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Towards more efficient selection for oil yield in the oil palm (Elaeis guineensis Jacquin)

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Towards more efficient selection for oil yield in the oil palm (Elaeis guineensis Jacquin)

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Abstract

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Detailed studies are made of the variability and heritability of a number of components of oil yield in the oil palm using published data of the breeding programme of the NIFOR in Nigeria and results of a number of experiments carried out at the OPRC in Ghana during the period 1965–1971. Estimations of h_n^2 for oil yield components are presented. Values are very high for some of the fruit quality components. A fairly high negative genetic correlation ($r_A = -0.58$) was found to exist between the two most important components, number of bunches and single bunch weight. Maximum selection progress for increased bunch yield may be obtained by intercrossing widely divergent subpopulations. Experimental evidence is produced of the nature of inheritance of the ratios shell to fruit and mesocarp to fruit in oil palm fruits. Consequently, selection for these components requires considerable revision. The efficiency of determinations of the oil-to-mesocarp ratio, an important oil yield component with a rather low heritability, can be enhanced considerably by applying a modified indirect method based on the fact that the dry fibre-to-mesocarp ratio has a high heritability. The effect of different periods of water stress on bunch yield and its two components, as well as on vegetative growth of the oil palm was investigated. The implications of the results of these studies for oil palm selection are discussed in detail and outlines of a modified breeding programme assuring continued selection progress are given. Essential are (1) the re-establishment of new, genetically highly variable and very divergent subpopulations, (2) the estimation of genotypic values of all components of oil yield from the first 3–4 years of production when the disturbing influence of competition for light between palms is still negligible, (3) information from special plant density-progeny trials about the optimum combination of genotype and spacing in a particular environment, required for a continued high production level beyond the first four years.

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Stellingen

I

Bij de veredeling van de oliepalm wordt nog steeds veel te weinig gebruik gemaakt van de zeer grote idiotypische variabiliteit die aanwezig is in de voor dit gewas belangrijke genencentra in West Afrika.

Dit proefschrift.

II

Antherencultuur als hulpmiddel bij de ontwikkeling van nieuwe rassen van overblijvende tropische zelfbevruchtende cultuurgewassen dient meer aandacht te krijgen dan tot nu toe het geval is geweest.

J. P. Braak, 1972. Landbouwk. Tijdschrift 84: 50-55.

III

Gezien de vrij hoge negatieve genetische correlatie tussen het aantal vruchttrossen en het gemiddeld trosgewicht in de oliepalm, dient al het voor de praktijk bestemde plantmateriaal verkregen te worden door kruising van ouderbomen die zijn geselecteerd uit genetisch zeer uiteenlopende subpopulaties.

Dit proefschrift.

IV

Voor de selectie van de oliepalm zeer waardevol kwantitatief genetisch onderzoek verliest aanzienlijk aan waarde, wanneer het uitgangsmateriaal bestaat uit genetisch zeer enge populaties.

J. J. Hardon, R. H. V. Corley & S. C. Ooi, 1972. Euphytica 21: 257-264.
S. C. Ooi, J. J. Hardon & S. Phang, 1974. In press.

V

Het aanplanten van overblijvende gewassen samen met vlinderbloemige bodembedekkers in de humide tropische gebieden in West Afrika kan dezelfde functie vervullen als herbebossing.

VI

Uit de dikte van de vezelmantel in door middel van groeihormonen geïnduceerde parthenocarpe vruchten van een *pisifera* oliepalm is niet vast te stellen wat voor schaaldikte de *tenera* nakomelingen zullen hebben.

NIFOR annual reports 1966-1968.
Dit proefschrift.

VII

Bij bemestingsadviezen voor de oliepalm op West-Afrikaanse latosols dient meer rekening gehouden te worden met de mogelijkheid van meeropbrengsten door fosfaatbemesting.

J. de Geus, 1973. Fertilizer Guide for the Tropics and Subtropics.
H. A. M. van der Vossen, 1970. Ghana J. agric. Sci. 3: 109-129.

VIII

Hoewel waterconservering door regelmatige grondbewerking in jonge oliepalmaanplanten in West Afrika, speciaal gedurende de droge tijd, aanvankelijk tot aanzienlijke oogstvermeerdering kan leiden, is een dergelijke methode te beschouwen als een ernstige vorm van roofbouw.

R. Ochs, 1963. Oléagineux 18: 231-238.
IRHO rapports annuels 1968-1971.

IX

Het selecteren op voor hoge plantdichtheid geschikte planttypen dient een centrale plaats in te nemen in veredelingsprogramma's van overblijvende tropische gewassen.

X

Bij de veredeling op resistentie tegen de koffiebessenziekte en bladroest in Arabicakoffie in Oost Afrika is het essentieel om tegelijkertijd te selecteren op 'tonic-'neutrale genotypen.

E. Griffiths, 1971. Proc. 6th Br. Insectic. Fungic. Conf., p. 817-825.

XI

Ook de buitenlandse in ontwikkelingslanden werkzame wetenschappelijke deskundigen behoren in de gelegenheid te worden gesteld om zich middels een periodiek verblijf aan een universiteit of hogeschool bij te scholen op hun vakgebied.

XII

De benaming 'althobo', voor een van de meest expressievolle instrumenten van de houtblazers groep, verdient verre de voorkeur boven 'Engelse hoorn' (E. en Fr.: cor anglais). De laatste algemeen gebruikelijke benaming berust op een verbastering van 'cor anglé'. Het instrument is evenwel noch van Engelse oorsprong, noch heeft het tegenwoordig een gebogen vorm.

Proefschrift van H. A. M. van der Vossen
Wageningen, 3 oktober 1974

Enige biografische gegevens

De auteur werd op 7 mei 1938 te Vught geboren. Hij ontving een opleiding gymnasium-β aan het Canisius college te Nijmegen, waarna hij in 1957 zijn studie begon aan de Landbouwhogeschool te Wageningen. In september 1964 werd het ingenieursdiploma behaald in de richting tropische landbouwplantenteelt met als specialisaties plantenveredeling, erfelijkheidsleer en planteziektenkunde. In datzelfde jaar vertrok hij met zijn vrouw naar Ghana om in dienst te treden van de Crops Research Institute te Kumasi met als opdracht een nieuw proefstation voor de oliepalm, het Oil Palm Research Centre, op te zetten nabij Kade. In 1971 kon hij zijn taak aan Ghanese staf overgedragen om vervolgens in dienst van de Directie Internationale Technische Hulp van het ministerie van buitenlandse zaken te worden aangesteld als hoofd van de nieuwe afdeling voor plantenveredeling op het Coffee Research Station te Ruiru in Kenya.

Acknowledgments

I am greatly indebted to my promotor, Prof. Dr Ir J. Sneep, for his guidance and for his helpful criticism and suggestions. I am also grateful for the hospitality offered by him at the Institute of Plant Breeding during the summer of 1973.

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I highly appreciate the work done by all the staff and other employees of the Oil Palm Research Centre. My thanks are especially due to Mr E. O. Koranteng, plantation manager, Mr W. A. Decker, plant production officer, Mr A. Nantwi, asisstant research officer, Ir B. Schut, who was on a 7-months assignment as postgraduate student in 1969/70, Dr J. B. Wonkyi-Appiah, research officer, the then scientific assistants Messrs S. W. Ohene-Tutu, C. S. K. Kanda and E. A. Agyepong, the draughtsman Mr A. K. Buabeng, and the pollinator Mr G. Mensah.

I am indebted to the Nigerian Institute for Oil palm Research for making use of published data of its breeding programme and to its senior plant breeder, Mr C. O. Obasola for providing unpublished data on the performance of some of the parent palms.

