CORRELATIONS BETWEEN VEGETATIVE AND YIELD CHARACTERISTICS AND PHOTOSYNTHETIC RATE AND STOMATAL CONDUCTANCE IN THE OIL PALM (*Elaeis guineensis* Jacq.)

KEYWORDS : Physiology; Photosynthesis; Transpiration; Stomatal conductance; Growth; Yield.

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Photosynthetic rate per unit leaf area (A) and stomatal conductance (g) were assessed during the dry season of 1988 for a mixed population of 6 progenies in a breeding trial in the Republic of Zaire. There were positive correlations between A or g and both yield and total biomass production, but there was no significant correlation between A or g and either Bunch Index or Harvest Index.

These results provide encouraging evidence that crossing high A palms with palms exhibiting superior partitioning characteristics could be a useful way to increase yields.

However, more work is needed to ensure that correlations between g or A and either dry matter production or yield arise because of genotypic effects rather than environmental variation.

INTRODUCTION

Dry matter production in any plant organ depends on the sunlight intercepted by the canopy, the efficiency with which the plant is able to use intercepted light for photosynthesis and the proportion of photosynthate partitioned into that organ (the Harvest Index, HI) (Monteith, 1977). In theory, yields should be improved by increasing any of the above components. In practice, most plant breeding for improved yield has succeeded because of alterations in allocation of photosynthate (Gifford and Jenkins, 1982). Oil palm breeding programmes in Malaysia (Hardon *et al.*, 1972) and Zaire (Rosenquist *et al.*, 1990) have attempted to increase HI or Bunch Index (BI) by reducing the proportion of assimilates directed into trunk, petiole or leaf growth, or by increasing the oil-to-bunch ratio.

In some crops, positive correlations between photosynthetic carbon fixation and biomass production have been obtained. A correlation between bi-weekly biomass production and a crude estimate of whole-tree photosynthesis based on measurements of CO_2 uptake with an Infra-Red Gas Analyser (IRGA) has been found in poplars, and clonal differences in photosynthetic capacity were related to shoot growth rate in poplars (Isebrands *et al.*, 1988). Correlations between A (photosynthetic rate/unit leaf area) and yield (root biomass production) have been found in cassava (El-Sharkawi *et al.*, 1990).

In oil palm there is evidence that vegetative growth is maintained at the expense of reproductive growth under unfavorable conditions (Corley *et al.*, 1971). A sensitivity analysis with a model prepared to simulate growth and yield indicated that any increase in crop photosynthesis, due to husbandry or genotype, would result in a proportional increase in bunch yield without much influence on vegetative growth (Van Kraalingen *et al.*, 1989). The 60% improvement in yield brought about by breeding the Deli *dura* oil palm population in Malaysia over 50 years has been achieved without significant changes in the vegetative growth characteristics of the palms (R.H.V. Corley and C.H. Lee, personal communication). This implies that there has been an increased rate of CO_2 assimilation per palm or per unit leaf area. Oil palm is therefore a good candidate for a search for relationships between yield and photosynthesis.

Since genetic variation in the rate of photosynthesis has been reported in oil palm seedlings (Corley, Hardon and Ooi, 1973), there is the potential for basing selection methods on the photosynthetic rate/unit leaf area (A), or photosynthetic rate/unit ground area. Palms with high rates of carbohydrate assimilation could also be crossed with palms exhibiting superior partitioning characteristics, in order to further improve HI.

Stomatal closure occurs in the middle part of the day during drought (Tees, 1961). This results in a considerable decrease in CO_2 assimilation, since conductance (g) and A are closely linked up to g values of approximately 200 $\mu mol/m^2/s$ (Dufrene 1989, Smith 1989). Therefore, in areas where there is a drought for a significant portion of the year, genetic variation in the stomatal response to dry soils and high vapour pressure deficits could be the most important factor affecting the photosynthetic capacity of the palm. Even in parts of Malaysia, midday closure of stomata may occur on up to 100 days a year (Corley, 1973). Since g can be monitored with less sophisticated equipment than is needed to assess A, stomatal conductance criteria may be better than photosynthetic rate criteria in certain selection programmes.

The main aim of the work described in this paper was to obtain preliminary data on relationships between g, A and yield in one progeny trial in Zaire. As vegetative growth has an important impact on yield, and g and A might be expected to affect vegetative characteristics as well as yield, interactions among g, A, vegetative characteristics and components of yield were all analysed. The potential for incorporating gas exchange characteristics (g and A) into oil palm breeding and selection programmes is discussed.

EXPERIMENTAL

Experimental Site

The Joint Research Scheme breeding trial described was located at Binga, Republic of Zaire, 2° N, 21° E. The trial (73/36), planted in 1973, is surrounded by commercial oil palm plantings or other breeding trials for at least 0.5 km on every side. Planting density was 143 palms/hectare. Potassium chloride fertilizer (KCl) was applied annually until the end of 1985, but was negligible thereafter. The soils in this area are sandy loams.

