AGE-RELATED CHANGES IN STOMATAL AND PHOTOSYNTHETIC CHARACTERISTICS OF LEAVES OF OIL PALM *(Elaeis guineensis* Jacq.*)*

Keywords: *Elaeis guineensis;* stomatal density; stomatal conductance; photosynthesis; palm age; sink activity.

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*Leaves from palms of different ages were examined for stomatal distribution, stomatal density, conductance to water vapour, and photosynthetic properties. Leaflets of mature (*c. *12-year old) palms had stomata predominantly on the lower (abaxial) surface with few, if any, on the upper (adaxial) surface. Adaxial stomata were more evident in young palms (up to the first year after field planting).*

*Stomatal density (defined as total number of stomata per unit leaf area) increased progressively with age up to the second year in the field. Leaf conductance and photosynthesis rates, although very dependent on environmental factors, also increased with age, most markedly during the time of first fruit maturation. Photochemical efficiency increased with age of palm in parallel with increases in maximum rate of photosynthesis, while other photosynthetic characteristics either changed little (*viz. *carboxylation efficiency, photorespiration) or varied more with long term light environment (light compensation point, dark respiration rate) than with palm age.*

The involvement of various factors in the increased photosynthetic capacity, and its significance for palm productivity and progeny selection, are discussed.

INTRODUCTION

A knowledge of the photosynthetic capacity of a species is an important prerequisite for modelling its growth and productivity. Photosynthetic rates of oil palm leaflets have been determined in several studies, but with considerable variation in the results obtained (*Table 1*). Much of this variation can probably be accounted for by differences in plant material, environmental conditions and measuring

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TABLE 1. LIGHT-SATURATED RATES OF PHOTOSYNTHESIS OF OIL PALM LEAVES AS DETERMINED BY VARIOUS WORKERS

Palm age	Photosynthesis rate (μmol m^{-2} s^{-1})	Method	Reference	Note
a) months from sowing				
8 – 12	4.1	IRGA	Hong (1979)	a
12	8.1	C14	Corley (1976)	b
<12	10.1	IRGA	Corley (1985)	c
12	13.6 – 19.3	C14	Corley *et al.* (1973)	d
b) years from field planting				
2	14.5; 16.7	IRGA	Gerritsma (1988)	e
3	15.0	C14	Corley (1983)	f
4	24.3	IRGA	Dufrene (1989)	g
11	21.4	IRGA	Dufrene (1989)	g
10 – 12	7.0 – 11.0	C14	Corley (1976, 1983)	h
–	≃ 2.0	IRGA	Smith (1989)	i

Notes:
[a] Semi-controlled conditions in laboratory.
[b] Unpublished data of Thiyagarajan and Corley as cited by Corley (1976); maximum rate in nutrition experiment.
[c] Unpublished data of W. Peace as cited by Corley (1985); measured in controlled environment; exact plant age not given.
[d] Range of values obtained in comparisons of 16 progenies.
[e] Mean results for two experiments; conducted in Papua New Guinea.
[f] Maximum rate interpolated from graph of rate against leaf number.
[g] Irrigated palms in Ivory Coast.
[h] Range of values obtained for fronds of different ages of same palms.
[i] Dry season measurements in Colombia; palm age not given.

techniques. But, the precise causes are unclear. There remains uncertainty concerning the representativeness of the data.

One factor commonly contributing to variation in photosynthetic capacity is the age of plant material. Like many perennial species, oil palm undergoes marked changes in leaf morphology as it matures (Hartley, 1988) and these are probably accompanied by anatomical and biochemical modifications. Also, as the plant becomes reproductive, the establishment of additional sinks for photosynthate in the form of developing fruits may also influence photosynthetic activity (Gifford and Evans, 1981). In addition to ontogenetically determined changes, alterations in environmental conditions associated with growth, in particular the light environment, can also affect the photosynthetic properties of leaves (Boardman, 1977).

Although photosynthetic rate is the outcome of a large number of processes, it is convenient to separate stomatal from non-stomatal influences. Stomatal conductance, which determines the rate of diffusion of CO_2 into the intercellular air spaces of the leaf, is closely linked to photosynthetic activity (*e.g.* Wong, Cowan and Farquhar, 1979). Conductance in turn depends on the stomatal aperture and on the size and density of the stomata. In explaining variation in photosynthetic capacity it is useful, therefore, first to examine the conductance properties of the leaf and the distribution and density of stomata.