I am most grateful to Dr Ir L. D. Sparnaaij for the many fruitful discussions we had during his visits as a consultant to the Oil Palm Research Centre. I am very grateful to him and to Ir I. Bos for critically reading the entire manuscript.

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My thanks especially go to my wife Riky for showing great patience while I was preoccupied with work on this thesis and for her assistance in sorting out some of the experimental data.

I am grateful to Mrs M. M. Pereira and Mr G. O. Akal of the Coffee Research Station in Kenya for typing the manuscript and to the editorial staff of the Pudoc for editing and publishing this thesis.

Contents

1 Background and objectives

The oil palm, *Elaeis guineensis* Jacquin, has been the subject of intentional selection since the advent of commercial oil palm plantations in Asia (Sumatra and Malaysia) and Africa (Zaire) around 1920 (Hartley, 1967).

The oil palm is an outbreeding perennial plant for which no practical method of asexual propagation has yet been developed. Improvement of total oil yield was initially pursued through phenotypic mass selection (individual selection) and applying independent culling levels to components of oil yield, starting from genetically narrow base populations (see Chapter 3). Based on biometric studies carried out by the INEAC[1] at Yangambi, Zaire (Beirnaert & Vanderweyen, 1941; Vanderweyen et al., 1945, 1947) a more systematic breeding programme, incorporating recurrent selection for specific combining ability, was initiated around 1950 by the INEAC (Pichel, 1957). Soon after a more comprehensive selection programme for good genotypic value was started by the NIFOR[2] in Nigeria (Sparnaaij et al., 1963) and a programme of reciprocal recurrent selection by the IRHO[3] in Ivory Coast (Gascon & de Berchoux, 1964). Exchange programmes between oil palm selection centres in Africa and Asia led to similar selection programmes being adopted in Malaysia (Hardon & Thomas, 1968). In recent years an impressive quantity of data on the performance of progenies, especially from the NIFOR and IRHO breeding programmes, has been published (NIFOR annual reports 1964–1968, IRHO rapports annuels 1967–1970).

A first interpretation of breeding results was attempted by Gascon et al. (1963, 1964 and 1966) and estimates of heritability of components of oil yield have been published by Blaak (1965), Thomas et al. (1969) and Meunier et al. (1970). The most fundamental contribution has been made by Sparnaaij (1969), who produced evidence of the additive inheritance of all major components of oil yield from data of the NIFOR breeding programme and showed how this could be applied to estimate genotypic values and thus to increase the efficiency of selection.

A new oil palm selection centre, the Oil Palm Research Centre (OPRC), was established in Ghana, near Kade, in 1964. The majority of the breeding material was identical to that of the NIFOR (van der Vossen, 1969a). By applying Sparnaaij's

1. Institut National pour l'Etude Agronomique du Congo.
2. Nigerian (formerly West African) Institute for Oil Palm Research.
3. Institut de Recherches pour les Huiles et Oléagineux.

method of estimation to the progeny means published in the NIFOR annual reports (1964–1968), we obtained genotypic values for most of the parent palms represented in the progenies planted in the OPRC selection fields (see Chapter 4). This formed the starting point of the estimation and interpretation of genetic variances and covariances for the components of oil yield presented in Chapters 5 and 6. The next two chapters deal with a special study to give experimental evidence of Sparnaaij's (1969) hypothesis on the inheritance of fruit quality components and experiments to develop reliable and less expensive methods of mesocarp oil content determinations. In Chapter 9 results are reported of investigations into important causes of environmental variance in bunch production.

The main object has been to contribute to a better understanding of the variability (and covariability) and inheritance of the components of oil yield in the oil palm and subsequently to indicate methods of selection which should result in maximum genetic improvement per unit of time and effort expended.

2 General introduction to oil palm breeding

2.1 Economic importance of the oil palm and prospects of further selection progress

The oil palm has the highest production potential per ha of all oil bearing crops. Its main products, palm oil and kernel oil, are important raw materials for the manufacture of margarine, compound cooking fats, soap, stearine candles, etc. In many countries in tropical Africa palm oil is also an essential ingredient of the local diet. With a total estimated world production of 1.9 million t palm oil and 0.5 million t kernel oil in 1972 (Randag, 1972) the oil palm ranks fifth (8.4%) in the order of importance of vegetable oils and fats producing crops.

National development plans aimed at planting vast new areas to oil palm have been initiated in the past 15 years in Malaysia and a number of countries in West Africa (e.g. Ivory Coast, Cameroon). These programmes, together with the rehabilitation and expansion of important existing oil palm industries in Indonesia, Zaire, Nigeria, and a number of smaller oil palm development programmes in West Africa (e.g. Ghana) and South America, are expected to cause a threefold increase in the world production of palm oil and kernel oil by 1985. The economic importance of the oil palm is, therefore, rapidly increasing.

Selected oil palm planting material may already produce, under favourable growth conditions, six to ten times the yield of the best semi-wild palm groves in West Africa. Annual production levels of 2.5–3 t oil per ha in mature plantations can be obtained in West Africa (IRHO rapport annuel, 1969) and even 5–6 t in the for oil palm cultivation optimal areas in Asia (Corley et al., 1971a). Improved cultural practices as a result of intensive agronomic research have, no doubt, contributed considerably to the spectacular yield increases.

Prospects of further improvement of oil yield by selection are still favourable, especially if one considers that present plant material is the result of only two to three generations of selection in sometimes genetically narrow base populations (Sparnaaij, 1971). However, a prerequisite to continued successful oil palm breeding will be the introduction of new germ plasm from the centres of high genetic variability.

2.2 Origin and centres of high genetic diversity

Elaeis guineensis Jacq., the most important of the two species in the genus *Elaeis* and commonly referred to as the (African) oil palm, has a West African origin (Zeven,

1964b, 1967). Its present geographical distribution in West Africa is the forest zone which extends from Guinea to Angola.

The heliophile but comparatively slow growing oil palm cannot compete with the faster growing tree species of the lowland tropical rain forest. Its natural habitat is, therefore, believed to be at the edges of fresh water swamps and along river banks where the large forest tree species are absent (Waterston, 1953; Zeven, 1967). The special structure of the roots with aerenchym in the cortex of the roots and the ability to form pneumatodes make the oil palm well adapted to seasonal inundation, although it cannot stand permanent waterlogging. Its abundance in the forest zone of West Africa must be largely attributed to unintentional spreading or deliberate propagation by man (Zeven, 1967), who in ancient times started to penetrate the closed primary forests and to open up parts of it for habitation and cultivation. Actually, one of the criteria used in West Africa to distinguish a true primary (undisturbed) forest from secondary forest is the absence of the oil palm in the former (Ahn, 1961).

It is now generally accepted that the semi-wild oil palm groves in Brazil are descendants of seeds brought from West Africa in the 16th century through the slave trade. The first introductions of oil palms to South-East Asia were made only about 125 years ago, i.e. in 1848 (Jagoe, 1952).

There are within the West African 'oil palm belt' some centres of high genetic diversity, notably in eastern Nigeria and south-eastern Cameroon. These centres are most important sources of new germ plasm. In recent prospections in eastern Nigeria some material was collected of remarkably good fruit quality (NIFOR annual report, 1965). Prospection for genetic variability outside these gene centres has been rather unreqarding (Vanderweyen, 1952; Meunier, 1969).

