levels of fertilizers.

Experiments one and two are discussed in more detail by BREURE & CORLEY (1983) and experiment three by BREURE (1977). In experiments one and three disbudding (castration, ablation), being a standard practice of removing all initial inflorescences, was carried out at monthly intervals during the first year of flowering. Experiment two followed the new practice and was not disbudded. All experiments were under assisted pollination because of poor natural pollination. Standards were different in the three experiments (BREURE, 1982). In experiment one assisted pollination was stopped in March 1979.

OBSERVATIONS

Bunch yield (weight of crop) was recorded at each harvesting round from the start

of production. From most of the palms in experiment two, at least two bunches were analyzed for bunch composition, following the method of BLAAK et al. (1963). Non-destructive measurements as developed by HARDON et al. (1969) and CORLEY et al. (1971) were carried out to estimate the following parameters:

BI – The proportion of total dry matter production (TDM) used per palm for fruit bunch production (Y).

LA – The area of the youngest fully expanded leaf.

LAR – The ratio of the new leaf area produced to new dry matter used for vegetative growth. It should be noted that this definition differs from that used for annual crops.

VDM – The vegetative, above-ground, dry matter production per palm.

The rate of crown expansion is expressed by LA against age from field planting (for practical purposes age is used instead of the temporal order of subsequently emerging leaves). The adopted system of determining these parameters has been fully described by CORLEY & BREURE (1981).

ESTIMATED LAI FOR OPTIMUM YIELD

During the fifth and sixth year from planting leaf pruning was kept at a minimum in experiment three. The mean number of leaves per palm, based on six series of counting, was 53.7 with an absence of a plant density effect. From the 7th year onwards, estate pruning standards were followed. HARDON et al. (1969) and MOELJONO (1983) found that standard estate practice is to retain circa 50 leaves until seven to eight years from planting and thereafter circa 40 leaves. CORLEY (1983) showed that this standard number retained in the crown remain all photosynthetically active. Further, CORLEY (1973) showed that this standard number of crown leaves is not affected by planting density in the range of LAI levels studied in experiment three. CORLEY (1976) also found that retaining more than 40 leaves in nine year old palms did not increase Y. Based on these results LAI in experiment three was therefore calculated using the recorded number of leaves found in the years five and six, 50 leaves in year seven, and 40 leaves for year eight to ten. When fitting a quadratic equation through Y and LAI, the LAI for optimum yield in the periods five to seven years and eight to ten years from planting was found to be 5.2 and 4.5, respectively.

GENERAL TRENDS OF CROWN EXPANSION

Logistic growth curve. In Table 1, mean values of LA calculated for various ages are presented for the three experiments. The general pattern was a rapid initial increase, followed by a decreasing expansion rate until LA stabilized at a more or less constant level. The following logistic growth curve gave a good fit to LA values against palm age.

$$L_t = \frac{L_m L_i e^{kt}}{L_i e^{kt} + L_m - L_i} \quad (1)$$

where: L_t = LA at a certain year t from field planting; L_i = LA at field planting (based on records from experiment two, estimated as 1,00 m²); L_m = LA at its maximum, constant, level; k = the relative rate of increase in the logistic equation. Para-

Table 1. Mean values for the actual area (m²) of the youngest fully expanded leaf (A) for different ages and those estimated (E) from the logistic growth curve (equation (1)). Experiments 1, 2 and 3.

Age (months from planting)	Experiment 1			Experiment 2			Experiment 3		
	A	E	s.e. ¹	A	E	s.e.	A	E	s.e.
0				1.00					
12		1.71		1.85	1.97	0.02		1.72	
24		2.81		4.08	3.51	0.06		2.81	
36		4.32		5.64	5.43	0.05		4.27	
48		6.13		6.62	7.22	0.07	5.94	5.92	0.06
60	7.86	7.97	0.14	8.57	8.49	0.10	7.59	7.49	0.11
72	9.98	9.51	0.17	9.25	9.22	0.09	8.93	8.73	0.06
84	10.55	10.66	0.20	9.74	9.59		9.43	9.59	0.13
96		11.41			9.77		9.90	10.13	0.12
108		11.87			9.86		10.58	10.44	0.17
120		12.14			9.89			10.62	
126	12.77		0.29				10.88		
129	11.43		0.31						
135	11.71		0.33						
138							9.48		
147	13.21		0.34						
150							11.74		
L_m^2		12.49			10.00			10.37	
$t_{0.95}$		106.8			77.6			94.5	
L_m^3		12.48			9.93			10.84	
$t_{0.95}$		107.3			77.7			101.6	

¹ s.e. represents the standard error of the mean across replicates.² Based on LA values at 60, 72, and 84 months from planting.³ Based on all available LA values.

meters of interest are L_m and the time required to reach L_m . The L_m value can be derived from equation (1). In equation (1), L is an asymptotic value which means that the time required to reach L_m is infinite. For practical purposes the time to reach $0.95 L_m$, referred to as $t_{0.95}$, was therefore chosen. From equation (1) it can be derived that

$$t_{0.95} = \frac{1}{k} \ln \frac{\frac{L_m}{0.95L_m} - 1}{\frac{L_m}{L_i} - 1} \quad (2)$$

Logarithmic curve. It was found that mean LA values against palm age can also be fitted, during the stage of LA expansion, by a logarithmic curve of the form

$$L_t = a + b \ln t \quad (3)$$

where L_t is LA at a certain age t , and a and b are constants. Since equation (3) could be more conveniently determined than equation (1) this logarithmic equation (3) was applied instead of equation (1) to compare LA expansion of single palms.

Table 2. Mean of progeny values of L_m ¹ and $t_{0.95}$ ² and correlation coefficients (r) between L_m and $t_{0.95}$ based on all available LA values (Table 6) and those derived from a reduced set of LA values. Experiment 2.

Parameter	Sets of LA values (years from field planting)						
	2, 3, 4 and 5		3, 5 and 7		5, 6 and 7		years 1-7
	mean	r	mean	r	mean	r	mean
L_m	8.91	0.74**	9.94	0.98**	10.16	0.94**	9.87
$t_{0.95}$	71.9	0.37	77.9	0.75**	84.2	0.67**	80.3

¹equation 1, m².

²equation 2, months from field planting.

**p < 0.01.

Sampling technique. For experiment two, the complete set of LA data from field planting until mature LA levels (year 1-7) were collected. To obtain information on sampling methods for establishing L_m and $t_{0.95}$, these values were calculated from different, reduced, sets of LA values and compared with those derived from all available LA data. Table 2 presents, for different sets of LA values, progeny mean L_m and $t_{0.95}$ values and also the correlation coefficients for L_m and $t_{0.95}$ between progeny values based on a reduced set of LA values and those based on the complete set of LA values.

Results show that L_m and $t_{0.95}$ were underestimated when based only on early results (years 2, 3, 4 and 5) but slightly overestimated when based exclusively on more mature LA data (years 5, 6 and 7). Clearly, L_m and $t_{0.95}$ were best estimated in the period ranging from the stage of maximum LA increase to the stage at which LA approaches its maximum level, i.e. years 3, 5 and 7.

Expansion Ratio (ER). Beside L_m and $t_{0.95}$, a characteristic of practical importance during the stage of LA expansion is the ratio of the estimated LA values, established from equation (1) and (3), at a stage of maximum expansion rate against when LA approaches its maximum level.

$$ER = \frac{LA_1}{LA_2} \quad (4)$$

where: ER = Leaf Expansion Ratio; LA_1 = Estimated LA at time of maximum expansion; LA_2 = Estimated LA at time of final expansion. This Expansion Ratio expresses both the speed of ground coverage of the canopy and its subsequent competitive ability. Palms with a low ER value are referred to as Slow Expansion Rate (SER) palms and those with a high ER value as Rapid Expansion Rate (RER) palms. To test whether it is justified to apply equation (3) for comparing ER values of single palms, a sample of ten palms was drawn from each of the three densities of experiment three, for which the ER 48/126 was determined both with equation (2) and (3). The rank correlations between the two sets of ER values were highly significant (ranging from 0.98 to 1.00).

To illustrate the range of differences in crown expansion within experiment two,

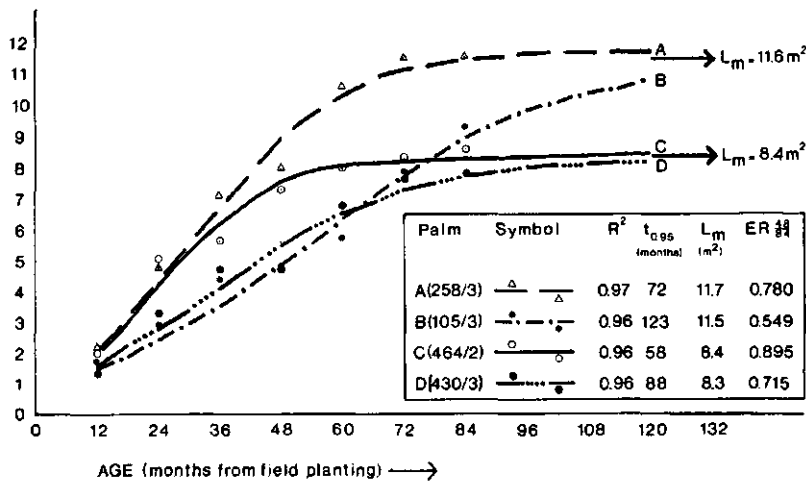
LA (m^2)

Fig. 1. LA versus time (months from field planting) of two RER palms (A and C) and two SER palms (B and D) each with a high and low L_m . Experiment 2.

Table 3. LAI¹ progression with age expressed as a percentage of LAI for optimum yield² for two RER and two SER palm types selected each for high and low L_m (Fig. 1). Experiment 2.

Age (months after field planting)	$L_m = 11.6 m^2$		$L_m = 8.4 m^2$	
	RER	SER	RER	SER
36	59	32	76	51
48	83	45	99	71
60	103	60	118	88
72	114	75	120	101
84	120	89	121	109
96	113	92	112	106
108	114	100	112	108
120	115	104	112	109

¹LAI's based on: - 50 green fronds/palm from year 3 to 7; - 40 green fronds/palm from year 8 to 10;
- Palms with $L_m = 11.6 m^2$, planted at 110 palms/ha; - Palms with $L_m = 8.4 m^2$, planted at 150 palms/ha.

²5.2 for year 3 to 7, 4.5 for year 8 to 10.

RER and SER palms were selected each with a high and a low L_m value. In fig. 1, the logistic growth curve (1) is fitted through annual LA values of these palms. Clearly, palms with high L_m values (palms A and B) should be planted at lower density than those with low L_m values (palms C and D) to reach similar LAI's at maturity. To compare their LAI progression with age it is assumed, in order to obtain a final LAI of approximately 5.00, that palms (A) and (B) will be planted at 110 palms per ha and that palms (C) and (D) at 150 palms per ha. In Table 3 LAI's for the first seven

Table 4. Mean actual leaf area values (m^2) for different ages of palms selected for slow and rapid leaf expansion ratio (SER and RER palms, respectively) together with L_m and $t_{0.95}$ estimated from the logistic growth curve (equation 1). Experiments 2 and 3.

Age (months after field planting)	Experiment 2		Experiment 3	
	high ER (SER)	low ER (RER)	high ER (SER)	low ER (RER)
0				
12	1.87	1.87		
24	4.03	4.20		
36	5.41	5.67		
48	5.82	7.21	5.64	6.50
60	8.10	8.66	7.18	8.04
72	9.43	8.76	8.83	9.10
84	10.87	9.07	9.69	9.16
96			10.38	9.44
108			11.33	10.26
120				
126			11.62	9.81
$L_m (m^2)$	11.55	9.21	11.86	10.00
$t_{0.95}$ (months)	96.7	68.4	112.4	87.0

Note: ER value are estimated using equation (3), based on estimated values for months 48 and 84 (Exp. 2) and for months 48 and 126 (Exp. 3).

years of bunch production (years 3 to 10 from field planting) are given as a percentage of LAI for optimum yield.

This sample indicates the marked differences between RER and SER ideotypes in time required to reach their optimal LAI, in particular for those ideotypes selected in a population with a high L_m .

DIFFERENCES IN CROWN EXPANSION BETWEEN EXPERIMENTS

Table 1 presents available mean LA values for the three experiments together with the L_m and $t_{0.95}$ values determined from equations (1) and (2). L_m and $t_{0.95}$ were established from the total set of LA values and also from those of identical age groups, i.e. 60, 72, and 84 months from planting.

Firstly, the similarity of the L_m and $t_{0.95}$ values based on the two sets of LA values within experiments should be noted. Secondly, there were marked differences between experiments in L_m and $t_{0.95}$ values. It is further of interest to note, in experiments one and three, that LA values showed considerable fluctuations during the stage at which LA had reached its final expansion stage.

DIFFERENCES IN CROWN EXPANSION BETWEEN SINGLE PALMS

To distinguish single palms for their crown expansion characteristics, ER values were calculated for each palm of experiments two and three. From Table 1 it can be seen that maximum LA expansion in experiments two and three occurred approximately

Table 5. Progeny mean values of area leaf 1 (m^2) for palms of different ages together with maximum leaf area (L_m) and time required to reach 0.95 L_m ($t_{0.95}$) estimated from the logistic growth curve (equation 1). Experiment 1.

Progeny	Age (months from field planting)								$t_{0.95}$ ¹	L_m ²	R^2 ³
	60	72	84	126	129	135	147	mean			
51	8.46	10.46	11.05	12.23	10.81	11.30	13.10	11.06	94.1	12.00	0.73
52	7.98	8.96	10.92	12.81	11.48	11.64	13.40	11.16	105.3	12.51	0.86
53	8.03	10.34	11.01	12.93	11.31	11.72	13.19	11.22	102.2	12.42	0.84
54	7.91	10.09	10.56	12.74	11.05	11.10	12.54	10.86	101.1	12.00	0.81
55	7.93	10.24	10.80	13.12	11.42	11.82	13.52	11.26	105.0	12.62	0.84
56	8.05	10.05	10.85	12.66	11.66	11.98	13.25	11.21	104.2	12.54	0.91
57	8.40	10.38	10.90	12.64	10.99	11.72	13.22	11.18	98.6	12.23	0.79
58	8.36	10.56	11.26	12.87	11.68	11.73	13.91	11.48	101.0	12.67	0.81
59	8.55	10.73	11.42	13.34	11.88	12.13	13.96	11.72	100.7	12.92	0.83
60	7.68	9.82	10.57	12.28	11.43	11.48	12.64	10.84	105.2	12.16	0.92
61	8.28	10.62	11.17	13.43	12.03	11.93	13.59	11.58	102.7	12.84	0.86
62	8.70	10.83	11.83	13.30	11.87	12.27	13.44	11.68	98.9	12.81	0.87
64	7.98	9.73	10.87	12.30	11.10	11.71	12.34	10.86	101.3	11.99	0.91
65	8.07	10.32	10.94	12.56	12.02	11.94	13.16	11.29	103.5	12.55	0.93
66	8.05	9.91	10.47	12.87	10.79	11.23	12.93	10.81	99.8	11.85	0.80
Mean	8.16	10.26	10.94	12.71	11.43	11.71	13.21	11.21	101.5	12.42	
LSD 5%	0.42	0.48	0.52	0.76	NS	NS	NS	0.47	6.6	0.34	

¹ Months from field planting.

² m^2 .

³ R^2 = Coefficient of determination.

48 months from field planting. ER values were therefore determined, using equation (3), based on estimated values for months 48 and 84 (ER 48/84) and months 48 and 126 (ER 48/126), respectively. Subsequently from each plot, palms with the two lowest (SER palms) and two highest ER values (RER palms) were selected. The pooled actual LA values of these SER and RER palms together with their L_m and $t_{0.95}$ values, are presented in Table 4. The marked differences in L_m and $t_{0.95}$ values between SER and RER palms should be noted.

GENOTYPIC DIFFERENCES IN CROWN EXPANSION

Tables 5 and 6 present available LA values for progenies of experiments one and two, together with their L_m and $t_{0.95}$ values established from equations (1) and (2). Progenies showed significant differences in mean LA, L_m and $t_{0.95}$ values. In Table 5, for example, progeny 51 had a significantly higher LA than progeny 55 at 60 months from planting, but at month 126 the reverse was observed although LA of progeny 55 was not significantly higher than progeny 51. In column 10 it can be seen that progeny 51 reached 0.95 L_m nearly one year earlier than progeny 55. As another example, in Table 6, progenies BM 119.16 and BM 119.26 showed the same L_m but the difference in their $t_{0.95}$ values was more than six months. These results indicate the potential progress which can be made in breeding for more desirable trends in crown expansion.

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Table 6. Progeny mean values of area leaf 1 (m^2) for palms of different ages together with maximum leaf area (L_m) and time required to reach 0.95 L_m ($t_{0.95}$) estimated from the logistic growth curve (equation 1). Experiment 2.

Progeny	Age (months from field planting)								$t_{0.95}$ ¹	L_m ²	R^{23}
	12	24	36	48	60	72	84	mean			
DM 742.112	1.92	4.23	5.57	6.70	8.69	9.29	10.34	6.68	81.1	10.46	0.98
205	1.75	3.95	5.46	6.34	8.32	8.86	9.81	6.36	81.8	9.97	0.98
207	1.91	4.44	5.89	7.07	9.22	9.97	10.93	7.06	79.5	11.00	0.98
307	1.78	3.77	5.51	6.37	8.07	8.78	9.45	6.25	78.7	9.55	0.98
316	1.91	4.08	5.81	6.53	8.85	9.59	10.54	6.76	82.2	10.69	0.98
503	1.82	3.98	5.62	6.70	8.29	9.04	9.81	6.47	78.4	9.89	0.98
Mean DM 742	1.85	4.08	5.64	6.62	8.57	9.26	10.15	6.57	80.3	10.26	
DM 743.202	1.69	3.74	5.48	6.06	7.58	8.52	9.16	6.04	80.2	9.26	0.98
207	1.81	3.93	5.43	6.10	8.20	8.87	9.31	6.24	80.0	9.61	0.98
210	1.72	3.57	5.32	5.79	7.70	8.72	9.48	6.04	87.5	9.91	0.98
302	1.81	4.02	5.54	6.53	8.49	9.03	9.67	6.44	78.8	9.88	0.98
510	1.68	3.79	5.23	6.02	8.19	8.73	9.33	6.14	82.6	9.65	0.98
514	1.69	3.58	5.36	6.26	7.99	8.05	8.75	5.95	76.1	8.90	0.99
Mean DM 743	1.73	3.77	5.40	6.13	8.03	8.65	9.28	6.14	80.9	9.54	
BM 119.16	1.82	3.87	5.38	6.06	7.97	8.62	9.59	6.19	82.2	9.68	0.97
26	2.07	4.38	5.62	6.58	8.54	9.17	9.75	6.59	75.8	9.75	0.97
Mean BM 119	1.94	4.13	5.50	6.32	8.26	8.90	9.67	6.39	79.0	9.72	
Trial Mean	1.81	3.95	5.52	6.37	8.29	8.95	9.71	6.37	80.4	9.87	
Progeny LSD 5%	0.07	0.16	0.28	0.38	0.48	0.45	0.55	0.39	5.8	0.54	
1%	0.09	0.22	0.38	0.52	0.67	0.60	0.73	0.52	7.8	0.72	

¹ Months from field planting.

² m^2 .

³ R^2 = coefficient of determination.

DENSITY AND FERTILIZER EFFECTS ON CROWN EXPANSION

Fertilizer and density effects on annual LA values were presented in an earlier publication (BREURE, 1982). In experiment three, no density effect on LA was found for measurements taken 60, 72, 84 and 96 months from planting, but thereafter (with LA approaching its maximum value) a highly significant reduction in LA was found due to higher density planting. Fertilizers increased LA only at a mature stage, viz. 96 to 120 months from field planting, and exclusively in the 110 palms per ha density. At this stage the F-test showed that the interaction between density and fertilizers was significantly negative ($p < 0.05$). Including some more recent results, equation (1) was fitted through the available set of sub-plot mean LA values. Results, as presented in Table 7, show a positive response of $t_{0.95}$ and L_m to fertilizers at the 110 palm per ha treatment, but an absence of response at the higher densities. This indicates a fertilizer \times density interaction which, however, just failed to be significant at the 5% level. Mean L_m and $t_{0.95}$ were significantly reduced by higher density planting.

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Table 7. Effects of planting density and fertilisers on maximum leaf area (L_m) and time required to reach 0.95 L_m ($t_{0.95}$) estimated from the logistic growth curve (equation 1). Experiment 3.

Fertiliser level	L_m (m ²)				$t_{0.95}$ (months)			
	density (palms/ha)				density (palms/ha)			
	110	148	186	mean	110	148	186	mean
0	10.58	10.42	9.87	10.29	98.3	96.7	90.5	95.2
1	10.94	10.57	9.85	10.45	107.4	95.4	91.8	98.2
2	11.41	10.57	9.94	10.64	105.2	97.3	89.8	97.5
3	11.57	10.23	9.82	10.54	106.2	93.8	88.0	96.0
Mean	11.12	10.45	9.87	10.48	104.3	95.8	90.0	96.7

Table 8. Dry matter production (kg/palm/annum) incorporated in fruit bunches (Y) and vegetative growth (VDM) of palms selected for slow (SER) and rapid (RER) leaf expansion in two planting densities. Experiments 2 and 3.

Age (months after field planting)	Experiment 2				Experiment 3			
	115 palms/ha		143 palms/ha		110 palms/ha		148 palms/ha	
	SER	RER	SER	RER	SER	RER	SER	RER
	Y	VDM	Y	VDM	Y	VDM	Y	VDM
24-36	69		69		64		65	
36-48	95	91	95	90	91	90	94	90
48-60	117	90	115	87	112	90	116	88
60-72	100	117	110	108	88	119	98	114
72-84	87	116	92	106	88	116	90	107
84-96							114	126
96-108							120	138
108-120							118	125
120-132							125	123
SUM	468	414	481	391	443	415	463	399
							905	882
							941	835
							651	822
							708	789

Note: the standard deviation values were within 11-29 (Exp. 2) and within 10-38 (Exp. 3).

COMPARISON OF DRY MATTER PRODUCTION BETWEEN RER AND SER PALMS

In Table 8, available mean values of Y and VDM are presented for RER and SER palms of two comparable densities of experiments two and three. As could be expected, SER palms stabilize at a relatively higher VDM level, in particular at the lower densities. The latter is probably due to the fact that potential differences in VDM between SER and RER palms can be better effectuated when light is less limiting. RER palms showed a higher cumulative Y than SER palms during the first seven years from field planting. At a later stage (experiment 3) differences in Y between RER and SER palms are less clear. It is, however, the yield of oil which is important economically. The determination of the oil content of fruit bunches in experiment two showed that RER and SER had a similar oil/bunch ratio, i.e. 23.6% and 23.3%, respectively. The benefi-

Table 9. Comparison of BI, TDM (kg/palm/annum) and LAR values between RER and SER palms of experiment 2 (143 palms/ha) and experiment 3 (148 palms/ha).

Age (months after field planting)	Experiment 2						Experiment 3					
	SER palms			RER palms			SER palms			RER palms		
	TDM	BI	LAR	TDM	BI	LAR	TDM	BI	LAR	TDM	BI	LAR
36-48	181	0.503	2.04	184	0.511	2.36						
48-60	202	0.554	2.11	204	0.569	2.43	224	0.567	2.11	242	0.583	2.26
60-72	207	0.425	2.14	212	0.462	2.20	204	0.505	2.16	217	0.548	2.24
72-84	204	0.431	2.16	197	0.457	2.02	200	0.405	2.14	198	0.449	2.13
84-96							200	0.360	2.06	197	0.406	1.97
96-108							205	0.395	1.96	197	0.401	1.85
108-120							200	0.360	1.98	210	0.395	1.79
120-132							176	0.290	1.96	173	0.312	1.74

cial effect of a more rapid crown expansion of RER palms on Y was expressed at an earlier stage in the higher densities. This could have been due to the well known effect of less competition for water on yield between palms and a more shaded ground cover, as occur in the higher densities. In Table 9, TDM, BI and LAR values are compared for RER and SER ideotypes selected from the two slightly suboptimal densities of experiments 2 and 3, i.e. 143 and 148 palms/ha, respectively (at present 130 palms/ha is the recommended density in West New Britain). The expected characteristics of RER ideotypes are confirmed. RER ideotypes showed higher TDM values prior to canopy closure, higher BI values and a decreasing trend in LAR values with age.

DISCUSSION

Results of LA (the area of the youngest fully expanded leaf) measurements in one experiment, as given in this paper, expose some of the limitations of earlier published conclusions which were based on restricted sets of LA data. For example, CORLEY et al. (1973) reported little effect of planting density on LA in four spacing experiments in Malaysia, and prematurely arrived at the conclusion that LA can be used to estimate optimal density for current yield independently of the yield potential of the environment. However, LA values in their experiments were established while the leaves were still expanding. Results of experiment three indeed confirmed an absence of density effect on LA during the expansion stage but at a later stage, with LA approaching its final size, our results showed a considerable decrease in LA due to higher density planting. Since the trend of LA with age is contingent upon planting density (Table 7) it is concluded that the equation, as formulated by CORLEY et al. (1973), to estimate optimal current density from LA, does not hold. Further, CORLEY & MOK (1973) reported a significant response to potassium chloride on LA in two experiments planted at densities of 114 and 138 palms per ha. This fertilizer effect was observed when LA in their experiments had reached a mature level of 10.6 m². Again, their results could only be confirmed when potassium chloride was applied to palms under similar

levels of inter-palm competition, i.e. 110 palms per ha in an environment where inter-palm competition is more intense (BREURE, 1982), and during the final stage of LA expansion. However, our results showed an absence of response to potassium chloride at higher densities or during the stage of rapid LA expansion.

Results of Table 7 and those reported in a previous paper (BREURE, 1982) may indicate that the supply of assimilates and mineral nutrition per palm only affect L_m but not the relative rate of increase (k -value in equation (1)). This suggests that L_m is determined by the sink strength of the leaves. The magnitude of L_m could therefore be regarded as a measure of the sink strength of the leaves.

Based on pooled results of LA measurements in plantations of different ages in Malaysia, CORLEY & GRAY (1976) observed that the size of a standard leaf increases progressively up to about eight or ten years, when it reaches a maximum which is maintained for at least 10 years. A similar trend of LA expansion over age was reported by HARDON et al. (1969). This trend could be confirmed when LA data of experiments one, two and three are combined (Table 1). CORLEY et al. (1973) and HARDON et al. (1969) assumed a linear relationship between palm age and LA until it reached its maximum level. However, the LA values against palm age as presented in their reports clearly indicate that the logistic equation (1) would have given a better fit through their LA data. GRAY (1969) found on the coastal soils in Malaysia a large fluctuation in LA. These LA values were obtained from several plantings of ten years and older, at which time these plantings presumably had reached their final stage of expansion. GRAY's results (1969) are not at odds with the present findings (see Table 1) in that seasonal differences in LA do exist in one particular planting (experiment one and three) and in that actual differences in L_m were obtained among the three different plantings (experiment one, two and three). It was found (BREURE, unpublished) that a seasonal difference in fruiting activity (number and fruit set of developing bunches on the palm) is responsible for the fluctuating LA values at mature levels. BREURE (1982) produced evidence that LA differences between experiments one, two and three were also associated with differences in fruiting activity (fruit set and the duration of disbudding during the early stage of flowering).

In experiments where different progenies and single palms within progenies are compared, one single set of LA measurements, as suggested by HARDON et al. (1969), had limited value in estimating relative mean LA. The ranking of progenies and, in particular, single palms, on the basis of LA, changed with age. This is clearly shown by frequently recorded progeny LA values (Tables 5 and 6) and by the comparison of LA values of SER and RER palms (Table 4).

This investigation proves that parameters derived from a logistic growth curve, i.e. L_m and $t_{0.95}$, are more meaningful for studying treatment effects on LA in breeding and agronomy experiments. Results of Table 1 and 2 indicate that reliable L_m and $t_{0.95}$ values can be estimated from only three series of LA measurements. Results of Table 9 show that the differences in TDM, BI and LAR between RER and SER palms are indeed as could be expected based on their distinct trends in crown expansion. The differences in TDM and BI between RER and SER palms were more pronounced in experiment three. This is probably due to the fact that in experiment three inflorescences were removed during the first year of flowering (resulting in a reduced sink size of Y) which results in a better expression of potential VDM as shown by CORLEY

(1976). The combination of a higher initial TDM and a higher BI from the start of mutual shading (Table 9) will give RER palms a higher bunch yield during the entire economic life of a planting. Since our results showed that RER and SER palms did not differ in oil to bunch ratio this also results in a higher oil yield. In particular, the higher early yield of RER palms should result in a more favorable discounted cash flow.

BREURE & CORLEY (1983) found that the palms in experiment three, which were exclusively selected for high LAR (as calculated at 48 to 72 months from planting) did not render palms tolerant of high density planting as expected on theoretical grounds (CORLEY, 1976). Results of Table 9 indicate that a combination of high initial LAR and a relatively low LAR at mature LA levels would have been a more effective method of selecting palms capable of yielding well at high density. Results of Tables 4, 5 and 6 indicate the feasibility of breeding and selection for the apparently more desirable RER ideotypes. The frequent and time consuming measurements required to establish reliable ER values might be considered to be a drawback to adopting ER as a parameter for selection. But fortunately, as pointed out by HARDON et al. (1982), the recent development of tissue culture techniques offers the possibility of a rapid multiplication of a good genotype, which justifies working with time consuming selection criteria.

The more intensive and earlier fruiting in experiment two had, presumably, induced an initially higher sink of generative growth at the expense of the sink size of vegetative growth with a long lasting residual effect. The recent introduction of oil palm pollinator insects, resulting in a higher percentage fruit set than the previous system of assisted pollination (SYED, 1979), may therefore also contribute to reducing both L_m and $t_{0.95}$. The implication would be that the presently adopted planting density could be increased, and that palms will have a higher BI.

In conclusion, to maximize oil yield, the importance of measuring LA expansion is stressed. The present paper shows that, in addition to breeding and selection, cultural practices (planting density, fertilizer rate, pollination standards, and ablation) are of relevance to achieving a more favorable trend in crown expansion. With respect to breeding and selection it is worth noting that the F_1 progenies tested in this paper are derived from highly inbred male and female parents. It is likely that more pronounced differences in magnitude of parameters describing crown expansion trends will be found when individual progenies would originate from a more heterogeneous and less inbred parental population. Clearly, the greatest progress in the near future will come from the multiplication of desirable phenotypes within existing populations through vegetative propagation.

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REFERENCES

- BEIRNAERT, A., & R. VANDERWEYEN, 1940. Note préliminaire concernant l'influence du dispositif de plantation sur les rendements. *Publs. Natn. Étude Agron. Congo Belge. Sér. Tech.* 27: 26 pp.
- BLAAK, G., L. D. SPARNAAIJ & T. MENENDEZ, 1963. Breeding and inheritance of the oil palm. Part II: Methods of bunch quality. *J. W. Afr. Inst. Oil Palm Res.* 4: 145-155.
- BREURE, C. J., 1977. Preliminary results from an oil palm density \times fertiliser trial on young volcanic soils in West New Britain. In: D. A. EARP & W. NEWALL (Eds), *International developments in oil palm. Kuala Lumpur, Incorporated Society of Planters.* p. 192-207.
- BREURE, C. J., 1982. Factors affecting yield and growth of oil palm *tenera* in West New Britain. *Oléagineux* 37: 213-228.
- BREURE, C. J. & R. H. V. CORLEY, 1983. Selection of oil palms for high density planting. *Euphytica* 32: 177-186.
- BREURE, C. J., J. KONIMOR & E. A. R. ROSENQUIST, 1982. Oil palm selection and seed production at Dami Oil Palm Research Station, Papua New Guinea. *Oil Palm News* 26: 6-22.
- CORLEY, R. H. V., 1973. Effects of plant density on growth yield of oil palm. *Expl. Agric.* 9: 169-180.
- CORLEY, R. H. V., 1976. Photosynthesis and productivity. In: R. H. V. CORLEY, J. J. HARDON & B. J. WOOD (Eds), *Oil palm research.* Amsterdam, Elsevier. p. 55-76.
- CORLEY, R. H. V., 1983. Photosynthesis and age of oil palm leaves. *Photosynthetica* 17: 97-100.
- CORLEY, R. H. V. & C. J. BREURE, 1981. Measurements in oil palm experiments. 35 pp. Internal report. London, Unilever Plantation Group.
- CORLEY, R. H. V. & B. S. GRAY, 1976. Yield and yield components. In: R. H. V. CORLEY, J. J. HARDON & B. J. WOOD (Eds), *Oil palm Research.* Amsterdam, Elsevier. p. 77-86.
- CORLEY, R. H. V., J. J. HARDON & G. Y. TAN, 1971. Analysis of growth of the oil palm (*Elaeis guineensis* JACQUIN) I. Estimation of growth parameters and application in breeding. *Euphytica* 20: 307-315.
- CORLEY, R. H. V., C. K. HEW, T. K. TAN & K. K. LO, 1973. Optimal spacing for oil palm. In: R. L. WASTIE & D. A. EARP (Eds), *Advances in oil palm cultivation.* Kuala Lumpur Incorporated Society of Planters. p. 52-69.
- CORLEY, R. H. V. & C. K. MOK, 1972. Effects of nitrogen, potassium and magnesium on growth of the oil palm. *Expl. Agric.* 8: 347-353.
- DONALD, C. M., 1968. The breeding of crop ideotypes. *Euphytica* 17: 385-404.
- GRAY, B. S., 1969. A study of the influence of genetic, agronomic and environmental factors on the growth, flowering and bunch production of the oil palm on the West Coast of West Malaysia. Ph. D. Thesis, University of Aberdeen. 947 pp.
- HARDON, J. J., R. H. V. CORLEY & C. W. LEE, 1982. Breeding and selection for vegetative propagation in the oil palm. In: *Proceedings of the VIII Long Ashton Symposium on 'Improvement of vegetatively propagated plants'.*
- HARDON, J. J., C. N. WILLIAMS & I. WATSON, 1969. Leaf area and yield in the oil palm in Malaysia. *Expl. Agric.* 5: 25-52.
- MARIJNEN, T., 1973. Contribution à l'étude de la densité de plantation chez les végétaux. *Publ. I.N.E.A.C., Série Scientifique* no 102: 79 pp.
- MOELJONO, T., 1983. Personal communication. Bah Lias Research station, North Sumatra, Indonesia.
- PREVOT, P. & J. DUCHESNE, 1955. Densités de plantation pour le palmier à huile. *Oléagineux* 10: 117-122.
- SLY, J. M. A. & L. S. CHAPAS, 1963. The effect of various spacings on the first sixteen years of growth and production of the Nigerian oil palm under plantation conditions. *J. W. Afr. Inst. Oil Palm Res.* 4: 31-45.
- SYED, R. A., 1979. Studies on oil palm pollination by insects. *Bull. Ent. Res.* 69: 213-224.
- WIT, C. T. DE, H. H. VAN LAAR & H. VAN KEULEN, 1979. Physiological potential of crop production. In: J. SNEEP & A. J. T. HENDRIKSEN (Eds), *Plant breeding perspectives.* Wageningen, Pudoc. p. 47-81.

THE EARLY DEVELOPMENT OF INFLORESCENCES AND FLOWERS OF THE OIL PALM (*ELAEIS GUINEENSIS* JACQ.) SEEN THROUGH THE SCANNING ELECTRON MICROSCOPE

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SUMMARY

The development of inflorescences and flowers of the African Oil Palm up to anthesis is illustrated by scanning electron microscopy images. The time of origin relative to the development of the foliage leaves of the basipetalous succession of flowering rachillae is determined, as well as the time of morphological sex definition. The logical stage when sex is determined is inferred to be not before the first appearance of the spikelet primordia. Female flower groups develop acropetally as triaxial cincinni, the male units as reduced ones. A developmental diagram is added.

INTRODUCTION

Various workers have contributed to the description of inflorescence development and mature flowers of the oil palm (*Elaeis guineensis* Jacq.); for a review see Hartley (1977) and Corley & Gray (1976). These descriptions, in some reports accompanied by illustrations (Beirnaert, 1935; Henry, 1961; Corley & Gray, 1976), are based on light-microscopical observations. Recently, there has been a growing interest in the use of scanning electron microscopy for this type of study which permits more detailed observation of the successive stages which can be more clearly described by means of scanning photographs.

The oil palm produces male and female inflorescences in separate leaf axils on the same palm, one in each axil. A succession of several inflorescences of one sex is followed by a succession of the other in alternating cycles, but occasionally hermaphrodite inflorescences occur. Developmentally, all flowers are bisexual, a feature already described by Beirnaert (1935). The initiation of inflorescences starts soon after the first leaf primordia are laid down, being 40 to 45 leaves before the stage at which a leaf attains its full expansion. As the expanding leaf is usually numerated as leaf 0, this corresponds to leaf -40 to -45. Anthesis occurs at about leaf 17.

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On male and female inflorescences a similar phyllotaxis and number of spikelets (rachillae) is found (Thomas et al., 1970). In contrast, the difference in early morphology between male and female spikelets is very pronounced in that the number of bracts subtending the flowers is greater on male spikelets (between 700–1200) than on female spikelets (10–20). This led Corley (1976) to suggest that sex cannot be distinguished by external morphology until growth of the floral bracts has commenced. In the present study the development stages will be, among others, composed for one palm with a continuous record of male inflorescences and one with only female inflorescences in order to confirm Corley's suggestion.

Furthermore, on male spikelets one single (male) flower per bract develops, whereas female inflorescences bear floral groups or floral clusters of which the central female flower normally reaches anthesis. Corley & Gray (1976) pointed out that these flower clusters appear very similar to those described by Tomlinson & Moore (1968) for the palm *Nannorhops ritchiana*, which is why they adopted the branching scheme given by these authors to illustrate the trifloral group in oil palm. The composition has been recognized as a monochasial sympodial branching system, i.e., a cincinnus. Uhl (1976) described the trifloral groups in *Ptychosperma* as cincinni.

The objective of this paper is to provide a description and comment on all stages of inflorescence development from the primordium of the central axis to up to anthesis of the flowers, with the relevant stages illustrated by scanning photographs. We feel that these photographs in particular will further contribute to the botanical description and our understanding of the developmental characteristics of the oil palm, which is one of the most important perennial crops in the tropics. Photographs of the fully formed inflorescences showing their eventual shape are given by Sparnaay (1969).