MATERIALS AND METHODS

Plant material

Tenera (dura × pisifera) palms were used in all studies. These were raised from seed with the exception of two tissue-cultured polyembryogenic clones used to examine stomatal density. Nursery palms, sampled at 12-15 months from germination, were grown in black polythene bags of well fertilized soil, watered daily. The plants were maintained in a glasshouse under partial shade. Older palms sampled were field planted at normal commercial spacing (*c.* 148 palms ha^{-1}).

For field palms, sampling and measurement was generally restricted to upper, fully expanded fronds well exposed to light. In some experiments with nursery palms, about six months old from sowing, all leaves on the plant were examined.

Measurements on nursery palms with lanceolate leaves, were made about half-way along the leaf, and for older nursery palms with pinnate fronds, on the fused, terminal, bifid lobes. In the field, measurements were made on leaflets about two-thirds of the distance from the base of the rachis, unless stated otherwise. Further details such as the age of the material are given in the relevant tables of results.

Measurements

Stomatal densities were determined from polystyrene surface replicas (Quarrie and Jones, 1977) at × 400 magnification. Both leaf surfaces were examined at approximately half-way along the leaflet. All stomata were counted in six fields of view to give a mean value for each sample. For other details see Henson and Chang (1990).

Measurements of leaf (stomatal) conductance were made using either a dynamic diffusion transit-time porometer (Delta-T Devices, Burwell, Cambs, UK) or a continuous-flow, steady-state gas exchange system (Analytical Development Co., Hoddesdon, Herts, UK). The former instrument permits separate determination of the conductances of the upper (adaxial) and lower (abaxial) leaf surfaces, while the gas exchange system measures total gaseous flux and hence total conductance of both surfaces.

Measurements of net photosynthesis were made using the gas exchange system, which incorporated an infra-red CO_2 gas analyzer. For a full description of the system see Long and Hallgren (1985).

Stomatal conductance measurements were made with natural light under clear sky conditions. Photosynthesis measurements were made under the same conditions except when determining light and CO_2-response curves, in which case light from a 55 Watt tungsten halogen lamp was used to illuminate the leaf via a fibre-optic cable. A maximum irradiance at the leaf surface exceeding 1900 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetically active radiation (PAR) was possible and was attenuated as necessary using varying numbers of intervening wire mesh filters.

Photosynthetic-light response curves were determined as previously described (Henson, 1991). The method assumes 85% transmission of PAR by the cuvette (chamber) window and 80% absorbtion by the leaf of the transmitted PAR.

The response of photosynthetic rate to CO_2 concentrations below ambient was determined at a constant irradiance of 800 $\mu mol\ m^{-2}s^{-1}$ PAR, also as earlier described (Henson, 1991).

Dry and wet bulb air temperatures, from which atmospheric vapour pressure deficits (vpd) were later calculated, were measured with an Assman psychrometer. Total radiation was measured with a Kipp solarimeter connected to a millivolt integrator.

RESULTS

Stomatal distribution and density

Data on stomatal density for *E. guineensis* material of different ages are summarized in *Table 2*. Stomata were detected on both leaf surfaces of palms of all ages, with the exception of palms sampled two years after field planting, on which no adaxial stomata could be detected. Adaxial stomata were only infrequently found on the 12-year old palms, and on some fronds of these palms (*Table 3*), none could be detected. The presence of adaxial stomata on fronds of 'mature' palms has, however, been recently confirmed using a scanning electron microscope (Mohd. Basri Wahid, personal communication).

The ratio of adaxial to total stomatal numbers declined with palm age while total stomatal density (sum of both surfaces) increased (*Table 2*). The stomatal density and distribution characteristic of the mature palm leaf appeared to be

TABLE 2. STOMATAL DENSITIES ON ABAXIAL AND ADAXIAL LEAF SURFACES OF OIL PALMS AT DIFFERENT STAGES OF GROWTH

Growth stage	Stomatal numbers per mm^2			
	abaxial	adaxial	total	% adaxial
In vitro				
plantlets[a]	53.1±1.9	27.3±0.8	80.4	34.0
Nursery palms				
6 months after sowing[b]	66.9±4.4	17.4±1.8	84.3	20.6
18 months after sowing[c]	92.4±1.7	17.5±1.6	109.9	15.9
Young field palms				
9 months after planting[d] (vegetative)	138.4±4.0	5.6±0.5	144.0	3.9
2 years after planting[e] (fruiting)	174.2±3.2	0	174.2	0
Mature palm				
12 years after planting[f] (fruiting)	175.0±4.8	0.4	175.4	0.2

Notes:

[a] Embryogenic tissue cultures. The largest fully-emerged leaf was sampled from two clones; five plantlets per clone. Each plantlet had 4–5 visible leaves. n = 10 ± s.e. mean.