2.3 Morphology, growth and floral biology

A detailed description of the morphology and growth of *Elaeis guineensis*, which is a feather palm with a single apical growing point, has been given by Hartley (1967) and Sparnaaij (1969). Broekmans (1957c), who has made a detailed study of the growth and floral biology of the oil palm, concluded that the leaf primordia are formed about two years before the spear stage. There is principally one inflorescence in the axil of each leaf and the floral primordia are formed at about the same time as the leaf primordia. The inflorescence is fully developed and reaches the flowering stage about nine to ten months after the supporting leaf has unfolded. The last four to five months are characterized by a rapid growth of the inflorescence and it is during this stage that floral abortion may take place. Floral abortion which may be up to 30–40% during the first year of production is generally not more than 5–10% in adult palms (Sparnaaij, 1960).

The oil palm is monoecious, producing inflorescences with either male or female flowers in alternate cycles of various lengths. In adult palms there is little variation in the number of leaves produced and thus in the potential number of inflorescences.

Plate 1. Female inflorescence (length c. 40 cm) about ten days before anthesis, still surrounded by inner spathe. All spines of the surrounding leaf bases removed. At right fruit bunch 3–4 months old.

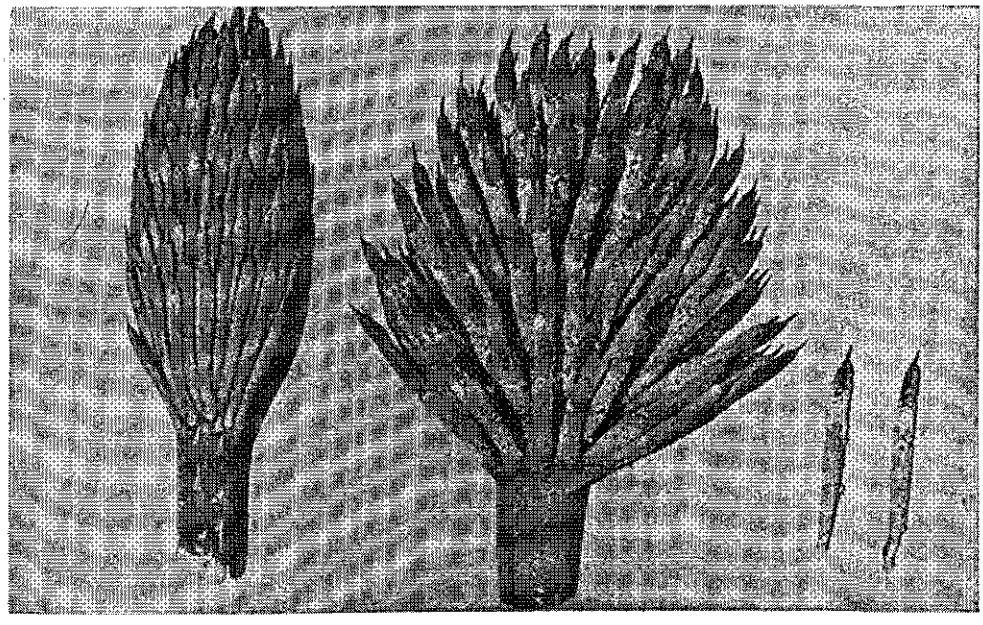

Plate 2. Male inflorescences: 2 weeks before anthesis with spathes removed (left); on day of anthesis (middle); two spikelets removed from central stalk (right).

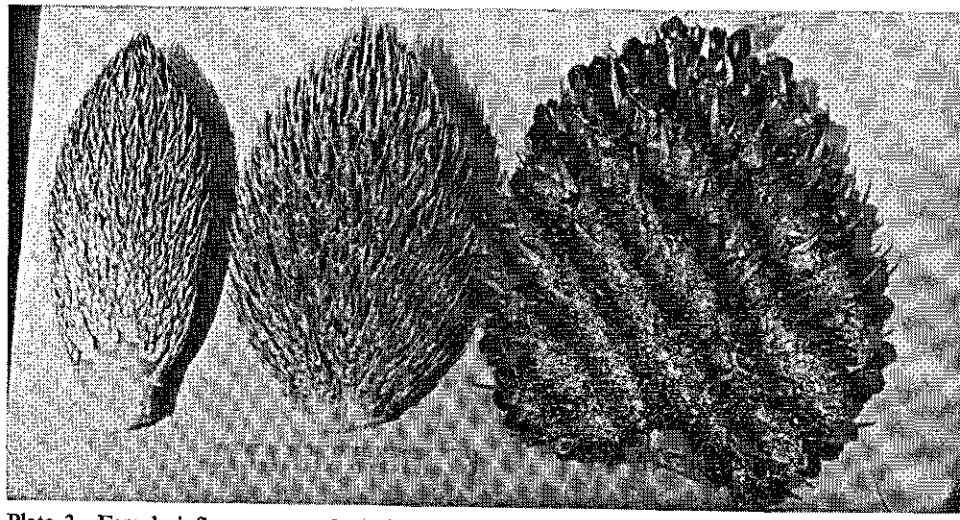

Plate 3. Female inflorescences: 2 weeks before anthesis with spathes removed (left); on day of anthesis (middle); ripe fruit bunch about 5.5 months after anthesis (right).

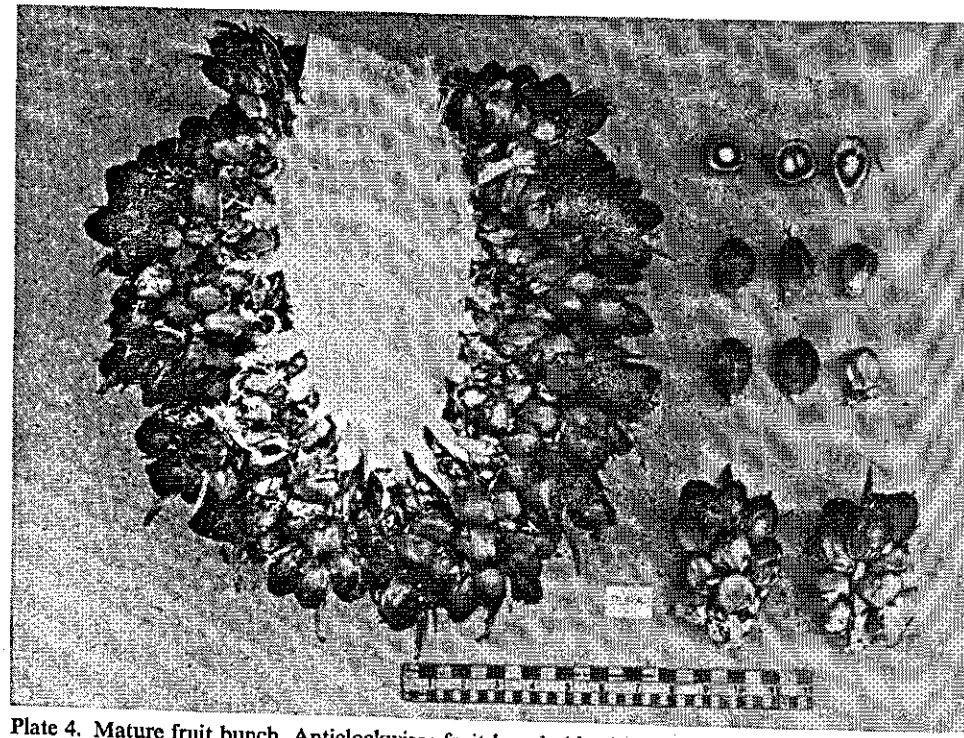

Plate 4. Mature fruit bunch. Anticlockwise: fruit bunch (*dura*) sectioned longitudinally, two spikelets removed from the central stalk, two outer (left) and four inner fruits; cross and longitudinal sections of a fruit (note double kernel in middle fruit).

