

THE BREEDING OF OIL PALMS IN MALAYSIA

S. C. Ooi *

Introduction

Taxonomic position. The oil palm, *Elaeis guineensis*, Jacq ($2n = 32$) is grouped together with the familiar coconut, *Cocos nucifera* under the tribe *Coccoineae*, in the family *Palmae* (or *Arecaceae*) (Hutchinson, 1934; Tomlinson, 1961; More, 1961). Two other palm species have also been included in the genus *Elaeis*, namely, *E. oleifera*, (HBK) Cortes, (also known as *E. melanococca*, Gaertner) and *E. odora*, (Wessels Boer, 1965). These two species have, at various times, also been placed in a different genus and were referred to as *Corozo oleifera* (HBK) Bailey and *Barcella odora* respectively (see for example, Moore, 1961, loc. cit.). However, at least insofar as the former species is concerned, this would not be appropriate, considering the great similarity between this species and *E. guineensis* for a great number of characteristics and the ease with which they hybridise and produce fertile offsprings. In fact as will be discussed later, *E. oleifera* through its hybrids with *E. guineensis* can have great potential in oil palm breeding for certain specific characteristics.

Origin and distribution. The oil palm is native to tropical Africa where it still exists fairly extensively to-day as wild and semi-wild groves along the western coast in a narrow belt from Senegal to Angola and towards the central regions in Congo, Southern Sudan, Uganda and Tanzania (Zevens, 1964.b).

The oil palm has been an important source of edible oil for the local population in Africa since ancient times. In Africa, its spread and distribution have been closely associated with human activity. At the present time, because of its economic importance, the oil palm has spread to other parts of tropical Africa, e.g. Zanzibar and Madagascar, the Far East and South America. In fact, today, the largest acreage of cultivated oil palms is found in the Far East, in particular Malaysia and Indonesia.

The oil palm was first planted in Malaysia during the early part of the 20th century and since then, the oil palm acreage has expanded very rapidly and at present, there are approximately 700 thousand hectares of oil palm making it the second major agricultural crop of Malaysia, after rubber. Malaysia is currently the largest producer and exporter of palm oil, accounting for two-thirds of the world trade in this commodity. The oil palm industry in Malaysia will continue to expand very rapidly, at approximately the rate of 50 thousand hectares annually. It is very easy, therefore, to visualise the importance of an effective breeding programme to produce adequate quantities of high quality seeds (10 million) annually to meet the needs of this rapidly expanding industry.

General Morphology and Breeding System. In common with other members of the palm family, the oil palm is characterised by a single stem which culminates in a crown of 40 to 50 feather-like leaves. The leaves of the adult palm are simply-pinnate with 150 or more leaflets on each side and arranged in two or more planes, giving it a rather ragged appearance very much different from that of a coconut frond. The leaves or fronds are arranged in a regular sequence on the stem and two opposing sets of spirals may be apparent. The most obvious is the arrangement into 8 spirals, which, depending on the direction of the spiral, may be described as left-handed

* Head, Oil Palm Branch, Malaysia Agricultural Research and Development Institute (MARDI), Serdang, Selangor, Malaysia.

or right-handed. The leaf bases remain persistent on the trunk for a very long period of time but when they are eventually shed, diamond shaped scars are visible.

The oil palm is monoecious, bearing male and female flowers in alternate cycles on the same palm. Normally, separate male and female inflorescences are formed but occasionally, hermaphrodite inflorescences do occur. The inflorescences (spadix) are borne at the leaf axil and as they emerge, they are still enclosed in a woody sheath or spathe. Eventually the spathe splits open to expose the inflorescence inside.

The female inflorescence is large, measuring up to one foot or more in length and consists of a central stalk or peduncle on which 100 to 200 spikelets are attached in a spiral arrangement similar to that for the attachment of the leaves on the trunk. The spikelets are thick and fleshy and carry 10 to 15 sessile female flowers on each.

The male inflorescence is borne on a longer peduncle than that of the female inflorescence, and consists of finger-like spikelets on which the male flowers are borne. Each of these male spikelets carries between 700 to 1200 male flowers. The male inflorescence produces large quantities of pollen (5 to 25 grams), adequate for use in hand pollinations of 25 to 125 female inflorescences.

Natural pollination is affected by wind, and although various insects are known to visit the flowers, their role in pollination has not been established. The alternate cycles of male and female inflorescences would appear to favour out-crossing and in fact, there is some evidence to suggest that the oil palm is not tolerant of severe inbreeding (Gascon, et. al. 1969; Hardon, 1970). Selfed progenies for instance, can suffer reduction in yields of up to 25% as compared to randomly mated progenies.

The female inflorescence eventually develops into a fruit bunch, each of which can contain up to 1500 fruits. The oil palm fruit is drupe and weighs between 10 to 30 gm. The fruit consists of an outer skin (or exocarp), the pulp (or mesocarp), the shell (or endocarp), and the kernel (or endosperm). The shell together with the kernel forms the nut or seed of the oil palm fruit. Considerable variations exist with respect to the fruit colour, shell thickness, carotenoid content and presence of additional carpels.

Economic importance. The oil palm is economically important for the oil it produces from the pulp of its fruit and kernel. The former is referred to as palm oil (and for which the oil palm is commonly associated with) while the latter is known as palm kernel oil. The residue from the kernel after extraction of the oil is also of economic importance as a source of animal feed.

In its natural state, palm oil is dark orange in colour, due to the presence of carotene. It is a semi-solid liquid at room temperature (25°C). Typical fatty acid composition of palm oil is as follows:

Fatty acid	Myristic(C ₁₄)	Palmitic(C ₁₆)	Stearic(C ₁₈)	Oleic(C _{18:1})	Linoleic(C _{18:2})
Percentage	0.6	49.2	2.2	40.2	7.8

The oil is well balanced in terms of saturated and unsaturated fatty acids (Iodine value, approximately 50). Palm oil finds application mainly in edible uses, particularly as blends for the manufacture of margarine, shortenings and cooking oil.

Palm kernel oil is a colourless liquid at room temperature (25°C) and it strongly resembles coconut oil both in physical and chemical characteristics. It is a relatively more saturated oil than palm oil and typical fatty acid composition is as follows:

Fatty acid	Caprylic(C ₈)	Capric(C ₁₀)	Lauric(C ₁₂)	Myristic(C ₁₄)
Percentage	3	6	50	16
	Palmitic(C ₁₆)	Stearic(C ₁₈)	Oleic(C _{18:1})	Linoleic(C _{18:1})
	6.5	1	16.5	1

It has applications similar to that for coconut oil and in addition to the edible uses listed for palm oil, palm kernel oil also finds good application in the manufacture of soaps with good lathering properties.