[b] Upper three leaves; n = 6 ± s.e. mean.

[c] Upper three leaves; n = 24 ± s.e. mean.

[d] Frond 6; middle leaflets; n = 9 ± s.e. mean.

[e] Frond 6; middle leaflet; n = 24 ± s.e. mean.

[f] Frond 19; every 10th leaflet along frond; n = 17 ± s.e. mean.

attained by at least the end of the second year in the field.

Stomatal densities given in *Table 2* represent average values for the palms and fronds examined. Stomatal density varied between fronds and between leaflets along a frond. For palms six months after sowing with six expanded lanceolate/bifid leaves, abaxial stomatal density decreased in a basipetal direction from 76.9 mm^{-2} on the youngest expanded leaf to 44.8 mm^{-2} on the oldest (sixth) leaf. Stomatal density of pinnate leaves (fronds) varied only slightly (<6% of the mean) along the frond in young palms sampled nine months after planting, but there was larger variation within the frond of a mature palm (*Figure 1*) with basal leaflets having lower densities than those near the frond apex.

Stomatal size differed between young and mature palms (*Table 3*). Thus, not only did mature palms have a higher stomatal density but the individual complexes were on average 1.36 times longer than those of nursery palms. Stomatal lengths did not differ significantly between leaf surfaces (*Table 3*).

Stomatal conductance

Several preliminary measurements were made using the diffusion porometer to determine variation in conductance between leaf surfaces and leaf or frond positions. In young nursery palms, while the abaxial surface contributed most to total conductance (*Table 4*), there was also appreciable adaxial conductance, which was significantly ($P<0.001$) correlated over time

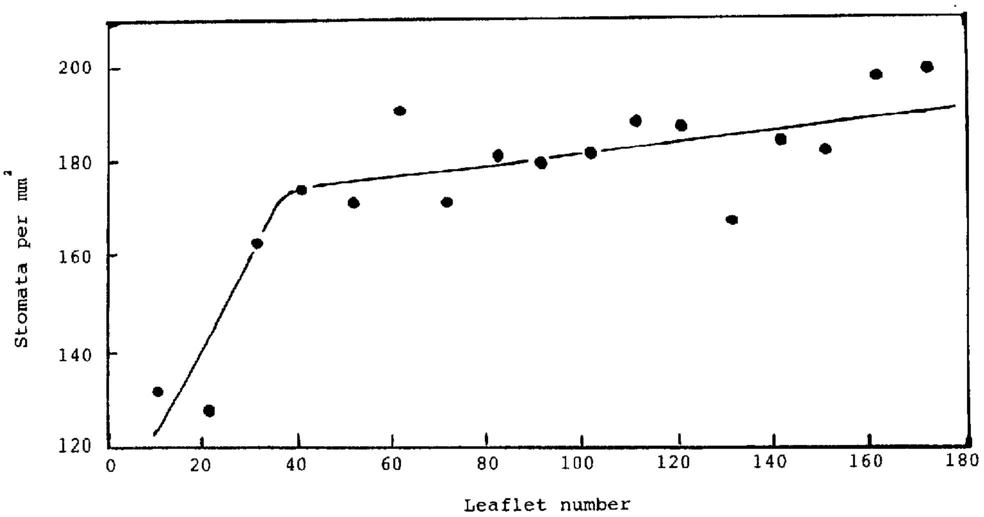

Figure 1. Variation in stomatal density of the abaxial surface of leaflets, along the frond of a mature fruiting palm (c. 12 years after field planting). The leaflets are numbered in an acropetal direction along one side of the rachis. Stomatal density was determined half way along each leaflet.