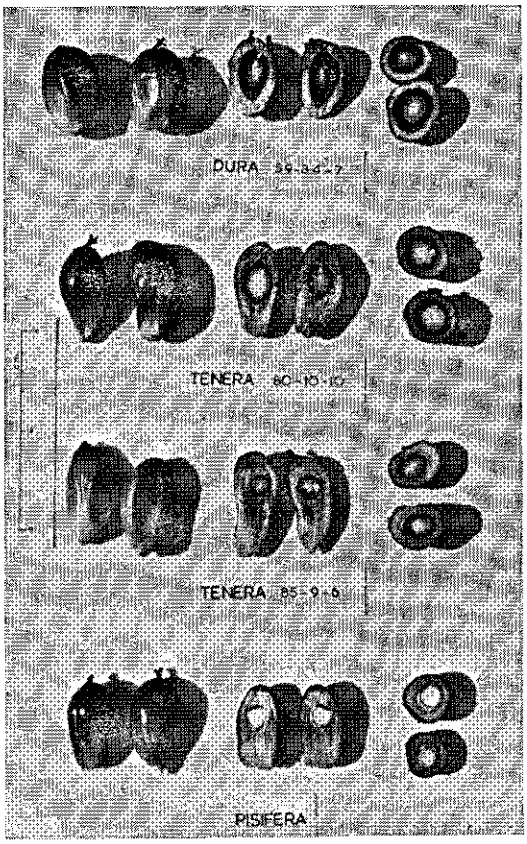

Plate 5. Oil palm fruit forms, with indication of the ratios mesocarp to fruit, shell to fruit and kernel to fruit for the *dura* and *tenera* fruits. The shell-less fruits at bottom are from a relatively rare fertile *pisifera* palm.

Plate 6. Individual palm yield recording. The weight of the bunch is recorded immediately after harvesting.

Plate 7. Oil palm bunches harvested from a selection field heaped along the roadside prior to collection. Note the hooked knife attached to a pole and the matchet (cutlass) used to harvest the bunches from 9 years old palms. Two bunches at lower right have been cut lengthwise for demonstration purposes.

Plate 8. Controlled pollination on a selected palm. The female inflorescence is surrounded by a terylene bag which has two celluloid observation windows. Pollen is blown into the bag through a small hole in the window.

As floral abortion plays an insignificant role and bunch failure is rare, except for *pisifera* palms, it is mainly the sex ratio – defined as the percentage female to total number of inflorescences – which will determine the number of fruit bunches, one of the most important components of oil yield.

Environmental factors strongly influence the differentiation of the floral primordia into male and female inflorescences, which takes place about two years before flowering (Broekmans, 1957c) or 28–30 months prior to maturity of the fruit bunch. Sparnaaij et al. (1963) found a high positive correlation between annual bunch yield and annual totals of effective sunshine – defined as sunshine hours during periods of moisture sufficiency – about two and a half years earlier.

The female inflorescence is a compact compound spadix consisting of a thick central stalk on which 100–200 spikelets are implanted, each carrying up to 25–30 sessile flowers. During anthesis only the three-lobed cream-white stigmas of the female flowers are visible from between the spiny floral bracts. The male inflorescence is basically of the same structure, but the central stalk is more elongated. The smooth fingerlike spikelets, about the same in number as on the female inflorescence, each carry several hundreds of small sessile male flowers. Both types of inflorescences are tightly surrounded by a double spathe. The outer one splits open about six weeks before flowering and the other inner one about 3–4 weeks later.

The female flower, which has a syncarpous trilocular ovary, remains receptive 36–48 hours after opening (Broekmans, 1957b). The oil palm fruit is a drupe, 2–5 cm long. When ripe, it has a soft and fibrous, orange-coloured, oil-bearing mesocarp. The stone-hard endocarp or shell envelops in about 80% of the cases a single kernel, which consists of oil-bearing white endosperm. Sometimes two or even all the three ovules develop into kernels. A little cream-yellow embryo lies embedded in the endosperm opposite one of the three germ pores. The oil palm thus produces two types of oil: *palm oil*, an orange to red oil extracted from the mesocarp, and *kernel oil*, a colourless oil extracted from the kernel. Quantitatively the palm oil is by far the most important economic product of this crop.

The oil palm is essentially an allogamous plant as simultaneous appearance of male and female inflorescences on the same palm rarely occurs. However, self-fertilization can be realized artificially by pollinating a female inflorescence with stored pollen collected from a male inflorescence on the same plant during a previous male cycle.

2.4 Classification within Elaeis guineensis

Existing systems of classification within *E. guineensis* are based on variation in fruit characteristics. Most fundamental for selection is the distinction of three basic fruit forms, *dura*, *tenera* and *pisifera* according to the variation in thickness of the lignified endocarp (shell). Beirnaert and Vanderweyen (1941) concluded from extensive biometrical studies in the selection fields at Yangambi (Zaire) that shell thickness is in the first instance determined by a single major gene with incomplete dominance action. The thin-shelled *tenera* form is the monohybrid between the thick-shelled

dura and shell-less *pisifera* forms which are both true-breeding. *Tenera* palms are preferred over *dura* palms because of the considerably higher ratio oil to bunch: 23–30% for *tenera* bunches to 12–18% for *dura* bunches. The *pisifera* palm is usually unproductive, i.e. female inflorescences do not develop into ripe bunches, but is used as male parent in *dura* × *pisifera* crosses to obtain a pure stand of *tenera* palms.

From a selection point of view there is no preference for the *nigrescens* (anthocyanin in the exocarp) or *virescens* (anthocyanin absent) fruit type, since no unfavourable characteristics are linked to either of the two alleles of the single major gene which determines the inheritance of these fruit types. On the other hand, the *albescens* fruit type is normally excluded from breeding programmes, because the extremely low carotenoid content in the mesocarp of *albescens* fruits, a recessive character, reduces the nutritive value of the mesocarp oil. Oil palm breeders have also lost all interest in the *poisonii* or mantled type of fruit (Sparnaaij, 1969).

All these different characters are inherited independently and the $3 \times 2 \times 2 \times 2 = 24$ possible combinations have all been found in natural palm groves. Beirnaert & Vanderweyen (1941) proposed a classification by arranging all the various types and forms in sub-species, varieties and sub-varieties, but in present literature this distinction is not made any more.

A very conspicuous character is the *idolatrica* leaf type, which Beirnaert & Vanderweyen (1941) considered a mutant of the normal type. Zeven (1964a) has given a detailed description of the *idolatrica* or king palm and its occurrence in West Africa. *Idolatrica* palms have no economical importance, but are sometimes used in border rows to mark experimental fields.

2.5 Components of oil yield

When selecting oil palms for breeding or seed production, a number of components of oil yield are considered. The relative economic value of each will be discussed in Chapter 6, but as a background of easy reference for the following chapters a brief account is given below of each of the components (see also Sparnaaij et al., 1963).

1. *Number of bunches* (n_b) *and single-bunch weight* (w), the product of which determines bunch yield. There is a wide variation between progenies and between individual palms for both characters. Number of bunches may vary from 0–25 per annum and is especially high during the first few years of production. Single bunch weights of over 50 kg are not uncommon in older plantations.
2. *Fruit-to-bunch ratio* (fr_b), i.e. weight of clean fruits to total bunch weight: range 40–80%.
3. *Fruit quality* which is, in the first instance, determined by percentage shell. There is a wide variation within the three fruit forms. The range of *shell-to-fruit ratio* (s) within the *dura* form is 25–55% and within the *tenera* fruit form 1–32%. The range of *dura* and *tenera* forms partly overlap, but *tenera* fruits can be distinguished from *dura* fruits by the presence of a coarse fibre mantle around the shell in the *tenera* fruits only. Similarly, the range in variation of the *mesocarp-to-fruit ratio* (m) is for *dura*

35–70% and for the *tenera* form 60–90%. The *kernel-to-fruit ratio* (k) may vary for both forms between 4 and 18%.