The experimental work was carried out in a randomized block progeny trial, but only four out of eight replicate blocks and six of the progenies available were assessed. The particular progenies were chosen from the trial because of resistance to wilt (*Fusarium oxysporum*), so there was usually complete canopy cover and there were few vacancies within the areas sampled. There was also less chance of results being confounded by *Fusarium* infection. Palms were planted in 9-palm blocks composed of palms of the same progeny; a high proportion of inter-palm competition would therefore be between palms of the same progeny.

The six progenies assessed were the offspring of three male and three female parents (*Table 1*).

Mesurements of Stomatal Conductance and Photosynthetic Rate

Palms in the breeding trial were investigated between January and March, during the 1988 dry season. There has been no significant rain for two months before the sampling period. At least 30 palms from each of six progenies (located within at least 3 separate blocks in the randomized block design trial) were assessed for stomatal conductance (g) and photosynthetic rate (A), using a portable Infra-Red Gas Analysis system (IRGA; Analytical Developments Company (ADC), Hoddesdon, Hertfordshire, U.K.) in conjunction with a Parkinson Leaf Chamber and data logger. The system was operated with a supply of dry air to the leaf chamber, and operation, calibration and calculations of physiological parameters were as described in the ADC manuals (Issue 1, 1985).

As the palms were all 4 – 6 m tall at the time of the experiment, it was impossible to sample the leaves while they were still attached to the palms. Accordingly, individual leaflets were excised from frond 15, 16 or 17 of the palms (taking the youngest fully-opened frond as frond 1), using a harvesting knife, and always placed in the leaf chamber within 1 minute of excision. In a trial using leaflets removed from adjacent palms which were 3m tall (results not shown), excision had no significant effect on the stomatal conductance or photosynthetic rate within 4 minutes. Gas exchange measurements were made in an adjacent clearing or road in open sun between 08:30 and 13:30. Only data collected at light intensity (PAR) > 500 $\mu mol/m^2/s$ Photon Flux Density (PFD), and therefore near to photosynthetic light-saturation (Smith, 1989), were analysed. Each palm was sampled on several occasions on at least two days during the experimental period. Data were discarded from palms from which two days of readings in full sun were not obtained.

As variation in temperature and vapour pressure deficit have important effects on A and g in oil palm (Smith, 1989), resulting in a marked fall in both A and g as the morning progresses during the dry season, the following procedure was adopted in order to reduce the data scatter and emphasize the phenotypic response of each palm; A and g for the entire population sampled on each day were modelled to a smooth quadratic curve against time of day. The difference between the actual values of A and g obtained and the mean values for the population at that time of day were then calculated, and the mean values of these 'residual values' over the experimental period calculated. The quoted values for A and g are therefore 'delta' values (*i.e.* the difference between progeny values and the calculated mean for the population studied at that time of day).

Yield and Growth Information

Information on the bunch number/year and total bunch weight/year was available for these palms from each year between 1976 and 1984 and for the first quarter of 1985. Vegetative characteristics of the palms were measured in 1982, and height was measured in 1982, 1984 and 1985. Data were missing for some characteristics in several palms, and oil/bunch was not available for a proportion of the population at the time of data

TABLE 1. PARENT PALMS OF THE PROGENIES ASSESSED

	Male Parents ♂		
Female Parents ♀	NF 14.263	NF 32.364	Bg 1080 Bi
1020/8	121	94	
161 Bi	154	97	142
132 S			69

TABLE 2. PALM CHARACTERISTICS

Character	Unit	Calculation	Definition	Reference
HEIGHT	cm	-	Height measured in 1982	-
HIGHINC	cm	-	Increase in height/year	-
VDM	kg/year /palm	((d**2) *3,1416*HIGHINC/ /4000)*((9*0.0076) + 0.0083) where d is the trunk diameter	Vegetative Dry Matter produced/year	Corley *et. al.*, 1971
TDM	kg/year /palm	VDM + (YIELD *0.52)	Total Dry Matter produced/year	
BN	no/year /palm		Mean Bunch Number/Year	
YIELD	kg/year /palm		Mean total fresh weight of bunches/year	
LAI			Leaf Area Index	Corley *et al.*, 1971
BI		(YIELD*0.52)/TDM	Bunch Index	
HI		BI*(oil-to-bunch)	Harvest Index	Donald , 1962
f		1-exp[-0.478 (LAI-0,43)]	Fractional light interception	Squire, 1985
e		TDM/f*S Where the total Solar Radiation (PAR) is estimated at 3 GJ/m^2, and each palm occupies 63.93 m^2	Conversion efficiency	
g	mmol/ m^2/s		Difference between mean progeny stomatal conductance and mean conductance for the population sampled	
A	µmol/ m^2/s		Difference between mean progeny photosynthesis and mean photosynthesis for the population sampled	

analysis. The characteristics were measured and calculated as in Corley and Breure (1981) and analysis of Leaf Area Index (LAI) and Vegetative Dry Matter production (VDM) was performed following Corley *et al.* (1971). Fractional light interception (f) and conversion coefficient (e) were calculated as in Squire (1985). Bunch Index (BI) and Harvest Index (HI) were calculated using the mean annual bunch weight (FFB) for the ten years for which bunch weight data were collected, and vegetative measurements compiled in 1982. The calculation of HI involves the oil-to-bunch ratio and a conversion factor for the energy content of oil. These measurements and calculations are summarized in *Table 2* for convenience.