TABLE 3. LENGTHS OF STOMATAL COMPLEXES ON ABAXIAL AND ADAXIAL SURFACES OF OIL PALMS AT THREE GROWTH STAGES[a]

Growth stage	**Stomatal length (µm)**	
	abaxial	**adaxial**
Nursery palms		
6 months after sowing		
Leaf 3	28.6 ± 0.3	26.6±0.4
Leaf 5	27.9 ± 0.5	27.6±0.5
12 months after sowing		
Leaf 2	25.8 ± 0.3	26.0±0.4
Leaf 3	24.9 ± 0.4	25.6±0.3
Mature palms		
12 years after planting		
Frond 19: sample 1	38.6 ± 0.5	Stomata not detected
sample 2	36.3 ± 0.6	Stomata not detected

Note:
[a] Leaves and fronds counted basipetally with youngest fully emerged leaf or frond as No. 1. Data are means of twenty ± s.e. mean.

with the conductance of the abaxial surface, indicating that the adaxial stomata were functional.

The virtual absence of adaxial stomata on mature oil palms leaves was reflected in the conductance of this surface being only 5 mmol m^{-2} s^{-1}, compared with up to 600 mmol m^{-2} s^{-1} for the abaxial surface.

In the nursery palms there were substantial variations in total conductance with leaf position (*Table 4*), which at least partly reflected changes in stomatal density. The second, fully expanded

TABLE 4. CONDUCTANCE TO WATER VAPOUR OF DIFFERENT LEAVES OF YOUNG D × P NURSERY PALMS

Leaf number (counting basipetally from youngest fully emerged leaf)	Abaxial conductance	Adaxial conductance	Total conductance
		(mmol $m^{-2} s^{-1}$)	
1	128 ± 15	19 ± 3	147 ± 16
2	170 ± 31	35 ± 5	205 ± 35
3	117 ± 24	31 ± 6	148 ± 29
4	99 ± 18	27 ± 4	126 ± 21
5	66 ± 5	26 ± 3	92 ± 7
6	41 ± 6	17 ± 1	58 ± 6

Data presented are for 0900 h, when conductance was maximal. Data are means of six plants ± s.e. mean. Plants were sampled about 6 months after 'sowing' of the germinated seed.

frond had the highest conductance, and so most measurements in subsequent studies were made using this frond.

In field palms sampled in the first year after planting, the third youngest frond (frond 3) had consistently higher conductances than frond 6, and conductances of both were higher than frond 1 (data not presented). In mature (c. 12-year old) palms, no substantial differences in conductance were detected amongst the youngest 10 fronds (excluding frond 1), and most subsequent measurements were made on frond 5.

TABLE 5. MAXIMUM RATES OF NET PHOTOSYNTHESIS (A) AND ACCOMPANYING VALUES OF STOMATAL CONDUCTANCE (g_S), INTERCELLULAR CO_2 CONCENTRATION (Ci), RATIO OF INTERCELLULAR TO ATMOSPHERIC CO_2 CONCENTRATION (Ci/Ca), SPECIFIC LEAF WEIGHT (SLW) AND PHOTOSYNTHETICALLY ACTIVE PHOTON FLUX DENSITY (PFD) OF OIL PALM LEAFLETS IN RELATION TO PALM AGE[a]

Palm type and age	A (µmol $m^{-2}s^{-1}$)	g_s (mmol $m^{-2}s^{-1}$)	Ci (Pa MPa^{-1})	Ci/Ca	SLW (g dry weight m^{-2})	PFD (µmol $m^{-2}s^{-1}$)
Nursery palms; about 18 months from sowing	i) 7.2 ± 0.2	243 ± 24	243 ± 6	0.68	61.0 ± 1.8	614
	ii) 8.2 ± 0.4	293 ± 43	232 ± 4	0.66		1980[b]
Field palms; years after planting:						
1.4[c]	13.2 ± 0.3	445 ± 26	259 ± 6	0.64	105.0 ± 1.6	1616
2.4[d]	21.3 ± 0.9	844 ± 75	349 ± 8	0.72	–	997
13.0[d]	17.8 ± 0.4	562 ± 62	252 ± 3	0.66	105.4 ± 1.5	1080

[a] Data are means ± s.e. of 6–16 measurements.

[b] Measurements made using an artificial light source; all other measurements made with natural light.

[c] Palms vegetative.

[d] Palms fruiting.