4. *Oil-to-mesocarp ratio* (o_m) in ripe fruits can be as low as 20% averaged over a progeny during the first year of production. The range of oil content in the mesocarp for mature palms is generally between 40 and 65%.

Oil content of kernels varies little (48–50%) and therefore does not lend itself to improvement by selection. The chemical composition of mesocarp and kernel oil, although distinctly different, is also fairly constant.

The relation between the components of oil yield per palm is given by the following equation:

$$\text{oil yield} = n_b \times w \times fr_b \, (m \times o_m + k \times 0.50) \qquad (1)$$

Number of bunches (n_b) and w are in absolute units, while the other components are expressed as ratios. The oil content of the kernel is taken as 50%.

2.6 Other selection factors

Secondary selection factors of importance in some oil palm breeding programmes, such as disease resistance and slow stem growth, are beyond the scope of the present studies, reason why they are left out in this introduction.

Recent work carried out in Malaysia (Corley et al., 1971a, 1971b; Hardon et al., 1972) indicates the possibilities of indirect selection for higher yield by selection for improved partition of assimilates between vegetative growth and bunch production. How and at what stage of selection this could be incorporated in an oil palm selection programme, to increase selection progress for higher oil yield, will be subject of discussion in Chapter 10.

2.7 Methods of analysis of components of oil yield

Methods of analysis of components of oil yield adopted in most present oil palm selection centres are basically those developed by the INEAC at Yangambi, where pioneering work was carried out in the years 1935–1945 to arrive at reliable techniques of analysis. A detailed description of methods of analysis of components of oil yield as applied at the NIFOR is given by Blaak, Sparnaaij & Menendez (1963). A complete analysis includes:

1. Individual palm recording of number of bunches and single-bunch weight by weekly harvesting rounds throughout the year as soon as the selection fields come into bearing (2.5–3.5 years after field planting). Each harvested bunch is immediately weighed at the foot of the palm.

2. Bunch and fruit quality analysis, which consists of a step-by-step weighing of the various components of the bunch to obtain the fr_b, m, s and k values, as well as the mean single-fruit weight (s. fr. w.).

3. Determination of the oil content of the mesocarp (see Chapter 8).

In large selection programmes, such as that of the NIFOR, it would be impossible to analyse all the bunches harvested from the progeny trials. Instead, a representative sample of bunches, usually 15–20, is analysed per progeny each month. The progeny means, i.e. means of full-sib families, published in the NIFOR annual reports (1964–1968) are thus averages of 180–240 bunches evenly taken over one full year (first year of production) from a representative number of palms within each full-sib family.

2.8 Controlled pollination

All breeding and seed production involves controlled pollination of individual palms. Artificial pollination is facilitated by the floral biology, since male and female flowers are borne on different inflorescences. However, the pollen, which is shed in large quantities by the male inflorescences, is mainly airborne, while also many small insect species are vectors in transferring pollen from the male to the female inflorescences (Sparnaaij, 1969). Efficient techniques of isolating the inflorescences are, therefore, essential to produce legitimate seed.

Techniques of preparation and bagging of male and female inflorescences, pollen collection and storage and actual pollination have been described by various authors: Blaak et al. (1963), Bénard & Malingraux (1965), van der Vossen (1969a) and Bénard & Noiret (1970). In fact, pollination techniques nowadays applied by the oil palm selection centres vary only in small details.

2.9 Seed production

Large quantities of *tenera* planting material for commercial use are produced by artificial hybridization between selected *dura* (female parent) and *pisifera* (male parent) palms which have been obtained through a breeding programme. The seeds issued by an oil palm selection centre are usually referred to as planting material of the *dura* and *pisifera* (D×P) hybrid variety. It is actually a mixture of several progenies obtained from crosses between selected *dura* and *pisifera* palms and genetically far from uniform, except that the resulting plantation will produce fruits of the *tenera* form only. Its genetic composition will also vary from year to year because of changes in the selected parent palms and variation in reproduction rate of each palm.

3 The base populations and the breeding programmes of the main oil palm selection centres

All planting material available today in the oil palm industry is the result of selection and breeding work carried out at three oil palm selection centres in Africa and a few in South-East Asia, most of which started from surprisingly small base populations. In the following review the centres have been arranged according to their historical order of importance for oil palm selection.

3.1 INEAC, Zaire

In West Africa there was already an important trade and export to Europe of palm oil and kernels, all derived from semi-wild palm groves, around the middle of the 19th Century, but in the Congo (now Zaire) it was first realized that the oil palm would be more profitable as a plantation crop (Hartley, 1967). Improvement by selection started there in 1922 when at Yangambi, the main station of the INEAC, a first experimental planting was established with illegitimate seed of nine *tenera* palms selected from nearby palm groves and one *tenera* palm from the botanical gardens at Eala. The latter, which is usually referred to as the Djongo palm, had a very good bunch and fruit composition (80–85% mesocarp to fruit) and would become the progenitor of important selection material of various other selection centres in Africa and South-East Asia (Hartley, 1967).

This first planting was subjected to rigorous selection and right from the beginning emphasis was laid on selection for good *tenera* palms only. A legitimate F_1-generation from crosses between the best *tenera* palms was established during the years 1933–1939. It formed the basis of the extensive biometrical studies by Beirnaert and Vanderweyen (1941) which led to the discovery of the hybrid nature of the *tenera* palm. The selection standards of the INEAC resulted in the characteristic Yangambi type of *tenera* palm producing well filled bunches of large ovoid fruits with a thin shell and comparatively large kernels. A negative aspect of the Yangambi type is its relatively rapid increase in stem height.

A recurrent selection programme for specific combining ability starting from 6 *tenera* 'elite' palms selected among the F_1 generation mentioned above, was initiated around 1950 and the first cycle, consisting of a complete diallel of 30 crosses and 6 selfings, was completed and planted out by 1956 (Pichel, 1957). The INEAC selection and breeding methods stood, in fact, as the example for two other important selection centres in West Africa, the IRHO and the NIFOR.

3.2 Oil palm selection centres in Indonesia and Malaysia

The oil palm was introduced to South-East Asia for the first time in 1848, when four palms were planted in the botanical garden at Bogor, Java. The seeds had been received directly or indirectly through Amsterdam from the island Bourbon (La Réunion) or Mauritius to where the oil palm had been introduced earlier in the 19th century from an unknown West African origin (Jagoe, 1952). Offspring of these four palms, most likely open-pollinated seed from one or two palms only, were planted as ornamental avenues on some Deli tobacco estates in Sumatra (Indonesia) around 1890. The oil palm's value as an oil crop with a high production potential was recognised soon after and the first commercial plantings were established in the period 1911–1920, on Sumatra's east coast and on the Malayan peninsula, with illegitimate seed collected from the avenue palms.

These palms, all the *dura* fruit form, formed the base population for selection programmes involving mass selection and artificial selfing or hybridization, initiated around 1920 at various research stations and commercial oil palm estates on Sumatra and Malaya. By maintaining high standards of selection a very attractive type of palm was obtained, generally referred to as the Deli *dura*, characterized by a high production potential and a very uniform and good bunch and fruit composition. Some research stations pursued increase in total yield by selecting for high number of bunches e.g. AVROS[1] in Sumatra and CRS[2] in Malaysia, while others placed emphasis on a high single-bunch weight, e.g. various commercial companies such as SOCFIN (Belgarric, 1951). Other selection factors were resistance to Crown Disease and slow stem growth (dumpies). One of the complications of the latter aim was that in pure dumpies, like the ones descendant of the E 206 palm selected at the Elmina estate by the CRS, slow stem growth is generally linked to lower production (Hartley, 1967).