MATERIALS AND METHODS

The inflorescence primordia of eight oil palms were prepared and fixed in formalin-acetic acid-ethanol solution at the Dami Oil Palm Research Station at Kimbe (Papua New Guinea). One of the palms produced almost entirely male inflorescences, another one female, based on continuous recording during six years.

The primordia were transferred to 50% ethanol, prepared, dehydrated in dimethoxymethane, critical point dried in carbondioxide, gold sputtered, and photographed in the scanning electron microscope at the Rijksherbarium, Leiden, the Netherlands.

RESULTS

The description should be compared with the series of photographs. In addition, an explanation of the photographs is presented at the end of this paper.

At a very young stage the inflorescence is an elliptic primordium which is surrounded by two spathes. This primordium is flattened on the side of the palm axis. First, two lateral bracts develop; the anterior and posterior bracts lagging behind (photo 1). This slight difference in rate of development is considered due to spatial

conditions, in that greater pressure is exerted on the primordium between the leaf and palm axis. In a similar way this difference in developmental rates occurs in later stages, as will be described below. On the further expansion of the primary apex of the inflorescence primordium more bracts are spaced out; this marks the starting point of the formation of the parastichies of bracts (photos 2 to 4). These parastichies develop acropetally.

We could not find differences by which male and female inflorescences could be distinguished at this stage (photo 5 to 7), neither in the form of the bracts nor in their phyllotaxis (compare Thomas et al., 1970).

Secondary, flowering axes originate in the axils of the bracts of the primary, central, axis of the inflorescence primordium (photo 8). They develop either into male or female spikelets (rachillae). There is a pronounced basipetal sequence in the origin and further development of the spikelet primordia, in other words their development starts somewhat below the apex of the primary axis and continues downwards (photos 9 to 10). The opening of the flowers at anthesis follows the same sequence. On the other hand, as the development of the spikelet primordia begins when the acropetal development of the primary axis is incomplete, spikelets also originate and further develop in an acropetal sequence which is, however, less pronounced. The first spikelets primordia originate in some lateral bracts, the development of which is more advanced than the dorsoventral bracts for reasons mentioned above. This critical stage when spikelet primordia are formed in the subapical region is easily observed because the first development of spikelet primordia in the axils of their subtending bracts causes the latter to stand out from the slope of the apex of the inflorescence. The origin of the flowering axes can also be observed with a powerful dissecting microscope using appropriate fixation and staining of the inflorescence primordium, with JKJ for example.

As on the primary axis, the two lateral bracts on the spikelets develop first (photo 11), and the anterior and posterior bracts lag behind. When the spikelet primordia are larger and less subject to pressure, the remaining bract parastichies are started and further develop acropetally. The distal part of a female spikelet remains sterile, and develops into a spine. It is a well known fact that the number of bracts and of their parastichies is much greater in male than in female spikelets (photo 12, 13, and 25). As also pointed out by Corley (1976), the difference in the number of early bracts arising on the base of the spikelet primordia is the first available morphological sign for sex definition. It can also be observed with a good dissecting microscope after proper staining as indicated above.

Flowers arise in the axils of each bract. Developmentally they are all bisexual, but in male spikelets numerous solitary male flowers occur, whereas on female spikelets a triad of flowers arises in the axil of each bract. Each such triad normally consists of a functional female in the centre of two non-functional male flowers. That the male flower is a reduced triad is explained later in this paper.

In some palms other than the oil palm the composition of the triad has been recognized as a monochasial sympodial branching system (see the review by Moore & Uhl, 1982). For oil palm this pattern was first investigated by Beirnaert (1935), but

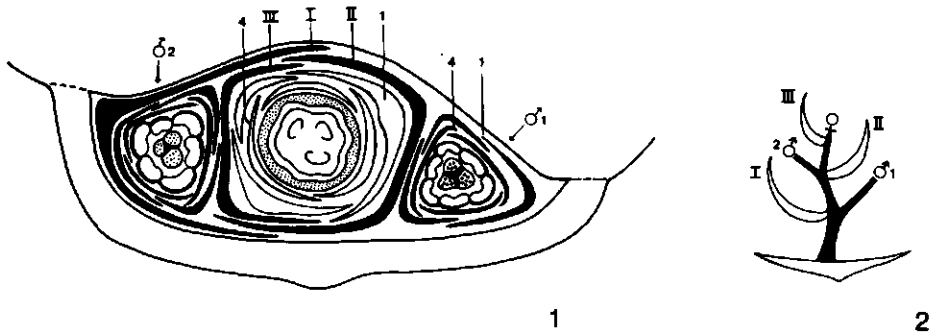


Fig. 1. Developmental diagram of a triad of flowers on a female spikelet. — Fig. 2. The cincinnal branching system explaining figure 1.

his diagram is incorrect in respect of the position of the bracteoles and the orientation of the male flowers and the carpels. Smit (1969) found that in the coconut palm triads represent cincinnal cymes. He pointed out that the triads are similar in the oil palm, a near relative within the *Coccoideae*. Corley & Gray (1976) presented an original diagram which conforms to our results. Figure 1 shows the composition of the triads on a developmental basis. It is idealised only in that the young male companion flowers in reality are located on a slightly higher level of cross-section. The ramification scheme explaining our diagram (fig. 2) shows the condensed axes in their theoretical position. There is only a minor difference to the scheme given by Corley & Gray (1976), which was based on Tomlinson & Moore (1968). They suggested a basal fusion between the axillary axes and the preceding axes, whereas in our scheme these parts are free at the base.

The developmental analysis of the triad as a cincinnus that was given by Uhl (1976) for the palm *Ptychosperma* is the only study of that kind for palms to date. In the present paper a similar approach is presented for the oil palm. The development begins with separation of a bracteole I from the triad primordium (photo 15). This occurs on the base laterally, to either side. The greater part of the primordium develops into the male flower 1. Development continues in the axil of bracteole I giving the reduced secondary axis of the triad (photo 17). From this axis bracteole II, and male flower 2 originate opposite bracteole I (photo 18). Similarly, in the axil of bracteole II the third reduced axis develops, from which bracteole III arises opposite bracteole II, and ending in the female flower (photo 19). Thus there is a succession of three reduced alternating axes each producing a bracteole and a terminal flower (photos 20 and 21). The result is a cincinnus. In contrast, in a male spikelet a solitary male flower and its bracteole are formed which correspond in position and time with female flower 1 and its bracteole I of the triad in a female spikelet (photo 27). As men-

tioned above, the development of the flowers on the male spikelet thus corresponds to the initial development on the female spikelet, but with its further development arrested. Basally, the whole triad is buried in a pit formed by its subtending bract and the flowering axis. The three flowers of a triad are arranged linearly, but the female flower may be shifted to the front or the back or turned slightly.

The angular form of the bracteoles II and III, as shown in cross-section, does not indicate that they are bicarinate prophylls as often found in monocotyledons as they are simple during development. The outer tepals may also be somewhat angular. However, this angularity is caused by mutual pressures in later stages of development.

It is remarkable that the first tepals of all flowers originate invariably opposite to the bracteoles of the flowers (photo 18, 20, and 27). The three outer tepals do not originate as a whorl of equidistant parts but rather the first tepal is advanced, the next two tepals together lagging behind. The same is true for the whorl of three inner tepals, the first of which (tepal 4) always originates opposite tepal one. Each whorl of tepals looks as if it is composed of a bract and two bracteoles. These features are also shown in figure 1.

The carpels originate free from each other as semi-globular primordia along the slope of the apex of the flower. They become slightly horseshoe-shaped. Later, when growing upwards, they are contiguous with their lateral faces (photo 22). Their lateral parts overarch the apex, on which one ovule primordium develops axillary to each carpel (photo 23). Later on, the young carpels are elevated by common zonal growth at the base, especially on the outside. By this 'fusion' the proximal part of the gynoecium which encloses the ovules is formed.

The ordinal leaf axil in which the different stages in inflorescence development are found may vary considerably according to the age of the palm, and its environment. The results obtained in various groups of dissected palms by Henry (1961), Corley & Gray (1976), and Breure & Menendez (in prep.), are compared with our results in table 1, which gives for mature palms the range of leaf axil numbers where the first bracts subtending the spikelets are initiated, the first spikelets initiated, and when the latter are differentiated. A possible explanation of these differences may be seasonal fluctuations in leaf production in that the stage of rapid expansion of the leaves is vulnerable to changes in environment as shown by Broekmans (1958). These changes can be due to the availability of water, stress on the palms consequent to the load of developing bunches etc.

CONCLUSIONS

Morphological definition of the sex of an inflorescence is possible only when the first bracts are initiated on spikelet primordia. We may suppose that the morphogenetic impulse causing sex differences acts before this. However, it is unlikely that this will be before the first appearance of the axillary meristems that give rise to the spikelets. The formation of spikelets starts in the axils of subapical bracts and proceeds mainly basipetally, whereas the development of the main axis of the inflorescence is acropetalous.

Table 1. The ordinal number of foliage leaves in which important stages in inflorescence development are found according to various authors.

	Henry, 1960	Corley & Gray, 1976	Van Heel, Breure & Menendez, 1987	Breure & Menendez (in prep.)
Initiation of first bract	-33	-20 to -29	-25, -26*	-18 ± 1.9 ¹
Spikelet initiation	-20	-7 to -13	-10 to -8	-4 ± 1.2
Spikelet differentiation (morphological sex definition)	-10	-2 to 0	-4 to -2	-2 ± 1.7
Number of palms dissected	not known	8-23	8 (*2)	48

¹) standard deviation.

The investigation has confirmed that the triads of flowers on female spikelets are triaxial monochasial systems, that is cincinni. The flowers on male spikelets are equivalent to the first monoaxial part of the female system.

A future publication will describe the further developmental morphology of flowers up to and beyond anthesis and of certain abnormalities, namely mantled fruits, androgynous inflorescences (see Hartley, 1977), and dysfunctional anthesis (Lawton, 1982).

ACKNOWLEDGEMENT

Our thanks are due to Bertie Joan van Heuven and Linda Putman for their technical cooperation.

REFERENCES

- BEIRNAERT, A. 1935. Introduction à la biologie florale du Palmier à huile (*Elaeis guineensis* Jacquin). Publications I.N.E.A.C., Série Scientifique 5: 1-42.
- BROEKMANS, A.F.M. 1957. Growth, flowering and yield of the oil palm in Nigeria. J. W. Afr. Inst. Oil Palm Res. 2: 187-220.
- CORLEY, R.H.V. 1976. Inflorescence abortion and sex differentiation. In: R.H.V. Corley, J.J. Hardon, B.J. Wood (eds.), Developments in Crop Science 1: 37-56. Elsevier, Amsterdam.
- & B.S. GRAY. 1979. Growth and morphology. In: Ibidem: 7-19.
- HARTLEY, C.W.S. 1977. The Oil Palm. 2nd Ed. Longman, London.
- HENRY, P. 1961. Recherches cytologiques sur l'appareil floral et la graine chez *Elaeis guineensis* et *Cocos nucifera*. I. La formation de l'appareil floral. II. Les fleurs et la graine. Rev. gén. Bot. 68: 111-132, 164-198.

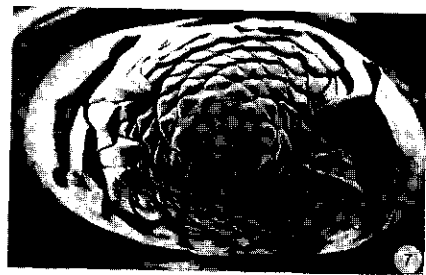
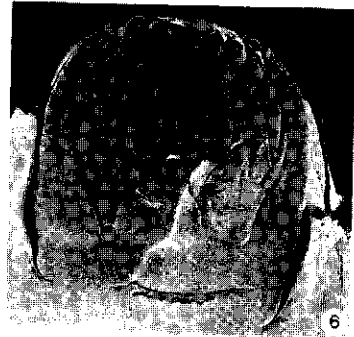
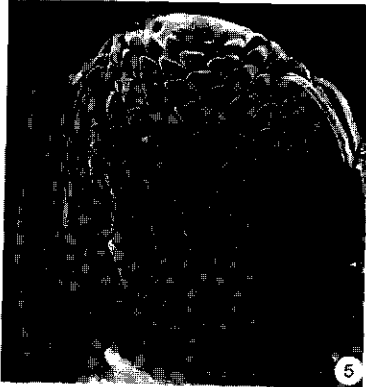
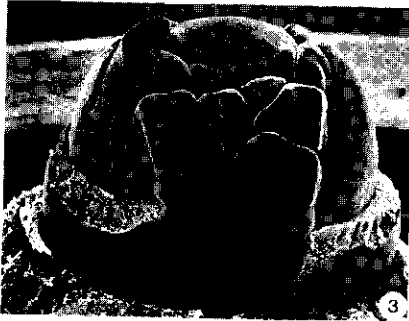
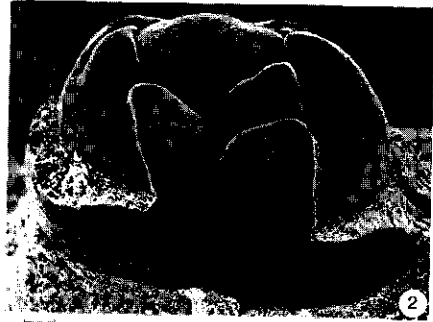
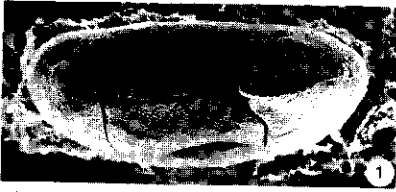
- LAWTON, D.M. 1982. Pollination and fruit set in Oil Palm (*Elaeis guineensis* Jacq.). In: Proc. Int. Conf. Oil Palm in Agriculture in the Eighties, Kuala Lumpur, June 1981: 241–262.
- MOORE, M.E. & N.W. UHL. 1982. Major trends of evolution in palms. Bot. Review 48: 1–69.
- SMIT, E.H.D. 1969. Morphological and anatomical studies of the coconut. Thesis. Wageningen.
- SPARNAAY, L.D. 1969. Oil palm (*Elaeis guineensis* Jacq.). In: F.P. Ferwerda & F. Wit (eds.), Outline of perennial crop breeding in the tropics. Misc. Papers 4: 339–387. University of Wageningen.
- THOMAS, R.L., K.W. CHAN & S.C. NG. 1970. Phyllotaxis in the oil palm: Arrangement of the male/female spikelets on the inflorescence stalk. Ann. Bot. 34: 93–105.
- TOMLINSON, P.B. & H.E. MOORE Jr. 1968. Inflorescence in *Nannorrhops ritchiana* (Palmae). J. Arn. Arb. 49: 16–34.
- UHL, N.W. 1976. Development studies in *Ptychosperma* (Palmae). I. The inflorescence and the flower cluster. II. The staminate and pistillate flowers. Amer. J. Bot. 63: 82–109.

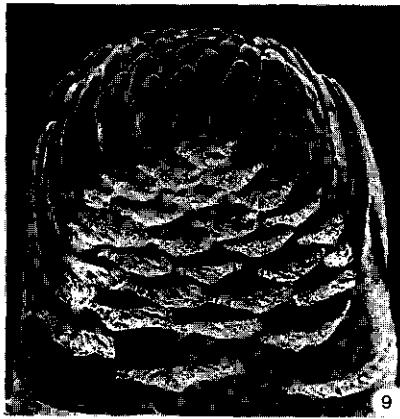
EXPLANATION OF THE PHOTOGRAPHS

(All bars represent 0.1 mm, except where indicated otherwise)

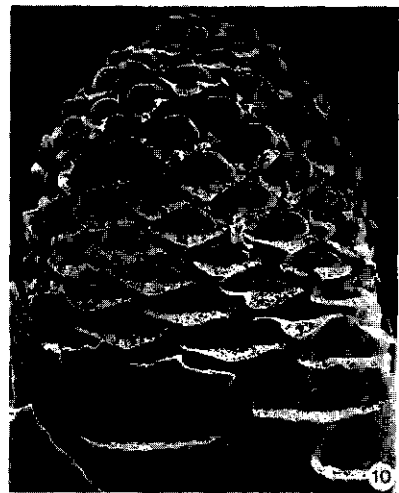
- Photo 1. Inflorescence showing primordial central axis with its bracts: seen from above, adaxial, flattened, side uppermost; anterior and posterior bracts lag behind in development.
- Photo 2. Inflorescence showing primordial central axis, slightly older, seen from the side. The first lateral bracts (prophylls) are removed. Their position is somewhat more to the abaxial side.
- Photo 3. Ibidem. The onset of parastichies of bracts which develop in acropetal direction.
- Photo 4. Ibidem, slightly older. The first lateral bracts have been left in position.
- Photo 5. Young inflorescence showing the spiral development of the bracts on the main axis. Tips of lower lateral bracts are removed. This is an inflorescence of a consistently male palm, in the axil of foliage leaf -9.
- Photo 6. Ibidem. This is an inflorescence of a consistently female palm (leaf -9). Its sex cannot be distinguished morphologically at this stage (compare photos 5 and 6).
- Photo 7. The same inflorescence, seen from above.
- Photo 8. Portion of the apex of a primordial inflorescence that is slightly older. The initiation of the flowering axis in the axil of two lateral, subapical, young bracts is shown as two bulging axillary meristems.
- Photo 9. Young inflorescence seen from the side. The bracts are removed to expose the axillary meristems giving the flowering axes.
- Photo 10. Central axis of young inflorescence, the bracts removed. Note the mainly basipetal, but also acropetal, development of the axillary flowering axes. Their development begins three quarters up the length of the central axis. Accordingly it is in that region that the flowering axes give rise to their two first lateral bracts.
- Photo 11. Portion of young inflorescence, the bracts removed, showing the primordial flowering axes. Their first two lateral bracts originate slightly shifted on the abaxial side. The further development of the flowering axes takes place in mainly basipetal but also acropetal sequence.
- Photo 12. Two very young female flowering axes. Their bracts originate in acropetal direction, the lateral ones being prominent. Compare the male counterpart in photo 25, that has more bracts. At this stage sex can be distinguished morphologically.
- Photo 13. Ibidem, slightly older. On the distal part no further primordial bracts develop.
- Photo 14. Upper portion of young inflorescence, carrying female spikelets in the axils of bracts. The spikelets themselves also show their bracts and their sterile tips. For this view no bracts have been removed.

- Photo 15. Portion of female spikelet, the bracts removed. The axillary meristems represent the primordial triads of flowers. First they give off the bracteoles I, either to the left or to the right.
- Photo 16. One young female flowering axis (spikelet, rachilla). Some bracts are removed, uncovering the development of the axillary triads of flowers. In this stage each triad shows the bracteole I and the male flower 1. The male flower shows the cap-shaped tepal 1 laterally and tepal 2. The counterpart of this stage on a male spikelet is shown in photo 27. On a male spikelet no further new development of flowers occurs.
- Photo 17. Young triad showing bracteole I on the left (removed) and male flower 1 with its tepal 1 – laterally – and tepal 2 (tepal 3 is not visible). In the axil of the bracteole I the triad is developing further.
- Photo 18. Young triad showing two male flower primordia. Young male flower 1 is on the right and its bracteole I on the left (removed). Its tepals 1 and 2 are removed. Male flower 2 and its bracteole II (removed) develop in the axil between bracteole I and flower 1. The tepals 1, 2 and 3 of each flower develop like a bract and 2 bracteoles in position and time. Tepal 1 of each flower is opposite to its bracteole. Likewise tepal 4 in male flower 1 is shown to be opposite to tepal 1. Compare with fig. 1.
- Photo 19. Ibidem, but older. The triad continues development in the axil between bracteole II and male flower 2, producing the female axis (in the lower background). The male flowers show the origin of a gynoeceium, that is arrested later on. In both male flowers one stamen primordium is replaced by two smaller ones.
- Photo 20. Triad showing bracteoles I and II (partly sectioned) and male flower 1 and 2 (removed). In the axil of bracteole II the female axis originates. This axis carries bracteole III and a primordial female flower with its tepal 1 opposite to bracteole III, and the tepals 2 and 3 lagging behind in development.
- Photo 21. Slightly older triad showing in the centre a very young female flower (with primordial tepals 1, 2 and 2) and its bracteole III. This female structure is axillary to bracteole II and male flower 2 (scar). The whole again is axillary to bracteole I and male flower 1 (stalk). This photograph is to be compared with figures 1 and 2.
- Photo 22. Young female flower (tepals removed) with three young carpels in the centre. The six stamen primordia are slightly connected at the base, and do not further develop.
- Photo 23. Young gynoeceium with four free carpels in the centre (two frontal ones removed). Around it a whorl of supernumerary arrested stamen primordia. The flanks of the carpels bulge over the apex. One ovule primordium originates on the apex in the axil of each carpel.
- Photo 24. Young ovule; the carpel removed.
- Photo 25. Portion of the main axis of a male inflorescence (bracts removed) showing young male spikelets. The numerous bracts on the spikelets develop in acropetal parastichies. The female counterpart of this stage is depicted in photos 12 and 13. This is the stage of morphological sex definition.
- Photo 26. Portion of male inflorescence (older stage) with young male spikelets axillary to the bracts (not removed). Numerous bracts develop on the spikelets acropetally.
- Photo 27. Portion of male spikelet (the floral bracts removed). The male flower units consist of a male flower 1 and the bracteole I (the tepals are in part removed). The cap-shaped tepal 1 originates opposite to the bracteole I, and the tepal 4 opposite to tepal 1. Tepals 2 and 3 lag behind in development. The female counterpart of this stage is given in photo 16.

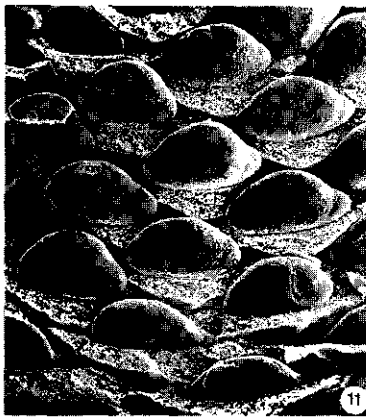




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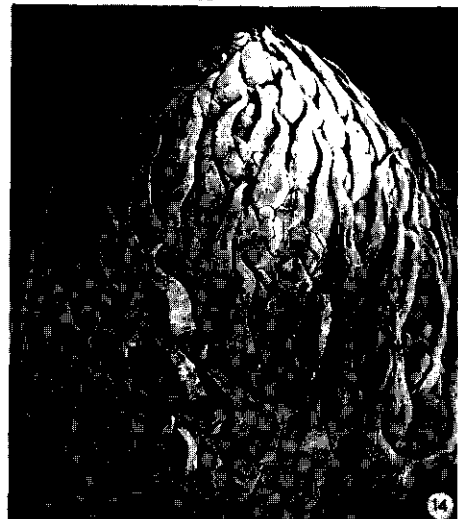
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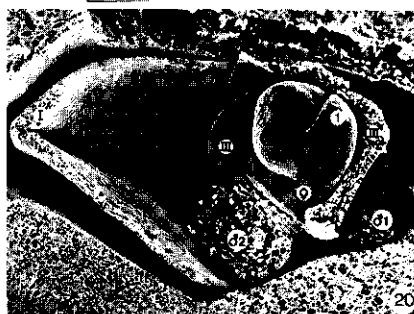
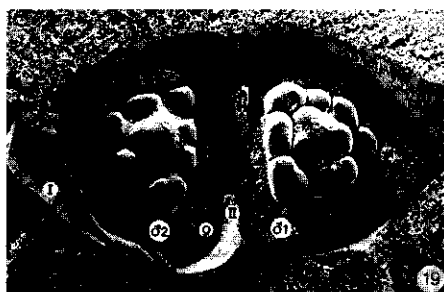
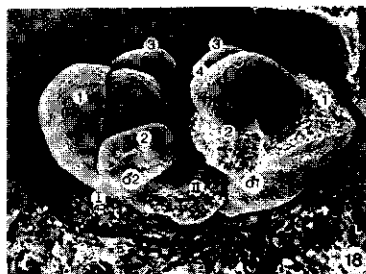
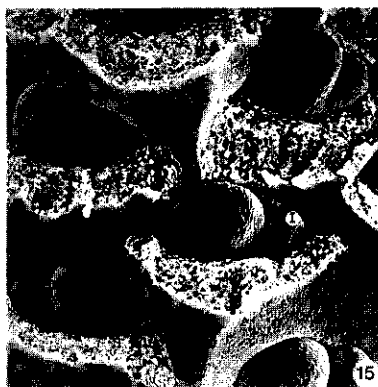
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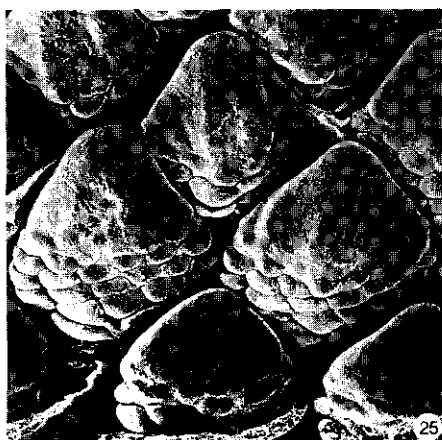


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THE DETERMINATION OF THE COMPONENTS OF BUNCH YIELD
IN THE DEVELOPMENT OF INFLORESCENCES IN
OIL PALM (*Elaeis guineensis*, Jacq.).
I. BUNCH NUMBER COMPONENTS.

C.J. Breure and T. Menendez

SUMMARY

The stage in oil palm inflorescence development at which abortion and sex differentiation, both determining the number of bunches produced, take place were identified by thinning (a part of) the 186 palms ha⁻¹ treatment of a spacing experiment at the Dami Oil Palm Research Station, Papua New Guinea. The developmental stage at which the resulting drop in abortion rate (the proportion of aborted inflorescences to total leaves produced) and that of the gain in sex ratio (the proportion of female to total inflorescences) occurred, was established by comparing abortions and sex of the surviving inflorescences of the unthinned and thinned group against sequentially numbered leaves (L-numbers). The corresponding scale in inflorescence development was derived by dissecting (a sample of) felled palms.

Sex differentiation appears to occur 6 to 7 leaves prior to spikelet initiation. Abortion occurred at the onset of rapid elongation of inflorescences, about 10 leaves prior to anthesis. Initially, abortion was preferential for female inflorescences, but later on both females and males aborted in equal proportion. The initial reduction in abortion and, at an earlier developmental stage, the rise in the proportion of females differentiated as a result of thinning, caused two peaks in the load of developing bunches (fruiting activity) on the thinned palms which apparently eliminated temporarily the gain in sex ratio. The occurrence of fruiting activity provided further evidence for the developmental stage at which sex

determination occurs.

Our study suggests that abortion and sex definition occur at a specific stage in inflorescence development. But considerable differences in time-lags between these critical developmental stages and anthesis may occur due to variations in environmental conditions and fluctuating levels of carbohydrate status of the palms.

INTRODUCTION

Bunch yield of oil palm (*Elaeis guineensis*, Jacq.) depends on the number of bunches produced (and their mean weight which is the subject of part II of the article). Bunch number, in turn, is mainly determined by the number of female inflorescences reaching anthesis as losses during bunch development are usually negligible.

The oil palm is monoecious producing on the same palm, in each leaf axil, either a male or a female inflorescence. Some inflorescences may abort before anthesis. The rate of leaf production thus sets an upper limit to bunch number; this potential number is only obtained in exceptional cases. In practice, bunch production depends on the proportion of female inflorescences differentiated (sex ratio) and on the abortion rate (the proportion of leaves with aborted inflorescences).

It is well documented that the critical stage for abortion is when inflorescences start to expand rapidly which occurs about 10 leaves, corresponding (at mature palms) to about 5 months, prior to anthesis (Henry, 1960; Broekmans, 1957; Gray, 1969; Corley, 1976). But there is uncertainty as to what extent abortion is preferential for either male or female inflorescences (Henry, 1960; Broekmans, 1957; Bredas & Scuvie, 1960). Corley (1976) concluded from results of a defoliation trial that, in his trial, the majority of the aborted inflorescences were females, which implies that abortion appeared to have reduced the sex ratio. But if abortion is mainly preferential for female inflorescences, males would frequently interrupt series of leaves with abortions, which is not supported by our observation on long term flowering

records of individual palms. To solve this inconsistency, we used a thinning intervention (sudden removal of interpalm competition for light) on palms of the 186 palms ha^{-1} density of a spacing experiment (at Dami Oil Palm Research Station, Papua New Guinea) at the start of a period with an exceptionally high rate of abortion. Thinning strongly reduces abortion (Breure et al, in prep.; Corley, 1976), and by comparing the sex ratio of the unthinned palms, for which abortion remained high, with those of the thinned palms to be regarded as a reference or zero level of abortion, we evaluated the effect of abortion on sex ratio. Further, in order to confirm other reports on the critical developmental stage for abortion, we recorded the response of abortion to thinning against sequentially numbered leaves (L-numbers). The corresponding scale in inflorescence development was derived by dissecting a sample of felled palms.

Corley (1976) introduced the thinning and dissection method to identify the stage in inflorescence development at which the sex is determined (fixed). He arrived at the conclusion that sex definition takes place just prior to the initiation of the first bract subtending the spikelets. This is at an earlier developmental stage than might be expected because male and female inflorescences do not differ in the number of spikelets, but they do substantially in the number of flowers per spikelet. More likely would therefore be the stage just prior to the appearance of the bracts subtending the flowers on the spikelet (spikelet differentiation), as pointed out by van Heel et al (1987). The present paper aims to substantiate the botanical viewpoint, for which the same thinning and dissection method of Corley (1976) is applied.

This implies that part of the present report is devoted to construct a developmental scale for inflorescence development based on the dissection of the felled palms, together with thinning, and to index the developmental stages in terms of successive leaf numbers. To identify the developmental stage of sex definition and other critical stages instead of counting actual time intervals can be argued by the fact that a developmental stage is more universally applicable than recording the time that elapses between a causative impulse,

such as thinning or heavy pruning, to the moment that changes in, for example sex ratio at anthesis, becomes manifest. The reason is that considerable fluctuations in speed of inflorescence development may occur (Broekmans, 1957; Corley, 1976), contingent on palm age and on seasonal and environmental differences in growing conditions. Indeed, the time intervals between sex determination and anthesis are generally shorter in the more favourable environments of Asia and the Pacific regions (cf Corley, 1986) than those of West Africa (Broekmans, 1957; Sparnaaij et al, 1963). Time-lags may be even less reliable in case of a severe drought because, in contrast to the abrupt thinning treatment of the present study, the actual start of the drought is not clearly defined. Moreover, because there is considerable evidence that variation in sex ratio depends on the carbohydrate level in the palms (Beirnaert, 1935; Broekmans, 1957; Sparnaaij, 1960), the timing may be delayed when the drought occurs at a favourable carbohydrate status.

To maximize the effect of thinning on abortion and on sex ratio, we thinned at the onset of a period with an unusually high load of developing bunches on the palms; from the report of Corley & Breure (in prep.) it can be derived that such a high "fruiting activity", as termed by Broekmans (1957), exerts a strong claim on carbohydrate supplied by the leaves. Because the very act of thinning results in an increase in photosynthetic production, this exceptional demand for carbohydrate will be better met in the thinned than in the unthinned group. In other words, thinning at high fruiting activity is expected to further enhance the difference in sex ratio and in abortion rate between the thinned and unthinned group.

Note, however, that the increase in number of bunches due to thinning must result, some time after thinning, in a corresponding rise in fruiting activity on the thinned palms. The first increase supposedly will come from a reduction in abortion rate so that the effect of fruiting activity is expected to be sudden and shortlived. The reason is that increasing the amount of light not only results in a gain in number of surviving females but, as pointed out by Broekmans

(1957), also in an accelerated inflorescence development.

The effect of fruiting activity is taken into account in the present study, which mainly aims to identify the stage in inflorescence development at which sex differentiation occurs, and to elucidate the aspect of preferential abortion of female inflorescences.

MATERIALS AND METHODS

Experimental palms were selected from a density experiment, planted at Dami Oil Palm Research Station, Papua New Guinea, in October 1970. The experiment compares 56, 110, 148, and 186 palms ha^{-1} density treatments which are arranged in randomized blocks with four replications. Palms of the highest density were divided into two groups. From one group at least three of the (six) surrounding palms were felled, in October 1981, to leave 80 experimental palms. These palms, for which the amount of light was enhanced, are referred to as the "thinned" group which is compared with 80 core palms of experimental plots of the "unthinned" group.

At the moment of thinning, the first fully opened leaf was given the ordinal number (L) +1. From that time onwards, all the leaves were sequentially numbered by giving leaves in the crown a positive and those emerging after thinning a negative number. Pairs of two sequential L-numbers are pooled in the analysis because a pair of two leaves corresponds, in mature palms, to the convenient time interval of approximately one month (Hartley, 1977).

At Dami mean daily sunshine varies from 3.9 hours in January to 6.5 in September, with a total of about 2000 hours per year. Rainfall is about 4000 mm per annum and is well distributed, so that there is usually no water deficit (Waringa, 1985). Nevertheless, in the course of the experiment a drought prevailed between July and November 1982 (Breure & Menendez, in prep.).

Pollination was outstanding at the moment of thinning because the activity of pollinating insects, introduced earlier in the year, was still undisturbed by predators. Further, thinning

coincided with a peak in anthesizing females. Joint occurrence of excellent pollination and high number of females caused a higher than usual "fruiting activity" on the palms at the time of thinning.

RECORDING

Inflorescence development

From all 80 felled palms the length of the inflorescences of both sexes, in L-numbers +1 to +13, was measured from the base of the proximal spikelet to the tip of the inflorescence. That range of L-numbers was chosen as it includes the developmental stage at which inflorescences are known to show a rapid expansion (Corley, 1976). Anthesis was recorded, against L-numbers, at the moment of thinning.

From a sample of 48 palms longitudinal sections were made of inflorescence primordia (referred to by their L-number). These primordia were examined under a light microscope (Staritsky & Breure, 1985), for the following main stages:

1. Initiation of the first bract subtending the spikelets.
2. Spikelet initiation.
3. Initiation of the first bract subtending the flowers on the spikelets.

These stages, and a summary of their corresponding L-number as reported by others, are described in greater detail by van Heel et al. (1987).

Stage of determination

The components of the number of bunches under study are sex ratio (the proportion of female to total inflorescences) and rate of abortion (the percentage of leaves with aborted to total leaves). Sex of the inflorescences and abortions were first recorded monthly for leaves opening between January 1973 and December 1977 (prior to thinning). Statistical analysis employed on these preliminary data (Fisher's exact two-sided χ^2 -test) revealed that sex ratio and abortion of the thinned and unthinned group were only significantly ($P < 0.05$) different in three and six out of 60 monthly pairs of records, respectively; these differences were unsystematically either

positive or negative. Thus by and large flowering of the two groups was the same, so that differences emerging after thinning cannot be ascribed to sampling error.

From October 1981 to November 1984 (the first three years after thinning) flowering was recorded against sequentially numbered leaf axils (L-numbers).

RESULTS AND DISCUSSION

INFLORESCENCE DEVELOPMENT.

Developmental scale

Dissection of felled palms revealed the following. Mean values of L-numbers (with standard deviation in brackets) for the main stages in inflorescence development were for (1) the initiation of the first bract subtending the spikelets, (2) spikelet initiation, and (3) initiation of the first bract subtending the flowers on the spikelets, L -18 (1.9), L -4 (1.2), L -2 (1.7), respectively. Anthesis was found at L +17 (1.3).

On palms of similar ages grown on the coastal alluvium of West Malaysia, Corley (1976) observed a similar ordinal distance in L-numbers between the first two stages, but his real scores indicate an earlier differentiation (L-27 and L -11, against L -18 and L -4 in our study). On the other hand, Corley's result agrees with that of a sample of palms dissected, in the same experimental area, about two years after thinning (van Heel et al, 1987). Because their method differed from the present study, an additional study on primordia of a sub-sample of six felled palms was done using the method of van Heel et al (1987), i.e. examining inflorescence primordia under a powerful dissecting microscope after staining with JKJ. Employing this alternative technique confirmed the present finding that spikelet initiation at the time of thinning occurred at L -4.

Variations between L-numbers are more rule than exception (cf Corley, 1976), which is likely due to the effect of environmental conditions on speed of inflorescence development.

Expansion of the inflorescences

Inflorescences grew slowly during the period shortly after leaf opening but in older leaves, around L +6, a more rapid expansion was observed (Figure 1).

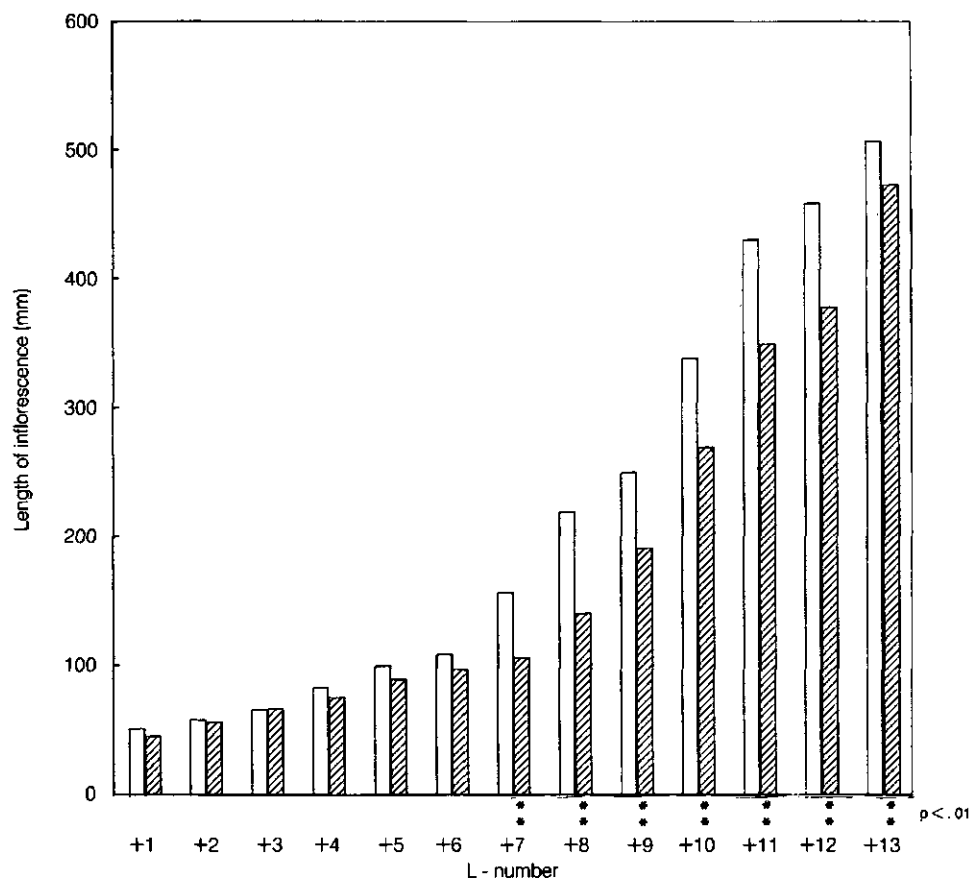


Figure 1 Length of male  and female  inflorescences in leaf axil (L-) number +1 to +13.