For both nursery and field palms there were considerable changes in stomatal conductance during the day which could not be accounted for solely by changes in radiation. *Figure 2* shows typical changes in conductance for palms of three ages. In each case conductance first rose to a peak in mid-morning, then declined, remaining at low levels in the afternoon despite adequate irradiance. Similar trends were found on many other occasions. As indicated in *Figure 2* and confirmed in other studies with the gas analysis system (*Table 5*), peak conductance generally increased with palm age. However, young palms measured 29 months after field planting were found to give higher conductances than older (13 years) palms (*Table 5*). This is further discussed below.

Photosynthesis

Photosynthetic rate was found to vary with time in a manner similar to that of conductance. *Table 5* gives the peak photosynthetic rates observed together with associated measurements, for palms of the different age groups. Measurements were made under natural light but nursery palms grown in the glasshouse (which transmitted only a portion of the natural radiation) were also measured with artificial irradiation to ensure that light was not limiting. Net photosynthesis rate paralleled conductance and increased in the order nursery palms < young field palms < older field palms.

A marked increase in peak photosynthesis rate occurred between *c.* 14 and 30 months

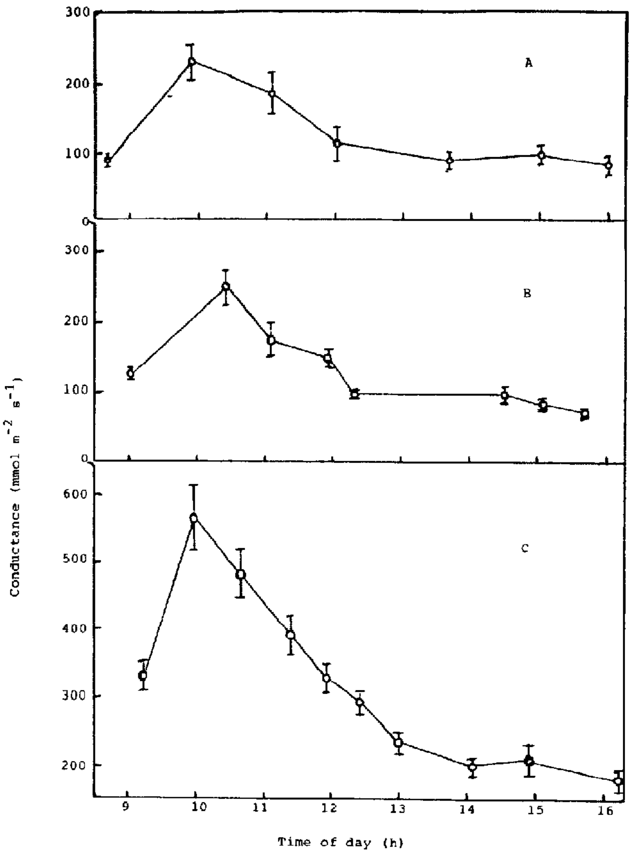

Figure 2. Representative daily time-courses of stomatal conductance for palms of three age groups: (A) nursery palms, 12 months after sowing, (B) field palms during the first year after planting, and (C) field palms during the 13th year after planting. Measurements were made on upper fronds, well exposed to light (clear sky conditions), using either (A, B) a diffusive porometer or (C) a gas exchange cuvette. Data are means of 6-12 measurements ± s.e. mean.

after field planting (*Figure 3*). The increase was at first gradual (months 14–24), then more rapid. The rapid increase coincided with maturation of the first harvested fruits.

Table 5 also shows that age-related increases in photosynthesis rate were partly associated with increases in conductance, as well as with increases in intercellular CO_2 concentration (Ci). The latter was related positively to the external ambient CO_2 concentration (Ca), such that the Ci/Ca ratio remained relatively constant. However, of these various factors, conductance remained the one most strongly correlated with photosynthesis rate ($r = 0.974$; $P<0.01$). Lower photosynthetic rate in nursery palms was also associated with a lower specific leaf weight (SLW), but it could not be ascribed to limiting irradiance during measurement.