All the palms were part of a *tenera* x *tenera* breeding programme. The population sampled was therefore expected to include 25% *dura* palms (thick-shelled fruit; sh^+sh^+), 50% *tenera* palms (medium shell-thickness; sh^+sh^-), and 25% *pisifera* palms (which normally have no shell sh^-h^-). *Pisifera* and unhealthy palms were excluded from the analysis of Bunch Number (BN) and Yield by including only data from palms which had produced more than 30 bunches between 1976 and 1985. Excluding low yielding palms and palms which had not been sampled on at least two days in full sun reduced the population of palms for which data were available to 192, and excluded all the data collected from one progeny (progeny 49) during the experimental period.

Statistical Analyses

All analyses were performed with the help of SAS Statistical Packages (SAS Institute Inc. SAS Circle. Box 8000, Cary, NC 27512-8000). Correlation analysis (PROC CORR in the SAS System) was used to investigate correlations between physiological parameters, biomass production and components of yield. The data were analysed in terms of both progeny and parental effects, but only the results of the progeny analyses are included in this report.

Although the original trial was a randomized block design, *Fusarium* infection killed or stunted approximately 20% of the palms in the trial. The palms sampled were therefore sometimes adjacent to gaps in the canopy and would have had access to more sunlight and water than their neighbours. Variation in the height, LAI and root growth of neighbours will also have affected the availability of sunlight, nutrients and water to individual palms. The analyses performed presume that this affected all progenies equally. Block effects were not significant in an analysis of variance, and were therefore excluded from the analyses presented.

Probabilities are presented in the text in full (*e.g.* $P=0.0012$) or in the form * ($P<0.05$), ** ($P<0.01$) and *** ($P<0.001$).

RESULTS AND DISCUSSION

Progeny Characteristics

The progenies investigated in this trial were chosen for their resistance to *Fusarium* wilt and for a relatively wide range of growth and yield characteristics. For most of the growth, yield and physiological parameters tested[a] (HEIGHT ***; HIGHINC *** ; VDM *** ; LAI *** ; LA * ; YIELD *** ; TDM ** ; BI ** ; g *** ; f *** ; e *) there were significant differences among the six progenies. There was no significant difference among the progenies for BN, HI or A. Since the oil/bunch ratio had not been determined for many of the palms in the trial, HI data were unavailable for all but one palm in progeny 97 and approximately 30% of the palms in all other progenies. Progeny mean values ± S.E. are presented in *Table 3*.

Correlations Between Parameters

Growth and Yield

There was no significant correlation between any of the vegetative characters tested and bunch number (BN) when the data were assessed as one population or as separate progenies. Palms intercepting more light, either because they were taller or because of high LAI, did not appear to produce more bunches except in progeny 154, where there was a positive correlation between LAI and BN ($r=0.5484$ $P=0.0017$).

BN had a highly significant positive correlation with YIELD (***). The correlation was significant in all progenies assessed. Within the whole populations, taller palms (***), and palms with a high

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[a] For definitions see *Table 2*.

LAI (*) also had greater YIELD. This result was derived from significant positive correlations between HEIGHT and YIELD in progenies 69 (*), 97 (***) and 121 (**), and between LAI and YIELD in progenies 97 (*) and 142 (**). All these progenies are of below average height for the population, and progeny 97 was, on average, shorter (***) than all the other progenies assessed (*Table 4*). Relatively tall palms with high LAI compete well for light when planted with shorter ones.

Palms with a high VDM also tended to have a high YIELD (**). This effect was significant in progenies 97 (***), 121 (*) and 154 (*), but there was also a significant ***negative*** correlation between VDM and YIELD in progeny 94 (**) (*Table 4*). Progeny 94 did not have an unusually extreme, or particularly wide range of VDM or LAR: It was, however, the tallest progeny in the trial (*).

There was no significant correlation between any vegetative characteristics and HI for the population as a whole, and significant negative correlations only between VDM (**), TDM (*), LAI (**) and HI in progeny 142 (*Table 5*).

Corley *et al.* (1971) found that faster growth rates lead to higher yield, but not necessarily higher Bunch Index. These findings were confirmed by the analyses in this trial. Indeed, there were significant negative correlations between HIGHINC and BI in the whole population (***) and progenies 69 (***), 94 (*), 121 (***) and 154 (*) (*Table 5*).