Our results agree well with those of Broekmans (1957), who referred to a phase 1 (slow expansion) and a phase 2 (rapid expansion). Fig 1 also shows that female inflorescences reached the rapid expansion stage about one leaf earlier, corresponding to about two weeks, than male inflorescences when females were also larger. The advantage in length of the female over the male inflorescences, reported earlier by Corley (1976), was highly significant ($P < 0.001$) at L +7 and from that number

onwards.

INFLORESCENCE ABORTION

Critical developmental stage

Figure 2 shows, regardless of sex of the inflorescences, the percentage abortions of the thinned and unthinned palms against age of the inflorescences at the moment of thinning (pairs of sequential L-numbers).

Abortion started to become significantly lower (Fishers's exact two-sided χ^2 -test) in the thinned than in the unthinned palms in axils of leaves L +11/+12. The reduction, however, became consistent and more pronounced in leaves younger than L +7/+8, indicating that L +7/+8 is, in general, the critical stage for floral abortion. Remember that at about L +7 we observed the beginning of a rapid expansion of the inflorescences (Fig 1). The observation that these two stages coincide is consistent with other reports (Henry, 1960; Broekmans, 1957; Corley, 1976).

Sex of aborted inflorescences

Table 1 presents, for both groups of palms, the total number of aborted inflorescences against L-numbers ranging from +9 to -6, i.e. the critical range in which, based on van Heel et al (1987), any difference in sex ratio between unthinned and thinned palms can only be attributed to preferential abortion.

The data pattern is consistent with the trend for the whole range under study (Fig 2) in that, on the average, much more inflorescences aborted in the unthinned than in the thinned group (26.3 against 3.9 in the thinned group). Because of the relatively low abortion rate of the thinned palms, this group can be regarded as a reference against which a decrease in sex ratio of the unthinned (high abortion) indicates preferential abortion of female inflorescences. The right column of Table 1 shows that abortion of the unthinned group by and large did not change the sex ratio of the surviving inflorescences (with averages of .33 and .29), except for L +5, L +6 and L +7 where a significantly lower ($P < 0.01$) sex ratio was observed for the unthinned (.18) than for the thinned (.35) group. Thus in this range, aborted inflorescences in

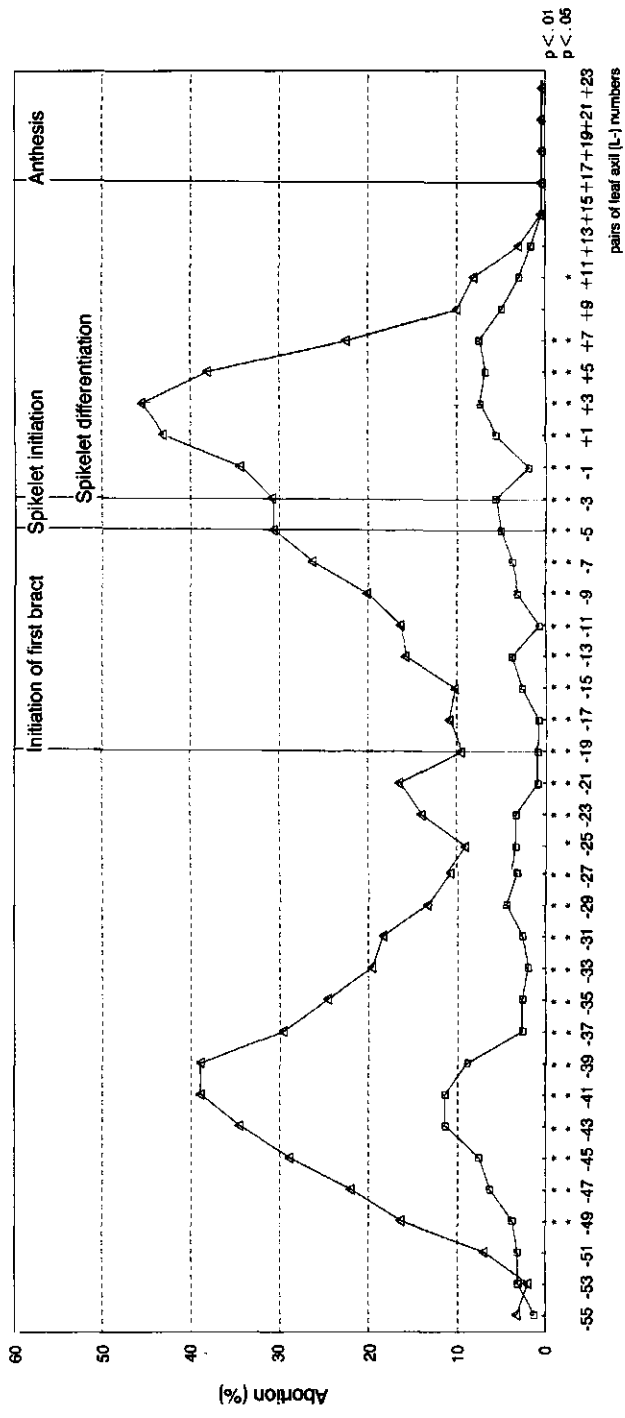


Figure 2 Abortion (%), plotted against two sequential leaf axil (L-) numbers, for thinned (\circ - \circ) and unthinned (Δ - Δ) palms.

Table 1. Number of aborted inflorescences of eighty thinned (T) and eighty unthinned (UT) palms for leaf numbers (L) +9 to +6, together with the sex ratio values of T and UT palms.

<u>L-number</u>	<u>Aborted inflorescences</u>			<u>Sex ratio</u>	
	T	UT	Difference	T	UT
+9	3	10	-7	0.29	0.33
+8	8	14	-6	0.33	0.29
+7	3	21	-18	0.36	0.19
+6	5	28	-23	0.39	0.21
+5	5	32	-27	0.31	0.13
+4	5	35	-30	0.17	0.22
+3	6	37	-31	0.16	0.09
+2	5	32	-27	0.08	0.10
+1	3	36	-33	0.10	0.18
0	1	26	-25	0.23	0.30
-1	1	28	-27	0.37	0.37
-2	4	23	-19	0.45	0.42
-3	4	25	-21	0.59	0.47
-4	2	21	-19	0.59	0.58
-5	5	27	-22	0.53	0.49
-6	3	24	-21	0.31	0.34
Mean	3.9	26.2	22.3	0.33	0.29

the unthinned group must have been mainly females. Note that L +5, +6, +7 were the first leaf axils in which abortion of the unthinned palms strongly increased (Table 1). Further, that in these leaves female inflorescences became larger, and rapid expansion started in a younger leaf, than males (Fig 1). Since the base of such young crown leaves is still tightly connected with its neighbouring leaf, female inflorescences would be more compressed during their expansion than males. The higher pressure on expanding females, following the hypothesis of Broekmans (1957), would possibly explain why females are more prone to abortion than males at the onset of the prolonged abortion phase.

The observation that the disadvantage in survival of female inflorescences is bound to this period only, is thus not consistent with results reported by Corley (1976). His results appear to indicate that preferential abortion of female inflorescences may occur for at least 6 months.

SEX DETERMINATION

Critical developmental stage

In Figure 3 the proportion of female to total inflorescences (sex ratio) of the thinned and unthinned palms is plotted against age of the inflorescence primordia at the moment of thinning (paired L-numbers). Sex ratio of the unthinned palms is used as a reference against which significant (Fisher's exact two-sided χ^2 -test) increments at the oldest developmental stage are indicative for the developmental stage of sex differentiation (only L-numbers prior to spikelet initiation should be considered because in older leaves, based on van Heel et al (1987), the sex must already be determined).

Figure 3 shows that L -11/-10, about 6 leaves prior to spikelet initiation, is the first candidate. Note that we found the same L-numbers for the determination of the number of flowers per spikelet (part 2 of this article), which is the key morphological characteristic to differentiate the sexes. This observation supports sex differentiation to occur at L -11/-10. It is also the approximate stage which van Heel et al (1987) concluded from their detailed morphological study on oil palm inflorescence development. Empirical support from field studies is further provided by Corley (1976), who also found the first significant increment in sex ratio of the thinned palms just prior to spikelet initiation in one of the two experiments studied. In his study the gain in sex ratio of the thinned palms disappeared in a set of younger leaves, similar to the virtual disappearance of response between L -17 to -23 (Fig 3). Such temporary lack of response to thinning might be associated with the expected increase in fruiting activity of the thinned palms.

Fruiting activity

The first peak in fruiting activity due to thinning must originate from the reduction in abortion of female inflorescence between L +5 and +12 (Table 1) and also from the coincidental higher sex ratio between L +13 and +14 (Fig 3). Inflorescences in these leaves reach anthesis about 3 to 5 months after thinning, resulting in a rise in fruiting activity shortly thereafter. Considering the inferred stage of sex

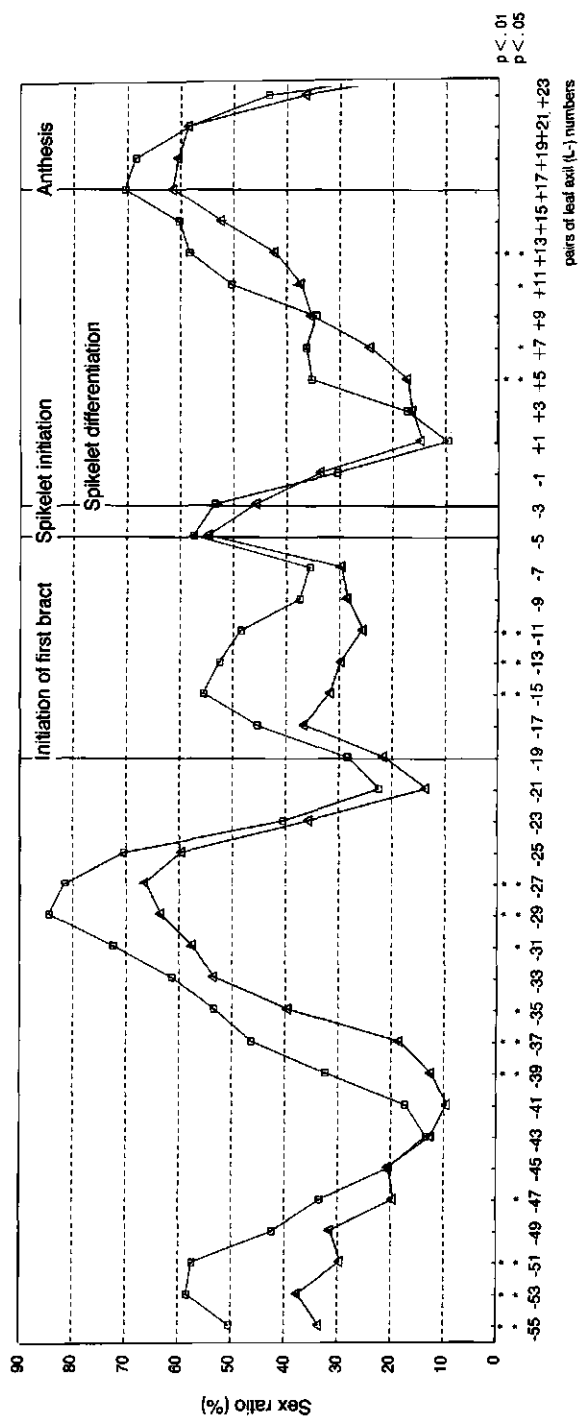


Figure 3 Sex ratio (%), plotted against two sequential leaf axil (L-) numbers, for thinned (□) and unthinned (△) palms.

differentiation 6 to 7 leaves prior to spikelet initiation (Fig 3), this peak might reasonably have negatively affected the sex ratio of primordia in L -17 to -23.

Fig 3 depicts another disappearance of response of sex ratio to thinning between L -40 and -44. In the same vein, a second peak in fruiting activity originating from the first strong increment in number of females differentiated as a result of thinning, between L -12 to -16 (Figure 3), looks a reasonable explanation for this temporary drop in response.

Thus, the apparent relation between these two peaks in fruiting activity and the inferred stage of sex differentiation provides additional confirmation that sex differentiation occurs about 6 leaves prior to spikelet initiation.

Time intervals

Assuming the usual production of two leaves per month, sex differentiation at L -10/-11 would correspond with a time-interval of 14 months between sex differentiation and anthesis (Fig 3). This value is at odds with Corley's (1976) observation of a drop in sex ratio 19 to 22 after a severe drought in Malaysia. There is a greater difference between our results and those of Sparnaaij et al (1963) who inferred time intervals between sex differentiation and anthesis of 24 to 26 months under West African conditions.

There are several possible reason for such discrepancies. First, the delay in spikelet initiation of the experimental palms at the moment of thinning (L -4 against L -10 reported by van Heel et al (1987) in the same experimental area some time after thinning). Further, while rate of leaf production in West Africa and Asia is quite similar (Sparnaaij, 1963), dissections of palms growing in the West African environment all suggest that here spikelet initiation occurs in lower L- numbers. For example, in West Africa Henry (1960) observed spikelet initiation at L -20; also, Henry (1960) , and Beirnaert (1935) appear to have observed spikelet differentiation (stage at which sex is distinguishable) in L -10 to -15 against L -2 usually found in Asia (Corley, 1976). Broekmans (1957) inferred from dissection of the bud that differentiation must take place 18 months before anthesis, which means that he appears to have

observed sex differentiation at about L -18. These reports indicate a slower speed in inflorescence development than in the Asian environment.

Second, because there is evidence that sex differentiation is influenced by the carbohydrate supply (Beirnaert 1935; Sparnaaij 1960), the level of carbohydrate status at the moment of treatment application may be relevant. In case of a drought, for example, it is quite likely that palms deplete their carbohydrate reserve first to a critical value before the number of females differentiated is reduced. In contrast, in our experiment, as can be inferred from the pronounced difference in abortion rate between unthinned and thinned palms shortly after thinning (Figure 3), the gain in carbohydrate supply of the thinned palms must have been sudden and quite pronounced. From these considerations the hypothesis may be put forwards that sex determination takes place at a specific stage in inflorescence development, but that time-lags between a causative impulse and anthesis may vary with the speed in inflorescence development and also with the carbohydrate status of the palms.

CONCLUSIONS

The developmental stage at which abortion of inflorescences occurs (about 10 leaves prior to anthesis) agrees very well with that reported by others (for a review see Corley, 1976). Both sexes appear to abort in equal proportion, except during the start of the abortion phase when we observe preferential abortion of female inflorescences. This phenomenon may be associated with our observation and that of Corley (1976) that, during rapid elongation, female inflorescences are larger, and thus more compressed by their subtending leaf axil, than male inflorescences; female inflorescences may thus be more sensitive to changing carbohydrate status than males.

Sex differentiation, in our experiment, occurs a few leaves prior to spikelet initiation which is at a later developmental stage than suggested by Corley (1976); but some of his results actually indicate the same developmental stage.

The hypothesis is put forwards that sex differentiation and

abortion are bound to specific stages in inflorescence development, irrespective of external conditions. Great variations in time intervals from sex differentiation or abortion to anthesis may then occur mainly due to differences in speed of inflorescence development. In this respect a slower speed in inflorescence development in West Africa than in the more favourable environment of South East Asia and the Pacific region may explain the generally larger intervals reported from Africa. Another contributing factor to varying time-lags may be the carbohydrate status of the palms at the moment of a stressful conditions.

In order to apply our results for yield prediction, therefore, more research is needed on factors associated with speed in inflorescence development and on the relevance of changing levels of carbohydrate status.

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REFERENCES

- BEIRNAERT, A. (1935). Introduction à la biologie florale du palmier à huile (*Elaeis guineensis* Jacq.). Publs. Inst. natn. Etude agron. Congo Belge. Sér. Sci., 5: 42 pp.
- BREDAS, J & SCUUVIE, L., 1960. Aperçu des influences climatiques sur les cycles de production du palmier à huile. Oléagineux, 15, 211-222.
- BROEKMANS, A.F.M. (1957). Growth, flowering and yield of the oil palm in Nigeria. J.W.Afr.Inst. Oil Palm Res., 2: 187-220.
- CORLEY, R.H.V. (1976). Inflorescence abortion and sex differentiation. In: R.H.V. CORLEY, J.J. HARDON & B.J. WOOD (Eds.). Oil Palm Research, Amsterdam, Elsevier: 37-55.
- GRAY, B.S. (1969). A study of the influence of genetic, agronomic and environmental factors on the growth, flowering and bunch production of the oil palm on the West Coast of West Malaysia. Ph.D Thesis, University of Aberdeen, 947 pp.
- HARTLEY, C.W.S. (1977). The oil palm. London, Longman. 806 pp.
- HENRY, P., (1960). Recherches cytologiques sur l'appareil floral et la graine chez *Elaeis guineensis* et *Cocos nucifera* L. La formation de l'appareil floral. Rev. gén. Bot., 68, 111-132.
- HEEL, van W.A., BREURE, C.J. & MENENDEZ, T. (1987). The early development of inflorescences and flowers of the oil palm (*Elaeis guineensis* Jacq.) seen through the scanning electron microscope. Blumea, 32, 67-78.
- SPARNAAIJ, L.D., (1960). The analysis of bunch production in the oil palm. J.W. Afr. Inst. Oil Palm Res., 3, 109-180.
- SPARNAAIJ, L.D., REES, A.R. and CHAPAS, L.C. (1963). Annual yield variation in oil palm. J.W. Afr. Inst. Oil Palm Res., 4, 111-125.
- STARITSKY, G. & BREURE, C.J. (1985). The morphogenesis of the inflorescences of the oil palm in relation to yield components. Acta Bot. Neerl., 34, 437-438.
- WARINGA, N.A. (1985). Soil moisture and climate in the West New Britain Area. Internal report, Agricultural University, Wageningen, Holland.

THE DETERMINATION OF THE COMPONENTS OF BUNCH YIELD
IN THE DEVELOPMENT OF INFLORESCENCES IN
OIL PALM (*Elaeis guineensis*, Jacq.).
II. BUNCH WEIGHT COMPONENTS.

C.J. Breure and T. Menendez

SUMMARY

Stages in inflorescence development at which components of bunch weight respond to external growing conditions were identified by reducing the density of one group of palms from 186 to 93 palms ha⁻¹ (sudden increment of amount of light). Bunch weight components of the unthinned and remaining thinned palms were recorded against sequential leaf (L-) numbers; the corresponding stages in inflorescence development were derived by dissection of a sample of felled palms.

Frame weight responded to thinning in three steps corresponding to (1) the rapid expansion phase of the inflorescences, (2) the completion of meristematic development of the primary axis, and (3) the stage of response of flowers per spikelet. The latter occurred about 4 leaves prior to spikelet initiation. Spikelet number responded at the stage of leaf opening, apparently as a result of prolonged meristematic development of the primary axis.

Thinning increased fruit weight shortly after anthesis with a minor response up to 6 leaves later. When flowers per spikelet increased the gain in fruit weight virtually disappeared and the response to fruit set became consistently negative. In contrast, frame weight increased when flower number per spikelet responded to thinning, so that fruit to bunch ratio diminished. There was apparently a sudden rise in fruiting activity of the thinned palms shortly after thinning, which counteracted temporarily the beneficial effect of thinning, and strengthened the interpretation of our results.

INTRODUCTION

Part II addresses to a second group of components of bunch yield in oil palm (*Elaeis guineensis*, Jacq.), being those which determine the weight of the bunch. The aim, as in part I, is to identify the stage in inflorescence development at which a specific component responds to external growing conditions. To (shortly) reiterate the method, a thinning intervention (sudden increment in amount of light) is employed reducing part of the 186 palms ha⁻¹ density of a spacing experiment at Dami Oil Palm Research Station, Papua New Guinea, to 93 palms ha⁻¹. For practical reasons the response to thinning can only be measured on the harvested bunch, but the actual stage in inflorescence development is traced by dissecting a sample of felled palms. From these palms a developmental scale is obtained in terms of the leaf axil number for the main stages in inflorescence development. The same numbering system is used to record, subsequently, the components of bunch weight of the thinned and unthinned palms.

The two groups of yield components, as studied in part I and II, may react differently to thinning. In respect of components determining the number of bunches, i.e. sex ratio and abortion, an inflorescence primordium becomes either a male or a female and, at a later stage, the inflorescence either aborts or survives. Such discrete responses will not occur for the bunch weight components of the present study in that more gradual responses are expected. Further, intrinsic relationships may emerge which either reinforce or reduce a certain component. As an example, an increase in the number of fruits must be accompanied by a strengthening of the supporting tissue. In spite of these confounding responses, the present study still aims at determining one or more developmental stages of the individual components. To serve this purpose, the morphological development of inflorescences, as described by van Heel et al. (1987), is used as a basis.

The components under study can be divided into those determining the weight of the frame (empty spikelets and stalk) and those of the total weight of fruit. The latter is the product of spikelet number, flower number per spikelet, fruit set (the

proportion of flowers which develop into fruit) and the mean weight of individual fruits. All these components respond positively to thinning except fruit set, as shown by Breure et al (in prep.). They argued that the negative response of fruit set to thinning is likely due to the diminishing efficiency of pollinator insects (Syed, pers. com.). Logically, fruit set must be determined at the time of pollination, so that no field study is required. It remains, however, of interest to establish the period which elapses before fruit set responds to thinning.

Of more interest are the basic components of bunch weight which must respond at an earlier stage in inflorescence development: the number of spikelets and flower number per spikelet. No field studies are known about the developmental stage at which these components are determined, but Corley & Breure (in prep.) inferred from a castration trial (removal of different levels of fruit bunches) that both the number of spikelets and flowers per spikelet respond at about the same time, between 14 to 15 months prior to harvest. Time intervals offer no reliable basis for the developmental stage at which the components are determined, however, even when rate of leaf production and speed of inflorescence development are taken into account. The reason is that both covary with palm age and environmental conditions (Broekmans, 1957). Thus, based on a production of two leaves per month, the Corley & Breure (in prep.) study might suggest that the determination of both spikelet number and flowers per spikelet took place at about the time that leaves attain their final size (central spear stage), corresponding with the approximate stage at which the primary axis ceases to be meristematic (W.A. van Heel, pers. com.; Corley, 1977). According to botanical observations (van Heel et al, 1987) such a coincidence is doubtful. Their study demonstrated that the development of spikelet primordia begins somewhere below the apex of the primary axis and progresses downwards (in basipetal sequence). At this time the primary axis has completed the greater part of its development and the space for most of the spikelets must already be fixed (W.A. van Heel, pers. com.). However, new spikelets arise, albeit to a lesser extent, in acropetal sequence until the meristematic

development of the primary axis is fully completed. For the present study it is relevant that the thinning intervention may prolong the meristematic development of the primary axis and thus spikelet initiation (in acropetal sequence). Because spikelet initiation is quickly followed by differentiation (part I), it is expected that mainly flower number on these additional spikelets can be enhanced by thinning; this increase may have little effect on the mean number of flowers per spikelet for the entire inflorescence. Thus number of flowers on the majority of the spikelets may be fixed shortly after the initiation of the first spikelet primordium, but the response of spikelet number is expected to be mainly linked with the response of the meristematic development of the primary axis. The extent of this development must also be crucial for frame weight, which, at an earlier developmental stage, is expected to respond in proportion to the number of flowers per inflorescence. But the oldest stage at which frame weight responds to thinning must be during the stage of rapid expansion of the inflorescences, which starts about 10 leaves prior to anthesis (part I). Thus one may predict that frame weight attains its final response to thinning at three stages in inflorescence development, being, with decreasing age of the inflorescence development, first, during rapid expansion of the inflorescences, second, when the meristematic development of the primary axis stops, and, third, when number of flowers per spikelet respond to thinning.

Concerning the developmental stage after anthesis, the response to thinning will be mainly restricted to fruit weight. Corley (1986) showed a gradual increase during the three-month period after pollination. The effect of thinning can thus only be fully effectuated on those fruits which are at the very onset of expansion.

As explained in much detail in part I, thinning took place at the moment of an unusually high load of developing bunches on the palm (fruiting activity), which must enhance the differences between components of the thinned and unthinned group. The resulting increase in yield due to thinning, in turn, must subsequently lead to a proportional rise in fruiting activity. As argued in part I, the first effect of fruiting

activity must be sudden and shortlived, occurring within 5 months after thinning. In particular, frame weight will respond to this enhanced fruiting activity, as Corley & Breure (in prep) showed. A strong response of frame weight was also obtained from decreasing planting density (Breure et al, in prep.). Thus the joint effect of thinning and fruiting activity should particularly show up in frame weight. In passing it is noted that this sensitivity to fruiting activity renders frame weight suitable as an index of (the influence of) fruiting activity.

Compensation effects between the components may occur. Broekmans (1957), for example, already suggested that an increase in number of flowers will be compensated by a decrease in fruit weight. Thus, at the time that the number of flowers per inflorescence in the thinned group rises, the gain in single fruit weight due to thinning may be reduced.

The contribution of such interactions and of the fruiting activity are taken into account to unravel the stages in inflorescence development at which the components of bunch weight are affected by thinning.

MATERIALS AND METHODS

Experimental details are fully described in part I. Briefly, part of the 186 palms ha^{-1} treatment of a spacing experiment, established at Dami Oil Palm Research Station, West New Britain, Papua New Guinea, was reduced to 93 palms ha^{-1} , in October 1981; at that time an unusually high number of bunches were developing on the palms (high fruiting activity).

At the moment of thinning, the first fully opened leaf was given the ordinal number (L) +1; from that time onwards, all the leaves were sequentially numbered by giving leaves in the crown a positive and those emerging thereafter a negative number. The following components of bunch weight were recorded, for 80 palms of each the "thinned" and "unthinned" group:

components of total fruit:

- spikelet number
- flowers per spikelet

- fruit set
- mean single fruit weight

Components of the frame. :

- the stalk
- empty spikelets

These components were analysed on about 75% of all bunches harvested, as follows:

On arrival of the bunch, a spikelet sample was marked by painting a band of about 5 cm from the base to the abaxial and one lateral side of the bunch. All spikelets were carefully removed and counted; the remaining stalk was weighed. From the marked spikelets only, all fruits were removed to determine the mean empty spikelet weight; fertile and parthenocarpic fruits (both oil-bearing and non-oil-bearing) were separately counted and weighed to derive (1) the percentage fertile fruit to total flowers (fruit set), (2) the average number of flowers per spikelet, and (3) the mean single fruit weight. Finally, in order to record the fruit to bunch ratio, the total weight of fertile fruit was inferred from the product of spikelet number, flowers per spikelet, fruit set and mean single fruit weight.

Components were recorded against pairs of ordinal L-numbers, which corresponds to a time interval of approximately one month

RESULTS AND DISCUSSION

The figures present components of bunch weight of the thinned and unthinned palms, the latter to be regarded as a reference. On the x-axis pairs of successive L-numbers are given which correspond, from left to right, to increasing age of the inflorescences at the moment of thinning. A significant (unpaired, two-sided t-test) change at the oldest developmental stage is indicative for the stage at which a particular component responds to thinning.

Number of spikelets

In spite of a first increment at L +10 to +7 (Fig 1), the second increment, at L +0/-1, is a more likely stage of actual response to thinning because it corresponds with the approximate stage at which spikelet initiation usually stops (W.A van Heel, pers. com.). Moreover, it agrees well with the time lag of 14 to 15 months prior to harvest, as Corley & Breure (in prep.) inferred from a castration trial.

The first increment at L+10 to +7 must be an artefact, which may be associated with the abortion score given in part I. In these leaves abortion started to become substantially higher in the unthinned than the thinned group. As argued in part I, the first abortions might have been preferential for the larger inflorescences. Because these are expected to have also the greater number of spikelets, the gain at L +10 to +7 of the thinned group may in fact be preferential abortion in the unthinned group of those inflorescences having the greater number of spikelets.

Flowers per spikelet

The number of flowers per spikelet is determined, at a cellular level, about 2 to 3 leaves after the spikelet is initiated (Part I). The first response to thinning can thus only be found on those spikelets which had just be initiated at the moment of thinning, i.e. on inflorescences younger than about L +3. Figure 2 shows that in this range, the first increment is observed at L +1/+2, but in younger leaf axils, between L -4 to L -7, the gain in flowers per spikelet of the thinned palms disappeared.

The positive effect of thinning becomes consistent in leaves younger than L -8/-9. For responses at both stages, L +1/+2 and -8/-9, arguments can be put forwards from botanical observations (van Heel et al, 1987). The developmental stage at L -8/-9 is about 4 leaves prior to the appearance of the first spikelet primordia (Part I). At this stage the majority of spikelets must already have been initiated at a cellular level (W.A. van Heel et al, 1987). Remember that, from that stage onwards the number of spikelet is contingent on the meristematic development of the primary axis (van Heel et al,

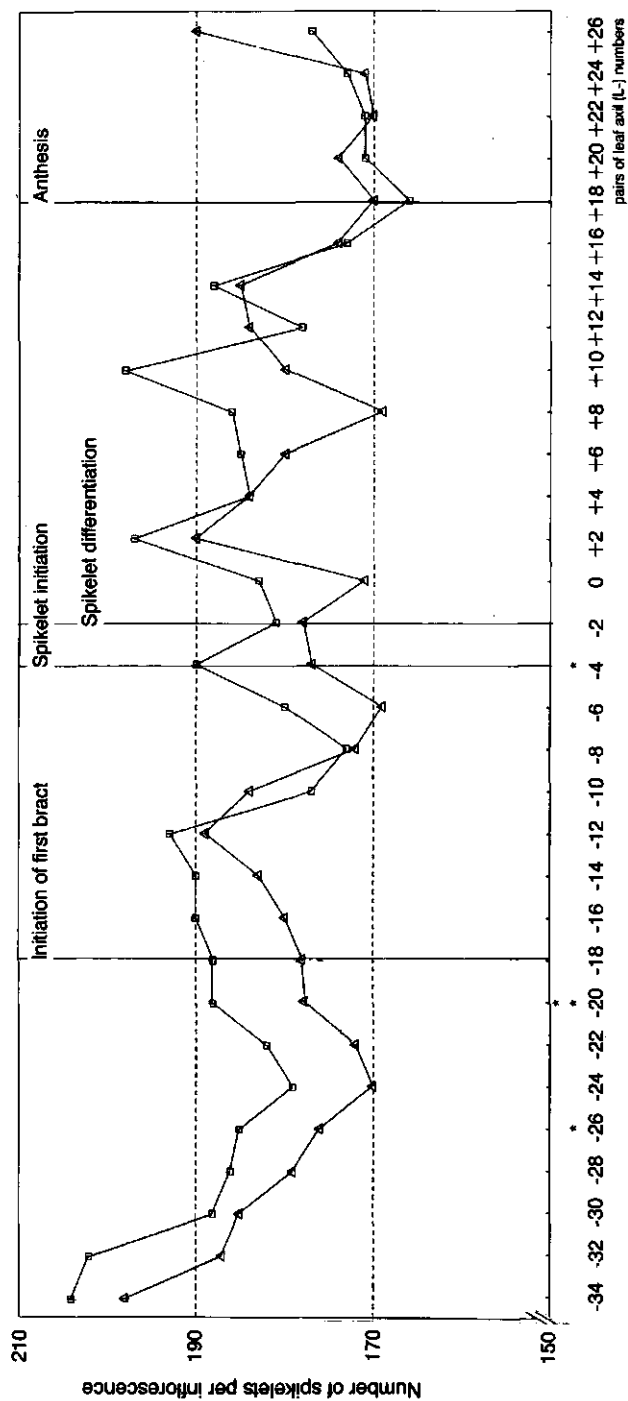


Figure 1 Number of spikelets per inflorescence, plotted against two sequential leaf axil (L-) numbers, for thinned (\square) and unthinned (\triangle) palms.

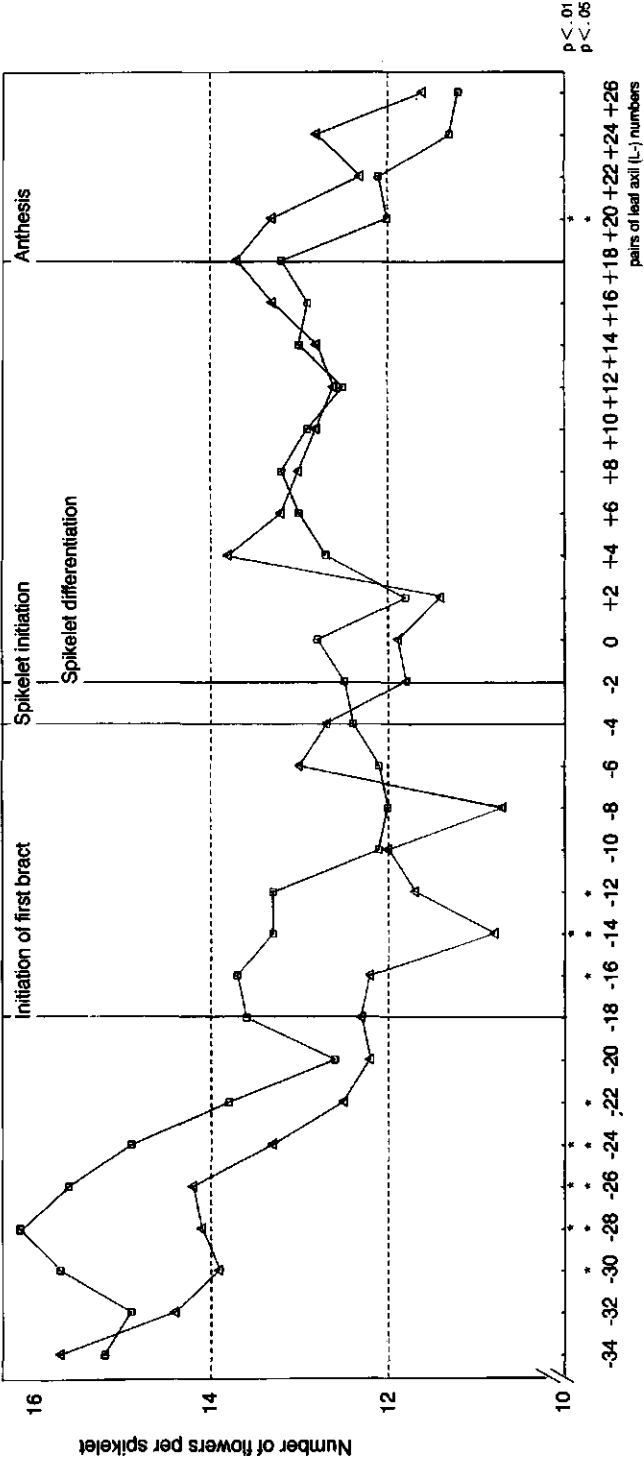


Figure 2 Number of flowers per spikelet, plotted against two sequential leaf axil (L-) numbers, for thinned (□) and unthinned (△) palms.

1987), so that only on these additional spikelets the number of flowers can still be increased. This may explain why a slight increment starts at $L +1/+2$. The possibility of an increase in flower number per spikelet on primordia as old as $L +1/+2$ supports the approximate time-lag reported by Corley & Breure (in prep.). One would expect, however, a subsequent gradual increase in leaves younger than $L +1/+2$, which is at odds with the diminishing and even negative response between $L -2$ to -7 . This unexpected response is likely due to fruiting activity, as will be explained later.

Thus it is reasonable to assume that flowers per spikelets on the majority of the spikelets responds about 4 leaves prior to the appearance of the first spikelet primordia while in older inflorescences, flowers per spikelet can only be increased on a minor proportion of total spikelets.

Fruit set

Logically, fruit set can only be determined at anthesis, which occurred at $L +17$ (part I). This stage could not be substantiated in the present study (Fig 3).

Remember that diminishing the planting density (thinning) had a negative effect on fruit set (Breure et al, in prep.). A second negative effect on fruit set could have been the enhancing fruiting activity (Corley & Breure, in prep.). Both effects may have governed fruit set shortly after thinning. The general trend is a reduction of fruit set due to thinning, which became particularly pronounced at $L +6$ to $+3$ which is likely the contribution of enhanced fruiting activity. It is more difficult to explain why a more pronounced decrease in the thinned palms occurred, from $L -16$ onwards. A connection with the increase in number of flowers per inflorescence is plausible.