Data obtained from photosynthesis-light response curves are presented in *Table 6*. Curves for nursery palms were initially constructed for plants growing in partial shade in the glasshouse. This, however, resulted in low light compensation points and dark respiration rates which were found not to be characteristic when palms were grown in the open (Henson, 1991). Data in *Table 6* thus refer to sun-grown plants only and show there to be no changes in light compensation point with age. Dark respiration rate increased with age but when expressed as a proportion of the maximum observed photosynthetic rate it decreased. Most significantly,

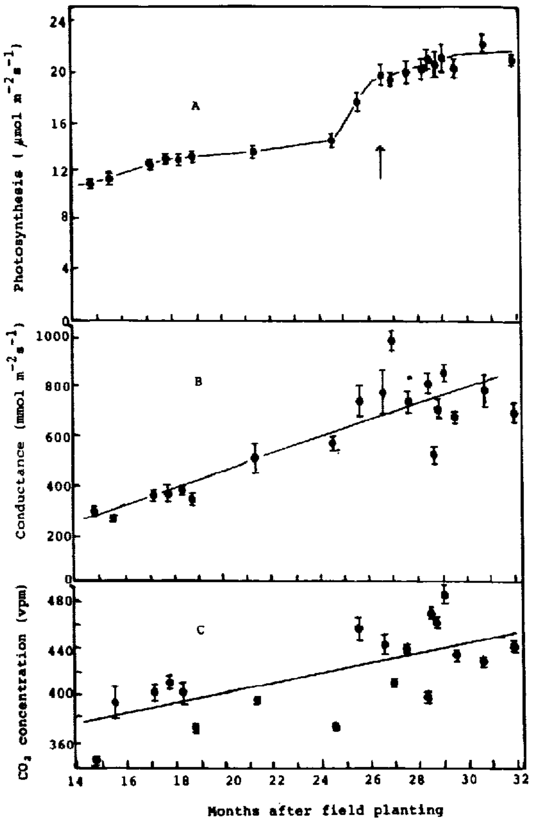

Figure 3. Changes between 14 and 31 months after planting in (A) the maximum observed photosynthetic rate of oil palm leaflets, (B) corresponding stomatal conductance, and (C) the corresponding ambient CO_2 concentration of air entering the leaf cuvette. Measurements were made on upper fronds, well exposed to light, under clear sky conditions. Data are means of 6-8 measurements ± s.e. mean. Arrow in (A) indicates time of harvest of first fruit bunches.

TABLE 6. PHOTOSYNTHETIC CHARACTERISTICS OF UPPER LEAVES OF OIL PALMS OF DIFFERENT AGES DERIVED FROM PHOTOSYNTHESIS – LIGHT RESPONSE CURVES[a]

Palm age	PAR at 85 per cent of maximum A (μmol $m^{-2}s^{-1}$)	Photochemical efficiency (mmol CO_2 mol^{-1} absorbed quanta)	Light compensation point (μmol $m^{-2}s^{-1}$)	Dark respiration rate (R) (μmol $m^{-2}s^{-1}$)	R as a per cent of maximum net CO_2 assimilation (A)
Nursery palms *c.* 18 months from sowing[b]	681 ± 69	29 ± 1.5	63 ± 7	1.19 ± 0.08	14.5
Field palms 2nd year after planting[c]	827 ± 57	40 ± 1.6	67 ± 11	1.83 ± 0.29	13.9
Field palms *c.* 13 years after planting[d]	755 ± 47	50 ± 1.1	65 ± 6	2.19 ± 0.18	12.3

[a] Data are means of 6–12 measurements ± s.e. mean.
[b] Measurements made on frond numbers 1 and 2; palms grown without shade.
[c] Mean value for frond numbers 2, 7, 13.
[d] Mean value for frond numbers 2–8.

TABLE 7. PHOTOSYNTHETIC CHARACTERISTICS OF UPPER LEAVES OF OIL PALMS OF DIFFERENT AGES DERIVED FROM PHOTOSYNTHESIS – CO_2 RESPONSE CURVES[a]

Palm age	Light growing conditions	Carboxylation efficiency (μmol CO_2 m^{-2} s^{-1} Pa^{-1})	CO_2 compensation point (Pa)	CO_2 efflux at zero C_i (μmol $m^{-2}s^{-1}$)
Nursery palms c. 18 months from sowing	shade	0.735 ± 0.034	7.43 ± 0.24	5.41 ± 0.28
	sun	0.445 ± 0.020	7.60 ± 0.10	3.37 ± 0.15
Field palms 2nd year after planting	sun	0.725 ± 0.027	7.65 ± 0.37	5.52 ± 0.28
Field palms c. 13 years after planting	shade	0.717 ± 0.038	7.73 ± 0.24	5.44 ± 0.14
	sun	0.690 ± 0.040	8.05 ± 0.29	5.48 ± 0.33

[a] Data are means of six ± s.e. Measurements made with PAR = 800 μmol $m^{-2}s^{-1}$. Other details as for *Table 6*.

the photochemical efficiency of leaves increased substantially with palm age (*Table 6*) in concert with the increase in maximum photosynthetic rate.