Initial results of further introductions of plant material from Africa around 1915 were very discouraging and it was generally decided to exclude this material from plantations, which consequently consisted exclusively of Deli *dura* populations until well into the 1950's (Janssen, 1959). A favourable exception was a consignment of seed, illegitimate offspring of the Djongo *tenera*, received from the Eala botanical gardens (Zaire) in 1922 and planted at Sungei Pantjur on the east coast of Sumatra. Particularly the offspring of one palm from this planting, SP 540, was used in many crosses with Deli *dura* palms which were extensively studies by Pronk (1953, 1954) and Pronk & Westenberg (1955). It formed also for a long time the main source of *pisifera* palms both in Sumatra as well as in Malaysia for the production of Deli *tenera* planting material, which became popular in South-East Asia after 1955.

Further introductions from African selection centres in more recent time have

1. Algemene Vereeniging Rubberondernemingen ter Oostkust van Sumatra (now RISPA).
2. Chemara Research Station.

widened the source of parent breeding stock and selection programmes similar to those carried out in Africa have now been adopted (Hardon & Thomas, 1968).

3.3 IRHO, Ivory Coast, Dahomey and Congo

When the IRHO started its oil palm selection programme in 1946 the following sources of plant material were available (IRHO, 1962; Gascon & de Berchoux, 1964).
1. Selfings of 29 *tenera* palms, planted between 1938 and 1942 at La Mé, Ivory Coast. These palms had been selected among an illegitimate planting derived from 60 open-pollinated bunches collected in 1924 – 28 from *tenera* palms in palm groves in the vicinity of the station. Selection criteria for fruit quality were mesocarp 60% and shell 20%. The selfings consisted of thick-shelled *dura* and *tenera* palms, producing a rather high number of small bunches. The low total yield was attributed to inbreeding depression.
2. The palm groves of southern Dahomey in which selection was carried out in a similar way. Seed from 34 open-pollinated bunches (number of different palms unknown) was planted at the oil palm station at Pobé in 1927. Later on an F_1 generation was planted, consisting of selfings and crosses from 38 palms selected in the 1927 planting. The quality of this material is similar to or even lower than that of the La Mé selections.
3. A planting established in 1944–1949 at the oil palm station at Sibiti (Congo), with selections made from earlier planting material originating from the original Yangambi selections. The material is of the Yangambi type with rather heavy bunches and large fruits with a low shell content.
4. A Deli *dura* plantation of 2000 ha at Dabou, Ivory Coast, established in 1925 with largely open-pollinated seed from selected Deli *dura* palms of the SOCFIN on Sumatra.

Following reports from Sumatra of very good results of Deli *dura* × African *tenera* or *pisifera* crosses, the IRHO carried out a large number of crosses between Deli *dura* palms of source (4) and *tenera* and *pisifera* palms of populations (1)–(3). It also organized an exchange programme between its own three research stations at La Mé, Pobé and Sibiti, the INEAC at Yangambi and SOCFIN in Malaysia which was called the 'Expérience Internationale'. Replicates of the same comparative trials were planted at the five different stations between 1950–1954. The results of these trials showed unequivocally that the progenies from Deli *dura* palms crossed with palms selected from sources (1)–(3) produced considerably more than the progenies from Deli *dura* × Deli *dura* or *tenera* × *tenera* crosses within the same population, i.e. interpopulation crosses were superior to within-population crosses.

This inspired the IRHO to a breeding programme based on reciprocal recurrent selection (Gascon & de Berchoux, 1964). Population A consisted of 80 Dabou Deli *dura* palms and later introductions of Deli *dura* material from Sumatra and Malaysia; population B was made up of 172 *tenera* and *pisifera* palms selected from sources (1)

and (3); the Pobé material was excluded from further breeding.

The in total 446 *tenera* × *dura* and *dura* × *pisifera* test crosses as well as 85 *dura* × *dura* and 79 *tenera* × *tenera* crosses and selfings of the best progenitors were planted out between 1958 and 1965 in 500 ha called the 'bloc semencier' at the IRHO's main station at La Mé (Anon, 1963). A second cycle of selection and hybridization was started in 1967 (IRHO rapports annuels 1967–1970).

3.4 NIFOR, Nigeria

A full account of the selection programmes of the NIFOR up to 1957 is given by Broekmans (1957a) and Hartley (1957). It largely consisted of phenotypic mass selection in offspring of grove palms from eastern Nigeria, to obtain parent trees for seed production at the main station near Benin and a number of outstations. Various introductions from South-East Asia, Zaire and other areas were made also. A large breeding programme, principally selection for good genotypic value of the components of oil yield, was drawn up in 1957 and the majority of the progenies from this programme was planted between 1959 and 1964 (NIFOR annual reports 1958–1964).

The *dura* and *tenera* parent palms were selected from the following base populations (NIFOR annual reports 1951–1962, Sparnaaij et al., 1963):

1. Eastern Nigeria origin

Calabar origin A plot of some 800 palms was established between 1912 and 1916 near Calabar from open-pollinated seed obtained from a number of grove palms. Yield recording started in this plot in 1922. Legitimate F_1 selfings of the best 12 *dura* and *tenera* palms were planted in 1930–1935 on agricultural stations near Ogba, Ibadan, Umudike (Umuahia) and Nkwelle. F_1 selfings and F_2 crosses were also planted at the main station near Benin during 1945–1947 and again in 1958.

Aba origin About 200 original grove palms were retained from an 11 ha palm grove improvement experiment. After 12 years yield recording and detailed analysis of bunch and fruit composition 5 *dura* and 6 *tenera* palms were selected for a programme of selfings and crosses. The progenies were planted at the main station near Benin during the period 1939–1941. However, segregation studies showed that controlled pollination had not been very successful and these F_1 plantings were to be considered as largely illegitimate offspring from the originally selected 11 palms.

Ufuma origin Yield recording started in 1939 in a 120 acres palm grove which contained an unusually high number of thin-shelled *tenera* palms. F_1 progenies of 166 selected palms were planted at the main station near Benin in 1956.

2. Deli origin

A first introduction of Deli *dura* palms to Nigeria consisted of two lots of seed, one from the SOCFIN Estate at Tandjong Genteng, Sumatra (a selfing of selection No. 8), and the other from the AVROS brought from Sumatra in 1926 and planted near Ibadan, Ogba and Umudike (Toovey & Broekmans, 1955). In 1939 seeds were obtained from ten crosses between high yielding palms at the Central Experiment Station at Serdang, Malaysia, including seven palms of the original avenue palms planted in 1922 and six palms from a field planted in 1926–1928. This material was planted in 1941 at the main station near Benin. Bunch and fruit composition were generally good, but bunch production was disappointing for most crosses, mainly due to the low number of bunches produced by these Deli palms under the less favourable environmental conditions prevalent in West Africa (long dry season, less hours of sunshine). Only the progeny from the cross between the Serdang avenue palms 19 and 65 gave a remarkably good production.

Other Deli *dura* palms included in the breeding programme were introductions (in some cases pollen only) from the IRHO at Dabou and Pobé, from Pamol Cowan Estate in Nigeria, direct from Malaysia and from Jamaica (origin unknown, but probably South-East Asia).

3. Angola origin

Introductions were made from an unknown source in Angola to the agricultural station at Njala in Sierra Leone. A few crosses and selfings from the six surviving palms were planted at the main station near Benin in 1942. A more comprehensive series of progenies was planted in 1961.

4. Yangambi origin (INEAC), Zaire

Introductions were made of seed and pollen from some of the *tenera* parent palms selected for the breeding programme of the INEAC.