Single fruit weight

Fig 4 shows that the increase in mean fruit weight follows the expected trend in that there was a minor positive effect during the expansion of the fruit ($L +18$ to $+24$) but a pronounced and highly significant effect on weight of those fruits which were just pollinated at the moment of thinning

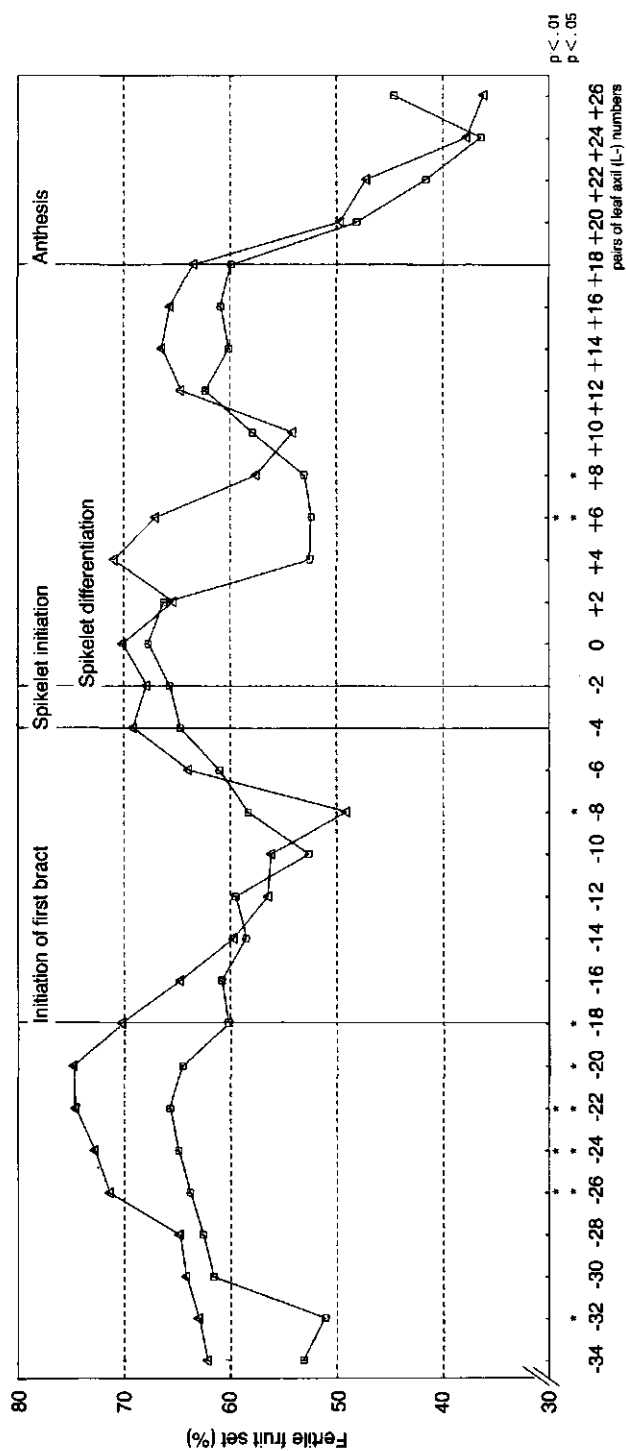


Figure 3 Fertile fruit set (%), plotted against two sequential leaf axil (L-) numbers, for thinned (□) and unthinned (Δ) palms.

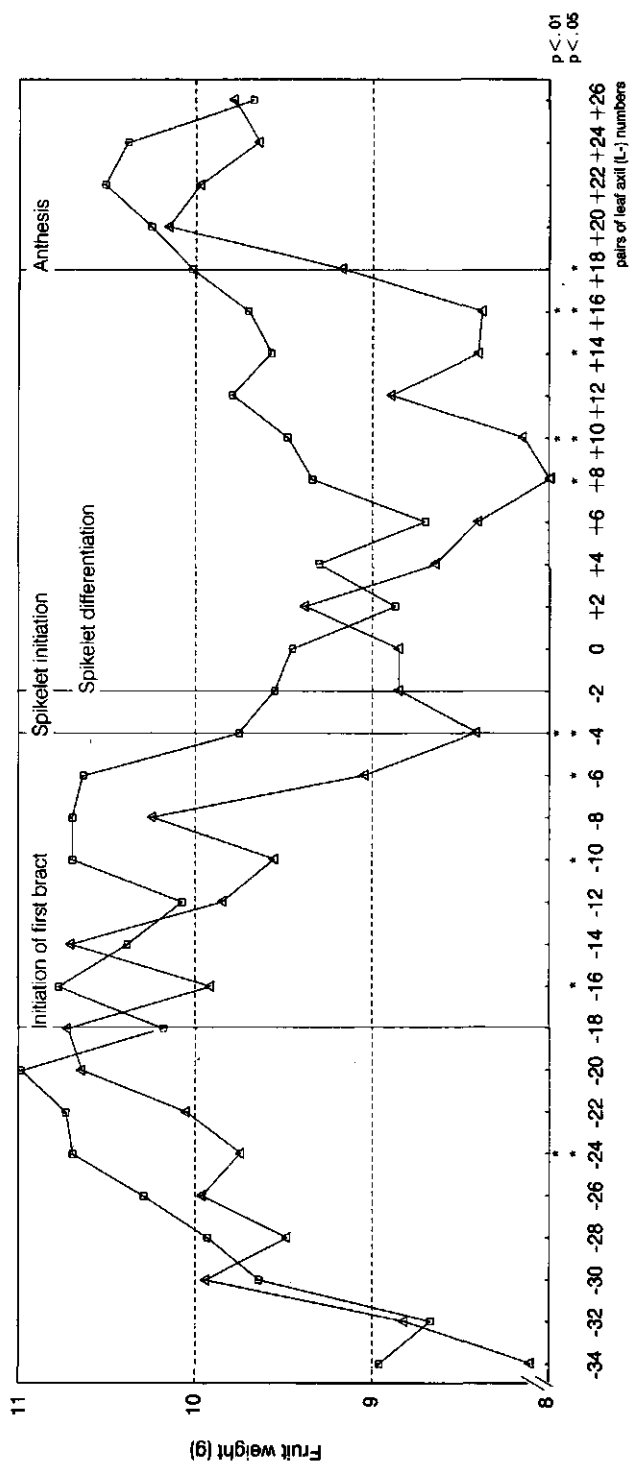


Figure 4 Weight of individual fruits (g), plotted against two sequential leaf axil (L-) numbers, for thinned (\square) and unthinned (\triangle) palms.

(L +17/+18).

The increase disappeared between L +6 to +1 and became even lower than the initial positive response in leaves younger than L -12/-13. The latter were the L-numbers at which flowers per spikelet increased (Fig 2), which may have had a counteracting effect on mean fruit weight, as already suggested by Broekmans (1957). The disappearance of the gain in fruit weight of the thinned palms at L +6 to +1, again, might be due to the sudden increment in fruiting activity on the thinned palms.

Frame weight

Considering the morphological development of inflorescences, frame weight is expected to increase in three steps, being (1) during the stage of rapid expansion of the inflorescences, (2) due to prolonged expansion of the primary axis and, finally, when the number of flowers per spikelet is increased. Our results (Fig 5,6, and 7) clearly support such three-step increase, in particular when looking at the weight of the stalk (Fig 7).

Frame weight and its components increased from L +16 to +7, followed by a further increase at L 0 to -13, and a final increment in leaf axils younger than L -14.

Note that the first increment reaches its maximum between L +10 and +7; this seems logical because their inflorescences were in a less advanced stage of expansion at the moment of thinning (part I). Subsequently the gain in frame weight and its components gradually decreased until even a negative response occurred at L +4/+3; thereafter the positive response resurrected. The range, between L +6 to +1, at which the initial significant response to thinning disappeared must be due to a strong rise in fruiting activity on the thinned palms. Fruiting activity apparently affected the growth rate of the frame only during the 3 to 5 months period after thinning. The positive effect of thinning, on the one hand, and the negative effect of fruiting activity, on the other hand, are very pronounced. This trend consistently supports results obtained in a spacing experiment (Breure et al, in prep.) as well as those of a castration trial (Corley & Breure, in prep.). The response of frame weight provides therefore the clearest

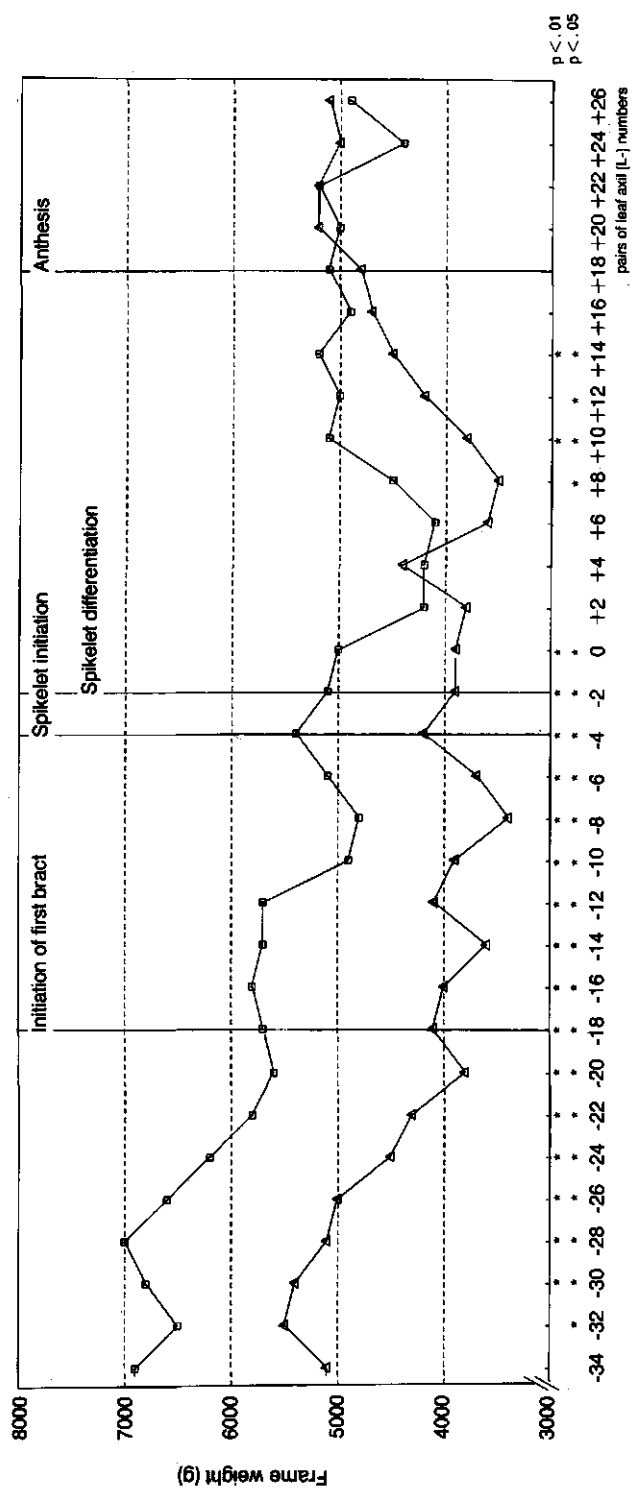


Figure 5 Frame weight (g), plotted against two sequential leaf axil (L-) numbers, for thinned (□) and unthinned (△) palms.

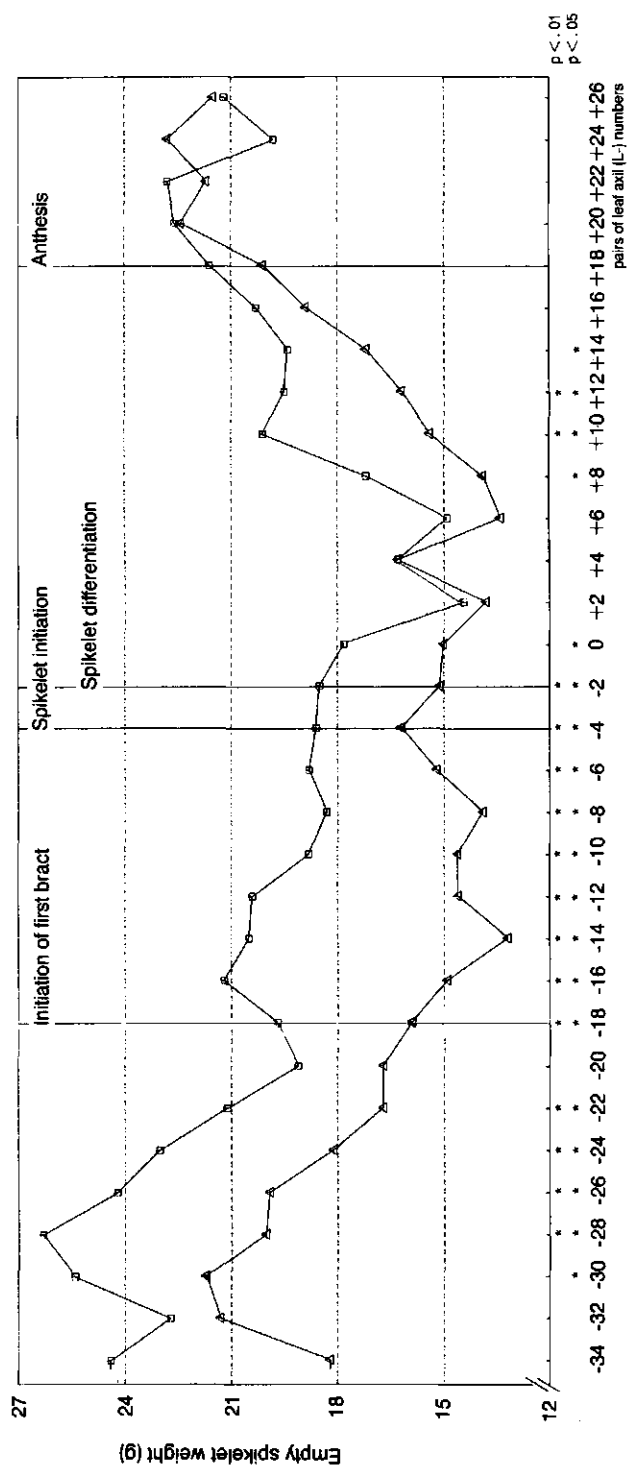


Figure 6 Mean weight per empty spikelet (g), plotted against two sequential leaf axil (L-) numbers, for thinned (\square) and unthinned (\triangle) palms.

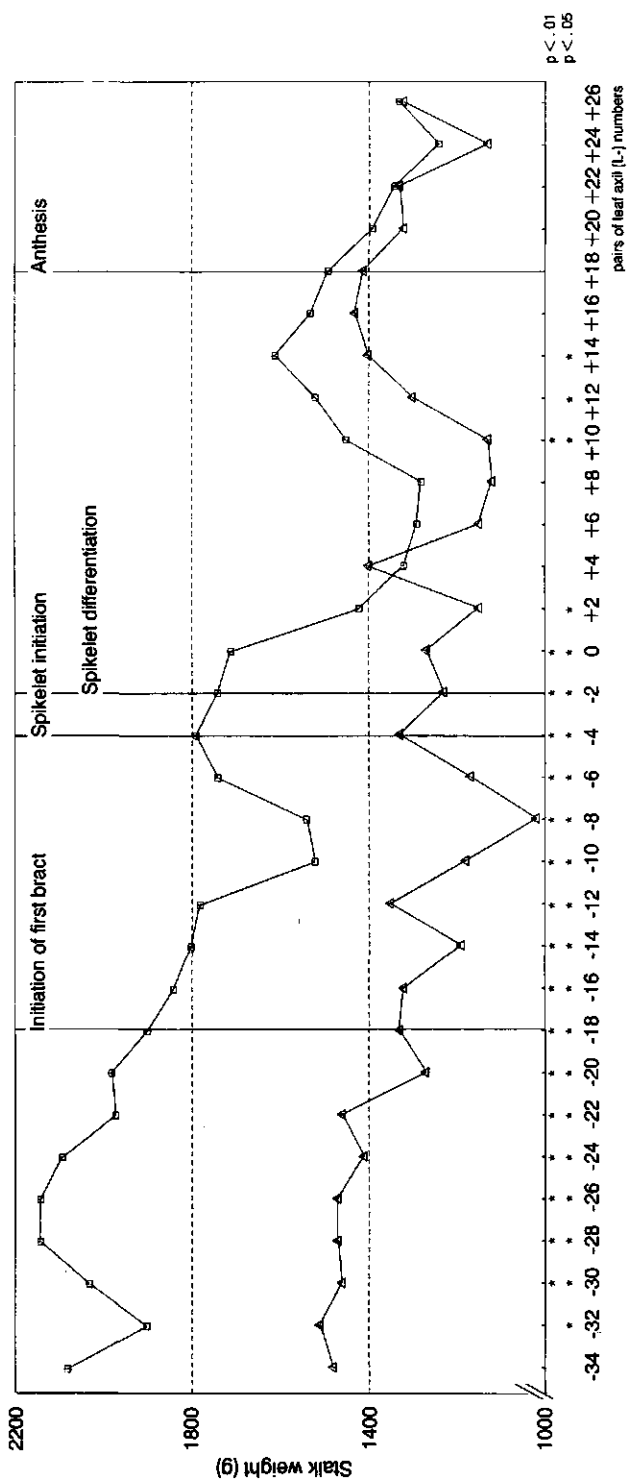


Figure 7 Stalk weight (g), plotted against two sequential leaf axil (L-) numbers, for thinned (\square) and unthinned (\triangle) palms.

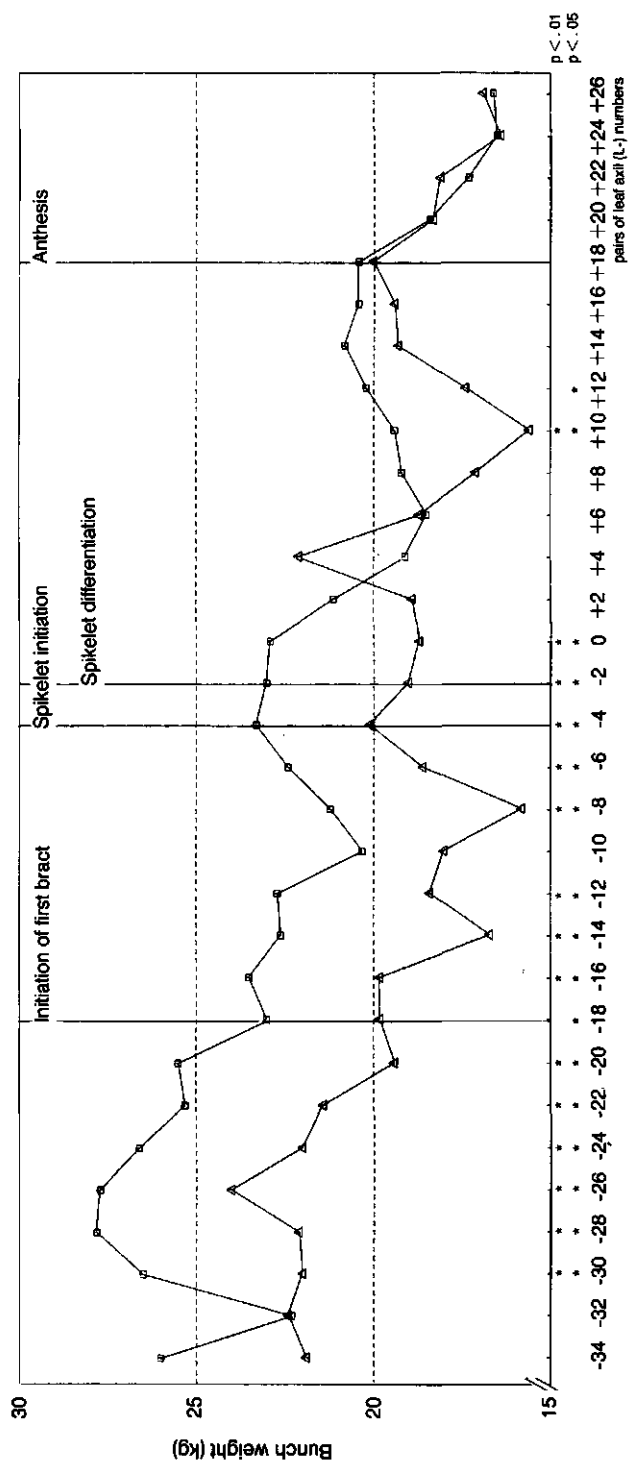


Figure 8 Bunch weight (kg), plotted against two sequential leaf axil (L-) numbers, for thinned (□) and unthinned (△) palms.

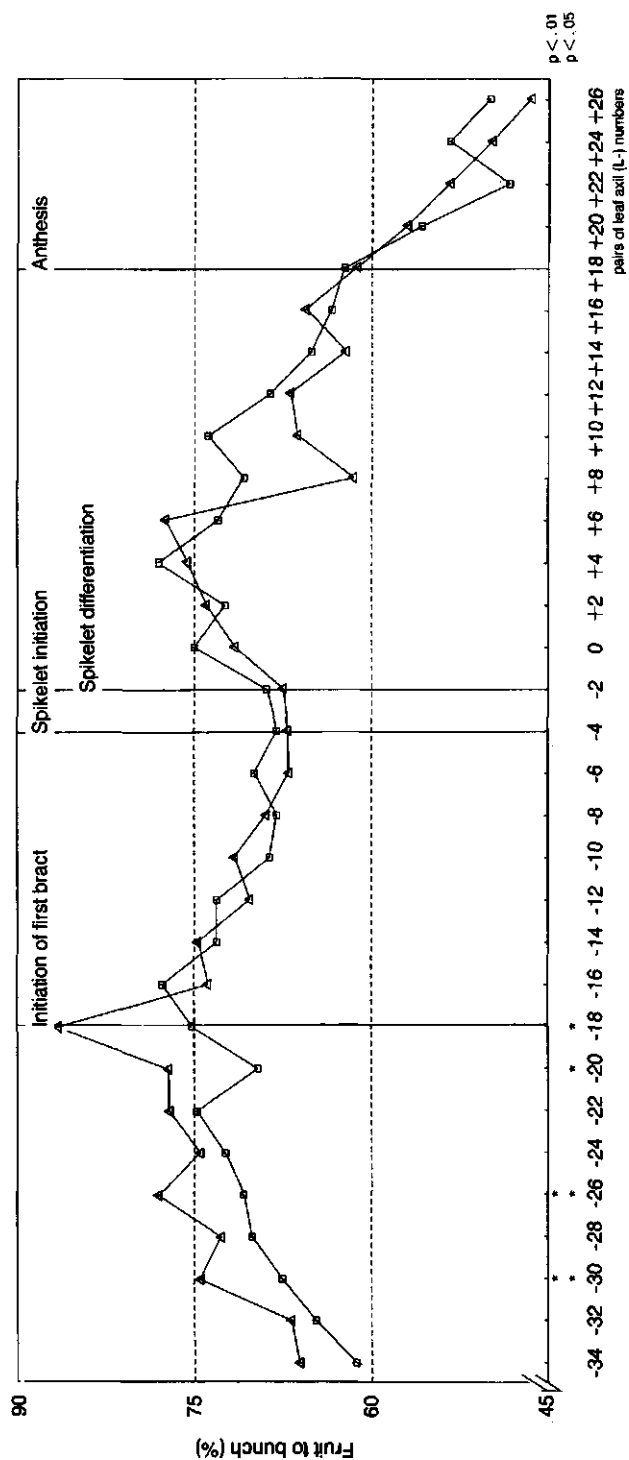


Figure 9 Fertil fruit to bunch (%), plotted against two sequential leaf axil (L-) numbers, for thinned (\square - \square) and unthinned (\triangle - \triangle) palms.

evidence of a strong, shortlived, counteracting effect of fruiting activity on the thinned palms, as assumed earlier.

Bunch weight

The first positive response of bunch weight to thinning, i.e bunches harvested in axils of L +12/+11 (Fig 8), is apparently due to the gain in frame weight (Fig 5) and in weight of single fruits (Fig 4).

The increase reached its maximal, by and large stable, level at about L +0/-1 when the positive response of spikelet number and of frame weight became manifest; from that stage onwards, bunch weight of the thinned palms remained about 5 kg higher than that of the unthinned palms. The fact that bunch weight did not further increase as a result of the positive response of flowers per spikelet, at about L -8, is due to a compensation effect from weight of single fruits (Fig 4) and, in particular, from fruit set (Fig 3). Such compensation did not occur on frame weight, which increased with 1203 g between L 0 and -11 to 1631 g in the younger L- numbers to L -35 (Fig 7). The end result is a significant decrease in the percentage fruit to bunch (Fig 9) in leaves younger than L -18/-19.

A decrease in fruit to bunch as a function of planting density is consistent with results reported by Breure et al (in prep.).

CONCLUSION

The developmental stages at which thinning affects the components of bunch weight agree reasonably well with those expected from the morphological development of inflorescence primordia. In particular, a three-phase response of frame weight could be substantiated.

Spikelet number, in contrast to the assumption of Corley & Gray (1976), responds at an older developmental stage than flowers per spikelet. The latter component appears to respond mainly some leaves prior to spikelet appearance. The positive response of flowers per spikelet is partly compensated for by a diminished response of single fruit weight. Further, when flowers per spikelet increase, the response of fruit set to thinning becomes negative. Because there is not such

compensation effect on frame weight, fertile fruit to bunch ratio starts to respond negatively to thinning in leaves younger than L -18.

The response of frame weight to thinning most strongly reflects the counteracting effect of fruiting activity, about 3 to 5 months after thinning. This strengthened the identification of the response of other components, which did not react so markedly to fruiting activity.

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REFERENCES

Broekmans, A.F.M. (1957). Growth, flowering and yield of the oil palm in Nigeria. J.W.Afr.Inst.Oil Palm Res., 2, 187-220.

Corley, R.H.V. & Gray, B.S. (1976). Yield and yield components. In: R.H.V. Corley, J.J. Hardon & B.J. Wood (Eds.) Oil Palm Research. Amsterdam, Elsevier: 77-87.

Corley, R.H.V. (1977). Oil Palm yield components and yield cycles. In D.A. Earp & W. Newall (Eds.), International Developments in Oil Palm. Kuala Lumpur, Incorporated Society of Planters, pp 116 - 129.

Corley, R.H.V. (1986). Oil Palm. In CRS Handbook of fruit set and development. MONSELISE, S.P. (Edt.) 253-258.

Heel, van W.A., Breure, C.J. & Menendez, T. (1987). The early development of inflorescences and flowers of the oil palm (Elaeis guineensis, Jacq.) seen through the scanning electron microscope. Blumea, 32, 67 - 78.

THE EFFECT OF DIFFERENT PLANTING DENSITIES ON YIELD TRENDS
IN OIL PALM

C.J. Breure

SUMMARY

Sixteen years' yield and growth data from a density experiment, comparing 56, 110, 148, and 186 palms ha^{-1} , and additional records from a progeny experiment, were used to study the effect of palm age and planting density on carbohydrates incorporated in total above-ground dry matter production per palm (TDM_c) and its components: fruit bunch yield (Y_c) and vegetative growth (VDM_c). Carbohydrates per unit intercepted radiation, the canopy efficiency (e), decreased from year 5 to year 8, then levelled off, and increased when crown expansion was completed. The decrease in e parallels the expansion of the intercepted leaf surface, and might therefore be linked to an increase in maintenance respiration losses. These losses were apparently not compensated by an increase in photosynthetic production. The subsequent increase in e appears to be due to improved light distribution consequent on an observed increment in light penetration. These effects of changing levels of interception and distribution of sunlight on e were more pronounced as the density increased, and resulted in marked differences in changes of TDM_c with age between densities. These differences were entirely reflected in those of Y_c , resulting in a decrease in optimum density for current yield until 12 to 13 years from planting, followed by a strong increase.

The results expose some relevant factors associated with the supply and distribution of assimilates per ha, and measures are discussed which might lead to an increase in yield per ha.

INTRODUCTION

Fruit bunch yield of commercial oil palms, grown in favourable environments, increases sharply during the first three years of production, after which it usually tends to decline slowly. According to Corley & Gray (1976) the decline seems to be an unavoidable consequence of planting at the optimal density. They explained their hypothesis by illustrating in one diagram the change in total dry matter (TDM) and vegetative dry matter production per palm (VDM) with time (Fig 1).

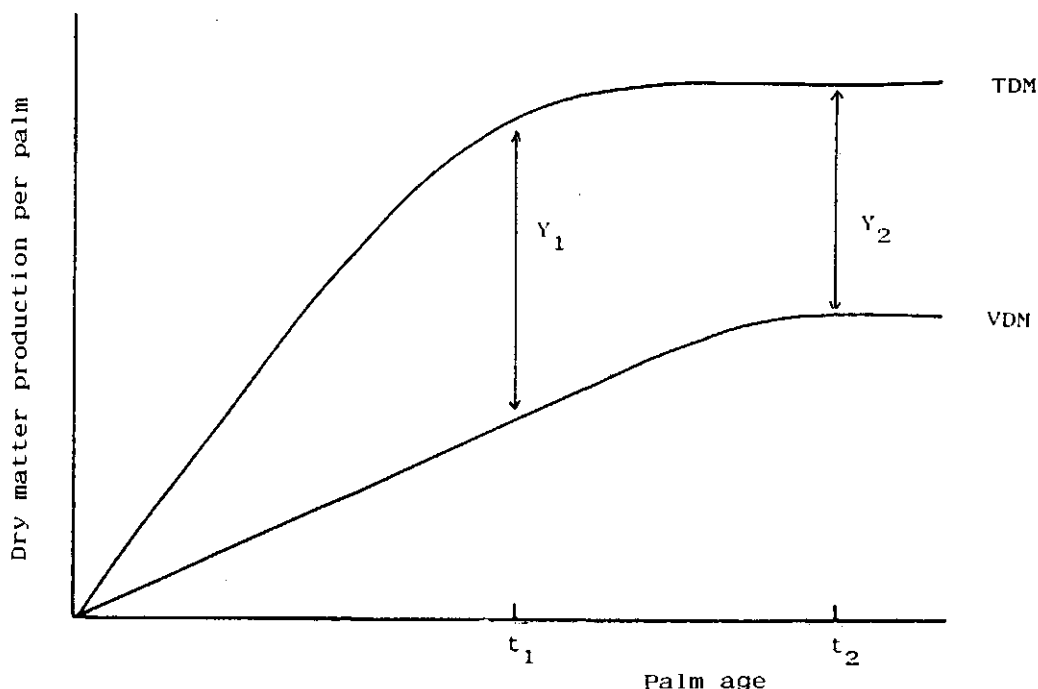


Figure 1. Diagram of trends, with age, of total dry matter production (TDM) and vegetative dry matter production (VDM) per palm. Competition between palms for light begins to limit TDM at t_1 . Bunch yield per palm (Y , the difference between TDM and VDM) increases to a maximum (Y_1), and then declines until it reaches a value of Y_2 when VDM becomes constant at t_2 . (diagram based on that presented by Corley & Gray, 1976).

This diagram shows that TDM increases linearly with time until, due to the expansion of the crown leaves, interpalm competition begins (t_1). Thereafter TDM becomes affected by the increasing

level of interpalm competition and the TDM/age gradient levels off, and finally from the diagram it can be inferred that TDM stabilises at a fixed value about the time that the canopy is practically closed. In contrast, VDM increases, unaffected by interpalm competition albeit at a lower rate than TDM, until leaf size attains its maximum. Since in their view vegetative growth takes priority over that of the other main component of TDM, i.e. dry matter incorporated in fruit bunches (Y), it may be inferred that Y increases initially, and then decreases from the commencement of mutual shading until VDM has reached its maximum value (t_2). This pictorial inference of yield decline assumes that TDM reaches its peak before VDM. Regarding the suggested change in VDM with time, there is sufficient evidence to accept their view (Breure, 1982, 1985), but the changes in TDM with time still requires empirical support; the alleged constancy at maturity, and the time when TDM reaches its peak, should be further elucidated. The latter depends on the planting density and indeed, at commercial planting densities where the canopy is closed before leaf size reaches its maximum, TDM is expected to reach its peak earlier than VDM. In this case the yield decline may be described in terms of TDM and VDM as suggested by Corley and Gray (1976). But the effect of changes in TDM on Y can only be properly understood when a range of planting densities is explored to provide information on, firstly, the time lag between canopy closure and the moment that TDM reaches its peak value, and, secondly, on the effect of planting densities on changes in TDM during maturity.

A constant mature TDM level, as suggested by Corley & Gray (1976), is based on the assumption that the difference between the supply of assimilates and those required for maintenance respiration remains unchanged after canopy closure. The effect of these factors on dry matter production can only be understood when this is expressed in carbohydrate requirements instead of as weight of dry matter formed. A further argument for this approach is that Y and VDM have different conversion factors (expressed in $\text{kg dry matter kg}^{-1}\text{CH}_2\text{O}$), and since the relative contributions of Y and VDM to TDM change with palm age and planting density (Breure, 1982, 1985; Corley, 1973), the

conversion factor for TDM does not remain constant. Thus trends in TDM at different planting densities can only be compared in terms of carbohydrate requirements (abbreviated as TDM_c , and its components Y_c and VDM_c). From trends in carbohydrate requirements for dry matter (DM) production, a deeper understanding of factors associated with the change in Y_c with time may be obtained. This then permits the exploration of measures which might increase the bunch yield during the economic life of a planting through a decrease in VDM_c and an increase in TDM_c . The latter depends primarily on the solar radiation absorbed by the canopy, which is directly related to leaf area index (L), i.e. the green leaf surface per unit ground area. To derive the light interception from L requires establishing the extinction coefficient (k), defined by Squire (1984b) as

$$k = \frac{-\ln(1-f)}{L - a}$$

where f is the light interception, and a is a constant.

The second factor which determines the supply of assimilates is the conversion rate of absorbed radiation which in turn depends on the assimilation-light response curve of the leaf surface. This curve is characterized by a region at low light intensity where assimilation rate is proportional to absorbed light leading to a plateau at light saturation which is reached at about 30% of full sunlight (Corley, 1976). It is thus clear that light is more efficiently utilised when the proportion of leaf surface in the linear portion of the curve is maximised, that is when light is evenly distributed over the leaf surface. An impression of light distribution may be obtained from the light penetration through the oil palm canopy, as shown by the vigour of the ground vegetation (to be considered as the lowest layer of the intercepting green leaf surface). This usually increases sharply in commercial plantings after crown expansion has stopped. For this reason Squire's (1984b) relationship between L and f should be established for different palm ages though in the present study it was only established when palms were 14 years old. The age trend in k-values, however, was studied for measurements carried out in commercial plantings of a wide range of ages in the same experimental

area.

The relative contribution of the alleged positive effect of improved light distribution and the negative effect of reduced light interception on gross photosynthetic production at mature crown size will be completely reflected in the change in TDM_c with time because maintenance respiration (the other main consumer of carbohydrates) will have become stable at this stage (Breure, in prep.). Therefore, in the present study light utilization is analysed, at different planting densities; in terms of the efficiency of the canopy to convert intercepted radiation into assimilates allocated to DM production (expressed in $g\ CH_2O\ MJ^{-1}$). A similar, but not identical, parameter was extensively reported by Squire (1984b), who concluded that there is little effect of palm age and size on the efficiency of the oil palm canopy. The present study offers an opportunity to test the validity of his conclusions.

But the main objective of this study is to study changes in the Y_c /age gradient as a function of planting density, as determined by the difference between those of TDM_c and VDM_c . The changes in Y_c with time have direct implications for establishing the optimal density for cumulative yields. Corley (1976) suggested that the optimal density for current yield remains constant after the leaf size reaches its maximum. This normally occurs about 9 or 10 years from planting after which Corley assumes that interpalm competition for light would remain unchanged. In the present paper the optimal density for current yield, which is required to extrapolate the optimum for cumulative yield over the entire economic life of a planting, is obtained over a longer period to test the validity of Corley's assumption.

The present paper differs from previous reports in that it provides long term data from the same experiment. Such a data base permits separating the age effect from other factors which, as pointed out by Corley & Gray (1976), might affect yield trends when calculated from a wide range of plantings; these factors include different sources of planting material, differences in fertiliser policy etc. There was, however, one potential confounding factor in that during the experiment insect pollination replaced the less consistent method of

assisted pollination, the efficiency of which might deteriorate with palm age and with increasing planting density, because these conditions make access for pollen application more difficult. Fortunately, for two planting densities, the bunch survival ratio, i.e. ratio of properly developed fruit bunches to total female inflorescences reaching anthesis, and the mean bunch weight were available for the entire period. These two parameters permit evaluation of any possible confounding effect of pollination efficiency on our results.

In our design the density treatments included one level with negligible interpalm competition for light; the effect of density on changes in the allocation of assimilates to DM production with time could thus be compared with this zero or reference level.

The ultimate objective of the present study is to obtain information on possible factors associated with changes with time in the allocation of assimilates to bunch yield. These factors, associated with the supply of assimilates and those utilised for maintenance respiration and vegetative growth, will be discussed in the context of formulating a breeding policy and of cultural practices aimed at increasing the amount of assimilates allocated to economic yield.

MATERIALS

The two experiments analysed in this paper were located at Dami Oil Palm Research Station, West New Britain, Papua New Guinea (latitude $5^{\circ}30'$ and longitude $150^{\circ}30'$), and planted with commercial dura x pisifera planting material. The details and the origin of the planting material are given by Breure et al (1982).

Experiment 1

This was a density experiment, comparing 56, 110, 148, and 186 palms ha^{-1} , and was planted in October 1970. This experiment is described in detail by Breure (1977).

Experiment 2 (additional)

This dura x pisifera progeny trial was planted in April 1976, with three replications at 115 palms ha⁻¹ and three at 143 palms ha⁻¹. More details are given by Breure (1986). Only the pooled growth data during the early years are used to supplement those of Experiment 1.

In Experiment 1, disbudding (castration or ablation, a former practice of removing initial inflorescences) was carried out at monthly intervals during the first year of flowering. Experiment 2 followed the new practice and was not disbudded. Both experiments were under assisted pollination, because of poor natural pollination in the environment. This method was very effective until about 1980 when pollination efficiency decreased, but from 1982 onwards excellent pollination was achieved by introduced insect pollinators.

OBSERVATIONS

Bunch dry matter production

Bunch yields from weekly harvesting rounds were recorded from the start of production i.e. from May 1973 to October 1986 (no yield records from Experiment 2 were used in this study). Yield recording was not done in November and December 1981, and for this period yield data were extrapolated from results of a census on inflorescence production (to estimate bunch number) in the 110 and 148 palms ha⁻¹ densities, and the mean weight of the bunches produced in the preceding months.

Above ground dry matter production

Annual values of non-destructive measurements, as developed by Hardon et al (1969) and Corley et al (1971) were obtained from the 5th to the 14th year from planting in Experiment 1, and from the 2nd to the 4th year from planting in Experiment 2. These early results from Experiment 2 were included to complete the set of growth measurements in Experiment 1. This is justified, because no density effect on growth was observed at this stage. The system of determining the growth parameters used in the present paper has been fully described by Corley

& Breure (1981). In Experiment 1 annual leaf production was recorded for all four densities during the 5th to the 9th year; thereafter recording only continued until the 14th year in the 110 and 148 plant densities. In the 56 and 186 plant densities annual leaf production was estimated for the 10th to the 14th years from planting as follows: first, the total number of leaves was determined as the difference between the estimated leaf production between the 5th and the 14th year, and the number actually recorded between the 5th and the 10th year. The former estimate follows the method of Breure & Powell (1987), and was obtained from counting the number of leaf bases of two (of the total of eight) spirals, for all densities: the estimated number of visible leaf bases was then corrected for those produced during the first four years from planting (this value was inferred from records in the 110 and 148 plant densities). The distribution into annual periods was based on the frequency distribution actually found in the 110 and 148 plant densities.