Method of breeding

Breeding objectives

Oil palm breeding may be carried out with the following main objectives:

1. Improvement of oil yield
2. Improvement of oil characteristics
3. Reduction in stem height increment
4. Resistance to diseases

The above ranking represents to some extent the relative priorities given to these objectives in the oil palm breeding programmes. These priorities would obviously vary from programme to programme. For instance, disease resistance breeding is given relatively higher priority in West Africa than in Malaysia, largely, because disease occurrence e.g. *Fusarium* wilt can account for substantial loss of crop through death of the trees in those countries. These objectives can also be expected to alter with changes in technology and use of the product. For instance, as a result of the trend towards greater consumption of unsaturated fats and oil, increasing interest and effort is being given in the oil palm breeding programme to improving the level of unsaturated fatty acids in palm oil and it is not unlikely that this objective may take precedence over oil yield in future breeding programmes.

1. Improvement of oil yield

As indicated earlier, two main economic products are derived from the oil palm namely, palm oil and palm kernel oil. Both products are derived from the fruit and are considered simultaneously in the oil palm breeding programme. A third economic product is also derived from the fruit namely, kernel cake or residue, which is used for animal feed, but no attention is given to this in the breeding programme.

1) Selection criteria

Oil yield of the oil palm may be regarded as a composite characteristic in that its final expression depends on a number of components. These are summarized in Table 1.

Table 1. Components of oil yield

Fresh fruit bunch yield components:		
a. Palm	—	{ number of bunches weight per bunch
Within bunch components (bunch quality characteristics)		
b. Bunch	—	{ fruits empty spikelets and stalk mesocarp
c. Fruit	—	{ shell kernel
d. Mesocarp	—	{ oil fibre moisture
e. Kernel	—	{ oil residue moisture

Data on all these parameters are collected in the breeding programme. Each palm is recorded for its fresh fruit bunch yield characteristics namely, total fresh weight of fruit bunches, bunch production per year and weight per bunch. This is carried out at regular intervals of 7 to 10 days throughout the year during harvesting of the palms. Recording of these fruit bunch yield characteristics normally commences during the 3rd to 4th year after the palms have been planted into the field and is normally continued for 5 years thereafter. The oil palm will continue to produce crop for the next 30 years or so, and the validity of this partial recording has therefore been examined and found to be satisfactory. Obviously, the precision could be improved if the period of recording were extended but this would also lengthen the generation interval.

For determination of the other components of oil yield (frequently referred to as bunch quality characteristics) a procedure termed as bunch analysis has been developed (Blaak 1963). Bunches are sampled from the palm during the 4th and 5th year of yield recording for this purpose. From this bunch analysis procedure, information is obtained on the percentages of fruit to bunch, mesocarp to fruit, shell to fruit, kernel to fruit, oil to mesocarp, fibre to mesocarp, moisture to mesocarp, and oil to kernel.

While data are collected on all these parameters, it is obviously not possible to give equal priority to all these parameters or in fact, even desirable, considering that the selection efficiency can be expected to be reduced as the number of parameters to be selected for are increased. Particular attention is focused on only certain of these components and the criteria used depend on

- i) the heritability of these characteristics
- ii) the relationship between these characteristics
- and iii) their contribution to increased oil yield.

Various studies have been carried out to obtain this information for the breeding populations currently in use in Malaysia and the current status with regard to knowledge on these is briefly summarized in the following sections.

a) Variation in fresh fruit bunch yield components

Two sub-components, namely, mean bunch production per palm (normally expressed on an annual basis) and mean weight per bunch constitute fresh fruit bunch yield (ffb per palm per year).

These parameters have been subjected to fairly extensive genetic studies. Some of the more recent information is summarized in Table 2. Data from similar studies in W. Africa have been included for comparison.

Table 2. Heritability estimates for fresh fruit bunch yield components

	Malaysia		W. Africa	
Bunch weight	0.18*	0.09**	0.51***	0.50****
Bunch number	0.25	0.23	0.21	0.13

Source: * Ooi S. C. et. al. (1973), ** Thomas. R. L. et. al. (1969),

*** Van der Vossen, H. AM (1974), **** Meunier, J. et. al. (1970)

The inflorescences are borne in the axils of the leaves and the rate of leaf production therefore represents the theoretical upper limit for the number of female inflorescences and consequently the number of fruit bunches that can be produced. In practice however, bunch production seldom reaches anywhere close to this level, due to the leaf axils occasionally bearing male inflorescences, and failure of initiated inflorescences to reach anthesis or maturity. Typically, the oil palm can produce between 20 to 30 leaves per year but bunch production seldom exceeds 15 bunches per year (Gray, 1969). However, considerable variation exists in

the number of bunches produced by the palm. For instance, in one progeny trial, the variation in bunch number ranged from 5 bunches to 18 or more bunches per palm per year. However, as suggested by the data from Table 2, most of this variation appears to be attributable to environmental and non-additive genetic causes.

Similarly, while considerable variation exists in the mean weight per bunch, this variation is also largely due to environmental and non-additive genetic reasons.

Frequently in selecting for fresh fruit bunch yield components, oil palm breeders are faced with the decision of whether to select for high bunch production or high weight per bunch. The relative merits of maximising for one against the other have not been established but considering the relatively low levels of heritable variation present for both these components, there is really very little to choose from between the two parameters. Nevertheless, it is clear from the relatively high negative correlation between these two parameters that it will not be possible to maximise for both in the individual. (Ooi et. al. 1973, loc. cit.; Van der Vossen, 1974, loc. cit). However, convenient arrangement exists in oil palm breeding, as described later, whereby each characteristic may be selected for in separate lines for final combination in the production and multiplication of the planting material.

b) Variation within bunch components (bunch quality characteristics)

The oil yield per bunch is a function of the level of fruit set in the bunch, the mesocarp and kernel content of the fruit and the oil content of the mesocarp and kernel.

i) **Level of fruit set:** The level of fruit set in the bunch can obviously be an important factor influencing the oil content in the bunch. However, genetic studies based on the percentage of fruit to bunch indicate the absence of heritable variation for this characteristic for the breeding populations currently used in Malaysia that were examined (Ooi, 1975a) although the studies in W. Africa on different breeding populations indicate fairly high heritability values for this characteristic (Van der Vossen, 1974, loc. cit.).