5. Other origins

Other introductions were made including pollen from a *tenera* palm planted at Cowan Estate descending from the 'Lisombe' *tenera* palms in West-Cameroon and seed from palms at Madagascar.

The design of the NIFOR breeding programme has been described by Sparnaaij et al. (1963) and only the main features will be reviewed here.

The F_0 of this breeding programme consisted in the first instance of 53 *dura* (and Deli *dura*) and 65 *tenera* palms selected from above mentioned origins and categorized in six groups according to their yield and bunch quality characters. Assuming

additive and quantitative inheritance of all the components which determine total oil yield, a programme of about 230 *dura* × *tenera* and 110 *tenera* × *tenera* crosses was carried out between palms of different groups which were as much as possible complementary in their yield and bunch quality factors. The full-sib families were planted out in statistically designed progeny trials at two different spacings with 48–60 palms per progeny. The best *dura* and *tenera* parents were selfed, while also *dura* × *dura* and *tenera* × *tenera* crosses were made between palms of similar yield and bunch quality composition to accentuate their specific qualities. These full-sib families were planted out in unreplicated blocks to form the seed gardens from which the *dura* and *pisifera* palms would be selected for commercial D × P seed production, after evaluation of the test crosses.

It should be noted that the NIFOR breeding programme is basically selection for good genotypic value starting from base populations of *dura* and *tenera* palms. As a special feature a type of assortative mating is applied by grouping palms according to their components of oil yield. In the NIFOR breeding programme no methods of reciprocal recurrent selection are applied as is stated in some publications (Hartley, 1967; Hardon, 1970).

4 Estimates of genotypic values for components of oil yield

4.1 Introduction

4.1.1 Definition of genotypic value

The continuous variation observed for the components of oil yield in segregating families of the oil palm indicates polygenic inheritance. Sparnaaij (1969) has given convincing evidence that, for the oil palm populations of the NIFOR, the genotypic component of variance is largely made up of additive variance. This was shown from an analysis of a systematic *dura* × *tenera* crossing design of the type usually referred to as a North Carolina Model II design. In this particular case 8 *tenera* parents were crossed with 11 *dura* parents. In other words, for the oil palm populations studied the gene effects in the components of oil yield are mainly additive, in which case the mean of a full-sib family will give a reliable estimate of the genotypic value of the midparent. Genotypic values of *individual* palms can then be calculated from sets of three F_1 full-sib families obtained from crosses between three palms (see 4.2). The values are actually *additive genotypic values* for which Falconer (1960) uses sometimes the term breeding values. However, the breeding value of an individual is twice the mean deviation of the progeny from the population mean, which is unknown in this case. The additive genotypic value only depends on the midparent and can thus be determined directly without previous knowledge of the population mean. The genotypic value will in this and following chapters be denoted with symbol A.

In the following paragraphs it will be shown how above principle has been applied to calculate A values, for the components of oil yield, from the mean of the full-sib families of the NIFOR breeding programme which have been published in the annual reports (NIFOR annual reports 1965–1968).

Most breeding material of the OPRC in Ghana is identical to that of the NIFOR (van der Vossen, 1969a), but planted some five to six years later. There is circumstantial evidence from earlier established field experiments that the effect of geographic and climatic differences, between the OPRC in Ghana and the NIFOR in Nigeria, on relative progeny performance is small (van der Vossen, annual reports OPRC 1965–1970). It is, therefore, justified to use the A values calculated from the NIFOR data to select for progenitors with good genotypic values for components of oil yield at the OPRC.

4.1.2 The use of genotypic values

The reasons for reporting here in some detail the results of the calculations of A values for the components of oil yield are twofold:

1. A values can be used to estimate the heritability in the narrow sense (h_n^2) for each component. Estimates of h_n^2 can be directly obtained from the regression of A on P (phenotypic) values (Falconer, 1960). Good agreement between these estimates for h_n^2 and those obtained from the regression of offspring on parent will then give additional proof of the additive nature of the genotypic variance in the oil palm populations under study (see Chapter 5).
2. The genetic correlation (r_A) between two components of yield is per definition the correlation between the respective A values (Falconer, 1960). The calculated A values can thus be used to estimate genetic correlations in a direct manner (see Chapter 6).

4.2 Calculation methods

The method of calculating individual A values for components of oil yield in the oil palm from the means of full-sib families was first proposed by Sparnaaij (1969). Required are the means of three full-sib families, which are the progeny of biparental crosses between three palms. The method amounts to a solution of three unknowns from three algebraic equations. One worked out example for percentage kernel to fruit including one *tenera* × *tenera* and two *tenera* × *dura* crosses of the NIFOR breeding programme is given below. The data are means of 48–60 palms per full-sib family.

Example 1

$$\left.\begin{array}{lll} T_1 \times D_3 : 4.3488 \times G145 = 9.4 = \dfrac{A(T_1) + A(D)_3)}{2} & & A(T_1) = 7.0 \\ T_2 \times D_3 : 2381D \times G145 = 12.4 = \dfrac{A(T_2) + A(D_3)}{2} & \therefore & A(T_2) = 13.0 \\ T_1 \times T_2 : 4.3488 \times 2381D = 10.0 = \dfrac{A(T_1) + A(T_2)}{2} & & A(D_3) = 11.8 \end{array}\right\}$$

If the A values for the components of oil yield are known for one of the palms in a biparental cross, the A values for the second palm can be calculated as follows:

Example 2

$$T_1 \times T_4 : 4.3488 \times 14.892 = 8.0 \qquad \therefore\ A(T_4) = 9.0$$

The degree of accuracy of above method of estimating A values will of course depend upon the proportion of the total phenotypic variance (σ_P^2) between progenies due to variation in general environmental factors (σ_E^2) such as availability of soil

moisture (see also Chapter 9) or soil fertility. Annual variations in climatic conditions, age effects and random errors should also be taken into account. Because most full-sib families of the NIFOR breeding programme have been planted in replicated field experiments, reliable means of *tenera* and *dura* palms per progeny (full-sib family) for bunch yield and its components were available at the time (NIFOR annual reports 1964–1968). Besides, since data on year of planting and experiment number for each progeny are available, it has been possible to correct the progeny means for between-year and between-experiment variation by making use of the standard cross 5.1450-T × 6.594-D which has been planted in most experiments. Apart from the standard cross, a number of other crosses were also planted in more than one experiment, thus increasing the possibilities for correcting the progeny means. In this way considerable between-experiment variation could be detected, some fields being appreciably more 'fertile' than others. Correction factors were calculated accordingly and all progeny means on yield data were multiplied with this correction factor before A values were estimated.

The NIFOR breeding programme had not been designed originally with the view to calculating A values in the manner described above and it was difficult to find sufficient sets of three crosses. However, it was possible to make two or more independent estimates of A values for each component from separate sets of three crosses for the following nine parents. In brackets the number of independent estimates:

1.2229-T	(4)	32.364-T	(3)
1.3352-T	(2)	32.3005-T	(6)
4.868-T	(3)	32.2612-T	(4)
4.1624-T	(4)	2381D-T	(3)
4.3488-T	(5)		

Means of the independent estimates of these 'test' parents were then used to calculate A for other parent palms as indicated in Example 2 above. Whenever possible, averages were taken over two or more independent estimates of A from crosses between the unknown parent and different 'test' parents. In fact, data from most of the 230 *dura* × *tenera* and 110 *tenera* × *tenera* crosses of the NIFOR breeding programme were used for these calculations.