Leaf area index

Total leaf area was calculated as the product of the number of palms per unit ground area, the number of crown leaves per palm and their mean individual leaf area. The latter was determined, for annual periods between the 5th and 14th year from planting, as the mean measurements on leaf 17 six months prior to, in the middle of, and six months after each year recorded. Corley (1976) reported a negligible contribution to gross photosynthetic production of crown leaves in excess of those maintained through regular pruning rounds for harvesting the fruit bunches in mature plantings. Therefore, this number of 35 mature crown leaves was adopted for annual periods recorded in Experiment 1. In contrast, for palms sampled to establish the relationship between L and fractional transmission of radiation, L was estimated from the actual number of crown leaves and the mean area of leaves 17 and 25. The biomass of these leaves was also of interest because of its contribution to maintenance respiration losses.

Carbohydrate requirements for dry matter production

Carbohydrate requirements ($\text{kg CH}_2\text{O palm}^{-1} \text{ a}^{-1}$) for the following components of dry matter production were established:

Y_c : carbohydrates for bunch yield production.

VDM_c : carbohydrates for above-ground vegetative DM production.

TDM_c : carbohydrates for total above-ground DM production

$$(\mathbf{Y_c + VDM_c}).$$

The conversion factors of assimilates to DM required for these components ($\text{g DM g}^{-1}\text{CH}_2\text{O}$) are as follows (Breure, in prep):

Leaves: 0.696

Trunk: 0.657

Bunches: 0.437

Roots: 0.649

Canopy efficiency (e) is defined as the amount of carbohydrates incorporated in above-ground DM production per unit absorbed photosynthetically active radiation (PAR) per ha ($\text{g CH}_2\text{O MJ}^{-1}$).

Absorbed photosynthetically active radiation

Absorbed PAR was measured at 25 equally spaced points in an area of $1/N$ per sampled palm, where N is the number of palms ha^{-1} (Squire, 1984a). L was measured for these palms and for their 6 neighbours. These measurements were done in Experiment 1 for 3 centre palms per sub plot, in 1984, and in commercial plantings for at least 36 palms per age group, covering the range between 5 to 14 years from planting, in 1986. A Bottemanne photosynthetic Radiometer type RA 200 Q was used. Based on these records intercepted PAR at different ages in the three higher densities of Experiment 1 was derived from estimates of L values and total available PAR. The latter is estimated as 50% of total solar radiation (Szeicz, 1974), which in turn is derived from the actual number of hours bright sunshine recorded at Dami (Waringa, 1985).

RESULTS

Carbohydrates for total above-ground and vegetative growth with time (TDM_c and VDM_c)

VDM_c continued to increase at all densities, until about 8 years from planting, and thereafter remained more or less constant (Fig 2) while TDM_c increased initially to a peak, reached earlier at lower values as the planting density increased.

The fitted curves are based on cubic regression equations with coefficients of determination (R^2) varying from 0.81 to 0.94. The peaks occurred at 132, 117, 92 and 87 months from planting, corresponding to maxima of 568, 474, 385 and 325 kg CH_2O palm⁻¹a⁻¹ or 31.7, 52.3, 57.1 and 60.4 t CH_2O ha⁻¹a⁻¹, at the 56, 110, 148 and 186 palms ha⁻¹ density levels, respectively. Initial production of carbohydrates per ha can be nearly entirely explained from the fractional light absorption, since, similar to TDM_c , canopy closure (maximum light absorption) occurs earlier and reaches a higher maximum as a function of planting density. After declining with age, TDM_c tended to increase again at higher planting densities.

The relative effect of planting density on carbohydrate requirements was calculated by expressing the requirements at 110, 148 and 186 palms ha⁻¹ as a percentage of that found at the 56 palms ha⁻¹ density (regarded as a reference level) (Fig 3).

VDM_c appears to be only moderately affected by planting density, and, in contrast to TDM_c stabilised from the 10th or 11th year from planting. Planting density strongly reduces Y_c until the 10th or 11th year from planting when it increases again, especially at higher planting densities.

Y_c expressed as a percentage of its value at 56 palms ha⁻¹ at any given number of years from planting is linearly related to the number of palms ha⁻¹ (N). This relationship may be expressed in the form $Y_c = a - bN$. The carbohydrate available for bunch production ($N Y_c$) is then given by

$$N Y_c = aN - bN^2$$

and reaches a maximum when $d(N Y_c)/dN = 0$, that is when a

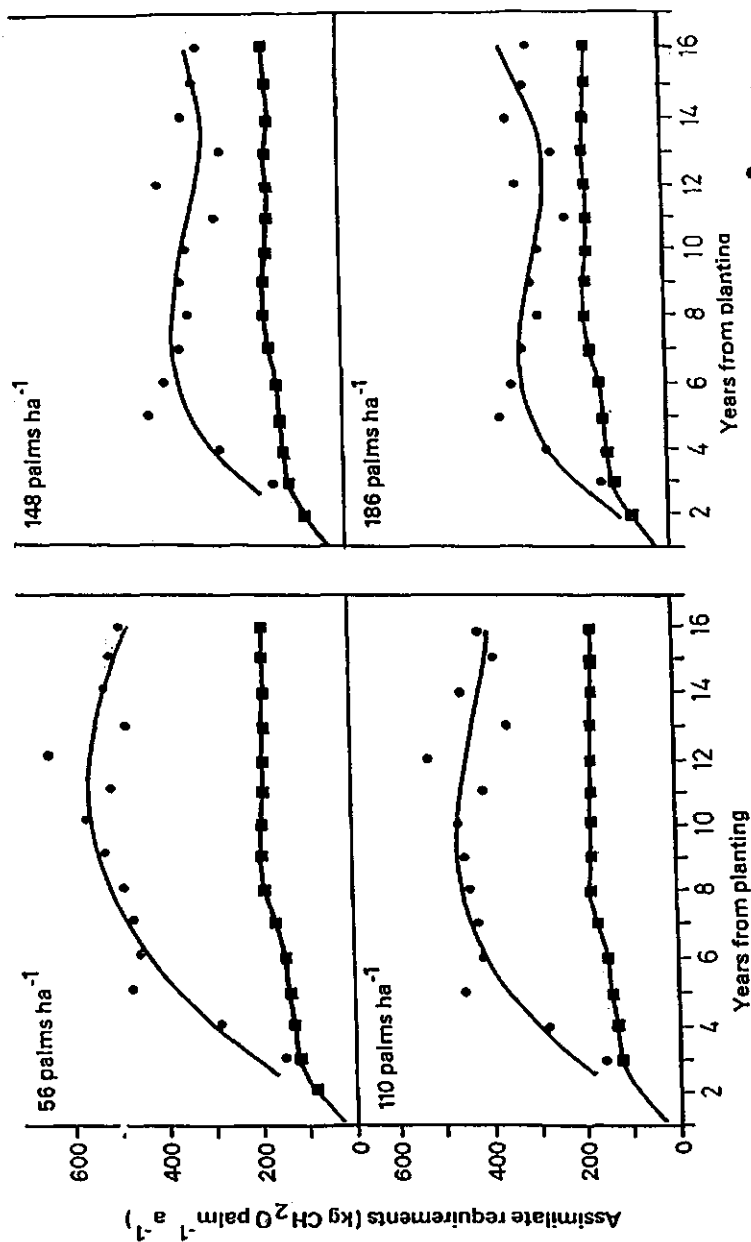


Figure 2. Carbohydrate requirements for total (TDM_C) and for vegetative (VDM_V) growth, plotted as functions of palm age (in years) for the planting densities of Experiment 1 (VDM_V for 3rd and 4th years adopted from Experiment 2, and for 15th and 16th years estimated as the mean of the three preceding years)

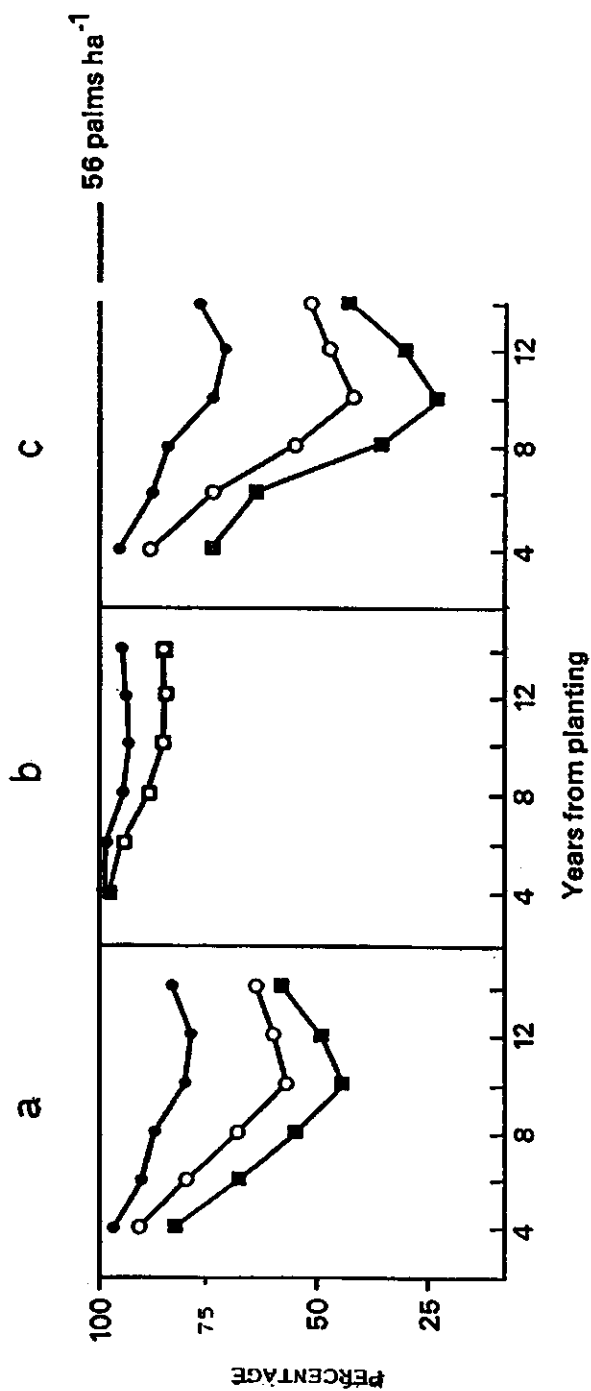


Figure 3. TDM_C (a), VDM_C (b) and Y_C (c), expressed as percentages of values with 56 palms ha⁻¹, plotted as functions of palm age (in years). ●—●, 110 palms ha⁻¹; ○—○, 56 palms ha⁻¹; ■—■, 186 palms ha⁻¹.

$$- 2bN = 0, \text{ or } N = a/2b.$$

The values obtained (Table 1) show that the optima decrease until the 11th or 12th year after planting, but then increase and appear to stabilise at a similar level to that of the 7th and 8th year.

Table 1. Estimated optimum density for carbohydrates supplied to bunch yield per ha for 7 successive two-year periods from the start of production, based on linear regression equations fitted through Y_c values of the 110, 148 and 186 palms ha^{-1} densities of Experiment 1.

Age (years from planting)	Linear regression ¹⁾	Coefficient of <u>determination</u>	<u>Optimum</u> <u>density</u> (palms ha^{-1}) ²⁾
3 & 4	$Y=236.10 - 0.37X$	0.92	320
5 & 6	$Y=846.07 - 2.19X$	0.93	193
7 & 8	$Y=913.42 - 3.59X$	1.00	127
9 & 10	$Y=1041.95 - 4.41X$	0.99	118
11 & 12	$Y=1149.32 - 5.13X$	0.99	112
13 & 14	$Y=779.41 - 2.98X$	0.93	131
15 & 16	$Y=772.43 - 3.05X$	0.94	126

1) $Y =$ carbohydrates for bunch DM palm⁻¹ (Y_c)
 $X =$ planting density (palms ha^{-1}).

2) estimated as $a/2b$.

Our results are not consistent with the suggestion of Corley (1976) that optima for current yield will remain constant after crown size has reached its mature level (9 or 10 years from field planting).

Light interception

Figure 4 depicts the linear regression equation fitted through sub-plot values of log transmission (1-f) of PAR and leaf area index (L) for fourteen year old palms in Experiment 1, together with the equation reported by Squire (1984b). Our equation ($\ln (1-f) = -0.32(L-0.6)$) resembles that of Squire ($\ln (1-f) = -0.47(L-0.3)$) in that it has an intercept on the L-axis, but our extinction coefficient (k) is substantially smaller than that reported by Squire (0.32 against 0.47 found by Squire).

W. Gerritsma (pers. com., 1987) repeated the measurements of absorbed PAR on the same palm sample in Experiment 1 in the 16th year after planting. He found a nearly identical k-value (0.33). Further, that the intercept of the regression line on the L-axis is not significantly different from zero. Therefore, the k-values from 6-14 year old commercial plantings in the environment as Experiment 1 (Table 2) were established from measurements of transmitted PAR and L-values, using the equation:

$$k = \frac{-\ln(1-f)}{L}$$

i.e without an intercept at the L-axis.

Table 2. Extinction coefficients (k) and leaf area index values (L) established in commercial plantings in West New Britain between 6 and 14 years from planting, together with measured transmission of PAR (1-f) and estimated values derived from Figure 1 and the formula presented by Squire (1984b).

Age (years)	L	k	<u>Transmission of PAR (1-f)</u>		
			<u>measured</u>	<u>estimated</u>	
				Figure 1	Squire
6	4.52	0.411	0.15	0.29	0.14
7	5.45	0.340	0.17	0.21	0.09
8	5.16	0.353	0.16	0.23	0.10
9	5.51	0.464	0.08	0.21	0.09
10	5.65	0.414	0.11	0.20	0.08
11	5.97	0.464	0.07	0.18	0.07
12	-	-	-	-	-
13	4.97	0.365	0.18	0.25	0.11
14	5.30	0.356	0.16	0.22	0.10

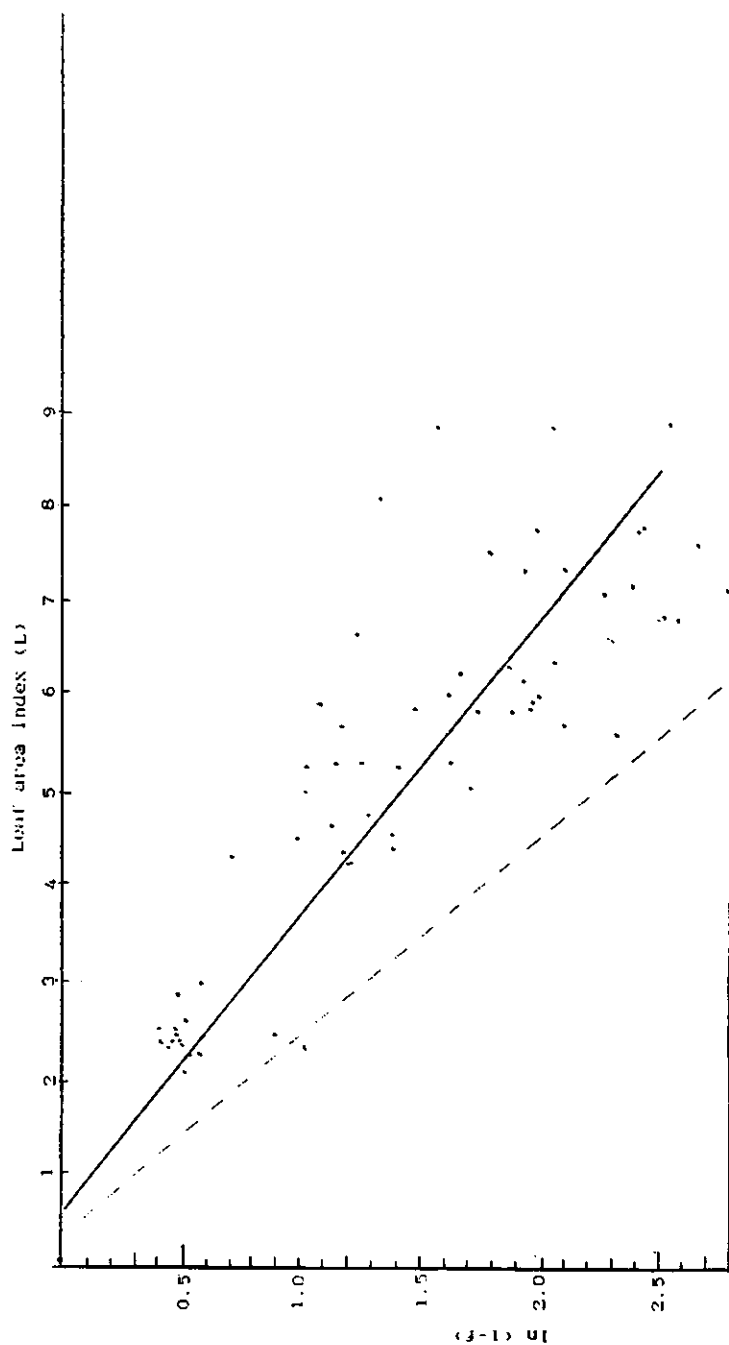


Figure 4. Relationship between interception of PAR (f) and leaf area index (L) based on sub-plot values of Experiment 1, 14 years from planting. The relationship of Squire (1984b) is also presented (dotted line).

The null hypothesis of one common regression line through the origin is rejected at the 5% significance level, i.e. the k-values differ between years of planting.

There was a clear peak in k-values for 9 to 11 year-old palms. A similar peak at about this age was obtained from measurements on plantings of different ages in North Sumatra (T. Moeljono, pers. com.). The observed trend in k-values is supported by visual observations in that ground vegetation sharply increased shortly after crown expansion was completed. The conclusion is that data derived from the formula of Squire (1984b) fit well for palms younger than 11 years, whereas the mean values obtained from Squire's formula and ours can be better applied for older palms, as can be observed from Table 2. Here measured transmission of PAR is compared with values estimated from both the Squire's equation and ours.

Efficiency of pollination

Changes in pollination efficiency over time are inferred from the mean bunch weight and the bunch survival ratio, i.e. the ratio of properly developed fruit bunches to total female inflorescences reaching anthesis (Table 3); these detailed records were not available for 186 palms ha^{-1} .

Table 3. Number of mature female inflorescences, bunch survival ratio and mean bunch weight (kg) for period of harvest 5 to 14 years from field planting, obtained in the 110 and 148 palms per ha densities of Experiment 1.

<u>Age</u> (years from planting)	<u>110 palms ha^{-1}</u>			<u>148 palms ha^{-1}</u>		
	<u>female</u> <u>inflores-</u> <u>censes</u> (palm^{-1})	<u>bunch</u> <u>survival</u> <u>ratio</u>	<u>bunch</u> <u>weight</u> (kg)	<u>female</u> <u>inflores-</u> <u>censes</u> (palm^{-1})	<u>bunch</u> <u>survival</u> <u>ratio</u>	<u>bunch</u> <u>weight</u> (kg)
5	26.5	0.82	12.0	25.9	0.81	11.5
6	23.8	0.79	12.0	22.0	0.82	11.3
7	18.3	0.78	15.1	16.1	0.72	13.1
8	12.0	1.00	18.1	9.2	0.96	15.9
9	13.8	0.98	17.0	10.9	0.91	15.7
10	14.3	0.91	18.3	11.2	0.81	16.1
11	15.8	0.73	17.0	10.8	0.63	14.9
12	14.0	0.97	21.4	11.4	0.95	19.2
13	9.7	0.76	20.8	6.4	0.70	19.0
14	11.5	0.91	22.4	9.0	0.88	20.8

Note: Assisted pollination from year 5 to 11
Insect pollination from year 12 onwards

Mean bunch survival ratio was 0.85 for both densities during year 5 to 8, but during year 11 (the last year under assisted pollination) bunch survival was relatively low in the 148 palms ha^{-1} density. Under insect pollination (from year 12 onwards) mean bunch survival ratio of the 110 and 148 plant densities was 0.88 and 0.84, respectively, which is thus similar to the initial period under assisted pollination. In contrast, bunch weight increased markedly following the release of pollinator insects.

Changes in canopy efficiency with time.

The efficiency (e) of conversion of intercepted photosynthetically active radiation (PAR) to assimilates required for dry matter production ($\text{g CH}_2\text{O MJ}^{-1}$) at the different palm ages for the three higher densities are shown in Figure 5 (the 56 density records were not available).

Efficiency diminishes at all planting densities until it reaches a minimum in year 8 to 10 and, in particular, in year 11, and thereafter improves with a clear peak in year 12. This improvement is more pronounced as the density increases but the minimum values were decreased as a function of planting density. The period of reduction in e parallels approximately that of the increase in L (Fig 5), and may be directly linked to the increase in leaf maintenance respiration consequent to the increase in leaf biomass. Apparently these losses are not completely compensated by the increase in photosynthetic production, and it is concluded that this effect is dependent upon planting density. The minima may be due to poor light distribution over the canopy, whereas an improvement thereafter may have caused the increase in e (periods with high and low k -values, respectively; Table 2). A contributing factor for the marked dip in e , in year 11, and the peak, in year 12, must be the sudden improvement of pollination after the release of the pollinating insects (Table 3). In turn this peak might have negatively affected e in year 13 due to a depletion of carbohydrate reserves.

Although our values of e cannot be directly compared with those reported by Squire (1984b), because his values are based on

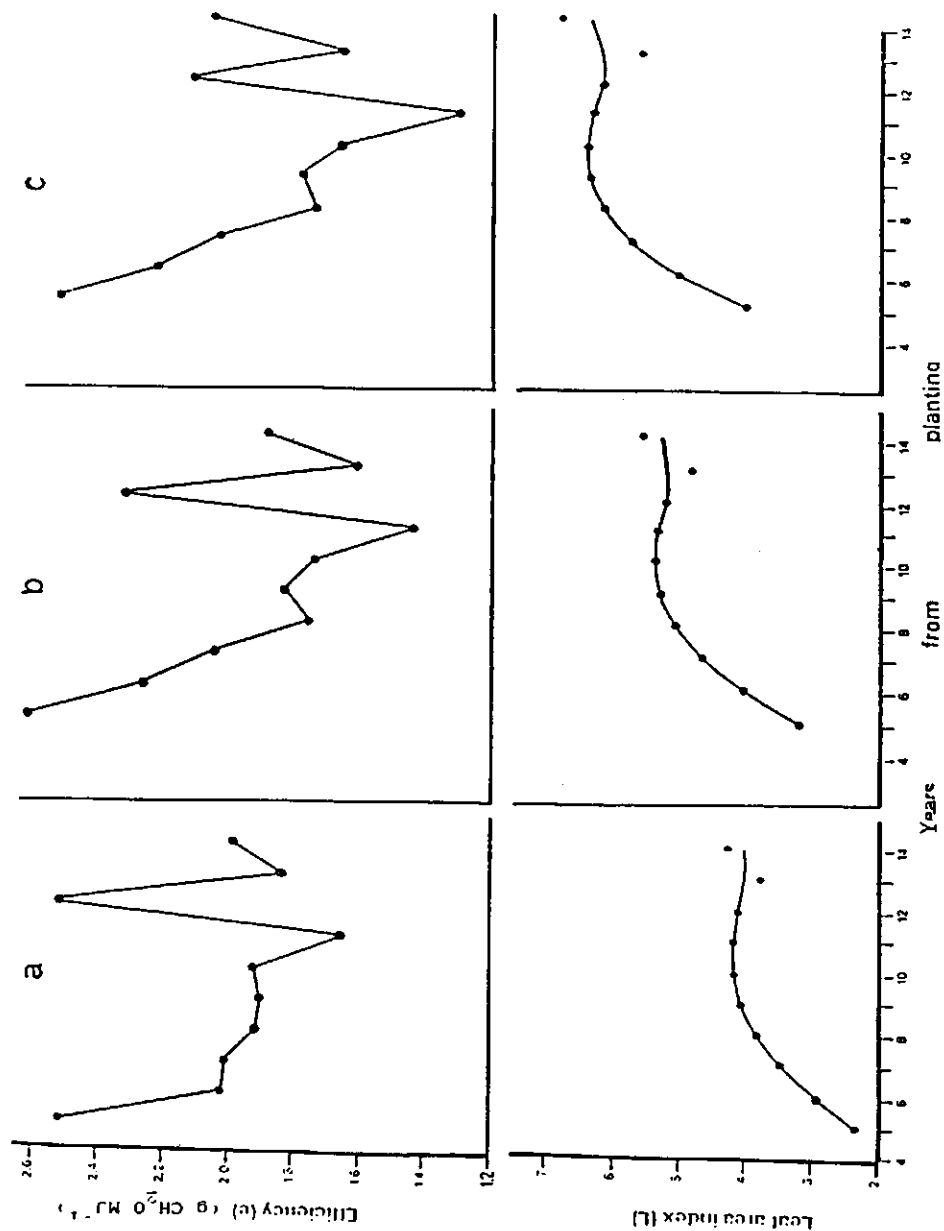


Figure 5. The efficiency (e), expressed in g CH₂O MJ⁻¹, of conversion of PAR to carbohydrates for above-ground dry matter production and leaf area index (L), plotted as functions of age, at 110 palms ha⁻¹ (a), 148 palms ha⁻¹ (b) and 186 palms ha⁻¹ (c).

weights of dry matter produced (albeit corrected for the higher energy content of oil), they differ from his as he reported a negligible effect of age or planting density on e .

DISCUSSION

Our observations of the assimilate requirements over time for the main components of dry matter (DM) production provide useful information about the factors determining the trend in economic yield. They confirm the trend in VDM with age as suggested by Corley & Gray (1976), but their assumed constancy of TDM after canopy closure appears to be a simplification.

At negligible interpalm competition for light (56 palms ha^{-1}) assimilates allocated to above-ground DM production (TDM_c) continued to increase until about 11 years from field planting (Figure 2). This is shortly after the crown leaves had attained their mature size (Figure 5) when gross photosynthetic production is expected to reach its maximum. This period became shorter, and a lower maximum was attained, as the planting density increased (Figure 2). Following the maximum a decline was observed at all densities (Figure 2), which can either be caused by a reduction in gross photosynthetic production or by an increase in maintenance respiration losses. These losses are stabilised when the crown approaches its maximum size (Breure, 1987) and their contribution to the decline depends thus on the planting density. In the two higher densities (148 and 186 palms ha^{-1}) leaf size still increases at a rapid rate after the canopy is practically closed, and the dominant cause of the decline in TDM_c at these densities might be the increase in maintenance respiration losses. These losses are apparently not compensated by an increase in photosynthetic production. This seems logical because the relationship between L and light transmission is asymptotic, which means that, for relatively high L -values, an increase in L results in a lower proportional increase in light interception. Moreover, our results suggest (Table 2) that after canopy closure, intercepted radiation becomes less evenly distributed over the foliage due to excessive interception

by the top layer of the canopy, thus decreasing photosynthetic production per unit green leaf. In contrast, the decline in TDM_c at the lower densities (56 and 110 palms ha^{-1}), and also the continuing decline at the higher densities, took place at a time when any increase in maintenance respiration would have stopped and must be due to a reduction in gross photosynthetic production. There are two factors which might be responsible for this decline when maintenance respiration has stabilised: first, a reduction in light interception, and, second, a decrease in efficiency of conversion of intercepted radiation to assimilates (e). Low e -values are indeed observed in years 8 to 11, in particular in the two higher densities (Fig 5); as mentioned, this might be due to poor light distribution consequent to an increase in light interception at that time (Table 2). From the subsequent reduction in k (Table 2) and also from the strong increase in vigour of the ground vegetation, it can be inferred that interception decreases thereafter. At the higher densities the increase in e (Fig 5) apparently more than compensated for this reduction in light interception, as TDM_c tended to increase (Fig 2); this, in contrast to the lower densities at which the increase in e appears, seems to be insufficient to compensate for the reduced interception, and TDM_c continued to decline (Fig 2). It might be argued that the increase in e (Fig 5) was a result of the improved pollination following the introduction of pollinator insects at the end of the 11th year from planting. This indeed resulted in an unusual peak in TDM_c in year 12 (Figure 5), while bunch weight clearly increased (Table 3). However, this effect of pollination efficiency on yield was subsequently compensated by a reduction in bunch number due to, initially, an abrupt and marked increase in abortion rate; this resulted in a negligible effect of improved pollination on yield, as also found by others (Gray, 1969; Syed et al, 1982). It is then concluded that pollination played no dominant role in the observed trends in utilization of intercepted light (e).

Our results suggest therefore that, at mature crown size, the trend in TDM_c is governed by a reduction in light interception. Reduced light interception is specially important at lower

plant densities and may be due to an increase in gaps of the canopy coupled with differences in height between palms (increase in depth of the canopy). At high planting densities the beneficial effect of improved light distribution becomes more dominant.

This differential effect of reduced light interception on gross photosynthetic production is mainly reflected in Y_c which depends on the surplus of assimilates after requirements for maintenance respiration and VDM_c have been met, and results in an increase in optimal density for current yield from the 13th year onwards (Table 1). A similar dip in optimal density, shortly after crown size reaches its maximum, can be obtained from long-term yield data of density experiments reported by Prevot & Duchesne (1955) and by Ramachandran et al (1972). Thus the suggestion by Corley (1976) that optimal density remains constant after the crown size reaches its maximum does not hold for palms grown in the environment of this study. Further, the suggestion by Corley et al (1973) that optimal density for current yield can be estimated from the mean area of the crown leaves does not appear to apply to plantings with mature crown size.

A further implication of the observed trends in optimal density for current yield (Table 1) is seen in the interpretation of results of thinning experiments in commercial plantings. Such experiments are usually laid down at the time of minimum light penetration (8 to 10 years from planting) and the quick yield responses to thinning at that time (Anon 1985) might be misleading when results are extrapolated for long term policy on thinning and even optimal planting density.

The above analysis of possible factors responsible for the trend in Y_c provides a basis for suggesting that yield might be improved by increasing TDM_c and reducing VDM_c . VDM_c can be diminished through breeding and selection for high bunch index (Corley et al, 1971; Hardon et al, 1972, Breure & Corley 1983; Breure 1986), while the period during which it increases can be reduced, and a lower mature value attained, by selection for so-called rapid expansion rate ideotypes, i.e. palms with rapid increase in mean leaf area and a reduced expansion period (cf Breure, 1985). Apart from a reduction in VDM_c these

ideotypes show increased initial TDM_c due to speed of ground coverage, combined with decreased leaf maintenance requirements due to reduced maximum leaf size. A reduction of losses due to leaf maintenance respiration may be possible through breeding as shown for rye grass by Wilson (1982). There seems to be little scope for breeding for favourable parameters of the assimilation-light curve for gross photosynthetic production because there is considerable evidence that there is little genetic variation in the slope of the curve at low light intensities in C_3 crops (Björkman, 1981; Ehleringer & Pearcy, 1983); but Corley et al (1973) reported significant differences between oil palm progenies in the nursery. Secondly, although the genetic variation in the assimilation rate at light saturation may be considerable, these differences would only be partly reflected in changes in photosynthetic production of the entire leaf surface, the response to selection being greater as interplant competition decreases (Spitters, 1986). On the other hand, our results indicate that there might be considerable possibilities in increasing gross photosynthetic production through measures which improve the light distribution over the leaf surface. This means that, for a given leaf area index (L), light penetration should be improved. This can, for example, be achieved through increasing the canopy depth by planting a mixture of clonal palms with distinct differences in height.

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REFERENCES

- Anon (1985). Annual report of the Papua New Guinea Oil Palm Research Association.
- Björkman, O. (1981). Responses to different quantum densities. *Encyclopedia of Plant Physiology New Series*, Springer-Verlag, Berlin 12A: 57 - 107.
- Breure, C.J. (1977). Preliminary results from an oil palm density x fertilizer trial on young volcanic soils in West New Britain. In: D.A. Earp & W. Newall (Eds), *International Developments in Oil Palm*. Incorporated Society of Planters, Kuala Lumpur. pp 192-207.
- Breure, C.J. (1982). Factors affecting yield and growth of oil palm tenera in West New Britain. *Oléagineux* 37: 213-228.
- Breure, C.J. (1985). Relevant factors associated with crown expansion in oil palm (*Elaeis guineensis*, Jacq.). *Euphytica*: 34, 161-175.
- Breure, C.J. (1986). Parent selection for yield and bunch index in the oil palm in West New Britain. *Euphytica* 35: 65-72.
- Breure, C.J. (1987). The effect of palm age and planting density on the partitioning of assimilates in oil palm (*Elaeis guineensis* Jacq.). *Expl Agric*.
- Breure, C.J. & R.H.V. Corley (1983). Selection of oil palm for high density planting. *Euphytica* 32: 177-186.
- Breure, C.J., J. Konimor & E.A. Rosenquist (1982). Oil palm selection and seed production at Dami Oil Palm Research Station, Papua New Guinea. *Oil Palm News* 26: 6-22.
- Breure, C.J. & M.S. Powell (1987, June). The one-shot method of establishing growth parameters in oil palm. Paper presented at the 1987 International Oil Palm Conference, Kuala Lumpur, Malaysia.
- Corley, R.H.V. (1973). Effect of planting density on growth and yield of the Oil Palm. *Expl. Agric*. 9: 169-180.
- Corley, R.H.V. (1976). Photosynthesis and productivity. In: R.H.V. Corley, J.J. Hardon & B.J. Wood (Eds.) *Oil Palm Research*. Amsterdam, Elsevier: 273-283.
- Corley, R.H.V. (1976). Planting Density. In: R.H.V. Corley, J.J. Hardon & B.J. Wood (Eds.) *Oil Palm Research*. Amsterdam, Elsevier: 273-283.
- Corley, R.H.V., J.J. Hardon & G.Y. Tan (1971). Analysis of growth of the oil palm (*Elaeis guineensis* Jacq.). I. Estimation of growth parameters and application in breeding. *Euphytica* 20: 307-315.

Corley, R.H.V., J.J. Hardon & S.C. Ooi (1973). Some evidence for genetically controlled variation in photosynthetic rate of oil palm seedlings. *Euphytica* 22: 48-55.

Corley, R.H.V., C.K. Hew, T.K. Tam & K.K. Lo (1973). Optimal Spacing for oil palms. In: R.L. Wastie and D.A. Earp (Eds.), *Advances in oil palm cultivation*. Incorporated Society of Planters, Kuala Lumpur, pp 52-69.

Corley, R.H.V. & B.S. Gray (1976). Yield and yield components. In: R.H.V. Corley, J.J. Hardon & B.J. Wood (Eds.) *Oil Palm Research*. Amsterdam, Elsevier: 77-86.

Corley, R.H.V. & C.J. Breure (1981). Measurements in oil palm experiments. Internal report, London, Unilever Plantation Group.

Ehleringer, J., & R.W. Pearcy (1983). Variation in quantum yield for CO₂-uptake among C₃ and C₄ plants. *Plant. Physiol.* 73: 555-559.

Gray, B.S., (1969). The requirements for assisted pollination in oil palms in Malaysia. In: P.D. Turner (Editor). *Progress in Oil Palm*. Incorporated Society of Planters, Kuala Lumpur, pp 49-66.

Hardon, J.J., C.N. Williams & I. Watson (1969). Leaf area and yield in the oil palm in Malaysia. *Expl. Agric.* 5: 25-52.

Hardon, J.J., R.H.V. Corley & S.C. Ooi (1972). Analysis of growth in the oil palm. II Estimation of genetic variances of growth parameters and yield of fruit bunches. *Euphytica* 21: 257-264.

Prevot, P. & J. Duchesne (1955). Densités de plantation pour le palmier à huile. *Oléagineux* 10: 117-122.

Ramachandran, P., R. Narayanan, & J.C.X. Knecht (1973). A planting distance experiment of dura palms. In: R.L. Wastie & D.A. Earp (Eds.), *Advances in oil palm cultivation*. Incorporated Society of Planters, Kuala Lumpur, pp 72-87.

Spitters, C.J.T. (1986). Toepassingen van gewasfysiologie en computersimulatie in de plantenveredeling. (Report Foundation for Agricultural Plantbreeding). Wageningen, the Netherlands.

Squire, G.R. (1984a). Techniques in environmental physiology of oil palm. I. Measurements of intercepted radiation. *Porim. Bull.*

Squire, G.R. (1984b). Light interception, productivity and yield of oil palm. *Palm Oil Res. Inst. Malaysia*, 73 pp.

Szeicz, G. (1974). Solar radiation for plant growth. *J. Appl. Ecol.* 11: 617-636.

Syed, R.A. (1979). Studies on oil palm pollination insects. *Bull. Ent. Res.* 69: 213-224.

Syed, R.A., I.H. Law & R.H.V. Corley (1982). Insect pollination of oil palms: introduction, establishment and pollination efficiency of Elaeidobius kamerunicus in Malaysia. Planter, Kuala Lumpur, 58: 547-561.

Waringa, N.A. (1985). Soil moisture and climate in the West New Britain area. Internal report, Agricultural University, Wageningen, the Netherlands. Limited circulation.

Wilson, D. (1982). Response to selection for dark respiration rate of mature leaves in Lolium perenne L. and its effect on growth of young plants. Ann. Bot. 49: 313-320.

FRUITING ACTIVITY AND YIELD OF OIL PALM

I. EXPERIMENTS WITH FRUIT REMOVAL

R.H.V. Corley and C.J. Breure

SUMMARY

The effect of different levels of fruit bunch removal (disbudding) on oil yield and its components, and on components of vegetative dry matter production, were studied in two oil palm experiments in Johor, Malaysia.

In one experiment disbudding commenced as soon as palms started to flower, and in the other experiment treatment commenced when palms were ten years old.

Disbudding resulted in a considerable compensation of bunch yield. Regarding the components of bunch number, the number of aborted and male inflorescences decreased, while the rate of leaf production increased. Inflorescence abortion and sex differentiation appear to have different thresholds for response to fruiting activity.

All components contributing to the weight of the bunch responded to disbudding, being spikelet number, flowers per spikelet, fruit set, mean fruit weight and the empty bunch. Of the latter components the greatest response was obtained for flowers per spikelet.

Disbudding also increased vegetative growth, which indicates that luxury production of vegetative growth can be restricted by maintaining a sufficiently high sink of bunch production.

Response of flowers per spikelet and number of spikelets occurred both 13 to 15 months after the change in fruiting activity. Response of sex differentiation was found after 16 months.