Photosynthetic responses to varying CO_2 concentration did not show any consistent differences due to palm age (*Table 7*). Although in a previous study (Henson, 1991) nursery palms were found to have a lower carboxylation efficiency than mature palms, this may not be a general trait, for on other occasions the reverse was found. *Table 7* shows the range of values obtained for different palm groups. No distinct age trends are apparent and palms of all ages show CO_2 compensation points and rates of photorespiration (measured as CO_2 efflux at zero C_i) which are typical of C_3 plants.

DISCUSSION

It is evident from this study that large changes occur in the physiological properties of oil palm leaves as the plant matures. The juvenile plant has stomata on both leaf surfaces but as the palm develops successively later-formed leaves, there is a loss of adaxial stomata, an increase in abaxial stomata and an increase in stomatal size. All these changes collectively favour the increase in stomatal conductance and gas exchange which was observed for palms between the nursery stage and up to the second and third year in the field.

Earlier observations of oil palms (WAIFOR, 1956 cited by Hartley, 1988; Rees, 1961; Corley and Gray, 1976) all infer that stomata are present on the lower leaf surface only. However, Ghose and Davis (1973) reported the presence of adaxial stomata on both 'young' and 'adult' oil palms although, as in the present study, they found that adaxial stomata were much less frequent than were abaxial stomata. So, stomata can occur on the upper surface even of mature palms, though this surface has a very low conductance to water vapour, and gas exchange is effectively confined to the lower surface of the leaf on all but juvenile palms. Such a hypostomatous characteristic is commonly found in various tall tree species and is considered (Jarvis and McNaughton, 1986) to increase the degree of control which can be exercised by the stomata over the rate of transpiration. The trait is therefore a useful one in situations where water may be seasonally limiting, as in much of West Africa (Rees, 1961).

The photosynthetic capacity of oil palm leaves was also observed to increase with plant age during the early years (*Table 5*). Examination of the results of other workers (*Table 1*) using the IRGA technique shows a similar trend, with the highest values being obtained for palms four years after planting by Dufrene (1989) and the lowest with nursery palms by Hong (1979). The limited data suggest that older field palms may have somewhat lower rates of net photosynthesis than those in the early years of fruiting; *cf.* 2.4- with 13-year old palms in *Table 5* and 4- with 11-year old palms measured in West Africa by Dufrene (1989) in *Table 1*. The ^{14}C method (*Table 1*) shows similar age trends if the results of Corley *et al.* (1973) (for a number of progenies) are excluded.

Reasons for the changes in photosynthesis rates with age could include:

i) An increase in stomatal frequency resulting in an increase in stomatal conductance and hence in CO_2 diffusion into the leaf. This is probably a major factor as photosynthetic rate (A) and conductance were similarly ranked (with age) and highly correlated ($r = 0.974$; $P<0.01$). However, changes in stomatal frequency did not account for differences in A between 2.4- and 13-year old palms. Here, differences in stomatal aperture must be involved.

ii) An increase in specific leaf weight. Greater mass per unit leaf area in older palms (*Table 5*) may imply more photosynthetic activity per unit area by virtue of a thicker leaf with more chloroplasts, enzymes, *etc.* This effect may contribute to the differences between nursery and adult palms but does not explain differences between young and mature field palms. In this respect it is pertinent to note that the carboxylation efficiency (which may be at least partly related to the amount per unit area of carboxylating enzyme) was potentially as high in young, as in mature palms (*Table 7*).

iii) An increase in demand for assimilates by developing sinks. It is noteworthy that an abrupt increase in A occurred in young palms just as the first harvestable fruits were reaching maturity. As described elsewhere

(Henson, 1990), the presence of fruits can markedly influence photosynthetic rate, which were much higher in fruiting than in non-fruiting palms of the same age. The increased photosynthetic rate found in fruiting palms was accompanied by an increased stomatal conductance, while intercellular CO_2 concentration did not differ (Henson, unpublished results). Thus, a restricted photosynthetic rate found in juvenile (non-fruiting) palms may be due in part to a lack of assimilate demand by sinks. The manner by which sinks stimulate stomatal opening and photosynthetic activity in source leaves is still a matter for debate (Gifford and Evans, 1981). However, there is some evidence (Henson, 1990) that in the oil palm a feed-back inhibition may occur through the accumulation of sugars within the leaflets.

iv) An increase in ambient CO_2 concentration. High ambient CO_2 concentrations (Ca) may have contributed to the higher photosynthetic rates of young field palms via an increase in C_i. Ca was highest with the 2.4-year old palms and early morning levels tended to increase in the field during the third year (*Figure 3*).