Gas Exchange Parameters

Stomatal conductance (g) and photosynthetic rate (A) were highly positively correlated for the population as a whole and in all progenies (***), except progeny 97 where there was a lower level of agreement between the two parameters (*Table 6*). The high degree of correlation between g and A in oil palm has been reported previously by Dufrene (1989) and Smith (1989).

The positive correlation between the conversion coefficient, e and A was significant (**) in the whole population, but only significant in progeny 97 (*) (*Table 6*) when the progenies were analysed separately. As e should reflect the photosynthetic efficiency of the canopy (albeit also incorporating respiratory losses and partitioning to roots in the whole palm, which were not assessed in this trial) this lack of correlation within progenies is disappointing.

There was no significant correlation between stomatal conductance (g) and any of the vegetative characters assessed in the population as a whole. Within the individual progenies, positive correlations between g and HEIGHT in progenies 94 ($r=0.3902$ $P=0.0297$) and 121 ($r=0.3357$ $P=0.0226$), and g and VDM ($r=0.4359$ $P=0.0204$) in progeny 94, were only significant at $P<0.05$.

There were, however, significant positive correlations between photosynthetic rate (A) and HEIGHT (*), VDM (***) and TDM (***) in the population as a whole. Whereas the correlation between HEIGHT and A was again almost entirely due to effects within progeny 94 (*), the positive correlations between A and VDM or TDM were not significant in particular progenies but arose through a general effect throughout progenies 69, 97, 121 and 154. Progenies 94 and 142, both of which had a high LAI and could therefore achieve a high rate of photosynthesis/palm without a high A had no indication of any correlations between A and TDM (*Table 6b*).

An approximation to relative photosynthesis/palm (in relation to the population mean) can be obtained by multiplying A by f (where f is the fractional light interception), as in *Table 6c*. This slightly increased the significance of the relationships between photosynthesis and dry matter production, but it is worth noting that the relationship still only accounted for slightly less than 10% of the variation in either VDM or TDM.

Although there was a significant (*) correlation between g and BN for the whole population, only progeny 97 (*) showed this effect when the progenies were analysed separately (*Table 5*).

The strong relationship (***) between g and YIELD for the whole population was largely due to correlations between g and YIELD in progeny 154 (***) (*Table 4*).

A and YIELD were correlated (*) mainly because of data collected from progeny 97 (*), and this progeny was the only one in which there was a significant correlation between A*f and yield (*Table 6c*). This level of correlation is similar to that found between A and yield by El-Sharkawi *et*

TABLE 3. PROGENY CHARACTERISTICS (Mean ± S.E.)

Number in brackets refer to number of palms in each sample.

Charateristics	**Progeny**					
	69 (33)	94 (31)	97 (16)	121 (46)	142 (33)	154 (33)
HEIGHT	243.9	288.3	189.3	264.1	262.4	266.4
(cm)	6.8	9.3	12.6	10.3	8.6	7.3
HIGHINC	66.43	62.97	62.44	82.48	58.72	78.83
(cm)	1.72	1.768	2.40	3.63	7.86	2.25
VDM	68.72	76.26	59.35	70.37	63.09	73.22
(kg/yr)	2.36	2.54	4.86	2.83	7.12	3.80
TDM	130.2	128.0	105.6	121.2	125.3	133.8
(kg/yr)	3.3	3.0	9.1	5.0	4.5	3.8
BN	8.693	8.693	8.025	9.260	8.154	8.100
(no/yr)	0.387	0.558	0.637	0.467	0.410	0.677
YIELD	79.01	74.06	58.01	75.28	58.55	63.01
(kg/yr)	2.99	2.78	5.85	3.19	2.39	3.42
LAI	4.371	4.921	4.107	4.529	4.648	4.384
	0.126	0.102	0.275	0.147	0.114	0.110
BI	0.3848	0.3455	0.3390	0.3567	0.2776	0.3166
	0.0105	0.0142	0.0146	0.0131	0.0100	0.0090
HI	0.0903	0.0794	0.1149	0.1088	0.0700	0.0847
	0.0112	0.0046		0.0262	0.0060	0.0059
	(22)	(23)	(1)	(32)	(17)	(11)
g (mmol /m^2/s)	7.92	1.65	4.66	4.11	0.77	-10.73
	2.84	2.73	6.92	2.32	2.01	3.66
A (μmol /m^2/s)	0.272	0.140	-0.189	-0.032	0.196	-0.116
	0.152	0.124	0.216	0.099	0.135	0.161
f	0.848	0.886	0.812	0.854	0.869	0.853
	0.010	0.006	0.032	0.009	0.007	0.007
	0.687	0.686	0.582	0.651	0.630	0.701
(g/MJ)	0.020	0.012	0.041	0.022	0.021	0.020

Progeny mean values for the whole population of palms in the trial.