INTRODUCTION

The yield of many crops is partly affected by the yield in previous years or seasons. A well known example of this is biennial bearing in temperate fruit trees. Such effects have been described for the oil palm, Elaeis guineensis Jacq., an important tropical crop (Haines, 1959; de Berchoux & Gascon,

1965; Corley, 1977). The number of bunches developing on the palm at any one time, described by Broekmans (1957) as "fruiting activity", may have large effects on both fruit bunch number and mean bunch weight. A detailed understanding of such effects, and the resulting yield cycles, is necessary for any attempt at computer simulation modelling of oil palm growth and yield. Such simulation modelling has proved a valuable research tool with other crops, and might also be used for yield forecasting.

The three main components of oil palm yield are fruit bunch number, mean bunch weight and oil to bunch ratio. Each can be considered in terms of several sub-components. Thus bunch weight is the sum of fruit weight and empty bunch (stalk and spikelets) weight; the former is the product of spikelet number per bunch, flower number per spikelet, fruit set (the proportion of flowers which develop into fruit) and mean weight of individual fruits. Oil to bunch is the product of the fruit to bunch, the mesocarp to fruit and oil to mesocarp ratios. Bunch number depends on the number of new leaves produced, since each leaf subtends an inflorescence primordium, and on the proportion of the primordia which are female (sex ratio). In addition, some inflorescences abort before anthesis, while some fruit bunches may fail to ripen, so the abortion and bunch failure rates are also important yield components.

We will also study the effect of fruiting activity on the components of vegetative growth. These are those which determine the vegetative dry matter production, i.e. dry matter incorporated in the leaves and trunk, and the green leaf surface.

In this paper we investigate the effect of fruiting activity on all these components of oil yield and vegetative growth. Fruiting activity was artificially varied by removing a proportion of young inflorescences, before anthesis. In a subsequent paper we shall examine the importance of the effects observed here in a population showing natural yield fluctuations.

MATERIALS AND METHODS

Both the experiments described were planted on Rengam series soils in Johor, Malaysia. The palms were of the commercial tenera fruit type, planted at 138 palms per hectare, and given regular dressing of N, P, K and Mg fertilizers in accordance with normal plantation practice.

Experiment 1 was planted in 1969; inflorescence removal commenced as soon as the palms started to flower, about 1.5 years after planting. The inflorescences were cut out from the leaf axil, before anthesis, with a knife.

There were four treatments, with ten palms per plot and seven replications in a randomised block design. The four treatments were as follows:

- 1 Control with no inflorescence removal, allowed to fruit normally.

- 2 50 percent of inflorescences removed before anthesis; the inflorescences were removed from all leaf axils in every other one of the eight conspicuous leaf parastichies on each palm.

- 3 75 percent of inflorescences removed; the inflorescences were removed from six of the eight parastichies.

- 4 Complete inflorescence removal.

Treatment continued for five years, until April 1976. Recording continued to allow study of the recovery period.

Experiment 2. Here treatment commenced when the palms were ten years old, and had already been fruiting for seven years. Although there were several treatments in the experiment, only two are considered in this paper:

- 1 Untreated controls, without inflorescence removal.

- 2 75 percent of inflorescences removed, as in experiment 1. The experiment was in a randomised block design with single tree plots, and 32 replicates.

In both trials yields were recorded by weighing fruit bunches

immediately after harvest; harvesting was done every ten days. Samples of bunches were taken at random for measurements of yield components. Analysis of bunch composition followed the procedure described by Blaak et al (1963).

Vegetative measurements were made as described by Hardon et al (1969) and Corley et al (1971). The number of new leaves and male and female inflorescences produced were recorded at three monthly intervals.

Fruiting activity for month n (FA_n) was estimated as the total dry weight of bunches developing on the palm in that month. From the relationship between bunch dry weight and the time described by Corley (1969), this is:

$$FA_n = 0.41Y_{n+1} + 0.32Y_{n+2} + 0.23Y_{n+3} + 0.14Y_{n+4} + 0.05Y_{n+5}$$

where Y_n is the actual yield harvested in month n .

RESULTS

Table 1 shows that yield of fruit was significantly reduced where inflorescences were removed. However, there was considerable compensation: yield from treatments 2 and 3 were reduced by only 25 and 42 percent respectively, in comparison with the control treatment 1, although 50 and 75 percent of the inflorescences were removed. Table 1 shows that mean bunch weight was significantly increased following inflorescence removal. Bunch number was greater than expected from the rates of inflorescence removal, indicating that the number of female inflorescences must have increased on the disbudded palms. Oil content of the bunches was not affected by the treatment. The sub-components of oil to bunch ratio are not considered further here.

Table 1. Effect of disbudding on yield of fruit, bunch number per year and mean bunch weight during years 2 to 5 after fruiting started, and oil content of bunches in year 5. Experiment 1.

Treatment	Yield of fruit kg/palm/ /year	Bunch number /palm /year	Mean bunch weight kg	Oil/ bunch %
1 No disbudding	154.6	20.5	7.6	25.2
2 50% disbudding	122.5	11.9	10.3	25.5
3 75% disbudding	84.2	6.6	12.7	25.6
Standard error	2.8	0.3	0.2	0.7

Treatment 4, complete disbudding, gave no yield during this period.

Table 2 shows components of mean bunch weight. The number of flowers per spikelet was increased most, but spikelet number per bunch and mean weight per individual fruit was also increased significantly. There was a slight trend towards increased fruit set in the disbudded palms, but the difference was not statistically significant.

Table 2 also shows that the weight of the empty bunch (stalk plus spikelets) was increased approximately in proportion to the overall increase in bunch weight. Mean bunch weight was 68 percent greater for treatment 3 than for treatment 1, and empty bunch weight was 74 percent greater.

Table 2. Effect of disbudding on components of mean bunch weight for years 4 and 5 after fruiting started. Experiment 1.

Treatment	Spikelet number /bunch	Flowers per spikelet	Fruit set %	Mean fruit weight (g)	Empty bunch weight (kg)
1 No disbudding	105	11.0	44.0	15.1	3.6
2 50% disbudding	114	13.0	45.9	15.8	5.2
3 75% disbudding	120	13.9	47.8	16.3	6.2
Standard error	2	0.3	1.6	0.4	0.2

Table 3 shows components of bunch number per palm. The sex of all inflorescences emerging on the disbudded palms was recorded at the time of removal, so, in effect, the table gives the components of potential bunch number. Actual bunch number was, of course, reduced by the disbudding treatment. Leaf production rate was significantly increased, and the number of male inflorescences was significantly reduced by disbudding.

Table 3. Effect of disbudding on components of bunch number for 4 years after fruiting started. Experiment 1.

Treatment	New leaves /palm /year	<u>Inflorescences/palm/year</u>			Sex Ratio %
		Aborted	Male	Female	
1 No disbudding	31.8	2.7	8.1	21.1	72
2 50% disbudding	32.6	1.6	7.1	23.8	77
3 75% disbudding	33.2	1.4	5.1	26.6	84
4 100% disbudding	34.9	1.3	3.0	30.6	91
Standard error	0.3	0.2	0.4	0.4	-

Note: The mean number of bunches per year which failed to develop after anthesis, ranged from 0.74 (no disbudding) to 0.14 (75% disbudding).

The number of aborted inflorescences was not recorded directly, but could be estimated from the difference between the number of leaves produced and the total number of inflorescences recorded. Table 3 shows that the number of aborted inflorescences was significantly reduced by disbudding. All these changes contributed to the increased number of female inflorescences on disbudded palms.

Rate of leaf production (Table 3), leaf dry weight, leaf area, trunk height and trunk diameter (Table 4) were all increased in the disbudded palms.

Table 4. Effect of disbudding on dimensions of vegetative parts, measured 3 years after disbudding started. Experiment 1.

Treatment	Leaf area (m ²)	Leaf dry weight (kg)	Trunk height (cm)	Trunk diameter (cm)
1 No disbudding	4.89	3.16	101	60
2 50% disbudding	4.97	3.23	110	62
3 75% disbudding	5.08	3.23	111	64
4 100% disbudding	5.24	3.46	122	70
Standard error	0.11	0.09	2.7	1.2

Experiment 1 therefore provided clear evidence that many yield components are affected by the number of bunches developing on the palm, or fruiting activity. For a full understanding of seasonal yield cycles, though, we need to know how soon after a change in fruiting activity each yield component may be expected to respond. Information on this aspect was obtained from experiment 2, and also from the recovery phase after disbudding stopped in experiment 1.

Figure 1 shows data on spikelet number and flowers per spikelet from experiment 2, over a period of two years. Both components increased in the disbudded palms approximately 14 months after treatment started. For statistical analysis, data were combined in 2-month periods, as the number of bunches harvested in any one month was often small. Analysis of variance showed that both spikelet number and flowers per spikelet were significantly greater in the disbudded palms in the period 14 to 15 months after disbudding started.

There were no clear trends in percentage fruit set or in fruit weight from experiment 2.

Further information on response times was obtained from experiment 1. Tables 2 and 3 show that both bunch weight and potential bunch number increased as the intensity of disbudding increased. Bunch number was potentially at its greatest in treatment 4, which was completely disbudded. The same probably applied to bunch weight, but this was not recorded in treatment 4.

When disbudding stopped, therefore, a period of intense fruiting activity ensued in the palms of treatment 4. Figure

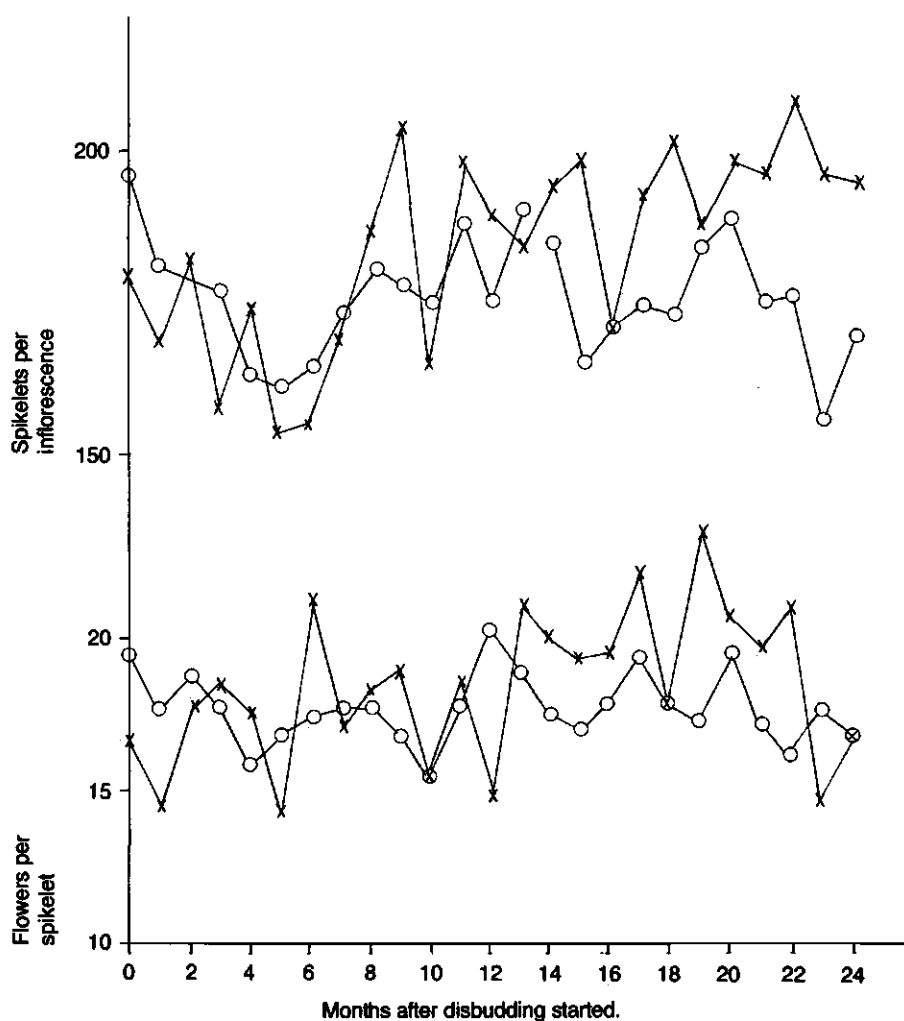


Figure 1. Number of flowers per spikelet and spikelets per inflorescence, plotted against months after disbudding started, for Treatment 1 (○—○) and for Treatment 2 (×—×). Experiment 2.

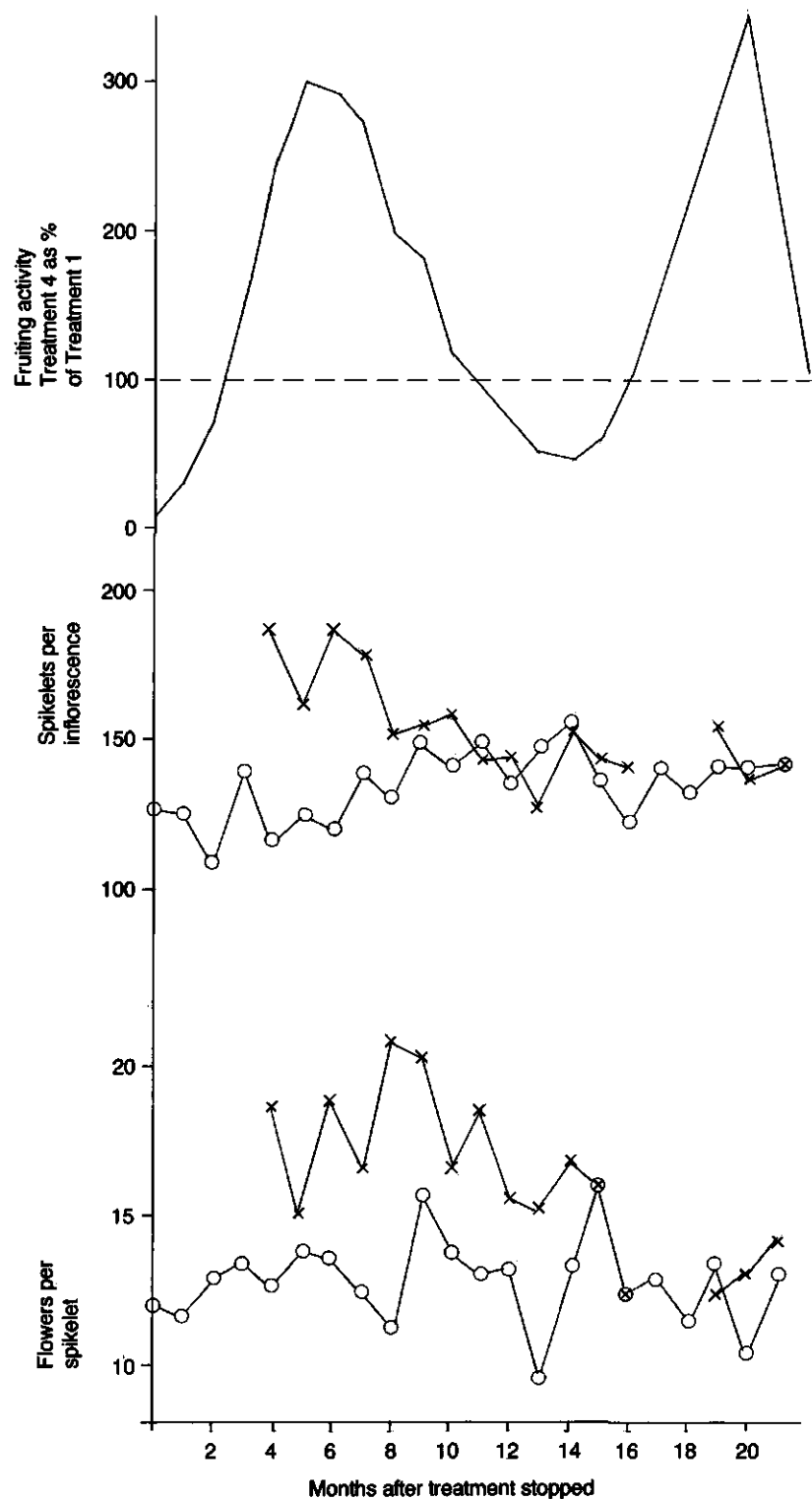


Figure 2. Number of flowers per spikelet and spikelets per inflorescence plotted against months after treatment stopped, for Treatment 1 (○—○) and for Treatment 4 (×—×). Experiment 1.

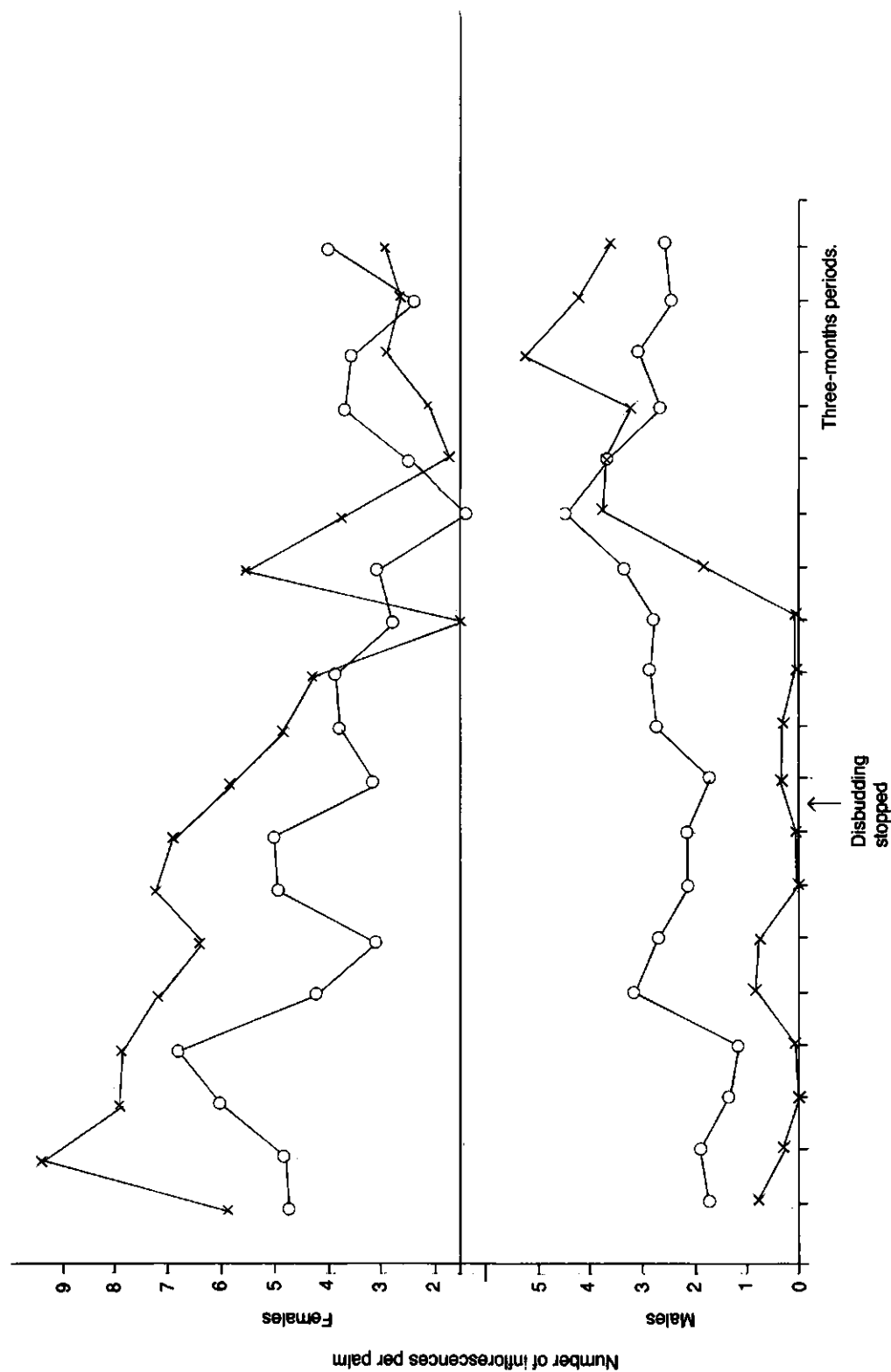


Figure 3. Number of male and female inflorescences per palm for treatment 1 (○—○) and for treatment 4 (×—×). Experiment 1.

2 shows that fruiting activity reached a level comparable to that in the control palms in June 1976, and increased to nearly three times that in the control by September, six months after treatment stopped. Flowers per spikelet in treatment 4 decreased abruptly to the control level in July 1977, 13 months after fruiting activity reached the control level. This is in reasonable agreement with the result of experiment 2.

Spikelet number decreased to the control level between January and March 1977, only 7 to 9 months after fruiting activity had reached the control level. This response was much quicker than that seen in experiment 2.

Over the two years before disbudding stopped, male flower number in treatment 4 averaged 20 percent of that in treatment 1 (Figure 3). For the first 12 months after disbudding stopped, male flower number was even lower, at 7 percent of the control level. In the three month period May to July 1977, male flower number in treatment 4 started to increase, and in August to October 1977 it was no longer significantly lower than in treatment 1.

Abortion rate was not recorded on a monthly basis, but harvested bunch number in treatment 4 dropped below the control level in March 1977; this cannot have been due to a change in sex ratio, as male flower number did not start to increase until several months later. Therefore, it is likely that this drop in bunch number was due to an increase in abortion rate, induced by the increased fruiting activity.

Bunch failure was negligible (less than 0.1 bunches per palm per year) in all treatments during the recovery period.

DISCUSSION

Artificial manipulation of fruiting activity has caused clear compensatory changes in most of the yield components studied. Fruiting activity is often thought of in terms of demand for assimilates (Broekmans, 1957). Because the oil content of bunches is unchanged by the disbudding treatments, demand for assimilates for bunch growth will be proportional to the final yield of fruit (Table 1). However, it is perhaps equally likely

that the effects of fruiting activity on yield components results from changes in levels of hormones produced by the developing seeds, as in apples (Luckwill 1970). If so, then the total number of seeds developing on the palm at any one time would provide a better estimate of fruiting activity than the total weight of bunches. In practice, both approaches give very similar estimates of fruiting activity: treatment 2 yielded 79 percent of treatment 1, and produced 78 percent of the number of seeds (calculated from bunch number per palm, spikelet number per bunch, flowers per spikelet and percentage fruit set). treatment 3 yielded 54 percent of treatment 1, and produced 51 percent of the number of seeds.

Whichever of these estimates of fruiting activity was used, flowers per spikelet, spikelet number, mean fruit weight and leaf production rate all decreased approximately linearly with increasing fruiting activity. However, it appears that flowers per spikelet is more tolerant to increasing fruiting activity than stalk weight. Of the bunch weight components, flowers per spikelet showed the greatest response.

Inflorescence abortion rate and male flower production (sex ratio) appeared not to respond linearly to fruiting activity. Abortion rate decreased from 8.5 percent in treatment 1 to 4.9 percent in treatment 2, but showed an insignificant further decrease in treatments 3 and 4. Thus a 20 percent decrease in fruiting activity was sufficient to cause the maximum observed change in abortion rate. Male flower production, on the other hand, was little different in treatments 1 and 2, but showed marked reductions in treatments 3 and 4. It appears, therefore, that inflorescence abortion and sex differentiation have different thresholds for response to fruiting activity.

The timing of response in flowers per spikelet appears clear. In both experiment, the response occurred 13 to 15 months after the change in fruiting activity. However, this response is faster than that observed by Breure & Menendez (in prep.). This might be partly associated with a gain in speed of inflorescence development in the disbudded palms.

The timing of the response in spikelet number is not clear. In experiment 2 the increase occurred 14 months after the start

of treatment. However, in the recovery period from experiment 1, a decrease occurred only 6 to 9 months after disbudding stopped. Inspection of developing inflorescences in dissected palms showed that spikelet initiation is complete several months earlier than this, and it seems most likely that spikelet number can actually be changed at such a late stage.

Breure & Menendez (in prep.) also observed a transient response in spikelet number at a similar stage. In their experiment, this coincided with an increased inflorescence abortion rate, and they suggested that there was a tendency for the largest inflorescences to abort preferentially. Thus where abortion rate increases, a reduction in average spikelet number in the surviving inflorescences would follow. A similar phenomenon may be occurring in our experiment, but in the absence of monthly abortion rate data this cannot be confirmed.

Studies of oil palm sex differentiation have often been confounded by the fact that female inflorescences are more prone to abort than males (Corley, 1976). In experiment 1, though, this complication does not arise. For two years before disbudding stopped male flower production by treatment 4 was only 20 percent of that of treatment 1, while inflorescence abortion was negligible. For 12 months after disbudding stopped, male flower production from treatment 4 remained at a low level, but it had returned to the control level by months 17 to 19 (Figure 3). It started to increase in the period 14 to 16 months after disbudding stopped, but recovery to the control level was not complete, suggesting that it commenced during the latter part of this period, at about 16 months. As anthesis normally occurs 5 to 6 months before harvest, this sex ratio response should cause a change in bunch number about 21 months after the change in fruiting activity. This response is at the lower limit of the range suggested by most other studies. Corley (1976) indicated a response time of 21 to 29 months to harvest, while Turner (1977) gave a range of from 21 to 32 months.

The responses of vegetative growth to disbudding are interesting. Several studies have shown that, when assimilate supplies are limiting, vegetative growth takes priority over reproductive growth in the oil palm (Corley et al 1971, Corley 1973, Breure, in press). Once a minimum level of vegetative

growth has been reached, surplus assimilates are then available for bunch production. However, the data in Table 4 show that, if sufficient bunch sinks are not available, then further assimilate can be diverted to vegetative growth. This additional vegetative growth, which might be termed luxury growth, clearly has a lower priority than reproductive growth.

Quantitative relationships between fruiting activity and yield components, such as have been established in this paper, will be very useful in simulation modelling and yield forecasting exercises. There have been many attempts to find statistical relationships between climatic factors and oil palm yield, with little success. We think that one reason for this lack of success is a failure to take account of the endogenous yield cycle or cycles which can result from the effect of current fruiting activity on future yield components. In a subsequent paper we shall investigate the extent to which these effects contribute to temporal variation in yield components in a natural population.

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REFERENCES

- De Berchoux, C. and Gascon, J.P. (1965). Caractéristiques végétatives de cinq descendance d'Elaeis guineensis Jacq. Premières données biométriques- Relations entre diverse caractères et la production. Oléagineux, 20, 1-7
- Blaak, G. Sparnaaij, L.D. & Menendez, T (1963). Breeding and inheritance of the oil palm. Part II. Methods of bunch quality analysis. Jl W. Afr. Inst. Oil Palm Res., 4, 145-155.
- Broekmans, A.F.M. (1957). Growth, flowering and yield of the oil palm in Nigeria. J.W.Afr.Inst.Oil Palm Res., 2, 187-220.
- Corley, R.H.V. (1973). Effect of planting density on growth and yield of the Oil Palm. Expl. Agric., 9, 169-180.
- Corley, R.H.V. (1976). Inflorescence abortion and sex differentiation. In: R.H.V. Corley, J.J. Hardon & B.J. Wood (Eds.), Oil Palm Research (pp 37-55), Amsterdam, Elsevier.
- Corley, R.H.V. (1977). Oil Palm yield components and yield cycles. In: D.A. Earp & W. Newall (Eds.), International Developments in Oil Palm. Kuala Lumpur, Incorporated Society of planters, pp 116-129.
- Corley, R.H.V., Hardon, J.J. & Tan, G.Y. (1971). Analysis of growth of the oil palm (Elaeis guineensis Jacq.). Estimation of growth parameters and application in breeding. Euphytica, 20, 307-315.
- Haines, W.B. (1959). The significance of cyclic peak yields in Nigerian oil palm. Empire J. exp. Agric., 27, 1-9.
- Hardon, J.J., Williams, C.N. & Watson, I. (1969). Leaf area and yield in the oil palm in Malaysia. Expl. Agric., 5, 25-52.
- Turner, P.D. (1977). The effects of drought on oil palm yields in South-East Asia and the South Pacific region. International Developments in oil palm. (pp 673-695). Kuala Lumpur, Incorporated Society of Planters.

THE EFFECT OF PALM AGE AND PLANTING DENSITY ON THE
PARTITIONING OF ASSIMILATES IN OIL PALM
(*Elaeis guineensis* Jacq.)

C.J. Breure

SUMMARY

Yield and growth records, assembled for several years from one density experiment, comparing 56, 110, 148, and 186 palms ha^{-1} , and one progeny experiment, planted at 115 and 143 palms ha^{-1} , were applied to estimate the partitioning of assimilates into those for structural dry matter (DM) production, and for growth and maintenance respiration losses.

Gross photosynthetic assimilation (A) for closed canopies was estimated from absorbed photosynthetically active radiation (PAR), derived from actual sunshine hours, and the assimilation-light response curve, to be $128 \text{ t CH}_2\text{O ha}^{-1}\text{a}^{-1}$. A for non-closed canopies was calculated by correcting for the degree of light transmission, which in turn was estimated from recorded leaf area index-values (L). i.e the total leaf area per unit ground area.

Of gross assimilation, 48 percent was needed for DM production, almost half of this being lost in growth respiration. The remaining 52 percent was lost in maintenance respiration. These losses appear to level off before crown expansion is completed, and since trunk biomass continued to increase, maintenance respiration per unit biomass (R) decreased with age.

Increasing planting density reduced assimilates for bunch DM, had little effect on those for vegetative growth, but strongly reduced maintenance respiration, and since biomass was little affected, reduced R. Assimilates for bunch DM per ha reached a maximum at $L = 5.6$.

The observed trends of R as a function of palm age and planting density should be further studied.

INTRODUCTION

Plant growth may be regarded as a balance between photosynthetic gains and respiratory losses. For oil palm (*Elaeis guineensis* Jacq.) the carbon budget has not been extensively reported, possibly because the supply and distribution of photosynthates change with age and are dependent on planting density. Therefore records of growth, covering a number of years, are needed for a range of planting densities. Records are required of leaf area index (L), i.e. the total green leaf surface per unit ground area, which is a function of planting density and palm age; of dry matter (DM) production; and of existing or accumulated DM (standing biomass).

Especially in perennials, where there is an accumulation of metabolically inactive stem tissue, it is meaningful to make a distinction between two types of respiration losses: those due to maintenance of existing biomass (maintenance respiration), and losses from the conversion of remaining assimilates into structural DM (growth respiration). Corley (1976) estimated total respiration losses in oil palm by measuring CO_2 -output on a sample of leaflets (assumed to represent the photosynthetic tissue) and on sections of trunk tissue (assumed to represent the non-photosynthetic tissue). However, maintenance respiration depends on the metabolic activity of the tissue (Penning de Vries, 1975); this probably differs substantially between palm organs and also with the level of growth rate (cf McCree, 1982). Corley (1976) estimated photosynthetic assimilation (A) from the pattern of light penetration to different levels in the canopy, the daily curves of incident light intensity, and the light-response curves of the leaves. This technique could not be applied in the present study because no long term data on light distribution within the canopy were available.

In the present paper respiration losses are calculated from estimates of A and annual growth data collected from one density experiment, comparing 56, 110, 148, and 186 palms ha^{-1} , and from one progeny experiment planted at 115 and 143 palms ha^{-1} .

Potential A for a closed canopy was first estimated by applying

the descriptive equations developed by Goudriaan & van Laar (1978); the required constants, which are assumed not to vary throughout the year or throughout the life of the palm, were obtained from the literature. These are the factor to convert solar radiation to PAR (Szeicz, 1979), the proportion of radiation reflected by the leaf surface (Monteith, 1972), the slope of the assimilation-light response curve, ϵ , (Ehleringer & Pearcy, 1983) and assimilation rate at light saturation (Corley, 1973). For non-closed canopies, A was corrected for the fractional transmission of PAR, estimated from recorded L-values. The adopted model assumes first that light is the sole limiting factor for gross assimilation, ignoring other limiting factors such as occasional water deficit and magnesium deficiency (Breure, 1982), and, secondly that there is a linear relationship between light interception and A; this does not take into account the effect of distribution of intercepted light on A. These simplifications are adopted in the present study because the environmental conditions at the experimental area are very favourable for oil palm (Breure, 1982), and because the interest focuses mainly on trends in the components of the carbon budget rather than on absolute values.

Annual records of DM production, assembled separately for bunches, leaves, and trunk are used to estimate growth respiration, by applying conversion factors calculated for oil palm by F.W.T. Penning de Vries (1985, pers. com.). Maintenance respiration (in terms of assimilate requirements) is assumed to be the difference between gross photosynthetic production and the quantity of carbohydrate needed for DM production. Since the latter can be determined quite accurately by our method, the uncertainty in estimating maintenance respiration depends mainly on that in estimating A. Despite this source of error the method of inference is adopted, because direct estimates, i.e. those derived from a fixed amount per unit biomass (R) appear to be quite unreliable (Amthor, 1984), particularly with perennials, where no further increase in gross assimilation occurs from the stage of canopy closure, although biomass continues to increase. The model would then predict a proportional decrease in carbohydrate available for structural growth, and, since carbohydrate needed for (vegetative dry matter (VDM) are known to have priority over

those for bunch DM (Corley et al, 1971), a negligible yield in older plantings would result. This is at odds with yield trends with age observed in commercial plantings (cf Corley & Gray, 1976).

The method used here to assemble the required DM data and the calculation methods to estimate photosynthetic production and respiration losses, are reported in detail for the interested reader. However, the objective of this paper is to provide an estimate of the partitioning of assimilates between maintenance respiration, growth respiration, and structural DM. The effects of age and planting density on this distribution, and, in particular on maintenance respiration per unit existing DM, are also studied.

MATERIALS

The experiments were located at Dami Oil Palm Research Station, West New Britain, Papua New Guinea (latitude $5^{\circ}30'$ N and longitude $150^{\circ}30'$), where environmental conditions are very favourable for oil palm (Breure, 1978;1982).

Experiment 1

This density x fertilizer experiment was planted with commercial tenera planting material in October 1970. There were four densities: 56, 110, 148, and 186 palms ha^{-1} . The three higher densities were divided into four sub-plots, each receiving different level of fertilizers. The zero fertilizer level was excluded to eliminate mineral nutrition as a potential limiting factor. More details of the experiment are given by Breure (1977).

Experiment 2

This was a dura x pisifera progeny trial testing 14 pisifera, each crossed with a set of four dura palms. Data are analysed for progenies derived from eight of the 14 pisifera, whose origin was similar to the commercial planting material of Experiment 1. The trial was planted in April 1976, with three replications at 115 and three at 143 palms ha^{-1} . The details

of this experiment are given by Breure et al. (1982).

In Experiment 1, disbudding (castration or ablation, the practice of removing the first inflorescences produced) was carried out at monthly intervals during the first year of flowering. Experiment 2 followed the new practice and was not disbudded. Both experiments were under assisted pollination, because of poor natural pollination in the environment. From 1982 onwards, more efficient pollination was achieved by introduced insect pollinators (Syed, 1979).

METHODS OF CALCULATING DRY MATTER PRODUCTION

Bunch DM

Fruit bunch yield was recorded at weekly rounds from the start of production, i.e. from May 1971 to October 1985 in experiment 1, and from June 1978 to April 1986 in experiment 2.

In Experiment 1, there was no yield recording in November and December 1981; yield data, for this period, were extrapolated from results of a census on inflorescence production in the 110 and 148 densities (to estimate bunch number), and the mean weight of bunches produced in the preceding four months.

Trunk and Leaf DM.

Annual, non-destructive growth measurements (Hardon et al, 1969; Corley et al 1971) were assembled between 4 and 14 years from planting in Experiment 1, and between 2 and 10 years from planting in Experiment 2.

Roots and male inflorescences

DM incorporated in these components was estimated as 10% of total DM production (R.H.V. Corley, pers.com.).

Conventional parameters

The method of growth measurement and the calculations to establish the relevant parameters have been fully described by Corley & Breure (1981). These parameters are DM incorporated in bunches (Y) and above-ground vegetative growth (VDM).

METHOD OF CALCULATING EXISTING DM (standing biomass)

Bunches

The estimated weight of bunches on the palm was based on results of Gray (1969) who found an increase from 1 to 6% of the fresh weight of the mature bunch during the six-month period prior to anthesis, and on Corley (1986) who found a further linear increase to 53% at harvest. From this it can be calculated that the mean DM of the bunches in year N_1 is approximately 7.5% of the total yield of fresh fruit bunches recorded in years N_1 and N_2 .

Leaves

Leaf DM is the product of the number of leaves and their mean weight. The number of leaves was assumed, based on values reported by others (Breure, 1985; Corley, 1976; Gray, 1969), to be 55 from year 2 to 6; 50 for year 7; 45 for year 8; 40 for years 9 and 10, and 35 leaves for years 11 onwards.

Mean leaf weight for year N_1 was calculated as that of leaves opening one year prior to, at the beginning of, and at the end of year N_1 . Leaf DM was divided into 65% non-photosynthetic tissue and 35% photosynthetic tissue, based on records presented by Ng et al. (1968).

Trunk DM

This was calculated as the mean of cumulative trunk DM at the beginning, and at the end of year N_1 .

Root, spear, cabbage, and male inflorescence biomass

These components were estimated, based on records of Gray (1969), to be 20% of total vegetative DM.

Calculated values of existing biomass ($t\ ha^{-1}$) of Experiments 1 and 2 are presented in Table 1.

Table 1. Standing biomass (t ha^{-1}) for two-year sequential periods. Experiment 1 (mean of 110 and 148 palms per ha) and Experiment 2 (mean of 115 and 143 palms per ha).

Age (years from planting)	Components of biomass				
	Bunches	Leaves	Trunk	Other	Total
<u>Expt. 1</u>					
5,6	4.3	18.3	7.5	6.5	36.6
7,8	3.6	21.7	12.2	8.5	46.0
9,10	3.5	21.6	17.2	9.7	52.0
11,12	3.7	19.4	22.4	10.5	56.0
13,14	3.2	20.4	28.0	12.1	63.7
<u>Exp. 2</u>					
3,4	3.4	13.0	3.0	4.0	23.4
5,6	3.7	19.0	7.6	6.7	37.0
7,8	3.8	21.1	12.2	8.3	45.4
9,10	3.6	20.9	17.3	9.6	51.4

METHOD OF ESTIMATING INTERCEPTION OF PHOTOSYNTHETICALLY ACTIVE RADIATION (PAR).