The absence of heritable variation for this characteristic may be partly explained by the relatively uniform nature of the breeding populations used in Malaysia and perhaps also by the fact that the percentage of fruit to bunch needs not necessarily reflect the full changes in the actual level of fruit set. The latter situation arises largely because the percentage of fruit to bunch is determined on a weight basis. Since increased fruit set may result in reduced individual fruit weight, the fruit to bunch percentage may remain the same or be altered only slightly while the actual number of fruits which is set may actually have changed more drastically.

Table 3. Pattern of fruit set in the bunch

	Regions within the bunch		
	Basal	Middle	Apical
Mean number of flowers per spikelet	25.03	26.92	16.18
Mean number of fruits per spikelet	2.64	7.07	6.18
Percentage fruit set	10.56	26.27	40.23

Source: Ooi & Tam, (1975)

A study carried out to examine the level of fruit set within the bunch (Ooi & Tam, 1975) reveals that only a relatively low proportion, less than 25%, of the flowers eventually develops into fruits (Table 3). There appears therefore to be good scope for increasing oil yield per bunch through improvement of the fruit set, but there is a need to develop appropriate selection criteria and this will be discussed in a later section.

ii) **Mesocarp and kernel content:** The next major factor which can influence the oil yield in the bunch is the mesocarp and kernel content of the fruit.

The mesocarp content is measured on the fresh weight and dry weight basis. Particular

emphasis is given to this parameter in the selection programme. Estimates of heritability (Table 4) indicate that this is most appropriate as the level of heritable variation for dry mesocarp to fruit (%) appears to be fairly good. In this particular study, no heritable variation could be detected for the percentage of wet mesocarp to fruit and this is unexpected as both parameters are highly correlated. The possibility of moisture interfering with the estimates was considered but could not be confirmed.

Table 4. Heritability estimates for mesocarp content

	Malaysia	W. Africa
Fresh mesocarp/fruit (%)	absent *	0.80–1.0 **
Dry mesocarp/fruit (%)	0.31	not available

Source: * Ooi, (1975a.), ** Van der Vossen, (1974).

At the same time as direct selection is carried out on the mesocarp content, attention is also given to reducing the shell content, thus increasing the economic value of each fruit. It has been established (Beirnaert & Vanderweyen, 1941) that the presence of the shell in the fruit is determined at single loci and as described later, this factor is fully exploited in the oil palm breeding programmes. However, sufficient variation in shell thickness exists within each genotype to suggest that perhaps modifier genes are present to permit further reduction in shell content. Genetic studies which were carried out (Ooi, 1975a, loc. cit.), however, failed to detect any genetic variation for shell content determined on a weight basis. This may partly be explained by the fact that fluctuations in the percentage of shell to fruit can arise from changes in the nut size as well as in the thickness of the shell. This was in fact demonstrated in the same study where, when the percentage of shell to nut was adjusted for variable nut size, significant heritable variation was detected.

Some variation in the kernel content exists but most of this variation appears to be largely environmental in origin and thus does not allow for any selection progress.

iii) Oil content: The final characteristic contributing to changes in the oil yield per bunch is the oil content of the mesocarp and kernel. No data are collected on the oil content of the kernel and therefore, they are not considered at all in the selection programme.

Table 5. Heritability estimates for oil content

	Malaysia	W. Africa
Oil / fresh mesocarp (%)	0.48 *	0.20 **
Oil / dry mesocarp (%)	0.30	Not available

Source: * Ooi (1975a), ** Van der Vossen (1974)

Insofar as the oil content of the mesocarp is concerned, fairly high levels of heritable variation are present (Table 5) and in all programmes, are given particular emphasis.

c) Relationship between yield components

So far, each of the characteristics has been considered individually, but clearly, the relationship between the various characteristics is of importance in determining the breeding method. Studies carried out (Ooi, et. al 1973, loc. cit; Ooi, 1975a, loc. cit) indicate the following relationships,

- strong negative correlation between bunch production and mean weight per bunch
- negative relationship between fruit to bunch percentage and average fruit weight

- positive relationship between fruit weight and percentage of mesocarp to fruit
- no relationship between oil content of mesocarp and other characteristics.

2) Selection and breeding method

It was established in 1941 by Beirnaert and Vanderweyen that the presence of shell in the oil palm fruit is inherited in a simple Mendelian manner. The material normally referred to as the "Dura" type is homozygous for presence of shell while the "Pisifera" type is homozygous for absence of shell. The F_1 hybrid between these two genotypes results in the "Tenera" type which has shell of intermediate thickness.

This factor has been fully exploited by oil palm breeders and all current breeding programmes are aimed at the production of "Tenera" type material for planting. The reason for this is obvious when we refer to Table 6. With the reduction in shell content, there is a corresponding increase in the mesocarp content of the fruit and since other components remain the same, the oil yield per bunch is improved quite substantially. In fact, an equivalent planting of "Tenera" type material is capable of giving an oil yield of some 25% to 30% more than that from the "Dura" type planting.

Instead of breeding for the intermediate shell type, i.e. "Tenera", it would seem more logical to use the "Pisifera" type since the latter is completely shell-less. The "Pisifera" is however, generally female sterile in that the female inflorescences do not develop to maturity or are only partially fertile. Even in the latter case, where the inflorescence may develop to maturity, the level of fruit set is usually very low and despite the advantage of a higher mesocarp to fruit content of 90% or more, the oil to bunch percentage seldom exceeds that for a tenera bunch. Some attempt however, has been made to breed for improved fertility in the "Pisifera" (Tang, 1971) and some success has been achieved in this direction.

While all breeding programmes at present are aimed at the production of "Tenera" type material, the exact breeding method differs, particularly between the breeding programmes of Malaysia and West Africa.

The breeding methods adopted for the different oil palm breeding programmes in Malaysia are generally similar except perhaps only with respect to the emphasis that is given to the various yield components.

The production of "Tenera" type planting material depends on the mating between "Dura" and "Pisifera" parents. The "Dura" parents and the "Pisifera" parents are largely maintained and selected for in independent lines. This procedure has been adopted largely to minimise the risk of inbreeding within the breeding populations. This is because the oil palm, which is a natural outbreeder, suffers from yield depressions as a result of inbreeding (Gascon, et. al., 1969; Hardon, 1970).

The selection of "Dura" parents is based on family and individual phenotypic values. Superior families are selected on the basis of fresh fruit bunch yield and its components, namely mean bunch production and mean weight per bunch, the assumption being that these characteristics, in having low heritabilities, would be more effectively selected for on this basis. Individuals are then selected from these superior families on the basis of the bunch quality characteristics i.e. percentage of mesocarp to fruit, shell to fruit, and oil to mesocarp. Attention is also given to the other characteristics, e.g. percentage of fruit to bunch, to ensure that these are at reasonable levels. Although this latter characteristic has a low heritability value it is correlated with the other parameters e.g. mesocarp to fruit percentage and thus may be expected to have an effect on the phenotypic value of these characteristics.