The increase in photosynthetic rate with palm age was also accompanied by an increase in photochemical efficiency, which is a measure of the photosynthetic rate per unit PAR *absorbed* under limiting radiation conditions. As most of the foliage of mature palms operates at low light intensities for much of the time, the higher photochemical efficiency of older palms would partially compensate for mutual shading and also ensure greater CO_2 assimilation even by upper fronds, as for example during cloudy weather.

There were also increases in dark respiration rate of leaves with palm age. However, when expressed as a percentage of maximum assimilation rate, the dark respiration rate actually declined. This could be one factor contributing to the maintenance over time of the light-use efficiency of the whole palm (Squire and Corley, 1987), despite the progressive increase with age in the proportion of non-photosynthetic tissue.

In contrast, photorespiration, as assessed by CO_2 efflux rate at zero C_i (*Table 7*), was similar for palms of all ages, with the exception of ursery palms grown in high light. Both the high photorespiration rates and high CO_2 compensation points are clear indications that the C_3 pathway of carbon fixation operates in oil palm.

The changes in maximum net photosynthetic rate, relative dark respiration rate, and photochemical efficiency with palm age would be expected, using current models of canopy photosynthesis (*e.g.* Goudriaan and Van Laar, 1978; Monteith, 1981), to lead to a substantial increase in canopy gross assimilation, more especially so as the leaf area index would also increase with age.

However, one restriction on the use of the measured photosynthetic parameters (maximum photosynthetic rate and photochemical efficiency) in current canopy photosynthesis models is that radiation does not appear to be the sole factor determining photosynthetic rates of oil palm under natural field conditions. Rates were observed to decline during the day despite high radiation and high soil moisture. The decline is considered (Henson and Chang, 1990) to be due to decreasing atmospheric humidity, which induces closure of stomata (Smith, 1989). Until the present models are modified to take this effect into account, some doubt must remain regarding their use for accurately estimating gross canopy photosynthesis.

A further remaining question is at what age photosynthetic capacity starts to decline after reaching its supposed peak, possibly around 2.4–4.0 years after planting. In Dufrene's (1989) work the change between 4- and 11-year old palms was not large, and amounted to only a 12% reduction or about 1.7% per year. The data in *Table 5* yield a similar value (1.6% per year between 2.4 and 13 years). Comparisons of Corley's data (*Table 1*) for 3- and 10–12 year old palms gives a minimum change of nearly 3.0% per year. If a linear reduction with time is assumed, then, using Dufrene's (1989) results, palms 25 years in the field would have a maximum photosynthesis rate of around 16.0 $\mu mol\ m^{-2}\ s^{-1}$.

Further studies are obviously needed on older palms; the main reason these have not been carried out is the obvious one of problems of access to the fronds of tall trees. The often-observed decline in yields of old palms could well be explained in part by declining photosynthetic capacity.

The present results may be of some consequence with respect to breeding and selection of palm progenies. Yield of oil palms is considered to be source-limited (Corley, 1976) and so selection for higher photosynthetic rates may be expected to lead to higher yields. Apparent genetic variation in photosynthetic rates of nursery palms has been observed previously (Corley *et al.*, 1973). However, there is now doubt, given the large, apparent influence of the bunch sink on leaf photosynthesis rate (Henson, 1990), whether differences observed in the juvenile stage would be expressed in the adult fruiting palm. It is possible that CO_2 assimilation may be governed more by sink strength, which would be determined by bunch load and hence inflorescence differentiation and development. This may confound any apparent genetic differences. This question has still to be resolved.

CONCLUSIONS

The oil palm undergoes considerable ontogenetic changes which are expressed not only morphologically but also in terms of physiological activity. There is a progressive increase with palm age in the capacity for gas exchange by the leaf surface, which changes most dramatically as the palm enters the reproductive phase. Further documentation is still needed on the changes occurring during the later life of palms up until the time of their clearance for replanting, and on the extent to which genetic differences in photosynthetic rate occur and are expressed at the different stages of growth.

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