Oil-to-bunch	23.2%	23.8%	n/a	23.9%	28.3%	n/a

n/a = *not available*

TABLE 4. CORRELATIONS WITH YIELD PEARSON CORRELATION COEFFICIENT/PROBABILITY OF EFFECT/NUMBER OF SAMPLES

Charac-teristics	Whole Population	Progeny					
		69	94	97	121	142	154
BN	0.6249	0.6461	0.7575	0.6099	0.7323	0.3682	0.6070
	0.0001	0.0001	0.0001	0.0121	0.0001	0.0350	0.0002
	192	33	31	16	46	33	33
HEIGHT	0.2590	0.4090	-0.135	0.7925	0.3827	-0.025	0.0574
	0.0003	0.0181	0.4666	0.0002	0.0087	0.8882	0.7510
	192	33	31	16	46	33	33
HIGHINC	0.0109	-0.143	-0.180	0.6520	0.0179	-0.239	-0.120
	0.8816	0.427	0.3594	0.0062	0.8596	0.2285	0.5056
	173	33	28	16	36	27	33
VDM	0.2364	0.0239	-0.526	0.7602	0.4205	0.2971	0.433
	0.0022	0.1802	0.0040	0.0006	0.0107	0.1686	0
	166	33	28	16	36	23	0.0168
							30
TDM	0.6831	0.6226	0.6912	0.9162	0.7879	0.5991	0.6753
	0.0001	0.0001	0.0001	0.0001	0.0001	0.0025	0.0001
	166	33	31	16	36	23	30
LAI	0.1877	-0.210	0.1164	0.5413	0.1147	0.5182	0.3306
	0.0101	0.2400	0.5329	0.0303	0.4478	0.0028	0.0744
	187	33	31	16	46	31	30
e	0.6853	0.7391	0.6289	0.7886	0.8057	0.5638	0.6521
	0.0001	0.0001	0.0003	0.0003	0.0001	0.0051	0.0001
	166	33	28	16	36	23	33
g	0.2483	-0.177	-0.151	0.3495	0.2751	0.078	0.5582
	0.0005	0.3219	0.4188	0.1844	0.0643	0.6643	0.0007
	192	33	31	16	46	33	33
A	0.1645	-0.041	-0.201	0.5475	0.2776	-0.024	0.2762
	0.0226	0.8182	0.2782	0.0282	0.0614	0.8967	0.1197
	192	33	31	16	46	33	33

n/a = *not available*

al. (1990) looking at 16 cultivars of cassava ($r=0.53$ $P<0.05$).

Whereas A had a significant positive correlation with the total above-ground dry mass produced/year (TDM) in the whole population (**; *Table 6b*), the correlation between A and YIELD was less significant (*) (*Table 4*). The main effect of increasing A was to increase total dry matter production, rather than the partitioning of carbon into bunches. This was also shown by the lack of correlation between either g or A and BI or HI for the population as a whole, although there were positive correlations between g (*) or A (*) and BI in progeny 97 (*Table 5*). No information on oil/bunch ratio was available for this progeny, so HI could not be calculated.

In order to assess the relative influence of HEIGHT, LAI and A on TDM, multiple linear regression analyses (PROC GLM in SAS) were

TABLE 5. CORRELATIONS WITH HARVEST INDEX AND BUNCH INDEX. PEARSON CORRELATION COEFFICIENT/PROBABILITY OF EFFECT/NUMBER OF SAMPLES

a) HI

Charac-teristics	**Whole Population**	**Progeny**					
		69	94	97	121	142	154
HEIGHT	0.1763 0.0707 106	0.2899 0.1903 22	-0.201 0.3570 23	n/a	0.3044 0.0902 32	-0.460 0.0630 17	-0.396 0.2285 11
HIGHINC	0.0214 0.8281 106	0.1610 0.4741 22	-0.596 0.0027 23	n/a	-0.010 0.9565 32	-0.288 0.2612 17	-0.674 0.0231 11
VDM	0.0012 0.9901 106	0.1822 0.4170 22	-0.682 0.0003 23	n/a	0.2293 0.2068 32	-0.662 0.0038 17	-0.556 0.0757 11
TDM	0.1643 0.0923 106	0.3185 0.1492 22	0.1259 0.5668 23	n/a	0.2820 0.1179 32	-0.625 0.0073 17	-0.203 0.5489 11
LAI	-0.064 0.5138 106	-0.124 0.5805 22	0.1439 0.5124 23	n/a	-0.036 0.8435 32	-0.561 0.0191 17	-0.069 0.8384 11
e	0.1921 0.0485 106	0.3664 0.0935 22	-0.183 0.4025 23	n/a	0.2931 0.1035 32	-0.567 0.0176 17	-0.173 0.6121 11
g	-0.018 0.8527 106	-0.051 0.8226 22	-0.441 0.0352 22	n/a	0.0323 0.8608 32	-0.321 0.2090 17	0.1868 0.5823 11
A	-0.048 0.6322 106	-0.021 0.9264 22	-0.464 0.0257 22	n/a	0.159 0.9313 32	-0.084 0.7480 17	0.110 0.7486 11