The "Pisifera" parents, being sterile, are normally bred from "Tenera" individuals. The selection of "Tenera" individuals follows that adopted for "Dura" selection. The selection of the "Pisifera" individuals, because of sterility or partial fertility, remains a difficult problem as no yield data on the palms can be collected. The selection of "Pisifera" parents is therefore dependent on actual test crosses with selected "Dura" parents, a procedure normally referred to as progeny testing. The testing is usually carried out by the top cross selection method

i.e. each "Pisifera" individual is mated with several "Dura" parents and the mean performance over all the crosses is taken as a measure of the breeding value of the "Pisifera". This method is clearly intended to exploit general combining ability and one which fits into the present method of seed production. All oil palms are currently grown from seed, and because of the large demand for seeds, no possibility exists for seed production to be confined only to those crosses which have actually been evaluated. The normal procedure would be to select "Dura" and "Pisifera" parents independently and any selected "Dura" parent would then be used in combination with any available selected "Pisifera" parent.

As indicated earlier, several of the yield components are correlated e.g. between bunch production and mean weight per bunch. When two characters are highly correlated negatively, it is clearly not possible to maximise for both in some individual except perhaps through severe selection pressure over several generations, a procedure which in the oil palm, is clearly not practical. The present method of oil palm breeding can conveniently overcome this to some extent as it allows for some characteristics to be emphasised in the "Dura" lines while others are emphasised in the "Tenera" lines.

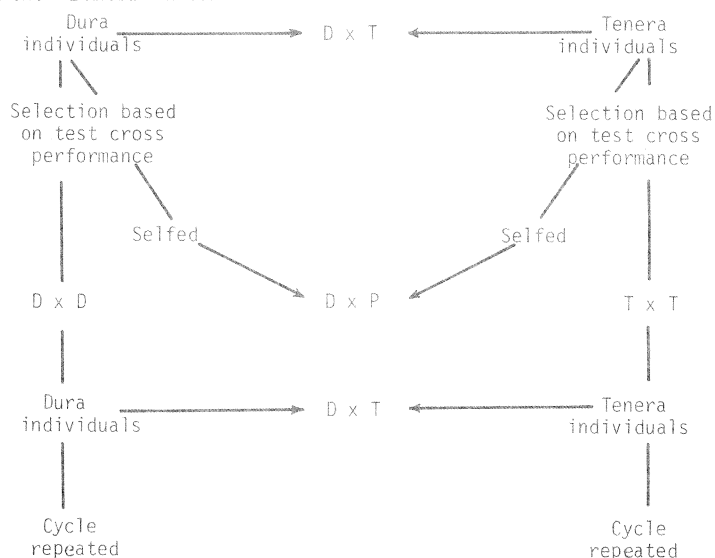


Fig. 1. Reciprocal recurrent selection for oil palm breeding (Meunier & Gascon, 1971).

As mentioned earlier, a different method of selection is adopted in some of the oil palm breeding programmes in West Africa, based on reciprocal recurrent selection method (Meunier and Gascon, 1971). The method is summarised in Figure 1. In this programme, the selection of "Dura" and "Tenera" parents is based on the test cross performance. The method would appear to be fairly effective in exploiting for specific combining ability but to what extent it is appropriate to maximise for general combining ability remains in doubt. Other criticism as to its suitability for oil palm breeding has also been raised (Hardon & Ooi, 1971) centered around the following aspects;

- a. limited number of individuals that can be tested
- b. no reason to assume that the selfed individuals will combine in the same manner as the parents in view of the role of specific combining ability.
- c. the long generation interval of oil palm of 10 years
- d. the limited number of seeds that can be produced.

3) Multiplication of planting material

All oil palms are currently raised from seed. The production and multiplication of seed

is carried out by hand pollination under very carefully controlled conditions so that only seeds of the desired combination are produced.

In the breeding programme, since only a few individuals are selected for producing the next generation of individuals for further selection, only the best need to be selected. On the other hand, for the actual production of seed, because of the large quantity of seeds required to be produced, the selection pressure cannot be so severe. Frequently, only minimum standards are set. Typical standards which are considered acceptable for selection as seed parents are summarised in Table 6.

Table 6. Typical bunch composition of Dura and Tenera type palms

		Dura	Tenera
Fruit to bunch	(%)	60	60
Mesocarp to fruit	(%)	60–65	75–85
Shell to fruit	(%)	25–30	8–15
Oil to mesocarp	(%)	50	50
Oil to bunch	(%)	18–19.5	22.5–25.5

4) Future prospects

The oil palm in Malaysia can yield well in excess of 5 tons of palm oil and 0.5 ton of palm kernel oil per hectare per year. At this level of productivity, the oil palm is by far the most efficient producer of vegetable oil per unit land area.

Systematic efforts to improve oil yields have been in progress for nearly 50 years in Malaysia but it is difficult to assess the actual improvements that have been brought about by breeding alone, because, during the same period, marked improvements in agronomic practices were also apparent. Nevertheless, it is clear that at least with the switch over from "Dura" type material to "Tenera" type materials during the early sixties, the oil yield would have been improved by at least 25%.

Although much progress has been achieved, oil palm breeders are still confident that the yield potential of the oil palm can be raised even further. This is based on expected developments in the following areas.

Firstly, it is clear that one of the constraints to further improvement is the fact that the level of heritable variation present for most of the parameters of interest is limited (Thomas, et. al. 1969; Ooi, et. al. 1974 loc. cit; Ooi, 1975b. loc. cit.). This is largely because the breeding populations currently in use have a very narrow genetic base i.e. derived from only a limited number of individuals. For instance, the "Deli Dura" population which forms the main source of "Dura" parents is derived from an introduction of 4 palms to Bogor Botanical Gardens, Indonesia in 1848 (Jagoe, 1952a; Hardon & Thomas 1968). As a result of inbreeding and selection under restricted population size, most of the heritable variation, particularly with respect to fresh fruit bunch yield and its components, appears to have been exhausted. Similarly, the "Pisifera" parents currently in use can also be traced to a small number of individuals (selected from natural oil palm groves) in the breeding programmes of West Africa particularly that of the INEAC programme of Zaire (Hartley, 1967). Steps to rectify this situation have already been taken. For example, the Malaysia Agricultural Research and Development Institute (MARDI) in collaboration with the Nigerian Institute for Oil Palm Research (NIFOR) undertook a large scale effort to collect oil palm genetic materials from natural oil palm groves in Nigeria (Arasu and Rajanaidu, 1976). These materials are currently being examined, and it is hoped that these natural populations will be able to yield new sources of variation for yield and other characteristics which, at present, cannot be obtained from the existing populations. The extent to which the genetic variability can be enhanced is apparent from a study (Ooi, 1975b) of

one population which was derived by outcrossing the "Deli Dura" population to an introduction from W. Africa. Heritability values for bunch yield components, which previously could not be detected, now reached very high levels.