Light penetration through a canopy decreases approximately exponentially with leaf area index, L (Monsi & Saeki, 1953). Squire (1984) established the following relationship for three to fifteen-year old palms in Malaysia:

$\ln(1-f) = -0.47(L-0.3)$, where f is the fractional interception of PAR. Breure (1987) found that, in the West New Britain environment, this relationship only applies for palms younger than 11 years; in older palms transmission of PAR was higher than estimated from Squire's formula. For palms 11 years and younger, light penetration will be estimated from Squire's formula and annually determined values of L . These were established as the mean of L one year prior to, at the beginning of, and at the end of the recording year, following the method developed by Hardon et al (1969). L is thus considered to be contingent upon palm age and planting density, these being the independent variables. L -values are then applied as independent variables to estimate light penetration.

CALCULATIONS OF GROSS ASSIMILATION AND THE DISTRIBUTION OF ASSIMILATES.

General structure of the model.

Assimilates from gross assimilation of the canopy are used first for maintenance of existing DM (maintenance respiration). An additional loss of weight (through CO_2 and H_2O) occurs when the remaining assimilates are converted into structural DM (growth respiration). The growth rate for a certain period (dt) can thus be described by the following general formula:

$$dW/dt = C_f(A - RW),$$

where W = weight of structural DM; C_f = the conversion factor of assimilates into structural DM; A = gross assimilation of the canopy; R = the amount of maintenance respiration per unit existing DM.

In the following sections methods will be developed to determine A, C_f and RW. Note that RW (total maintenance respiration) in the carbon budget of the plant probably has the first priority, but its value in our model is estimated by difference.

Gross assimilation (A)

Available PAR: The mean annual solar radiation at Dami for the period 1970 to 1984 was $66.4 \text{ TJ ha}^{-1} \text{ a}^{-1}$ (Waringa, 1985), of which approximately 50% was photosynthetically active (PAR), and of this 8% is assumed to be reflected by the leaf surface (Monteith, 1973). The mean day time flux of PAR is usually calculated for the period that solar height exceeds 8 degrees, which, following Goudriaan & van Laar (1978), gives an average 10.9 hr d^{-1} at the Dami latitude. Hence, the day time flux of PAR available for absorption by the canopy amounts to

$$\frac{66.4 \times 0.50 \times 0.50 \times 0.92 \times 10^{12}}{365 \times 10.9}$$

$$8.01 \times 10^9 \text{ J ha}^{-1} \text{ hr}^{-1} = 222 \text{ W m}^{-2}.$$

Assimilation-light response curve: This curve is characterized by a region, at low light intensity, where assimilation rate is proportional to light intensity (slope at the origin is labelled α), and a region where assimilation rate is no longer

dependent on light intensity (assimilation rate at light saturation, A_{\max}). We adopted a value for A_{\max} of $11 \cdot 10^{-9}$ kg CO₂ J⁻¹ as proposed by Ehleringer & Pearcy (1983) for C₃ plants at 27°C. This is an empirically established value which appears to apply for a variety of C₃ plants. Moreover, several authors (Ehleringer & Pearcy, 1983; Bower & Martha, 1981) showed that differences between C₃ plants are small. For A_{\max} a value of 30 kg CO₂ ha⁻¹ h⁻¹ was derived from data presented by Corley et al (1973).

Gross assimilation for closed canopies: Potential A, defined as gross assimilation of a closed canopy optimally supplied with water and nutrients and free from pests and diseases, was calculated from the PAR, ϵ , and A_{\max} -values established above, following the method of Goudriaan & van Laar (1978). The canopy photosynthesis values thus obtained were 589 and 250 kg CO₂ ha⁻¹ d⁻¹ for clear and overcast skies, respectively. The proportion of canopy photosynthesis under an overcast sky was calculated as 0.47 from tabulated data for incoming PAR at a standard clear sky and an overcast sky (Goudriaan & van Laar, 1978) and actual PAR observed at Dami. This fraction is to be squared (Lantinga, 1985) for the best interpolation of A between clear and overcast sky. Potential A thus amounted to 516 kg CO₂ ha⁻¹ d⁻¹ or 128 ton CH₂O ha⁻¹ a⁻¹. This is less than values reported in the literature. Corley (1976) estimated actual gross assimilation of a ten-year old oil palm canopy (density 138 palms ha⁻¹) to be 160 t CH₂O ha⁻¹ a⁻¹. This estimate was obtained at Johor, where Squire (1984) reported a mean solar radiation of 61.2 TJ ha⁻¹ a⁻¹.

Gross assimilation for non-closed canopies was estimated by correcting for fractional transmission of PAR (f):

$$A_{\text{non-closed}} = f \cdot A_{\text{closed}}$$

RESPIRATION LOSSES

Growth respiration losses: The conversion factors (C_f) of carbohydrate required for the production of the main components

of structural DM formed ($\text{g DM g}^{-1} \text{CH}_2\text{O}$) were adopted from F.W.T. Penning de Vries (pers. com., 1985) (Table 2).

Table 2. Percentage composition and conversion factors (C_f , $\text{g DM g}^{-1} \text{CH}_2\text{O}$) of the main components of oil palms.

	Conversion factor	<u>Percentage composition</u>			
		Leaves	Trunk	Bunches	Roots
Carbohydrates	0.761	75	68	41	71
Protein	0.503	6	4	3	3
Lipids	0.304	5	2	48	2
Lignin	0.435	5	20	4	2
Organic acid	1.017	5	2	2	2
Minerals	10.0	4	4	2	2

C_f 0.696¹⁾ 0.657 0.436 0.649

1)

1

$$(.75/.761+.06/.503+.05/.304+.05/.435+.05/1.017+.04/10.0$$

Growth respiration losses are calculated from the difference between carbohydrate requirements (calculated from recorded DM production and C_f -values of Table 2) and the weight of DM formed.

Table 3 presents, as an example, calculations of growth respiration losses for the 110 palms ha^{-1} density during year 6 to 9. (see Table 4).

Table 3. Calculated method for determining carbohydrate requirements and growth respiration losses ($\text{kg CH}_2\text{O}$ per ha per day) from "measured" dry matter growth of the 110 palms per ha treatment of experiment 1 during the 6th to 9th year from planting.

	<u>DM Component</u>				Total
	Bunch	Leaf	Trunk	Root	
DM ($\text{kg palm}^{-1} \text{a}^{-1}$)	117	103	19	27	266
Carbohydrate ($\text{kg CH}_2\text{O palm}^{-1} \text{a}^{-1}$)	268	148	29	42	487

Total growth respiration losses: $487 - 266 = 221 \text{ kg CH}_2\text{O palm}^{-1} \text{a}^{-1}$ or $67 \text{ kg CH}_2\text{O ha}^{-1} \text{d}^{-1}$

Maintenance respiration losses: The amount of assimilates needed to maintain existing DM is in our model inferred as the difference between gross assimilation (A) and carbohydrate required for total DM production.

For example, maintenance respiration losses for the 110 palms ha^{-1} density during year 6 to 9 (see Table 4) amounts to:

308 (gross assimilation) - 147 (carbohydrate needed for DM production) = 161 (amount of maintenance respiration (expressed in $\text{kg CH}_2\text{O ha}^{-1} \text{d}^{-1}$).

RESULTS

Partitioning of photosynthates

Results are only assembled for the 6th to 9th years from planting, because for this period the complete set of records was available for both experiments.

Mean weight losses in respiration amounted to 73% (21% for growth respiration and 52% for maintenance respiration) (Table 4).

Table 4. Gross assimilation ($\text{kg CH}_2\text{O}$ per ha .per day) and assimilates needed for maintenance² and growth respiration, and carbohydrate incorporated in structural DM formed. Two planting densities of experiments 1 and 2 during the period 6 to 9 years from planting. (In brackets requirements as a percentage of gross assimilation).

<u>Density</u> (palms per ha)	<u>Gross</u> <u>assimilation</u>	<u>Carbohydrate needed for</u> <u>structural DM production</u>		<u>Maintenance</u> <u>requirements</u>
		growth respiration	incorporated in structural DM	
110 1)	308	67	80	161
148 1)	331	73	92	166
115 2)	315	63	78	174
143 2)	333	72	90	172
Mean	322	68 (21)	86 (27)	168 (52)

1) Experiment 1

2) Experiment 2

Maintenance respiration is thus clearly the most important component in the carbon budget. Our estimate for total respiration losses agrees very well with results reported for some other tropical perennials (Corley, 1983).

Changes in partitioning of assimilates

Results are only presented for sequential two-year periods between the 3rd and 10th year from planting for Experiment 2 (Table 5) because, in contrast to Experiment 1, vegetative growth was recorded from the start of bunch production, and no potential bunches were removed during the first year of flowering (castration).

Table 5. Carbohydrate ($\text{kg CH}_2\text{O ha}^{-1}\text{d}^{-1}$) needed for total DM production and maintenance² respiration, together with maintenance respiration per unit biomass ($\text{g CH}_2\text{O kg}^{-1}\text{DM d}^{-1}$). Mean values for the 115 and 143 densities of Experiment 2.

Age (years from planting)	Gross assimilation	Carbohydrate requirements for		Daily maintenance per unit biomass
		Growth	Maintenance	
3	243	107	136	7.1
4	287	134	153	5.6
5	311	155	156	4.1
6	325	149	176	4.4
7	327	145	182	4.1
8	326	168	158	3.4
9	323	146	177	3.7

This shows that carbohydrate requirements for DM production and for maintenance respiration appeared to stabilise when palms were about 7 years old. In contrast, total biomass continued to increase with age (Table. 1), which, since leaves and bunches are regularly removed, was mainly due to increases in trunk DM. As a result, there is a clear diminishing trend in R with age.

The effect of planting density on the carbon budget

Mean values per palm of gross assimilation, carbohydrate required for the production of the main components of DM (bunches and vegetative growth), and those for maintenance respiration for Experiment 1 are presented in Table 6. Results are assembled for the period for which actual single palm records of above-ground DM production were available, i.e. years 6 to 9 from planting.

Table 6. Gross assimilation ($\text{kg CH}_2\text{O ha}^{-1}\text{d}^{-1}$) and assimilates needed for maintenance and growth respiration, and carbohydrate incorporated in structural dry matter (DM) formed. Two planting densities of experiments 2 and 3 during the period 6 to 9 years from planting. (In brackets requirements as a percentage of gross assimilation).

Density (palms ha^{-1})	Gross assim. ilation	Carbohydrate needed for Bunch growth	Veget ative growth	Maint. enance respir.	Mean total biomass	Daily maint enance per unit biom ass
56	3.96	1.01	0.62	2.33	356	6.5
110	2.92	0.74	0.60	1.58	358	4.4
148	2.22	0.55	0.55	1.12	345	3.2
186	1.83	0.37	0.54	0.92	341	2.7

The decrease in gross assimilation per palm due to increasing planting density affected both assimilates needed for m

The decrease in gross assimilation per palm due to increasing planting density affected both assimilates needed for maintenance respiration and those available for total DM production. Moreover, it is apparent that the reduction in carbohydrate for DM production is almost restricted to those needed for bunch DM. Increasing planting density had little

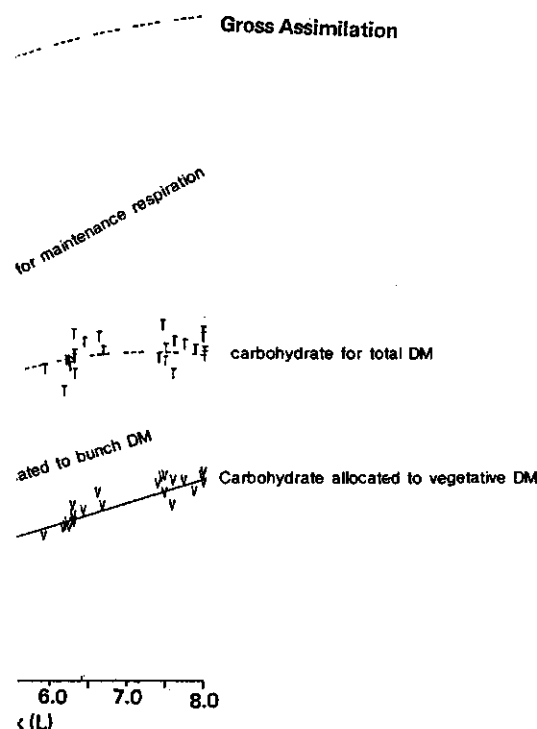
ERRATA

p. 220. Heading Table 6 should read:

Table 6. Gross assimilation ($\text{kg CH}_2\text{O palm}^{-1}\text{d}^{-1}$) at four densities and its partitioning into carbohydrates needed for growth and for maintenance respiration, compared with mean total biomass (kg palm^{-1}) and its maintenance ($\text{g CH}_2\text{O kg}^{-1}\text{DM d}^{-1}$). Experiment 1 during the period 6 to 9 years from planting.

ss; the decrease in maintenance
 long decrease in R. These results
 reported for white clover by McCree

of increasing interpalm competition
 carbon budget on a per ha basis (Fig.
 between L and (1) gross assimilation,
 carbohydrate incorporated in total DM
 vegetative DM production.



leaf area index (L) and carbohydrate
 allocated to vegetative DM (V____),
 the total of measured vegetative DM
 and bunch DM, T----T). Points being sub-plot values of the
 four planting densities of Experiment 1, from 6 to 9 years
 from planting. The relationship between L and Gross assimilation
 (--- --- ---) is derived from the formula of Squire (1984).
 Maintenance respiration is in the adopted model inferred as
 the difference between Gross assimilation and carbohydrate
 allocated to total DM production.

The latter fitted a linear regression line ($R^2 = 0.97$), whereas the former relationship was best fitted by a quadratic curve ($R^2 = 0.91$). The distance between these regression lines is the amount of carbohydrate allocated to bunch DM. This amount, which is based on actually recorded bunch DM production and C_f -values presented in Table 2, showed an optimum at $L = 5.6$. This was estimated by fitting a quadratic regression through sub-plot values of L and carbohydrate needed for bunch DM.

Note that the oil palm is an indeterminate species, which means that the main growing point remains vegetative and the yield originates from axillary buds. The apparent priority of carbohydrate allocated to vegetative growth over that to bunch DM (Fig. 1) is a typical characteristic of several of such species in that when the flow of photosynthates per plant is reduced, through increasing the level of interplant competition for light, there may occur at extreme levels of light competition, a monopolization of this flow by vegetative growth at the expense of economic yield (De Wit et al., 1979).

DISCUSSION

Our model which is novel for oil palm in that it is based on annual growth data, quantifies the components of the carbon budget and permits the separation of growth and maintenance respiration losses. The latter is determined by inference, and its accuracy depends to a large extent on the reliability in estimating A . For example, if the true value for A in Table 4 were 25% higher than estimated, the maintenance respiration inferred would be increased by 80 units; this would increase the proportion of gross assimilation from 52 to 62%. However, provided that there is no bias in estimating carbohydrate needed for DM production, or in A , as a function of planting density and palm age, the observed trends with density and age should be valid. Considering first carbohydrate for DM production, the only uncertainty is in estimating root DM, because other DM components were actually recorded; roots are a low proportion of total DM, though, and a possible error in root DM does not appear important. It is also unlikely that a systematic error

in estimating A could explain our calculated trends in R (Table 5 and 6). On the contrary, there is evidence (Breure, 1987) that the increases in A values with age and planting density are overestimated by the method adopted in this paper. If so, the increase in maintenance respiration per hectare would also be overestimated. Consequently it is likely that there is an even more pronounced decrease in R with planting density and palm age than shown in Tables 5 and 6, respectively. The decrease in R with age might be partly due to a decrease in leaf maintenance requirements, associated with a reduction in photosynthesis per unit leaf surface as L increases (McCree, 1982). Since there is a close, positive, relationship between maintenance requirements and the N-content of biomass (de Wit et al, 1978), the reduction in R might also be associated with the decrease of N-content of the leaves with palm age (Ochs & Olivin, 1976). However, the main conclusion must be that, despite its steady accumulation (Table 1), most of the trunk tissue is inactive, and respiration losses must be mainly restricted to the younger part of the trunk. This appears reasonable, since phloem bundles from the leaves to developing bunches and vegetative parts, and also cambium tissue (both metabolically very active components) are particularly abundant in the young, leaf bearing, part of the trunk (van Kraalingen, pers. com.). This is in contrast to the older trunk tissue, in which phloem bundles leading to abscised leaves show signs of collapse of the sieve walls (Parthasarathy and Tomlinson, 1962). Our results (Table 5) do not support the suggestion of Rees (1963), that the respiration load of the accumulating trunk DM might take an increasing proportion of total photosynthetic production. Respiration losses of the leaves appear to be more important than those of the trunk for three reasons: firstly leaf biomass has a higher maintenance respiration (Corley, 1976; de Wit et al, 1978)), secondly, its weight in mature palms is approximately double that of the leaf bearing trunk tissue (Table 1), and, thirdly, leaf tissue remains metabolically active, irrespective of palm age (leaves are regularly removed). Results of Wilson (1982) proving that selection for reduced leaf maintenance respiration is feasible, and appears to result in a proportional increase

in DM production, is thus of direct interest for oil palm breeding. The trend we observed in R with planting density (Table 6), is consistent with results reported by others (McCree and Kresovich, 1978; Wilson et al, 1980; McCree, 1982) in that there appears to be a positive relationship between maintenance respiration and growth rate on a per plant basis.

The proportion of total assimilates lost by respiration (Table 4) is similar to that estimated for ten-year old oil palms by Corley (1976). In contrast, our absolute values of the two components, i.e respiration losses and gross assimilation, are both substantially lower. There are two possible reasons why Corley's estimates of respiration losses are higher than ours: first, he extrapolated CO_2 -output of small plugs of unspecified trunk tissue to the entire non-photosynthetic part of the palm, while our study suggests that part of this is metabolically inactive. Second, he estimated leaf respiration by extrapolation of photosynthetic light response curves adopting an initial light use efficiency which was probably too large, namely $18.8 \times 10^{-9} \text{ kg CO}_2 \text{ J}^{-1}$ (Corley et al, 1973) compared with our value of 11.0×10^{-9} adopted from Ehleringer & Pearcy (1983) and recently confirmed for oil palm by Gerritsma (pers. com.). This higher initial light use efficiency appears to be also the cause of Corley's higher estimate of gross assimilation ($160 \text{ t CH}_2\text{O ha}^{-1} \text{ a}^{-1}$, against 118 obtained from our method in the same age group).

In conclusion, it is apparent that maintenance respiration losses are of paramount importance in the carbon budget. The observed diminishing trend in R with age and planting density (Tables 5 and 6; Fig. 1) appears to be a consequence of an increase in inactive biomass and a reduced growth rate per palm. This implies that maintenance respiration ($\text{kg CH}_2\text{O ha}^{-1} \text{ d}^{-1}$) becomes by and large stable when the canopy is closed and appears to be proportional to A rather than to the standing biomass. A more precise quantification of the effect of varying conditions on R than that derived from our model is needed for developing simulation models for oil palm growth and production. For such a study our method of inference looks suitable, provided crop photosynthesis can be measured or calculated accurately.

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REFERENCES

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

BOWER & MARTHA (1981).

BREURE, C.J. (1977). Preliminary results from an oil palm density x fertilizer trial on young volcanic soils in West New Britain. In D.A. Earp & W. Newall (Eds.). *International Development in Oil Palm*, Kuala Lumpur, Incorporated Society of Planters, 192-207.

BREURE, C.J. (1978). Research Report Dami Oil Palm Research Station 1971 - 1977, Vol I and II, 215 pp.

BREURE, C.J. (1982). Factors affecting yield and growth of oil palm tenera in West New Britain. *Oléagineux*, 37, 213 - 228.

BREURE, C.J. (1985). Relevant factors associated with crown expansion in oil palm (*Elaeis guineensis* Jacq.). *Euphytica*, 34, 161 - 175.

BREURE, C.J. (1986). Parent selection for yield and bunch index in the oil palm in West New Britain. *Euphytica*, 35, 65-72.

BREURE, C.J. (1987). The effect of different planting densities on yield trends in oil palm. *Expl. Agric.*

BREURE, C.J., KONIMOR, J., & ROSENQUIST, E.A.R. (1982). Oil Palm selection and seed production at Dami Oil Palm Research Station, Papua New Guinea. *Oil Palm News*, 26, 6 - 22.

CORLEY, R.H.V. (1976). Photosynthesis and Productivity. In: R.H.V. CORLEY, J.J. HARDON & B.J. WOOD (Eds.). *Oil Palm Research*, Amsterdam: Elsevier, 1976, 55 -76.

CORLEY, R.H.V. (1986). Oil Palm. In: CRC Handbook of fruit set and development. MONSELISE, S.P. (Edt.) 253- 258.

CORLEY, R.H.V. (1983). Potential productivity of tropical perennial crops. *Expl. agric.*, 19, 217 - 237.

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

CORLEY, R.H.V., HARDON, J.J., and OOI, S.C. (1973). Some evidence for genetically controlled variation in photosynthetic rate of oil palm seedlings. *Euphytica*, 20, 48 - 55.

CORLEY, R.H.V. & GRAY, B.S. (1976). Yield and yield components. In: R.H.V. CORLEY, J.J. HARDON & B.J. WOOD (Eds.). *Oil Palm Research*, Amsterdam, Elsevier: 77 - 86.

CORLEY, R.H.V., and BREURE, C.J. (1981). Measurements in oil palm experiments. Internal report, Unilever Plantation Group, London, 35 pp.

EHLERINGER, J. & PEARCY, R.W. (1983). Variation in quantum yield for CO₂-uptake among C₃ and C₄ plants. *Plant Physiol.* 73, 555 - 559.

GOUDRIAAN, J., and van LAAR, H.H. (1978). Calculation of daily totals of the gross CO₂ assimilation of leaf canopies. *Neth. J. of Agric. Sci.* 26: 373 - 382.

GRAY, B.S. (1969). A study of the influence of genetic, agronomic and environmental factors on the growth, flowering and bunch production of the oil palm on the West Coast of Malaysia. Ph.D. Thesis, University of Aberdeen, 947 pp.

HARDON, J.J., WILLIAMS, C.N., & WATSON, I. (1969). Leaf area and yield in the oil palm in Malaysia. *Expl. Agric.* 5, 25 - 52.

LANTINGA, E.A. (1985). Productivity of grasslands under continuous and rational grazing. Thesis, University of Wageningen. 61 pp.

MC CREE, K.J. (1982). Maintenance requirments of white clover at high and low growth rates. *Crop Science*, 22, 345 - 351.

MC CREE, K.J. and KRESOVICH, S. (1978). Growth and maintenance requirements of whtie clover as function of daylength. *Crop Sci.* 18, 22 - 25.

MONSI, M. and SAEKI, T (1953). Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Jap. J. Bot., 14, 22 - 52.

MONTEITH, J.L. (1973). Principles of environmental physics. Edward Arnold, London, 241 pp.

NG, S.K., THAMBOO, S., and DE SOUZA, P. (1968). Nutrient contents of oil palms in Malaya. II: Nutrients in vegetative tissue. Malay. Agric. J. 46, 332 - 390.

OCHS, R. and OLIVIN, J. (1976). research on mineral nutrition by the IRHO. In: R.H.V. CORLEY, J.J. HARDON, & B.J. WOOD (eds.) Oil Palm Research, Amsterdam; Elsevier, 182- 213.

PARTHASARATHY, M.V. & TOMLINSON, P.B. (1967). Anatomical features of metaphloem in stems of Sabal, Cocos and two other palms. Amer. J. Bot. 54, 1143 - 1151.

REES, A.R. (1963). Relationship between growth rate and leaf area index in the oil palm. Nature, 197, 63 - 64.

SQUIRE, G.R. (1984). Light interception, productivity and yield of oil palm. Palm Oil Res. Inst. Malaysia, 73 pp.

SYED, R.A. (1979). Studies on oil palm pollination by insects. Bull. Ent. Res. 69, 213 - 224.

SZEICZ, G. (1974). Solar radiation for plant growth. J. Appl. Ecol., 11, 617 - 636.

WARINGA, N.A. (1985). Soil moisture and climate in the West New Britain Area. Internal report, Agricultural University, Wageningen.

WILSON, D.R. (1982). Response to selection for dark respiration rate of mature leaves in *Lolium perenne* L. and its effect on growth of young plants. Ann. Bot., 49, 313 - 320.

WILSON, D.R., van BAVEL, C.H.M., and MC CREE, K.J. (1980) Carbon balance of water deficient grain sorghum plants. Crop Sci. 20: 153- 159.

WIT, C.T. de, van LAAR, H.H. and van KEULEN, H. (1979). Physiological potential of crop production. In: J. Snee and A.J.T. HENDRIKSON (Eds), Plant breeding perspectives. Wageningen, Pudoc. p 47-81.

WIT, C.T. de et al (1978). Simulation of assimilation, respiration and transpiration of crops. Simulation monographs. PUDOC, Wageningen, 140 pp.

THE ONE-SHOT METHOD OF ESTABLISHING GROWTH
PARAMETERS IN OIL PALM.

C.J. Breure and M.S. Powell

SUMMARY

Mean growth parameters, for year 3 to 10 from planting, calculated from annual yield and growth records, were compared with those determined from annual yield records and two sets of growth measurements made six years and ten years after planting. The growth parameters compared in this study were Bunch Index (BI, the proportion of total dry matter used for bunch yield), Leaf Area Ratio (LAR, the ratio of leaf area produced to dry matter used for vegetative growth), and parameters derived from the logistic growth curve fitted through leaf area values against palm age, of a dura x pisifera progeny trial, established at Dami Oil Palm research Station, West New Britain, Papua New Guinea.

The records used to calculate the estimated growth parameters are, in addition to conventional yield records, height, trunk diameter, frond weight, leaf area, and the number of frond bases and crown leaves in all eight spirals. High correlations between actual and estimated BI and LAR are found; results demonstrate that one round of growth recording, at the end of the usual period of yield recording, is sufficient to select progenies for these parameters. Precision was not improved by using frond base counts of more than two spirals.

To permit establishing the logistic growth curve and to select individual palms on the basis of LAR, an additional recording round is required at the end of yield recording.

Our method, which is described in detail, greatly reduces recording intensity and permits selection for growth characteristics in trials for which only limited growth records are available.

INTRODUCTION

There has been a growing interest in including vegetative characteristics in the selection of oil palm, in addition to economic yield and its components.

Frequent recording, at reasonable cost, has become feasible since the development of non-destructive vegetative measurements (Hardon et al, 1969; Corley et al, 1971). These techniques have been adopted at the Dami Oil Palm Research Station, West New Britain, Papua New Guinea, since 1973.

In this favourable environment for oil palm growth, Breure & Corley (1983) provided evidence that selection for Bunch Index (BI, the proportion of total dry matter production used for fruit bunches) would increase yield per hectare. further, Breure (1986) showed that additional selection for leaf area ratio (LAR, the area of new leaf produced to total new vegetative growth) would result in a more rapid increase in BI in the offspring than would direct selection for BI itself. In passing it should be noted that the benefit of selection for high LAR had been suggested earlier on theoretical grounds (Corley et al, 1971; Hardon et al, 1972; Corley, 1973).

Breure (1986) showed that selection for rapid crown expansion and reduced expansion after canopy closure is another method to increase BI. Crown expansion is described by fitting a logistic growth curve through leaf area (LA) of a standard leaf against palm age; characteristic parameters derived from this curve are the maximum asymptotic value of LA (L_m), the time required to reach 0.95 L_m ($t_{0.95}$) and the so-called leaf expansion ratio (ER, the ratio of LA at maximum expansion rate to LA at its final size, L_m). Both high LAR and high ER increase the area of the light intercepting photosynthetic tissue with a minimum increase in those vegetative parts which are inactive in photosynthetic production. Therefore, the success of selection for these characters in increasing BI was to be expected, and these can be considered valuable selection criteria.

At least one year elapses before BI and LAR can be determined by the method of Corley et al (1971) because essential variables for estimating dry matter production, i.e. height increment

and rate of leaf production, are measured between annually marked reference points. Their method involves measuring a standard leaf, at annual intervals, to estimate the mean area and the weight of the leaf. Clearly, more rapid methods would be an advantage.

Detailed growth records using the conventional method were assembled annually from all palms of a dura x pisifera progeny trial at Dami for the first ten years from field planting. This extensive set of records will be used to determine whether reliable estimates of BI and LAR can be obtained from one single round of growth measurements. The advantages of such a "one-shot method are obvious: first, it would permit immediate selection on the basis of growth parameters of those progeny trials for which only yield records are available, and second, it would greatly reduce recording costs. The key to such a method is to obtain reliable records of the rate of leaf production, because this is the most important component of vegetative dry matter production.

Counting the total number of leaf bases on the trunk appears to be an obvious method, but the older leaf bases are no longer visible, due to expansion of the trunk during the early years in the field. The corresponding period of leaf production can only be determined when the actual leaf production from the time of field planting is known. Moreover, the validity of the method of counting the fronds on the trunk depends on whether or not progenies differ in the period during which leaf bases are concealed under the trunk.

Equally important is to find an instant method of determining annual height increment since this is, in addition to being a variable required for establishing vegetative dry matter production, a characteristic which determines the economic life of an oil palm planting. A mature rate of increase is reached several years after field planting, so that measured height must be corrected for age to arrive at a mean annual increment. If this correction is a characteristic of a particular environment, once established it could be applied to all material in breeding programs conducted in that environment.

Finally, mean area and weight of the leaves can be conveniently

determined in one single recording round from measuring a set of two leaves in the crown, because leaf growth stops as soon as the leaf is fully opened (spear leaf stage). Leaf measurements at a certain age, however, do not lead to the actual mean values for the entire recording period because both leaf weight and leaf area of subsequent spear leaves increase with palm age for at least the first ten years after field planting; data thus obtained should be considered of relative value. Moreover, because of differences in ER-values, the pattern of increase in leaf area may differ between progenies so that their ranking on the basis of LAR may change with age. Thus, to obtain reliable estimates of LAR, an additional set of recording may be required.

A more extensive set of LAR values than can be obtained with a single round of recording is definitely necessary to fit the logistic growth curve (Breure, 1985), and with little extra work the petiole can be measured to estimate frond weight. This would give an additional set of LAR estimates, based on the ratio leaf area/leaf dry matter production only. Since trunk dry matter production makes only a minor contribution to the variation of total vegetative dry matter production, the error in relative progeny values of this alternative LAR measurement is expected to be negligible.

In the present paper both methods of estimating LAR will be compared with that based on the complete set of growth records. In addition, we will compare parameters derived from the logistic curve based on a reduced set of LA-values with those determined from annual leaf area measurements for the first ten years from planting. The final objective is to evaluate the reliability of estimating BI from a single set of growth measurements made at the end of the usual period of recording.

MATERIALS AND METHODS

Records are from a dura x pisifera progeny trial testing 14 pisifera, each crossed with a set of four dura palms. The adopted crossing scheme is generally referred to as the North Carolina mating design I (Comstock & Robinson, 1952). Progenies

were planted in a split-plot design with pisifera parents determining main plots of 16 palms and with dura parents determining sub-plots of four palms each.

The experiment was planted at Dami in April 1976, with three replicates at 115 palms per ha and three at 143 palms per ha.

Observations

Bunch yield was recorded at each harvesting round from the start of production in June 1978.

Non-destructive measurements as developed by Hardon et al (1969) and Corley et al (1971) were carried out on the first fully opened leaf, each year between April 1977 and April 1986. From these records the area and the mean weight of the leaves were estimated.

In August 1982 the number of leaf bases was counted on spiral 1 (the spiral of the youngest fully opened leaf) and spiral 5. In September 1986 leaf bases on all eight spirals were counted.

Rate of actual leaf production was determined annually, from the time of field planting until April 1986. In order to determine actual leaf production until the time of a leaf base count, a correction was made on the basis of the previous year's values.

Height was measured to the base of leaf 25, each year from April 1979 to April 1986; the adopted reference point is a little below the growing point.

Trunk diameter was measured at the level of the base of leaf 56 in August 1980.

From these records values of Bunch Index (BI), leaf Area Ratio (LAR), the logistic growth curve of leaf area (LA) against age, are derived. These are considered actual values against which those based on a reduced set of records are tested (estimated values).

RESULTS

Leaf production

The difference between actual production of leaves and those

of a frond base count represents the number of frond bases concealed under the expanding trunk. The corresponding period of production was estimated based on the mean monthly leaf production during the first two years in the field. The period during which initial leaf production was concealed did not differ significantly among progenies derived from each of the 14 pisifera, or between densities (Table 1).

Table 1. Actual number of fronds produced for the first ten years after field planting (FP 86A) and those estimated from a single frond base count at the end of the recording period (FP 86E), together with the corresponding period (months) of concealed leaf bases (PCL). Dura x pisifera progenies derived from 4 crosses of 14 different pisifera, planted at 115 palms palms per ha (D_1) and 143 palms per ha (D_2).

Progeny	FP 86A		FP 86E		PCL (months)	
	D_1	D_2	D_1	D_2	D_1	D_2
1	303	296	255	247	15.5	16.2
2	321	307	274	262	15.0	14.7
3	304	301	259	253	14.9	16.0
4	308	301	259	254	16.1	15.9
5	314	308	269	259	14.7	16.2
6	317	306	265	258	16.3	15.6
7	306	307	260	258	15.9	16.4
8	319	311	271	266	15.8	15.0
9	332	318	275	267	17.6	16.2
10	313	305	265	258	15.6	15.6
11	323	314	267	259	17.9	17.7
12	304	301	254	250	16.3	17.2
13	316	307	266	259	16.5	15.8
14	300	296	252	250	15.9	15.7
Mean	313	306	264	257	16.0	16.0

Therefore, the mean period of all progenies can be used to correct the frond base count for the number of concealed frond bases. As this amounts to about one year (actually 16 months), the annual leaf production for the present paper is estimated by the formula:

number of visible fronds at year t

t-1

where t is the number of years after field planting at the moment of the frond base count.

Counting frond bases in all spirals may be excessive. To determine the loss in precision by counting a reduced number of spirals, we calculated correlation coefficients between the actual number of leaves produced and those estimated by counting frond bases and green leaves on two, three, four and all eight spirals (Table 2).

Table 2. Correlation coefficients ¹⁾ between the actual number of fronds produced for the first ten years after field planting (FP 86A) and those based on a single frond base count for different number of spirals at the end of the recording period (FP 86E). Dura x pisifera progenies derived from crosses of 14 different pisifera, planted at 115 palms per ha (D₁) and 143 palms per ha (D₂).

<u>Number of spirals</u> <u>to estimate FP 86E</u>	<u>FP 86A (D₁)</u>	<u>FP 86A (D₂)</u>
8 (D ₁)	0.92 ^{xx}	
8 (D ₂)		0.90 ^{xx}
4 (D ₁)	0.92 ^{xx}	
4 (D ₂)		0.90 ^{xx}
3 (D ₁)	0.91 ^{xx}	
3 (D ₂)		0.90 ^{xx}
2 (D ₁)	0.92 ^{xx}	
2 (D ₂)		0.90 ^{xx}

1) based on mean values of 48 palms per pisifera.

High and identical correlations are found between actual and estimated values, so that no further improvement in accuracy is obtained by counting more than two spirals.

Height increment

The mean height increment of the 14 progenies stabilises in the fourth year after planting (Fig 1).

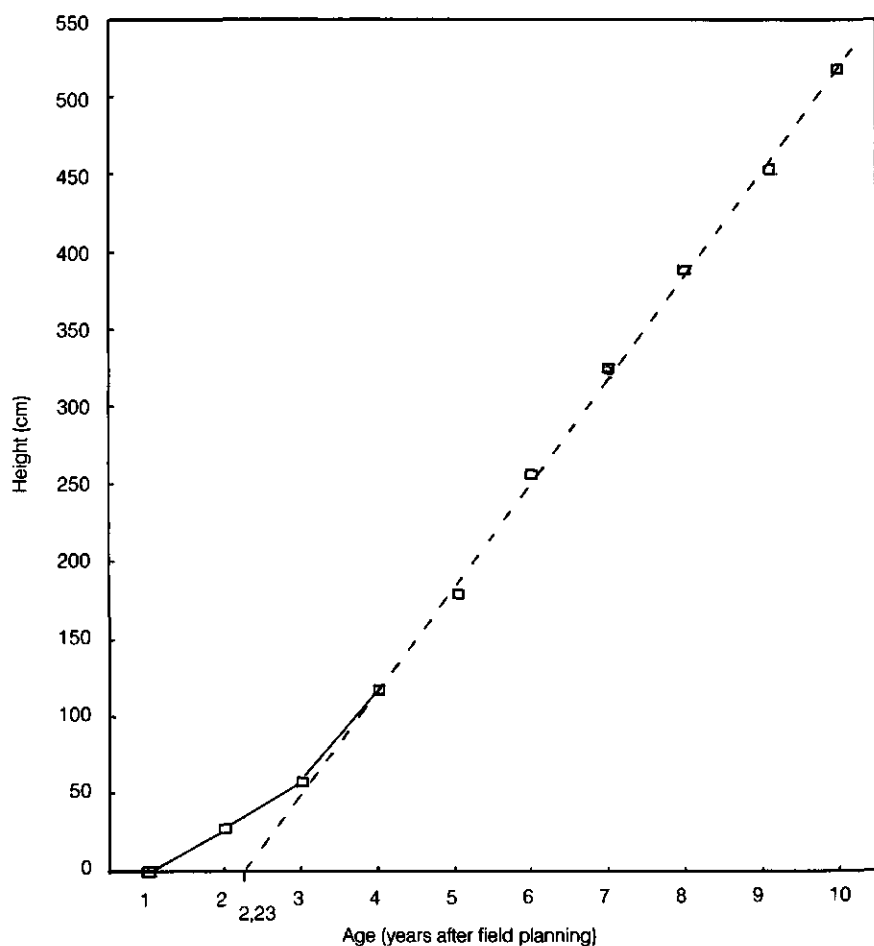


Figure 1. Height to the base of leaf 25 for palms of different ages. Expt. 3.

From that time, the following linear regression line gave an excellent fit to height at different ages:

$$\text{Height}_t = -150 + 67 t$$

where t is years after planting.

The intercept with the x-axis is reached at $t = 150/67$. In the present paper an age correction of two years is applied,

so that annual height increment is

$$\frac{\text{Height at year } t}{t-2}$$

Bunch Index (BI) and Leaf Area Ratio (LAR)

Estimates of BI and LAR are made six (82E) and ten (86E) years after planting, based on records of height, number of visible frond bases at these ages, and two sets of measurements of fronds marked at opening 5 and 6 years after planting, and 9 and 10 years after planting.