n/a = *not available*

performed as shown in *Table 7*. In the population as a whole, both HEIGHT and LAI had highly significant effects on both YIELD and TDM, while the effect of A was not significant. However, each progeny appeared to respond differently. Progenies 69, 121 and 154 showed positive relationships between both HEIGHT and LAI and TDM. These progenies behaved like those described by Hardon *et al.*, (1969), who found a positive correlation (P=0.01) between leaf area and bunch yield in some families (8/12 in their population) after a partial correlation to eliminate the effect of height on yield. Progenies 97 and 142 only showed correlations between HEIGHT and TDM. Only progeny 94 showed no relationship between either HEIGHT or LAI and TDM. Progeny 154 was the only one in which a significant relationship between A and TDM remained in the model, when HEIGHT and LAI were taken into account at the same time.

TABLE 5. (Continued)

b) BI

Characteristics	Whole Population	Progeny					
		69	94	97	121	142	154
HEIGHT	-0.145 0.0631 166	-0.155 0.3881 33	-0.442 0.0184 28	0.2694 0.3130 16	0.1371 0.4252 36	-0.661 0.0006 23	-0.367 0.0461 30
GHI-=NC	-0.205 0.0081 166	-0.285 0.1075 33	-0.285 0.1415 28	0.2172 0.4190 16	-0.192 0.2618 36	-0.365 0.0872 23	-0.511 0.0039 30
VDM	-0.416 0.0001 166	-0.562 0.0007 33	-0.830 0.0001 28	0.0997 0.7133 16	-0.099 0.5665 36	-0.734 0.0001 23	-0.447 0.0131 30
TDM	0.0787 0.3136 166	-0.079 0.6602 33	-0.171 0.3833 28	0.3621 0.1682 16	0.3969 0.0165 36	-0.565 0.0049 23	-0.070 0.7122 30
LAI	-0.114 0.1410 187	-0.657 0.0001 33	0.1341 0.4963 28	0.0091 0.9734 16	-0.022 0.8996 36	-0.243 0.2627 23	-0.052 0.7844 30
e	0.1635 0.0353 166	0.2539 0.1539 33	-0.238 0.2223 28	0.4842 0.0573 16	0.4017 0.0152 36	-0.581 0.0036 23	-0.053 0.7802 30
g	0.1085 0.1640 166	-0.151 0.4031 33	-0.297 0.1243 28	0.5172 0.0402 16	0.2795 0.0987 36	-0.229 0.2941 23	-0.054 0.9733 30
A	-0.074 0.3434 166	-0.332 0.0591 33	-0.321 0.0958 28	0.5238 0.0201 16	0.1440 0.4019 36	-0.541 0.0076 23	-0.006 0.9755 30

GENERAL DISCUSSION

Progeny Characteristics

Progeny 97 was the shortest progeny assessed, and also had the lowest VDM, TDM, YIELD, LAI, A and e. Within this progeny, there was good agreement between carbon assimilation per unit leaf area measured as A and calculated as e. Moreover, there were consistent correlations between carbon assimilation parameters and yield, and between factors enhancing competition (height, height increment, LAI) and yield.

At the other extreme of vegetative development, the results obtained for progeny 94 (tall, with a high LAI and slightly above average VDM and YIELD) show that palms with a high competitive ability for sunlight can achieve good yields without high A. e or superior BI or HI. The taller palms within this progeny demonstrated higher g and A, possibly because these individuals had more water available to them and they were therefore able to grow taller. Superior competitive ability for sunlight or water is **not**, however, a desirable characteristic, as a monoclonal stand of such palms would divert an unnecessarily large proportion of assimilates into trunk growth and

TABLE 6. CORRELATIONS BETWEEN A AND g OR e
CORRELATION COEFFICIENT/PROBABILITY OF EFFECT/NUMBER OF SAMPLES

a) A and either g or e

A				Progeny			
	ALL	69	94	97	121	142	154
g	0.6290	0.7955	0.9091	0.4856	0.6424	0.6568	0.5652
	0.0001	0.0001	0.0001	0.0565	0.0001	0.0001	0.0006
	192	33	31	16	46	33	33
E	0.2422	0.2176	-0.041	0.6282	0.1842	0.0113	0.2761
	0.0017	0.2237	0.8384	0.0092	0.2823	0.9591	0.1397
	166	33	28	16	36	23	30