Secondly, all oil palm plantings are established from seed. If we examine a particular progeny or family, the variation in yield between the individuals of the same progeny can be quite substantial, e.g. from 100 kgs. per palm per year to 300 kgs. per palm per year. Clearly, part of this variability is environmental but it is not unlikely that genetic differences play a part. If the palm with the yield of 300 kgs can be reproduced exactly, yield improvement will be quite substantial and oil yields of 10 tons per hectare per year would not be unexpected. Research is currently at hand to develop vegetative methods of propagation by tissue culture (Ong, 1973; Corley et. al 1976) and the results obtained so far are encouraging.

Thirdly, all the breeding efforts have so far been concerned with raising the yield potential of the individual palm. Yield can obviously also be increased by increasing the number of palms per unit area. If this is to be achieved, the approach and selection criteria will need to be different, i.e. to deliberately select for palms which would tolerate a higher density of planting. Studies have been carried out to examine the effect of density on oil palm dry matter production (Corley, 1972) and the relationship is shown in Figure 2.

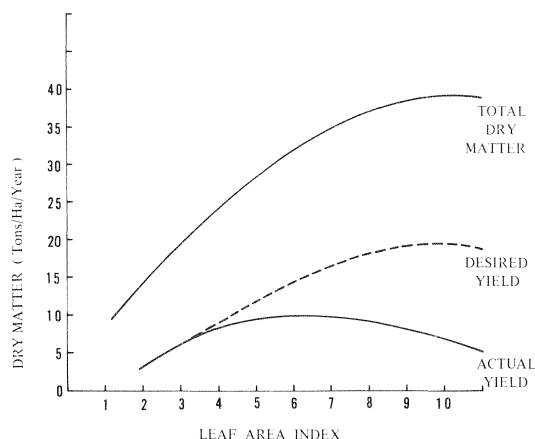


Fig. 2. Relationship between density and total dry matter production and yield (Corley, 1972).

For the present breeding materials, the fruit bunch yield reaches a maximum at a Leaf Area Index of 6 while total dry matter production is maximum at a Leaf Area Index of 8 to 10. At this point, the total dry matter production reaches a level of 40 tons per hectare per year while yield accounts for less than 25% of the total dry matter produced. Clearly, if the proportion of the total dry matter for yield can be raised to 50%, bunch yield equivalent to 10 tons of oil per hectare per year can be expected.

The problem however, remains on the type of selection criteria suitable for breeding such a palm. Two possibilities have been proposed, one based on partitioning of dry matter production or Bunch Index (Corley, et. al. 1971) and the other on the basis of the response to severe frond removal (Corley, 1976). Both possibilities have not been evaluated but genetic studies (Hardon, et. al. 1972) suggest that these parameters are under genetic control although again, the extent of the genetic variability present for these parameters in the breeding populations is unfortunately limited (Ooi, 1977, in press). Nevertheless, these alternative selection criteria are considered to hold considerable promise and hopefully, sources of genetic variability will be available from the germplasm collections to make the breeding of this new plant type possible.

Fourthly, possibilities exist for further improving the selection criteria whereby better response can be achieved from the selection efforts. This is particularly so for the within bunch components (bunch quality characteristics) of oil yield. It is suggested that more effective response can be expected if the selection pressure is exerted on the factor (or factors) responsible for the greatest change in the mean value of the desired component instead of the component itself. This may well be illustrated by the case of the fruit to bunch percentage. As indicated earlier, the fruit to bunch percentage is an important component of oil yield per bunch. A study carried out to examine the actual level of fruit set in the bunch (Ooi & Tam, 1975) reveals the relatively low proportion of flowers (less than 25%) which eventually develop into fruits (Table 3). The scope is therefore good for increasing the level of fruit set further and thereby the oil yield. However, difficulties may exist in attempting to select directly for a higher level of fruit set. Apart from the practical difficulties of collecting data on fruit set, this characteristic can also be expected to be subjected to a considerable degree of environmental fluctuation, one of the most important being the uneven distribution of pollen reaching the individual female inflorescences. Furthermore, it is apparent from Table 3, that greater improvements are possible within certain regions of the bunch than in others.

An alternative and perhaps more promising approach would be to identify and select for those bunch characteristics which would contribute to a more complete pollination of the bunch. For instance, it is of interest to note from Table 3 that the spikelets in the basal regions of the bunch are especially low in their level of fruit set. This is largely because the basal regions of the bunch are normally embedded in the frond base, making it difficult for pollination to occur. Clearly, the level of fruit set can be improved if selection can be carried out to provide for a longer bunch stalk so that the whole female inflorescence would become more fully exposed for pollination. It has also been suggested (C. Teo, 1975, unpublished) that the low level of fruit set in the bunch may be due in part to the tight packing of the spikelets in the bunch, reducing access of the pollen to the flowers at the base of the spikelets. Some gain in fruit set could therefore be achieved if greater spacing could be provided for in between the spikelets.

Similarly, in attempting to improve the mesocarp content, attention could, more beneficially, be given to selecting for greater fruit size. This is because it is quite clear from the correlation studies that changes in fruit size will give rise to proportionally greater changes in the mesocarp content than in the other components. This will also avoid problems of displacement of the kernel content which the selection for high mesocarp to fruit percentage can result in.

2. Improvement of oil characteristics

Palm oil is a semi-solid liquid at room temperature. For this reason, it is not directly suitable for use as cooking oil which requires the oil to be uniformly liquid at room temperature. With the development of fractionation techniques, palm oil can now be separated into several fractions, the two main being:

- liquid, "olein" fraction with a low cloud point
- solid, "stearin" fraction with a high melting point.

It is normally possible to recover up to 70% of palm oil as "olein" fraction and 30% as "stearin" fraction. The "olein" fraction can be marketed directly for blending in liquid cooking oils and other uses, and fetches a price higher than that for crude palm oil. The "stearin" fraction, on the other hand, is difficult to market and fetches a lower price than that for crude palm oil. The yield of the "olein" fraction can therefore be an important economic factor.