High correlations are obtained between mean values of BI calculated from actual growth parameters assembled annually between years 4 to 6 (BI 82A) and BI 82E, and those annually determined between years 4 to 10 (BI 86A) and BI 86E (Table 3).

Table 3. Correlation coefficients ¹⁾ between Actual (A) and Estimated (E) values of Bunch Index (BI) made at 6 years (82) and 10 years (86) after planting. Dura x pisifera progenies derived from crosses of 14 different pisifera, planted at 115 palms per ha (D₁) and 143 palms per ha (D₂).

<u>Estimated values</u>	<u>Actual values</u>			
	BI 82A (D ₁)	BI 82A (D ₂)	BI 86A (D ₁)	BI 86A (D ₂)
BI 82E (D ₁)		0.98 ^{xx}		
BI 82E (D ₂)			0.90 ^{xx}	
BI 86E (D ₁)				0.96 ^{xx}
BI 86E (D ₂)				0.97 ^{xx}

1) based on mean values of 48 palms per pisifera.

Indeed screening of the 56 dura x pisifera progenies on the basis of 86E is very efficient, as shown in Fig 2.

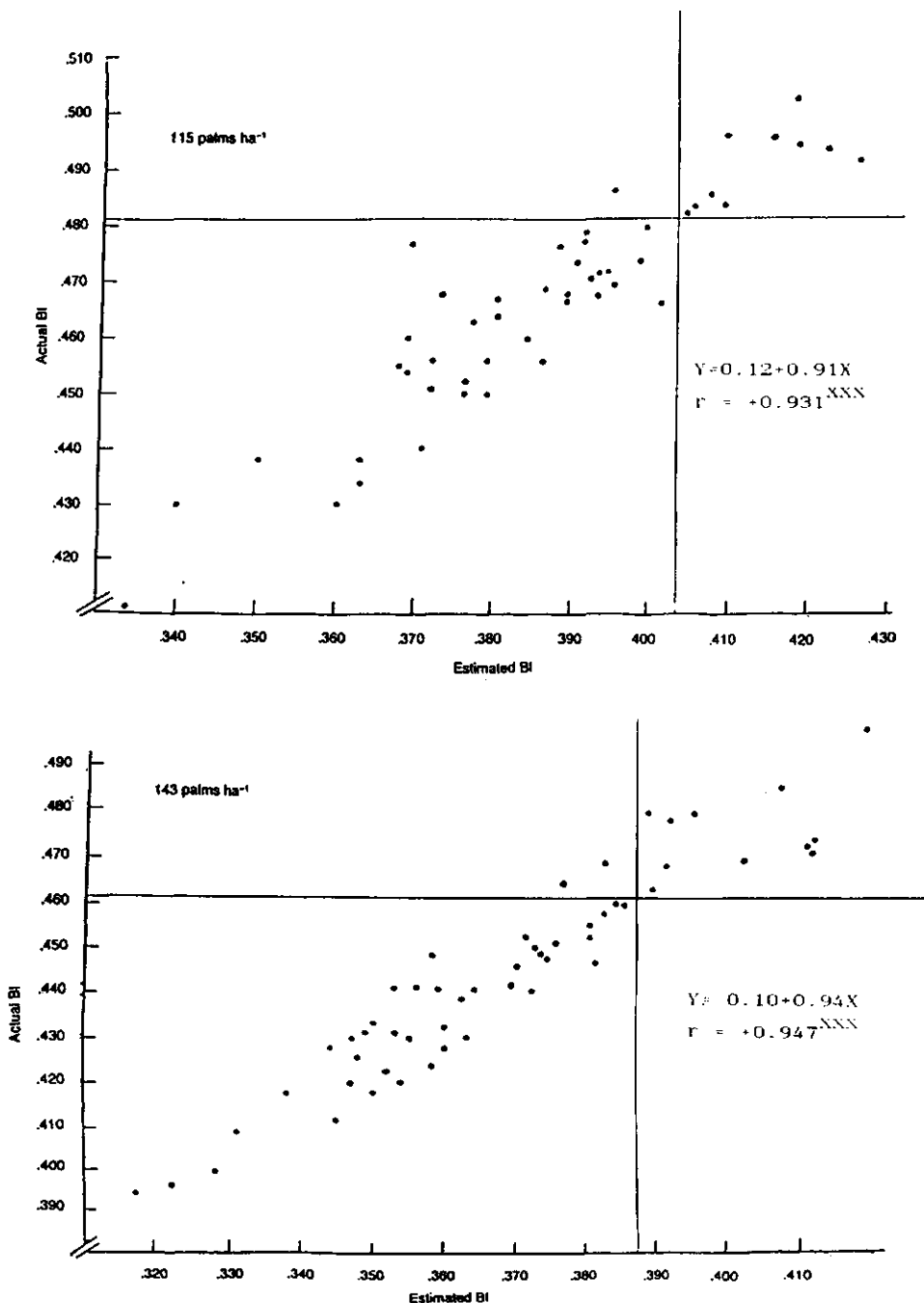


Figure 2. Plotted progeny values of Bunch Index (BI) estimated from growth measurements made ten years after planting, and those derived from mean actual values of years 4 to 10 after planting. 56 dura x pisifera progenies, at two planting densities.

Here, ten dura x pisifera families selected, in both densities, on the basis of high BI 86E values, were virtually the same as those selected on actual values (BI 86A).

We found equally high correlations between mean LAR of years 4 to 6 (LAR 82A) and LAR 82E, and those annually determined between years 4 to 10 (LAR 86A) and LAR 86E (Table 4).

Table 4. Correlation coefficients ¹⁾ between Actual (A) and Estimated (E) values of Leaf Area Ratio (LAR), based on total vegetative dry matter (VDM), and frond dry matter (FDM), made at 6 years (82) and 10 years (86) after planting. Dura x pisifera progenies derived from crosses of 14 different pisifera, planted at 115 palms per ha (D₁) and 143 palms per ha (D₂).

<u>Estimated</u> <u>values of LAR</u> (based on VDM or FDM)	LAR 82A (D ₁)	<u>Actual Values</u>		LAR 86A (D ₁)	LAR 86A (D ₂)
		LAR 82A (D ₂)	LAR 86A (D ₁)		
VDM 82E (D ₁)	0.96 ^{XX}				
VDM 82E (D ₂)		0.92 ^{XX}			
VDM 86E (D ₁)			0.89 ^{XX}		
VDM 86E (D ₂)				0.91 ^{XX}	
FDM 82E (D ₁)	0.91 ^{XX}				
FDM 82E (D ₂)		0.81 ^{XX}			
FDM 86E (D ₁)			0.88 ^{XX}		
FDM 86E (D ₂)				0.80 ^{XX}	
FDM 82/86 (D ₁)			0.93 ^{XX}		
FDM 82/86 (D ₂)				0.87 ^{XX}	

1) Based on mean values of 48 palms per pisifera.

The same Table presents the relationships between actual LAR and that estimated on the basis of frond dry matter only (FDM) for (1) years 5 and 6, (2) years 9 and 10, and (3) years

5,6,9,and 10. Again, these values show very high correlations with actual LAR-values, with a slight gain in precisions for the latter set of 4 year's records.

Leaf expansion

Table 5 presents correlations between characteristic parameters of the logistic growth curve (L_m , $t_{0.95}$ and ER) derived from LA measurements in years 5,6,9,10 and from those mesured annually for the first ten years after planting; correlations are given for the 115 and 143 palms per ha densities. Remember that these leaf measurements can be assembled six (years 5 and 6) and ten years (years 9 and 10) after planting.

Table 5. Correlation coefficients ¹⁾ between Actual (A) and Estimated (E) values of parameters describing crown expansion, based on four sets of leaf measurements. Dura x pisifera progenies derived from crosses of 14 different pisifera, planted at 115 palms per ha (D_1) and 143 palms per ha (D_2).

Estimated values	Actual values (1,2,3,4,5,6,7,8,9,10) ²⁾							
	L_m (D_1)	L_m (D_2)	$t_{.95}$ D_1	$t_{.95}$ D_2	ER D_1	ER D_2		
L_m E 5,6,9,10 (D_1)	0.99 ^{XX}							
L_m E 4,5,8,9 (D_1)	0.99 ^{XX}							
L_m E 5,6,9,10 (D_2)		0.96 ^{XX}						
L_m E 4,5,8,9 (D_2)		0.89 ^{XX}						
$t_{.95}$ E 5,6,9,10 (D_1)			0.91 ^{XX}					
$t_{.95}$ E 4,5,8,9 (D_1)			0.93 ^{XX}					
$t_{.95}$ E 5,6,9,10 (D_2)				0.92 ^{XX}				
$t_{.95}$ E 4,5,8,9 (D_2)				0.93 ^{XX}				
ER E 5,6,9,10 (D_1)					0.92 ^{XX}			
ER E 4,5,8,9 (D_1)					0.94 ^{XX}			
ER E 5,6,9,10 (D_2)						0.89 ^{XX}		
ER E 4,5,8,9 (D_2)						0.88 ^{XX}		

1) based on mean of 48 palms per pisifera.

2) Age of leaf opening (years after planting).

L_m = Maximum leaf area derived from logistic growth curve

$t_{.95}$ = Time to reach .95 L_m .

In the same Table estimates based on years 4, 5, 8, and 9 are compared with actual values. Equally high correlations are obtained for both sets of estimates.

DISCUSSION

Good estimates of BI and LAR are obtained from a single set of growth measurements made in one year. The reliability of progeny screening for BI on the basis of one round of growth measurements at the end of the usual period of yield recording (between 6 and 10 years after field planting) is of particular interest (Table 3; Fig 2). It should be noted that mean values of Fig 2 are only based on 12 palms, which is much less than the usual number of palms per progeny. Furthermore, differences in BI among progenies in this paper are quite small. Thus more precise estimates may be expected in trials with a more conventional, higher, number of palms per progeny.

The frond base count accounts for only 85% of the variation in actual frond production of progenies (Table 2), the loss in precision probably due to differences in rate of trunk expansion. As the proportion would be expected to be lower for individual palms, there is a need for an improvement in precision. To eliminate any possible error due to differences in numbers of concealed leaf bases, a fixed starting point on the spiral is required. If, for example, the two youngest fully expanded leaves were marked at a known date in the second year after field planting, the mark transferred to the frond base at a later date can be used as the starting point when counting the two spirals is done, and the period of frond production can be determined to the nearest month. This would eliminate any possible errors due to differences in trunk expansion, and permit efficient selection of individual palms. For an evaluation of progenies for trends in crown expansion, LA records assembled during maximum expansion at year 4 to 5 and at the end of yield recording are sufficient. It is reasonable to assume that this set of four leaf measurements will also permit a reliable selection for LAR of individual

palms (no leaf production records are required). In passing it is relevant that parent selection for LAR is more effective in increasing BI of their offspring than direct selection for BI (Breure, 1986). Thus, a second set of recordings, in addition to that required for establishing BI of progenies, will permit parent selection, on the basis of LAR, for seed production or for further breeding.

In conclusion, one single round of growth measurements at the end of the usual period of yield recording is sufficiently reliable to screen progenies on the basis of BI. This permits the inclusion of this important characteristic in the final evaluation of those current progeny trials for which only yield records have been assembled.

For future experiments, however, a greater precision, in particular for individual palms, might be achieved by leaf marking in the second year after planting.

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REFERENCES

- BREURE, C.J. (1985). Relevant factors associated with crown expansion in oil palm (*Elaeis guineensis*, Jacq.). Euphytica, 34, 161-175.
- BREURE, C.J. (1986). Parent selection for yield and bunch index in the oil palm in West New Britain. Euphytica, 35, 65-72.
- BREURE, C.J. and CORLEY, R.H.V. (1983). Selection of oil palm for high density planting. Euphytica, 32, 177-186.
- COMSTOCK, R.E. and ROBINSON, H. (1952). Estimation of the average degree of dominance of genes. In: J.W. Gowan (ed.), Heterosis. Ames, Iowa State College Press.
- CORLEY, R.H.V. (1973). Effect of planting density on growth and yield of the Oil Palm. Expl. Agric. 9, 169-180.
- CORLEY, R.H.V., HARDON, J.J. and TAN, G.Y. (1971). Analysis of growth of the oil palm (*Elaeis guineensis* Jacq.). I. Estimation of growth parameters and application in breeding. Euphytica, 20, 307-315.
- HARDON, J.J., WILLIAMS, C.N. and WATSON, I. (1969). Leaf area and yield in the oil palm in Malaysia. Expl. Agric. 5, 25-52.
- HARDON, J.J., CORLEY, R.H.V. and OOI, S.C. (1972). Analysis of growth in the oil palm. II. Estimation of genetic variances of growth parameters and yield of fruit bunches. Euphytica, 21, 257-264.

THE EFFECT OF PLANTING DENSITY ON THE COMPONENTS
OF OIL YIELD IN OIL PALM
(*Elaeis guineensis* Jacq.).

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SUMMARY

Response of components of oil yield were studied in a spacing experiment, comparing 56, 110, 148, and 186 palms per ha densities, at Dami Oil Palm Research Station, Papua New Guinea. Bunch weight components were studied under assisted pollination (5th year from planting) and under insect pollination (year 12 to 14). In both periods bunch weight decreased significantly as a function of planting density, due to an effect on frame weight (stalk and empty spikelets), and on flowers per inflorescence (spikelet number and flowers per spikelet); single fruit weight was little affected. Fruit set (the proportion of fertile fruits to total flowers) did not respond under assisted pollination but with insect pollination closer spacing increased fruit set. This resulted in an enhanced kernel and oil extraction to the extent that optimal planting density was 5 palms per ha higher for oil and kernel yield than for yield of fresh fruit bunches.

The rate of response of flowers per inflorescence indicates that seed production per palm can be increased by 15% by any practical method of reducing shade from surrounding (unselected) palms.

Bunch number was reduced in response of higher density planting density, due to a rise in the number of both aborted and male inflorescences.

Sex definition, and the flower number per inflorescence are less sensitive to increasing interpalm competition for light than floral abortion and the weight of the frame of the bunch.

INTRODUCTION

The relationship between planting density in oil palm (Elaeis guineensis Jacq.) and the number and weight of bunches produced per palm has been the topic of study of several workers (Prevot & Duchesne, 1955; Sly & Chapas, 1963; Corley et al, 1973; Breure, 1977), but information on components determining the economic product is scarce. This concerns components which determine the kernel of the fruit and the oil extracted from the mesocarp. Further, when the production of oil palm seed is at issue, it concerns the number of seed per bunch, for which the number of flowers per inflorescence is relevant.

In each leaf axil either one male or one female inflorescence is differentiated. Only in exceptional cases, do all leaf axils bear female inflorescences. Some inflorescences may abort before reaching anthesis, but losses during subsequent bunch development are usually negligible. In practice, therefore, bunch number is mainly determined by the number of male and aborted inflorescences.

In the present study on the response of these components to interpalp competition for light, competition is expressed by the leaf area index (L), i.e. the total leaf area per unit ground area. The reason is that L not only rises with increasing planting density but, in young palms, also with the expansion of the crown leaves with age.

Weight components are conveniently divided into those of the empty bunch (stalk and empty spikelets) and the fruit. Components contributing to the weight of total fruit are the number of flowers per inflorescence (the product of spikelet number and flowers per spikelet), the fruit set (the proportion of flowers which develop into fertile fruit) and mean single fruit weight. We also analysed the percentages of kernel and mesocarp to fruit, and the oil content of the mesocarp, to test planting density effect on extraction rate.

Corley & Breure (in prep.) studied response of components of oil yield to different levels of fruit bunch removal (castration). Castration may be compared with planting density as both regulate the amount of carbohydrate available for the

development of inflorescence primordia. Their study identified differences in threshold of response to level of castration. This phenomenon may also occur in response to light competition. In this respect, one may expect that those components which are determined at an advanced stage in inflorescence development (and thus have a high demand for carbohydrate), such as weight of the frame and floral abortion, are more sensitive to competition than those which are fixed at an earlier developmental stage (when demands are low), such as sex differentiation and flowers per spikelet. We stress that differences in thresholds of response to interpalm competition are of paramount importance for computer simulation modelling of oil palm yield.

The effect of leaf pruning is similar to that of increased planting density, as both directly influence the amount of photosynthetic production on a per palm basis; this is why Corley (1977) suggested to use leaf pruning to simulate high density planting in progeny selection. It is relevant to the present study that Corley & Hew (1976) found that leaf pruning increased the number of male and aborted inflorescences, and, hence, decreased bunch number. Regarding bunch weight, Corley (1973) found a negative effect of leaf pruning on spikelet number, flowers per spikelet and weight of individual fruits. Again, we extrapolate that similar responses will be found to higher density planting. Fruit set responded positively, however, which is at odds with the above mentioned study of Corley & Breure (in prep.). An explanation of Corley's (1973) result could be the artificial application of pollen which supplemented natural pollination at that time. Assisted pollination, the efficiency of which must benefit from removal of obstructing leaves, was standard in Asia and the Pacific regions. Currently, very satisfactory pollination is obtained by introduced pollinator insects (Elaeodobius kamerunikus). These insects prefer a cool dark environment with little wind disturbance, as prevails between palms in the higher density plantings (R.A. Syed, pers. com.). This tendency may be reflected in a positive response of fruit set. This, in turn, results in an enhanced kernel and oil extraction rate, as shown by Syed et al (1982). On the other hand, an accompanying

decrease in fruit size may partially counteract the gain in extraction rate. Nevertheless, from an economic point of view, insect pollination might be favourable as it may shift optimal planting density to a higher level than was standard under assisted pollination. To compare, under insect pollination, optimal planting densities both for extracted product and exclusively for weight of fresh fruit (the conventional method), is another objective of the present study.

We evaluated the role of pollinator insects in a spacing experiment in which records of components of weight and composition of the bunch were assembled before and after the arrival of the pollinator insects (at the beginning of the 12th year after planting). Because bunches under assisted pollination were analysed in younger palms (during the 5th year after planting) than under insect pollination, methods of pollination may be confounded with age related factors; these include the usual increase in the proportion of male inflorescences and variation in palm height, which potentially benefit pollination in the higher density plantings. In that respect Breure's (1987) study is of relevance. He observed that in the period just preceding the introduction of the insects, efficiency of (assisted) pollination deteriorated with increasing planting density (cf Turner & Gillbanks, 1974). Hence any positive or even absence of response of fruit set to planting density after insects were introduced cannot be attributed to palm age.

At Dami oil Palm Research Station where the study took place, the chief interest is oil palm seed production. Seed is produced by a group of selected mother palms which suffer from shade of their unselected neighbours. It is of practical importance to extrapolate this disadvantage in respect of potential number of seed produced per palm by comparing number of flowers per inflorescence between different planting densities.

This paper further aims to determine the optimal planting density with insect pollination as an intervening variable, and to test differences in sensitivity of yield components to increasing interpalm competition for light.

MATERIALS AND METHODS

Records were from a density x fertilizer experiment, planted at Dami Oil Palm Research Station, West New Britain, Papua New Guinea in October 1970. The experiment compared 56, 110, 148, and 186 palms per ha⁻¹ treatments in a split plot design, with densities determining the main plots (of about 0.75 ha) and four rates of fertilizers determining the sub-plots, except the 56 density which was split into two sub-plots which received the two higher rates. Different fertilizer treatments were stopped in 1979. Sub-plot values are pooled for each density in the analysis, because it is effects of density treatments which are of interest.

The experiment was under assisted pollination until October 1981 when insect pollinators were introduced in the region of the experiment. During the last year prior to their establishment pollination was poor, but at the time that records were assembled for the present study assisted pollination was very satisfactory (Breure 1982).

RECORDING

Bunch number components

Inflorescences in axils of monthly marked leaves were recorded, when reaching anthesis, as either female, male, or aborted. Between January 1973 and June 1977 flowering was recorded in all density treatments, but thereafter recording continued only in the 110 and 148 densities until June 1983.

Bunch weight components

Bunches were sampled from as many different palms as possible. Under assisted pollination, in the 5th year after planting, these were analysed for spikelet number, the number of flowers per spikelet, fruit set (the proportion of flowers which develop into fertile fruit), the mean fruit weight, and the weight of the stalk.

Under insect pollination, between the 12th and 13th year after planting, the same analysis was repeated but this time the

weight of empty spikelets was included.

The analysis method has been fully described by Breure & Menendez (in prep.).

Bunch composition

Bunches were analysed for the components of oil to bunch ratio (fruit to bunch, mesocarp to fruit and oil to mesocarp ratios), and for the percentage kernel to fruit, following the method of Blaak et al (1963). This analysis was done under assisted pollination (5th year after planting) and under insect pollination (between the 14th and 15th year after planting).

Leaf area index

The total leaf area per ha (LAI) was calculated as the product of the number of palms per unit ground area, the number of crown leaves per palm and their mean leaf area. The latter was determined, for annual periods, as the mean of measurements on leaf 17 six months prior to, in the middle of, and six months after each year recorded. The number of crown leaves at different ages was adopted from Gray (1969).

RESULTS

Bunch number components

The relative proportion of leaves with female inflorescences changed in favour of male and aborted inflorescences as a function of planting density (Table 1).

Note that of the two sets of five-year flowering periods, only the first period presents results for the full range of densities. In this earlier period, the increase in the proportion of aborted inflorescences was by and large linear. Percentage leaves with males, in contrast, only markedly responded at the higher density level (the transition from 148 to 186 palms ha^{-1}). During the 6th to 10th year of flowering, on the other hand, there was an increase in male inflorescences in response to a change from 110 to 148 palms ha^{-1} . This corresponded to a rise in leaf area index (L) from 4.5 (110 palms) to 5.8 (148 palms), against 3.7 to 4.9 for these densities in the first period. Thus, although in these

two periods the response of sex definition occurred at different density levels, the level of L was similar and higher than that for the response of floral abortion. Remember that Corley & Breure (in prep.) also found, for these components, a difference in thresholds of response to level of fruit bunch removal (castration).

Table 1. Female, male and aborted inflorescences, as percentage of leaves produced, for the first five years of flowering (four planting densities) and for the sixth to tenth year of flowering (110 and 148 palms per ha densities), together with values of mean leaf area (L).

<u>Component</u>	<u>Density (palms per ha)</u>			
	56	110	148	186
<u>Years 1 to 5</u>				
Female inflorescences (%)	58.3	56.9	53.5	44.5
Male inflorescences (%)	37.7	36.9	38.4	44.2
Aborted inflorescences (%)	4.0	6.2	8.2	11.6
L	1.8	3.7	5.0	6.2
<u>Years 6 to 10</u>				
Female inflorescences (%)	-	51.4	40.7	-
Male inflorescences (%)	-	44.1	51.7	-
Aborted inflorescences (%)	-	4.9	7.6	-
L	-	4.5	5.8	-

Note: Results were not statistically analysed.

Bunch weight components

Weight of the bunches analysed, both in year 12 & 13 (insect pollination) and year 5 (assisted pollination), diminished as a function of planting density (Table 2).

Stalk weight, in both sets of records, decreased linearly. On the other hand, spikelet number and, to a greater extent, flowers per spikelet mainly started to respond at the higher density levels. Fruit weight tended to be slightly decreased.

Note that in the younger palms fruit set remained unaffected by planting density, while in the second period, under insect

Table 2. Effect of interpalms competition (expressed by the planting density and the leaf area index) on the components of bunch weight (values of the higher planting densities expressed as a percentage of the real values presented for the 56 palms per ha density), together with the Probability (P-tail) values for significance of pairs of density treatments. Years 12 and 13 after planting (insect pollination), and Year 5 (assisted pollination).

<u>Components</u>	<u>Density</u> (palms per ha).					
	<u>Low</u> (L)		P	<u>High</u> (H)		L/H ³⁾
	56	110		148	186	
<u>Years 12 & 13</u>	real	%		%	%	P
<u>insect pollination)</u>						
Bunch weight (kg)	23.4	91	x	80	74	N.S.
Stalk weight (g)	1869	85	xx	71	64	N.S.
Spikelet weight (g)	16.3	91	xx	84	80	N.S.
Frame weight (g)	5310	87	xxx	75	68	xx
Spikelet number	212	98	N.S.	92	87	xx
Flowers/spikelet	15.1	99	N.S.	91	87	N.S.
Fruit set (%)	49.0	104	N.S.	109	117	N.S.
Fruit to bunch (%)	62.5	107	x	107	111	N.S.
Fruit weight (g)	8.8	99	N.S.	99	98	N.S.
Number of bunches analysed	321	408		328	172	
Leaf area index	1.90	3.71		4.80	5.81	
<u>Year 5</u>						
<u>(assisted pollination)</u>						
Bunch weight (kg)	16.7	94		84	83	
Stalk weight (g)	1324	89		77	75	
Spikelet number	132.2	100		99	99	
Flowers/spikelet	12.1	100		95	95	
Fruit set (%)	60.0	96		96	100	
Fruit weight (g)	15.0	97		97	94	
Number of bunches analysed	210	351		409	470	
Leaf area index	1.65	3.38		4.72	5.94	

1) x if $0.01 < P < 0.05$

xx if $0.001 < P < 0.01$

xxx if $P < 0.001$

2) Not statistically analysed.

3) Mean of 56 and 110 against 148 and 186 palms ha⁻¹.

pollination, fruit set clearly improved with density.

We studied the sensitivity of response of bunch weight components to increasing planting density in detail in the older palms, because these records permit a statistical analysis. We tested, first, the contrasts in the two lower and in the two higher density levels and, further, those of the differences of the mean of the lower (56 and 110) against the mean of the higher densities (148 and 186 palms ha^{-1}). Levels of significance (P-tail) for these test are also given in the upper part of Table 2. Frame weight (empty spikelets and stalk) mainly decreased in response to a rise from 56 to 110 palms ha^{-1} . Spikelet number and flowers per spikelet, in contrast, showed the highest response in the upper range of density treatments, but the response was only significant for spikelet number. However, when the lower and higher densities were compared the decrease in these components was very highly significant. Fruit set clearly increased with planting density, but the response was only significant when the means of the lower and higher densities are compared. Of paramount importance for oil and kernel extraction is the significant increase in fruit to bunch; the largest response was found when density increased from 56 to 110 palms ha^{-1} .

Bunch composition

Under assisted pollination (year 5), we clearly see no effect of planting density on bunch composition, but for bunches analysed when insects were fully established (years 14 to 16) components of oil and kernel extraction rate can be significantly described as a linear function of the planting densities (first degree polynomial; the higher degree polynomial components were not significant). It should be noted that mesocarp to fruit, in contrast to the other components, decreased as a function of planting density (Table 3). Table 3 shows, as in the previous set of bunches analysed under insect pollination (Table 2), a rise of fruit set in response to planting density with an absence of response of fruit weight. As in Table 2, the rise in fruit set is accompanied by an increase in fruit to bunch ratio. The main interest from an economic view point is, however, the composition of the fruit.

Table 3. Effect of planting density on bunch composition for years 14 to 16 after planting (insect pollination) and for year 5 (assisted pollination).

<u>Component</u>	<u>Density (palms per ha)</u>				linear component.
	56	110	148	186	
<u>Years 14 to 16</u> (insect pollination)					
Mesocarp/Fruit (%)	75.4	74.3	74.1	73.6	x
Oil/Mesocarp (%)	52.0	52.3	52.8	52.7	xx
Fruit/Bunch (%)	67.4	69.6	70.5	70.9	xxx
Kernel/Fruit (%)	7.8	8.5	8.8	8.9	xx
Single Fruit wt.(g)	12.3	12.4	12.6	12.5	
Oil/Bunch (%)	26.4	27.1	27.7	27.5	xx
Fruit set (%)	66.3	68.3	70.0	69.2	x
Number of bunches analysed	426	608	629	345	
<u>Year 5</u> (assisted pollination)					
Mesocarp/Fruit (%)	-	80.7	80.8	80.4	
Oil/mesocarp (%)	-	48.6	48.8	48.1	
Fruit/Bunch (%)	-	68.2	68.0	69.5	
Kernel/Fruit (%)	-	8.2	8.1	8.4	
Single Fruit wt (g)	-	12.0	12.1	12.0	
Oil/Bunch (%)	-	26.7	26.8	26.9	
Number of bunches analysed		197	253	315	

Table 3 shows a significant increase in kernel to fruit which, as found in other experiments (cf Breure, 1982; Foster et al, 1987), is at the expense of the mesocarp to fruit. The negative response of mesocarp was, however, more than compensated for by a rise in the oil content to the extent that, as can be derived from Table 3, oil to fruit increased in response to

planting density.

In order to evaluate the relative contribution of fruit to bunch in the oil extraction of the bunch (OB), we studied the three components of OB by a multiplicative model of components of OB, i.e. mesocarp to fruit (MF), oil content of the mesocarp (OM), and fruit to bunch (FB). In our model the relationship was given as

$OB = C \times (MF)^{b_1} \times (OM)^{b_2} \times (FB)^{b_3}$, where C and b_1 , b_2 , and b_3 are constants,

or $\log(OB) = b_0 + b_1 \log(MF) + b_2 \log(OM) + b_3 \log(FB)$, where $b_0 = \log(C)$.

We found no significant difference of this relation between density treatments, and therefore density treatments were pooled in our model, giving a very high coefficient of determination (0.86). The contributions of all components were significant, but the relative importance differed, as can be learned from the t-values and their significance levels. These were 2.95^x , 3.82^{xx} , and 5.75^{xx} for $\log(MF)$, $\log(OM)$, and $\log(FB)$, respectively. Thus fruit to bunch is the main contributor to the (rise in) OB. In order to explore, in turn, which components contributed to fruit to bunch, we employed the same multiplicative model on its components, being spikelet number (NS), flowers per spikelet (FLSP), fruit set (FS), fruit weight (FWT) and, finally, the weight of the bunch (BWT). The t-values obtained were .72, 1.71, 3.03^x , 1.49 and 2.13, respectively. Thus, the only contributing factor to increase significantly was fruit set (P-tail of 0.013). It is therefore concluded that the increase in fruit to bunch in response to planting density is mainly due to a rise in fruit set. Remember that kernel to fruit increased with planting density, so that the increase in fruit to bunch additionally contributed to a rise in kernel extraction rate. Thus the rise in fruit set had a direct effect on oil and kernel extraction.

We compared the gain in optimal density for kernel and oil extraction by contrasting this against the optimum for fresh fruit bunches (the conventional method). The usual method was followed, that is by fitting linear regression lines through yield per palm (Y) and planting density (Corley, 1976; Breure, 1987). This relationship can be expressed in the form

$Y = a - bN$ with $b > 0$, where N is the number of palms ha^{-1} . Yield per ha is then given by $NY = aN - bN^2$. This reaches a maximum when $d(NY)/dN = 0$, that is when $a - 2bN = 0$, or $N = a/2b$, and $d^2(NY)/(dN)^2 = -2b < 0$.

Table 4 presents optima for yield of fresh fruit bunches (assuming an absence of response of bunch composition) and of the yield of the economic product (kernels and mesocarp oil) for the five years under insect pollination (years 12 to 16).

Table 4. Comparison of estimated optimum density (palms per ha) of yield of kernel and oil, and of fresh fruit bunches, based on linear regression equations fitted through values of four planting densities, during the period 12 to 16 years after planting (5 years).

Optimal density (palms ha^{-1}) ¹⁾.

Kernel and oil	Bunches
131 (.99) ²⁾	126 (.99)

1) Estimated as $a/2b$, in which a = intercept and b = slope of the fitted regression lines.

2) In brackets coefficient of determination of the two regression lines.

This Table shows that optimal planting density for the economic product was 5 palms ha^{-1} higher than for fresh fruit bunches (131 against 126 palms ha^{-1} for fresh fruit bunches).

DISCUSSION

Oil and kernel extraction increased as a function of planting density due to a positive effect on both the kernel and oil content of the fruit and, more importantly, on the fruit to bunch ratio. Of the components studied, we found that fruit set is the most important contributor to the rise in fruit to bunch. The amelioration of fruit set is likely to be coupled to insect pollination, because these insects are known to prefer the cool environment which prevails in closely spaced palms. The resulting gain in extraction rate (Table 3) bears upon optimal planting density. We estimated, for mature palms under insect pollination (Table 4), an optimal density for kernel and oil yield of 131 palms ha^{-1} against 126 for fresh fruit bunches (the conventional method of estimating optimal density). Note that the optimum which is based exclusively on fresh fruit bunches assumes a zero response of extraction rate to density. However, under assisted pollination the response of extraction rate to higher density planting may be negative for two reasons. First, there are indications that with assisted pollination fruit set, and thus extraction rate, decreased as a result of closer spacing. Corley (1972) found that pruning had a beneficial effect on fruit set; this may have been due to improved exposure of female inflorescences, which would also occur at the lower planting densities. The gain in fruit set in Corley's experiment might have been higher in the present environment where interpalm competition is more pronounced, due to excessive vegetative growth (Breure, 1982).

Second, vegetative growth, as can be derived from the study of Breure (1982) and Corley & Breure (in prep.), must have slowed down when more adequate pollination was achieved by the introduced insects. Thus it is reasonable to assume that, following the introduction of the insects, optimal density must also have increased due to reduced interpalm competition for light, in addition to improved fruit set at higher density planting.

It might be argued that the positive response of fruit set as a function of planting density could have been due to the more pronounced positive effect of planting density on male

inflorescence production (Table 1). However, there are several reasons why such an increase could not have been reflected in that of fruit set. First, response of insect pollination to number of male inflorescences would not become manifest on a plot level, because the diameter of the plots is less than the usual distance over which pollinator insects carry pollen (R.A. Syed, pers. com.) and, second, plots are not sufficiently bordered to prevent insect movement to neighbouring plots.

As expected, differences in sensitivity of response to planting density were obtained for sex ratio and number of flowers per spikelet on one hand, and abortion and frame weight on the other hand. This might be partly due to differences in time-lag of response, which the study of Breure & Menendez showed to be about one year later for the first group of components. This would show up to only a minor extent in period of response studied and the main cause appears to be differences in demand for carbohydrate coupled to the developmental stage of response. For seed production per palm, which is contingent on the number of flowers per inflorescence, it is interesting to observe that the greatest response to density in mature palms was obtained in the transition from 148 to 110 palms ha^{-1} (an increase from 2677 flowers per spikelet to 3120 or about 15%). A similar response may also be expected from heavy pruning or removal of palms surrounding selected seed parents. Two advantages of removal of interpalm competition can be mentioned: First, it permits the discarding of a substantial number of lower grade seed palms. Second, annual height increment will be reduced (Breure, 1982) which, because artificial pollination work becomes more difficult in tall palms, would prolong the productive life of a seed garden.

To summarize, insect pollination increased the optimal planting density by at least 5 palms ha^{-1} . Yield components respond differently to increasing interpalm competition, which appears to be associated with carbohydrate requirements at the responsive stage. An extrapolation of our density study is that removal of interpalm competition in oil palm seed gardens appears to be worthwhile.

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REFERENCES

Blaak, G., Sparnaaij, L.D. & Menendez, T. (1963). Breeding and Inheritance of the oil palm. Part II. Methods of bunch quality analysis. Jl W. Afr. Inst. Oil Palm Res., 4, 145-155.

Breure, C.J. (1977). Preliminary results from an oil palm density x fertilizer experiment on young volcanic soils in West New Britain. In D.A. Earp & W. Newall (Eds.), International developments in oil palm (pp 192-207). Kuala Lumpur, Incorporated Society of Planters.

Breure, C.J. (1982). Factors affecting yield and growth of oil palm tenera in West New Britain. Oléagineux, 37, 213-227.

Breure, C.J. (1987). The effect of different planting densities on yield trends in oil palm. Expl. Agric. (in press).

Corley, R.H.V., Hew C.K., Tam, T.K. & Lo K.K. (1973) Optimal spacing for oil palm. In: R.L. Wastie and D.A. Earp (Eds.) Advances in oil palm cultivation. Incorporated Society of Planters, Kuala Lumpur, pp 52-69.

Corley, R.H.V. (1973). Oil Palm physiology- A review. In: R.L. Wastie and D.A. Earp (Eds.), Advances in oil palm cultivation. Incorporated Society of Planters, Kuala Lumpur, pp 37-49.

Corley, R.H.V. (1976). Planting density. In : R.H.V. Corley, J.J. Hardon & B.J. Wood (Eds.) Oil Palm Research. Amsterdam, Elsevier: 273-283.

Corley, R.H.V. (1977). Effects of severe leaf pruning on oil palm, and its possible use for selection purposes. MARDI Res. Bull., 4, 23-28.

Corley, R.H.V. & Hew, C.K. (1976). Pruning. In: R.H.V. Corley, J.J. Hardon & B.J. Wood (Eds.), Oil Palm Research (pp 307-313), Amsterdam, Elsevier.

Foster, H.L., Mohd Tayeb Hj Dolmat & Gurmit Singh. (1987). The effect of fertilizers on oil palm bunch components in

Peninsular Malaysia. Paper presented at the 1987 International Oil Palm Conference, Kuala Lumpur, Malaysia.

Gray, B.S. (1969). A study of the influence of genetic, agronomic and environmental factors on the growth, flowering and bunch production of the oil palm on the West coast of West Malaysia. Ph.D. thesis, University of Aberdeen. 947 pp.

Prevot, P. & Duchesne, J. (1955). Densités de plantation pour le palmier à huile. Oléagineux, 10, 117-122.

Turner, P.D. & Gillbanks, R.A. (1974). Oil Palm cultivation and management. Incorporated Society of Planters, Kuala Lumpur, 672 pp.

Sly, J.M.A. & Chapas, L.S. (1963). The effect of various spacings on the first sixteen years of growth and production of the Nigerian oil palm under plantation conditions. J.W.Afr.Inst. Oil Palm Res., 4, 31-45.

Syed, R.A., Law, I.H. & Corley, R.H.V. (1982). Insect pollination of oil palms; introduction, establishment and pollination efficiency of Elaeidobius kamerunicus in Malaysia. Planter, 58, 547-561.

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De auteur werd geboren op 5 november 1938 te Aalsmeer, volgde een 4-jarige MULO-B opleiding te Hoofddorp, en van 1956 tot 1958 de HBS-b opleiding in Haarlem. In 1958 begon hij zijn studie aan de Landbouwhogeschool te Wageningen (studierichting Tropische Plantenteelt), waar hij in 1967 het ingenieursdiploma behaalde. In dat zelfde jaar aanvaarde hij een functie als assistent deskundige aan de landbouwuniversiteit, La Molina, Lima, Peru. Hierna volgde een kort werkverband aan het Internationaal Agrarisch Centrum te Wageningen.

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