b) A and growth and yield characteristics

A	ALL	69	94	97	121	142	154
HEIGHT	0.1542	0.2658	0.4279	0.3106	0.1133	0.0815	-0.106
	0.0328	0.1350	0.0163	0.2415	0.4532	0.6521	0.5558
	192	33	31	16	46	33	33
HIGHINC	-0.026	0.1916	0.3880	0.1399	-0.023	0.0846	-0.113
	0.7351	0.2854	0.0413	0.6053	0.1642	0.6748	0.5306
	173	33	28	16	36	27	33
VDM	0.2843	0.3978	0.4334	0.2800	0.2194	0.2562	0.1701
	0.0002	0.0219	0.0212	0.2935	0.2124	0.2372	0.3640
	166	33	28	16	36	23	30
TDM	0.2409	0.3056	0.1358	0.4004	0.1927	-0.015	0.2960
	0.0018	0.0837	0.9453	0.1243	0.2602	0.9448	0.1122
	166	33	28	16	36	23	30
LAI	0.0851	0.2209	0.1916	-0.117	-0.031	0.0774	0.1496
	0.2470	0.2167	0.3055	0.6650	0.8339	0.6791	0.4302
	187	33	31	16	46	31	30
e	0.2423	0.2176	-0.040	0.6282	0.1841	0.0113	0.2761
	0.0012	0.2237	0.8384	0.0092	0.2823	0.9591	0.1397
	166	33	28	16	36	23	30

c) A*f and growth and yield characteristics

A*f	ALL	69	94	97	121	142	154
VDM	0.2976	0.4216	0.4433	0.3153	0.1980	0.2738	0.1832
	0.0001	0.0145	0.0181	0.2342	0.2471	0.2061	0.3324
	166	33	28	16	36	23	30
TDM	0.2480	0.3126	0.0270	0.4352	0.1854	0.0029	0.3073
	0.0013	0.0765	0.8915	0.0921	0.2791	0.9895	0.0986
	166	33	28	16	36	23	30
YIELD	0.1239	-0.056	-0.197	0.5870	0.2782	-0.010	0.1137
	0.0910	0.7568	0.2880	0.0168	0.0612	0.9585	0.5495
	187	33	31	16	46	31	30

TABLE 7. MULTIPLE LINEAR REGRESSION OF TDM AGAINST HEIGHT, LAI AND A

Estimate/S.E. of estimate/probability
TDM = INTERCEPT +{T + (X*HEIGHT) + (Y*LAI) + (Z*A)

TDM	All	Progeny					
		69	94	97	121	142	154
INTERCEPT	27.44	-7.368	83.82	-9.435	12.38	20.39	-35.50
	8.96	17.264	34.53	20.143	17.86	25.87	23.10
	0.0026	0.6727	0.0231	0.6479	0.4933	0.4403	0.1365
HEIGHT	0.2342	0.3642	0.1074	0.5138	0.2818	0.3001	0.3313
	0.0249	0.0498	0.0664	0.1708	0.0484	0.0709	0.0528
	0.0001	0.0001	0.1187	0.0109	0.0001	0.0005	0.0001
LAI	8.265	11.11	2.859	4.6859	7.032	6.628	18.78
	1.750	2.66	5.762	7.4640	3.072	6.462	3.67
	0.0001	0.0003	0.6243	0.5419	0.0288	0.3180	0.0001
A	3.082	0.3939	-3.431	8.238	1.8153	-17.33	5.436
	1.849	2.2933	4.735	6.846	5.5338	8.453	2.362
	0.0976	0.8648	0.4757	0.2520	0.7450	0.0543	0.0292

high LAI at the expense of bunch production.

Progeny 69 produces a better type of palm for use on commercial plantations; the palms are generally short, with good partitioning characteristics (high BI and HI), and high g, A and e. Again, as in progeny 94, a positive correlation between height and yield is seen which is not accompanied by an increase in BI; indeed there is a negative correlation between height increment and BI.

Progeny 121 has a high height increment, but below average VDM, TDM and e. Again height correlates positively with yield but height increment correlates negatively with BI. Height also correlates positively with g.

Progeny 142 is average in most characteristics, but has a high LAI and low BI and height increment. Here it seems to be the LAI which is important in affecting competitive ability for light and so influencing yield. LAI has a negative effect on Harvest Index. This progeny is of interest in a breeding scheme because of its exceptionally high oil-to-bunch ratio (28.3% for the whole progeny; E.A. Rosenquist, personal communication).

Progeny 154 has a high height increment, VDM and TDM combined with low g and A and high e. The high A and low e in this progeny need further examination, as e is an estimate of conversion efficiency and should therefore be related to A. Progeny 154 showed the closest relationship between YIELD and A and TDM and A.

GENERAL DISCUSSION

The Use of Gas Exchange Selection Criteria in Oil Palm Breeding

The potential for incorporating selection for g or A into breeding schemes can only be assessed against the background of the relationship among growth, partitioning and yield characters. Considerable caution is needed to interpret correlation data since the significant correlations will inevitably have arisen by chance when so many correlations have been performed on the same data set.