Another important economic factor is the nature of the fatty acids present in the oil. With the present concern on the health hazards of the consumption of saturated fats and oils, oils which are highly unsaturated are favoured for use in edible purposes. Palm oil has approximately equal proportions of saturated and unsaturated fatty acids and it has been suggested that palm oil could possibly be used in higher proportions in margarine blends if its level of unsaturation were higher.

All the breeding effort is, at present, concerned primarily with raising the level of unsaturation in palm oil, but since the proportion of liquid "olein" fraction that can be recovered is partly related to the level of unsaturated fatty acids, a corresponding improvement in the "olein" fraction may be expected from the same breeding programme.

The present method of breeding for a higher level of unsaturated fatty acid involves intercrossing the present oil palm species, *E. guineensis* with another oil palm species *E. oleifera*. Although some variation exists within the species, *E. guineensis*, as shown by Noiret and Wuidart (1976), the range in fatty acid composition is nevertheless, limited. While differences in the fatty acid composition within the species can usefully be exploited, it is very doubtful that selection within the species alone could result in much improvement in the level of unsaturated fatty acids. The other species, *E. oleifera*, on the other hand, produces an oil which is highly unsaturated but it is extremely low yielding and as such, cannot be directly used for commercial exploitation.

The two species, fortunately, hybridise and produce fertile offsprings (Hardon & Tan, 1969; Obasola, 1973). It is from these hybrids that the desired combination of oil yield and oil characteristics is likely to be achieved and a fairly extensive hybrid programme is now under way in Malaysia, West Africa and South America (Meunier, et. al., 1976; Obasola, et. al., 1976; Tam, et. al., 1976).

In Malaysia, the earliest *E. oleifera* (a single palm) was introduced and planted at the Dept. of Agriculture gardens, Kuala Lumpur, during the early 1950's. Subsequently, crosses were made to this particular palm and it is from studies on the progenies derived from these crosses that most of the current knowledge on the behaviour of the hybrids in Malaysia is known.

The difference in levels of unsaturated fatty acids between *E. guineensis* and *E. oleifera* is apparent from Table 7. The F_1 hybrid between the two species produces an oil which is approximately intermediate between the parents, with respect to the composition of the fatty acids. The backcross progenies, as expected, tend to have an oil composition which resembles more that of the recurrent parent. The F_2 generation is intermediate in the oil characteristics between the two types of backcross generations. As expected, the backcross and F_2 generations show a greater degree of variability (values of the standard deviation are given in the brackets) than either the parents or the F_1 hybrids.

Table 7. Fatty acid composition* of *E. guineensis*, *E. oleifera* and hybrids

Fatty acid Composition		<i>E. guineensis</i>	<i>E. oleifera</i>	F_1 hybrid	$F_1 \times$ <i>E. guineensis</i>	$F_1 \times$ <i>E. oleifera</i>	$F_1 \times F_1$
Lauric	(C12)	—	0.2 (0.4)	—	—	—	—
Myristic	(C14)	0.6 (0.1)	0.1 (0.2)	0.3 (0.1)	0.2 (0.1)	0.3 (0.3)	0.5 (0.2)
Palmitic	(C16)	49.2 (1.3)	21.2 (3.1)	41.2 (2.0)	40.0 (3.6)	33.0 (6.7)	35.3 (5.6)
Oleopalmitic	(C16:1)	—	0.8 (0.2)	—	—	0.4 (0.4)	0.1 (0.1)
Stearic	(C18)	2.2 (0.5)	1.5 (0.4)	1.5 (0.3)	3.0 (1.4)	1.4 (0.6)	2.7 (0.8)
Oleic	(C18:1)	40.2 (0.6)	57.9 (5.9)	47.8 (2.0)	46.5 (4.1)	54.1 (5.7)	49.5 (6.0)
Linoleic	(C18:2)	7.8 (0.7)	19.2 (2.8)	9.2 (0.9)	10.3 (1.6)	10.8 (2.6)	11.7 (2.2)
% Unsaturation		48.0 (0.9)	77.9 (3.8)	57.0 (2.0)	56.8 (3.6)	65.3 (7.5)	61.3 (6.4)

* Values in brackets give the standard deviation. Source: Tam, et. al. (1976)

It thus appears very simple to raise the level of unsaturation in the oil through recurrent backcrossing to the *E. oleifera* parent but as seen from Table 8, this can also lead to a decline in the oil yield per bunch because it is accompanied by most of the undesirable characteristics of this species. *E. oleifera* has an extremely low oil yield per bunch, 4% as compared to 23.3% for an average *E. guineensis* (Tenera type) material currently grown commercially for oil

production. The low oil value can be attributed to the poor mesocarp (very thick shelled) content of the fruit and the low oil content of the mesocarp. The F_1 hybrid results in a considerable improvement in the oil yield as both the mesocarp and oil content are increased quite substantially. This is improved even further in the backcross to the *E. guineensis* parent. It should be noted however that the phenotypic value of the F_1 and backcross generation with respect to the fruit characteristics is dependent on the type of *E. guineensis* parent that is used, i.e. whether of "Pisifera", "Dura" or "Tenera" type. Hybrids of *E. oleifera* with "Pisifera" type parents tend to give a markedly thinner shell and a higher mesocarp content than those with "Dura" type parents. The data presented in Table 8 are based on crosses in which the *E. guineensis* parents are all of the "Pisifera" type and in view of its desired effect on the fruit characteristics, will most likely be the source of *E. guineensis* parents in all hybrid programmes.

Table 8. Bunch composition* of *E. guineensis*, *E. oleifera* and hybrids

Bunch Components		<i>E. guineensis</i> (Tenera)	<i>E. oleifera</i>	F_1 hybrid	$F_1 \times$ <i>E. guineensis</i>	$F_1 \times$ <i>E. oleifera</i>	$F_1 \times F_1$
Fertile fruit/bunch (%)		55.6 (6.1)	20.7 (6.3)	12.5 (5.5)	41.4 (10.2)	33.2 (18.5)	26.6 (9.6)
Parthenocarpic fruit/bunch (%)		4.2 (3.1)	22.3 (5.2)	31.4 (8.6)	5.8 (4.0)	20.7 (4.3)	24.6 (8.7)
Mesocarp/fruit (%)**		80.2 (4.3)	41.4 (11.9)	73.9 (4.8)	75.0 (9.4)	47.3 (19.1)	49.9 (5.0)
Shell/fruit (%)**		10.2 (2.1)	42.2 (8.4)	18.9 (3.5)	15.0 (6.6)	33.2 (13.5)	39.7 (4.1)
Oil/W. mesocarp (%)**		49.6 (3.3)	19.8 (5.8)	41.2 (7.1)	46 (6.4)	35.3 (17.7)	39.6 (5.0)
Oil/Bunch (%)		23.3	4.0	13.3	15.8	9.4	12.4

* Values in brackets give the standard deviation, ** Fertile fruits only. Source: Tam, et. al. (1976)

The pattern of inheritance of the within bunch characteristics is similar to that for the oil characteristics. The phenotypic value of the F_1 progenies falls in between the two parents for most of the fruit characteristics. The backcrossed progenies tend towards the recurrent parent while the F_2 generation is somewhat intermediate between the values for the two backcrossed generations. The consequence of this in respect of the oil yield per bunch is that it is intermediate between the parents for the F_1 hybrids and improves with the backcross to *E. guineensis* but declines with that to *E. oleifera*. It is of interest to note that as was the case previously, the backcrossed and F_2 progenies show a relatively greater degree of variation.

The results obtained so far would suggest that the best immediate possibility of breeding for the desired oil characteristics and oil yield lies within the F_1 hybrids. One obvious advantage is the highly uniform nature of the F_1 population. Backcrossed generations appear to be limited by the fact that any attempt to improve the fruit characteristics and thereby the oil yield results in a deterioration in the oil characteristics and vice-versa. Furthermore, it is doubtful whether improvements in the fruit characteristics alone can contribute much to improvement in the oil yield because the fertilised fruits form only a small proportion of the fully developed fruits. The proportion of parthenocarpic fruits (which are similar in size to the fertilised fruits) can be quite considerable. This is a characteristic acquired from the *E. oleifera* parents and because of the absence of a fully developed nut, the parthenocarpic fruits contain a higher mesocarp content than the fertilised fruits. Therefore, better scope exists in breeding for a higher level of parthenocarpic fruits in the bunch as a means of improving the oil yield per bunch.

Data are available on the fresh fruit bunch yield only for the F_1 hybrids, and the data suggest that this is comparable to that for an average *E. guineensis* stand (Rajaratnam, 1974). The F_1 hybrids appear to hold a very good scope for breeding for the desired oil characteristic

especially, when we consider that the present data are based on a single *E. oleifera* palm which was never selected, either, for good oil characteristics or for high oil yield. It can be expected therefore, that if more *E. oleifera* genetic materials are examined and evaluated against a wide range of *E. guineensis*, progenies with good oil characteristics and higher oil yield will soon be forthcoming. In fact, in one of the crosses recently evaluated, a hybrid progeny with good oil characteristics and oil yield per bunch of 30% was recorded (Ramachandran, personal communication). This is a very good oil yield indeed, and one which exceeds even most *E. guineensis* progenies.

While the F_1 hybrids offer immediate prospects of producing seeds for commercial exploitation, the backcross and F_2 progenies cannot be ignored because, as a result of recombination, individuals with both high oil yield and good oil characteristics are apparent within the progenies. If vegetative methods of propagation become available, there should be little difficulty in multiplying such individuals. Alternatively, these individuals could, obviously, also form parents for future combinations.

Apart from the obvious advantage of the oil characteristics, the hybrids also possess other desirable attributes e.g. disease resistance (Meunier, et. al. 1976, loc. cit.) and reduced height increment (Obasola, et. al., 1976, loc. cit.). With all these advantages, there is little need to emphasize the importance of the hybrid programme in oil palm breeding and considerable attention is now being given to introducing new sources of *E. oleifera* genetic materials and to evaluating them in combinations with the various *E. guineensis* parents that are currently available. There is obviously also a need to obtain a better understanding of the combining ability between the two species, so that the selection of individuals for evaluation can be made on a more systematic basis and thus increase the probability of obtaining the desired combinations in the progenies.

3. Reduction in stem height increment

Although the oil palm can grow and produce crop for up to 150 years or more, its economic life span is only 30 years or so. The main reason for this limited life span, is the decline in the productivity of the palms while, because of the rapid increase in the height of the palms, harvesting becomes more difficult and costly. With increasing labour costs, the prospects of breeding for reduced height increment become very attractive.

Two possibilities exist in the breeding for reduced stem height increment. Within the *E. guineensis* species, a mutant has been identified, which has a height increment of approximately half of that for normal palms (Jagoe, 1935b). This mutant type breeds true and the F_1 hybrid is approximately intermediate between the mutant parent and the tall parent. The "mutant" type however, has a poorer oil yield, due largely to the poorer fruit set within the bunch and to the poorer fruit characteristics. Some attention is being given to improving the yield characteristics while, at the same time, retaining the useful height properties.

The second possibility lies in the hybrid crosses with *E. oleifera* (Obasola et. al., 1976, loc. cit.) which also possess a much reduced height increment. Considering the other advantages of the hybrid, this line of approach would appear to be more attractive.

4. Breeding for disease resistance

Malaysia is fortunate in having few diseases of economic importance, and considering the long generation interval of 10 years for oil palms, breeding for disease resistance is to a large extent, neglected. A small effort is being made to develop a screening method (at the seedling stage) for resistance against *Ganoderma*, the main disease of some importance, but as yet, the technique has not reached a satisfactory level for application (C.F. Loh, personal communication).

The hybrid with *E. oleifera* appears to offer some resistance to the disease (Moktar, 1968) and studies are being conducted to confirm this possibility.

Summary

Oil palm breeding in Malaysia is carried out with the objective of improving oil yield, oil characteristics, and to a lesser extent, reduced stem height increment and disease resistance. The method of oil palm breeding currently used is described. Future trends and possible developments are also discussed.

Acknowledgement

The author is grateful to the Director-General of MARDI for permission to present the paper.