Palms with high VDM and TDM tended to produce more bunches. However, the only other significant factor found to be related to BN in this analyses was g. The relationship between g and BN is consistent with a model where an important cause of inflorescence sex determination and/or bunch abortion is the degree of water stress to which the palm is subjected. Stomatal conductance (g) could be seen as an indicator of the water available to the palm, either through environmental variation, or variation in the efficiency with which the palm is able to extract water from dry soil. The analysis performed here is unable to distinguish between these two hypotheses.

It has previously been shown that palms with high leaf areas outyield others because they are more competitive for light (Corley *et al.*, 1971). Height and LAI are clearly major factors in competition for light, and both had significant interactions with many yield, growth and physiological parameters. It is important to develop selection criteria which result in high YIELD, BI or HI without enhancing competition, implying increased efficiency in the use of available resources. The question as to whether tall palms become so ***because*** of high g, or whether tall palms ***develop*** high g (perhaps because their leaves achieve photosynthetic saturation at higher PFD, and g and A are closely linked) is therefore of considerable importance. This question can be answered if palms are assessed when still relatively young, before they begin to compete for light and nutrients with their neighbours, and are then assessed again at a later date, once competition has had a chance to have major effects. This type of experiment is clearly required.

Oil palm is a good crop in which to search for a relationship between yield and photosynthesis, as yield appears to be sink-limited under most circumstances (Corley *et al.*, 1979), and the intimate relationship between leaf age and frond position allows easy standardization of leaves on which to measure photosynthesis. The strong (P=0.0018) relationship between A and TDM, arising from an accumulation of data in most progenies, is encouraging evidence that measured rates of photosynthesis do influence the total CO_2 assimilated by the palm. A is therefore a potentially important selection criterion in breeding and clone selection programmes. There are, however, caveats:

-TDM only refers to the dry matter production in above ground parts of the palm. Roots may account for up to 40% of dry matter production by a palm (Dufrene, 1989). This proportion may be sufficiently variable for misleading correlations to be obtained between A and dry matter assimilated.

-the variation in A in these data cannot be ascribed definitively to genotype effects and may result from environmental variation.

-A (or A*f) only accounted for less that 10% of the variation in VDM or TDM.

-the effects of A may be noticeable only in some progenies, and other factors may have more influence on yield in other progenies.

Corley *et al.* (1971) suggested that vegetative requirements took priority over reproductive sinks for assimilates after comparing palm dry matter production in Malaysia and Nigeria. In populations differing only in A, this should mean a positive correlation between A and YIELD, HI and BI. However, in these trials, high A had a higher positive correlation with vegetative growth (VDM) (***) or vegetative and reproductive growth combined (TDM) (**) than with high YIELD (*) or superior partitioning characteristics (n.s.). However, there are also data from disbudding experiments which indicate that when reproductive sinks are not available for assimilates, assimilate can be diverted into additional vegetative growth (Corley and Breure, 1992). Drought-induced reductions in reproductive sinks during the dry season in Zaire might have had the same effect in this trial.

Crossing palms selected for high A with palms selected for superior partitioning characteristics (high BI or HVIN) should therefore be a profitable procedure if the correlation between A and YIELD or TDM seen here is indeed due to genetic effects.

There is evidence from elsewhere (Adjahahossou, 1983) that low conductance correlates well with survival in extremely harsh dry season conditions. There is therefore a good reason to develop selection methods based on g to use for palms which will be planted in such extreme areas. In less extreme climates, the main type of 'drought resistance' which will be required is the ability to continue to yield relatively well in spite of a regular dry season. This paper has presented evidence that breeding programmes incorporating selections for ***high*** g or A in the dry season could be useful in conditions such as those seen in many areas of West Africa and South America. Further experiments are needed to assess g and A in breeding or clone trials in irrigated and rainy season conditions before recommendations are made for particular climatic zones.

Desirable characteristics (high YIELD, BI and HVIN) are clearly affected by both genetic and environmental factors. In this trial, conducted in a part of the world which suffers a regular dry season, environmental variation in water availability and competition between adjacent palms will have had a strong influence on these characteristics, and also on the measured values of A and g. It is important to establish that there are positive correlations between g or A and desirable characteristics in trials where the results can be ascribed to genotype rather than environmental variation before expensive breeding programmes are started. Trials where the same genotypes (preferably clones rather than progenies) are planted in different environments, in larger blocks, where heritability can be estimated, and palms assessed when both juvenile and mature are needed before the confounding genetic and environmental components of the results presented here can be unravelled.

CONCLUSION

The work described in this paper provides encouraging evidence that high photosynthetic rate/unit leaf area (A) contributed to high yield. This was due to effects on total dry matter production rather than assimilate partitioning. The results suggest that breeding schemes combining high A with other desirable characteristics should be worthwhile.

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