References

1. ARASU, N. T. & RAJANAIDU, N. (1976). Oil palm genetic resources, *Mal. Int. Oil Palm Agric. Conf.*, Kuala Lumpur.
2. BEIRNAERT, A. & VANDERWEYEN, R. (1941). Contribution a l'étude génétique et biometrique des variétés d' *Elaeis guineensis*. *Publ. Inst. Nat. Etud. Agron. Congo-Belge*. Série Scientifique 27, 101.
3. BLAAK, G., (1963). Breeding and inheritance of the oil palm. II. Methods of bunch analysis. *J. West Afr. Inst. Oil Palm Res.* 4, 146.
4. CORLEY, R. H. V., HARDON, J. J. & TAN, G. Y. (1971). Analysis of growth in the oil palm (*E. guineensis*, Jacq) I. Estimation of growth parameters and application in breeding. *Euphytica* 20, 304.
5. CORLEY, R. H. V. (1972). Oil palm physiology - a review. *Third Incorporate Soc. of Planters Conf.* Kuala Lumpur.
6. ——— (1976). Effects of severe pruning on oil palm and its possible use for selection purpose. *MARDI Res. Bull.* 4, (2), 23.
7. CORLEY, R. H. V., BARRET, J. N. & JONES, L. H. (1976). Vegetative propagation of oil palm via tissue culture. *Mal. Int. Oil Palm Agric. Conf.*, Kuala Lumpur.
8. GASCON, J. P., NOIRET, J. M. & MEUNIER (1969). Effects de la consanguinité chez *Elaeis guineensis* Jacq. *Oleagineux* 24, 603.
9. 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, Univ. of Aberdeen.
10. HARDON, J. J. & THOMAS, R. L. (1968). Breeding and selection of oil palms in Malaya. *Oleagineux* 23, 85.
11. HARDON, J. J. & TAN, G. Y. (1969). Interspecific hybrids in the genus *Elaeis*. I. Crossability, Cytogenetics and Fertility of F₁ hybrids of *E. guineensis* x *E. oleifera*. *Euphytica* 18, 372.
12. HARDON, J. J. & OOI, S. C. (1971). To what extent should inbreeding be avoided in oil palm seed production. *Chemara Communications* 9.
13. HARDON, J. J., CORLEY, R. H. V. & 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.
14. HARTLEY, C. W. S. (1970). *The Oil Palms*. Longman, Lond.
15. HUTCHINSON, J. (1934). *The families of the flowering plant. II. Monocotyledons*. Macmillan. Lond.
16. JAGOE, R. B. (1952b). Deli oil palms and early introductions of *Elaeis guineensis* to Malaya; *Mal. Agric. J.* 35, 3.
17. ——— (1952). The "dumpy" oil palm. *Mal. Agric. J.* 35, 12.
18. MEUNIER, J. & GASCON, J. P. (1971). General scheme for oil palm improvement at IRHO. *Oleagineux* 26, 1.
19. MEUNIER, J., VALLEJO, G. & BOUTIN, D. (1976). *E. melanococca* x *E. guineensis*

- hybrid and its improvement. *Oleagineux* **31**, 519.
20. MOORE, H. E. (1961). Botany and classification of palms. *Amer. Hort. Magazine* **40**, 17.
 21. NOIRET, J. M. & WUIDART, W. (1976). Possibilities for improving the fatty acid composition of palm oil - results and prospects. *Oleagineux* **31**, 465.
 22. OBASOLA, C. O. (1973). Breeding for short stemmed oil palm in Nigeria. I. Pollination, compatibility, varietal segregation, bunch quality and yield of F₁ hybrids *Grozo oleifera* x *Elaeis guineensis*. *J. Nig. Inst. Oil Palm Res. S.* **18**, 45.
 23. OBASOLA, C. O., OBESAN, I. O. & OPUTE, F. I. (1976). Breeding of short-stemmed oil palm in Nigeria. *Mal. Int. Oil Palm Agric. Conf.* Kuala Lumpur.
 24. ONG, H. T. (1976). Studies into tissue culture of oil palm. *Mal. Int. Oil Palm Agric. Conf.* Kuala Lumpur.
 25. OOI, S. C., HARDON, J. J. & PHANG, S. (1973). Variability in the Deli dura breeding population of the oil palm (*E. guineensis*, Jacq) I. Components of bunch yield. *Mal. Agric. J.* **49**, 11.2
 26. OOI, S. C. (1975a). Variability in the Deli dura breeding population of the oil palm (*E. guineensis*, Jacq) II. Within bunch components of the oil yield. *Mal. Agric. J.* **50**, 20.
 27. ——— (1975b). Variability in the Deli dura breeding population of the oil palm (*E. guineensis* Jacq) III. An outcrossed population. *Mal. Agric. J.* **50**, 147.
 28. ——— (1977). Variability in the Deli dura breeding population of the oil palm (*E. guineensis* Jacq) IV. Vegetative and growth parameters. *Mal. Agric. J.* (In press).
 29. OOI, S. C. & TAM, T. K. (1975). The determination of the within bunch components of oil yield in the oil palm (*E. guineensis*, Jacq) I. Pattern of variation. *MARDI. Res. Bul.* **3** (1), 44.
 30. RAJARATNAM, J. A. (1974). Prospects of planting *E. oleifera* x *E. guineensis* hybrids in Malaysia. *Ann. Rep. Negeri Sembilan Planter's Association*, p. 27.
 31. TAM, T. K., LIM, C. S., YEOH, G. H. & OOI S. C. (1976). The oil and other characteristic of interspecific (*E. guineensis* x *E. oleifera*) hybrids planted in Malaysia and their significance for future breeding programmes. *Mal. Int. Oil Palm Agric. Conf.*, Kuala Lumpur.
 32. TANG, T. L. (1971). The possible use of pisifera in plantations. *Mal. Agric. J.* **48**, 57.
 33. TEO, C. (1975). *MARDI, Oil Palm Ann. Report.* (Unpublished).
 34. TOMLINSON, P. B. (1961). *Anatomy of the monocotyledons. II. Palmae.* Oxford. Land.
 35. Van der Vossen, H. A. M. (1974). Towards more efficient selection for oil yield in the oil palm (*E. guineensis* Jacq). Ph. D. thesis, Univ. of Wageningen.
 36. WESSELS BOER, J. G. (1965). The indigenous palms of Surinam. Ph. D. thesis, Univ. of Utrecht.
 37. ZEVEN, A. C. (1964b). On origin of the oil palms. *Grana. Polynol.* **5**, 121.

Discussion

K. Sakai, Japan: In the plateau present in the curve for yield against leaf area index, could the leaf area index vary depending on environmental conditions?

Answer: It would be correct to say that under different environmental conditions the optimum plant density would be different but given the same genotype the optimum LAI may be approximately the same.

J. T. Carlos, Jr., The Philippines: Under what level of technology do you breed for oil palm?

Answer: The main production input for oil palm cultivation is fertiliser's. No specific attempt is made to breed for response to high fertiliser levels but the selection of oil palms in Malaysia is carried out uniformly under a fairly high fertiliser regime.

N. Yamada, Japan: Regarding the relationship between total dry matter and actual yield shown in fig. 2, I would like to know whether the number of fruit bunches increased parallel to the increase of total dry matter. It seems to me that the number of fruit bunches might increase with the increase of total dry matter because fruit bunches are produced in parallel with the successive development of leaves.

Answer: The number of fruit bunches will increase with total dry matter production only up to a certain level and then decline as the plant competition becomes more severe. The number of leaves produced is not the main determining factor for the number of bunches produced. In fact, even under optimum environmental conditions only about 50% of the leaf axils contain fruit bunches.