4.3 Components of bunch yield

4.3.1 Available data

At the time of investigation yield records were available for most full-sib families over the first three years (year 1+2+3) of production, i.e. from $3\frac{1}{2}$-$6\frac{1}{2}$ years after field planting. Blaak (1965) and Sparnaaij (1969) demonstrated that, for palms planted at a conventional triangular spacing of about 9 m, the first 3–4 years of

Table 1. Components of bunch yield.
Phenotypic and genotypic mean annual values per palm in some groups of *tenera* and *dura* palms.

Group size and fruit form	P[1]			A[2]		
	n_b	w (kg)	yield (kg)	n_b	w (kg)	yield (kg)
21 *tenera*	11.5	5.5	62.3	10.0	4.8	48.0
coeff. of variation (%)	28	23	34	26	29	28
15 *dura*	9.0	7.0	63.0	9.6	4.0	38.6
coeff. of variation (%)	44	54	32	39	49	48
9 Deli *dura*	7.5	8.4	62.2	6.9	7.4	51.5
coeff. of variation (%)	16	19	19	30	31	43
45 *tenera* + *dura*	9.8	6.6	59.2	9.2	5.1	46.0
coeff. of variation (%)	37	41	32	34	43	39

1. P: mean values over year 1+2+3+4.
2. A: mean values over year 1+2+3.

production are little influenced by competition for light. At a later age this competition so much affects the sex ratio (number of bunches), one of the most important components of oil yield, that differences between progenies may be leveled out. Genotypic (A) values for the components of bunch yield can thus be estimated most accurately from the early, pre-competition years, since such estimates are independent of the effect of competition for light on bunch yield. In West Africa the correlation between early and mature yields in the oil palm is usually rather low, especially when the bunch number is inherently high (Sparnaaij, 1969).

Nevertheless, the A values for the bunch yield components derived from the early years of production can be used to select material with a high production potential. The beneficial effect of this increased production potential can be extended over the whole economic lifespan of the plant material, provided the spacing is adapted on the basis of data from specially designed plant density-progeny trials. This will be discussed in Chapter 10.

Estimates of A values for number of bunches, single bunch weight (kg) and total yield (kg) were made for 21 *tenera*, 15 *dura* and 9 Deli *dura* parent palms from annual means per palm over the first three years of production, after the original full-sib family means had been corrected for year effect and between-experiment variation (see 4.2). Mean P and A values and coefficients of variation for the 45 palms are given in Table 1. A values have also been calculated for total yield, but it is more valid to make comparisons between the components which determine yield.

4.3.2 Comparing phenotypic and genotypic values

Single-bunch weight increases rapidly in the first 4–5 years of production. This

Table 2. Coefficients of correlation between phenotypic and genotypic values for bunch yield and its two components, calculated over different sets of years.

	P (1+2+3+4)-A (1+2+3)	P (1+2+3+4)-A (1+2)	P (1+2+3+4)-A (2+3)
n_b			
tenera	0.487* (n=21)	0.456* (n=24)	.
dura	0.691*** (n=24)	0.654*** (n=26)	.
tenera + *dura*	0.632*** (n=45)	0.586*** (n=50)	0.698*** (n=30)
w			
tenera	0.491* (n=21)	0.258 (n=24)	.
dura	0.478* (n=24)	0.460* (n=26)	.
tenera + *dura*	0.441** (n=45)	0.450*** (n=50)	0.382* (n=30)
Total yield			
tenera	0.328 (n=21)	.	.
dura	0.281 (n=24)	.	.
tenera + *dura*	0.297* (n=45)	.	.

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

explains why the mean phenotypic value (6.6 kg) which has been calculated over the first 4 years of production is slightly higher than the mean A value (5.1 kg), for which only the first 3 years records were available. For the phenotypic values of the parent palms only four-year totals were available.

The data on phenotypic values for the *tenera* and *dura* palms are in accordance with frequently made observations (Beirnaert & Vanderweyen, 1941; Vanderweyen et al., 1945) that *tenera* palms produce at an average a higher number of bunches of a somewhat lower single-bunch weight than *dura* palms. However, the mean A values, which are calculated from the means of *tenera* plus *dura* palms within the same full-sib family, are much more similar for both groups of palms.

A group apart are the nine Deli *dura* palms. While their phenotypic values are on the whole of the same order as those for the *dura* palms, their mean A value for single bunch weight is almost double that of the *dura* palms. This is accompanied by a lower mean for number of bunches. It is not surprising that the coefficient of variation for the phenotypic values of the nine Deli *dura* palms is much lower, since five out of nine are full-sibs, whereas three have one parent in common with the other five palms. However, the c.v. of their A values is of the same magnitude as in the *tenera* and *dura* palms.

Coefficients of correlation between phenotypic and genotypic values are presented in Table 2. Values for number of bunches are generally much better correlated than for single-bunch weight, while the lowest coefficients were found for total yield.

Correlation coefficients are generally not substantially different when A is estimated over year 1 + 2 or year 2 + 3.

4.4 Components of bunch and fruit quality

4.4.1 Available data

The progeny means for bunch and fruit composition, as published in NIFOR's annual reports (1964–1968) are based on analyses of 15–20 bunches per month per progeny over the first 12 months of production (see 2.7). For *tenera* × *tenera* and *dura* × *tenera* crosses progeny means are given for the *tenera* and *dura* palms separately. Genotypic (A) values have been calculated for the percentages fruit to bunch (fr_b), mesocarp to fruit, shell to fruit and kernel to fruit (m, s and k), oil to mesocarp (o_m) and for single fruit weight (s. fr. w.).

For o_m nonsensical A values were obtained, in some cases zero or even negative figures. This is an indication of the inadequacy of the oil analysis data on which these calculations were based. The oil content of the mesocarp is usually very low for the small bunches produced during the first four to six months of production and it does apparently not bear any relation to the oil content of larger bunches produced afterwards. Not all the palms of a progeny may have come into production at the same time and during the first year of production the sampling variance may thus be extremely large due to 'age' differences between palms within a progeny. This difficulty would be evaded to a large extent if oil analysis were to start in the second year of production only. However, such data were not available. Investigations into possible improvements of mesocarp oil content determinations will be discussed in Chapter 8.

4.4.2 Comparing phenotypic and genotypic values for dura and tenera

The ultimate goal of an oil palm breeding programme is the production of *tenera* palms. *Dura* parent palms should, therefore, be judged by the performance of their *tenera* progeny for their bunch and fruit composition and consequently genotypic values for components of bunch and fruit quality were estimated from means of the *tenera* full-sib families and denoted as A_t. Nevertheless, for the *dura* and Deli *dura* palms A values were also estimated from means of *dura* offspring (A_d) in order to be able to compare A_t and A_d values. Phenotypic values of the parent palms were obtained from averages of fruit and bunch analysis data of these palms accumulated over several years of production.

Means and coefficients of variation of P and A_t values for 31 *tenera* palms and mean P, A_t and A_d values for 18 *dura* and 19 Deli *dura* palms are presented in Table 3. Coefficients of variation between means of P and A values are of the same magnitude in all cases. The higher coefficients of variation for s and k for P_t compared to P_d values, and for A_t compared to A_d values, is the consequence of the greater flexibility

Table 3. Components of bunch and fruit quality.
Phenotypic and genotypic mean values of some groups of *tenera* and *dura* palms. In brackets coefficents of variation (%).

Group size and fruit form	fr_b (%)	m (%)	s (%)	k (%)	s. fr. w. (g)
31 *tenera*					
P	63.8 (9)	83.1 (7)	9.0 (45)	7.9 (34)	8.0 (35)
A_t	65.6 (7)	79.0 (7)	12.5 (35)	8.5 (21)	6.5 (42)
18 *dura*					
P	66.7 (6)	55.9 (8)	33.0 (11)	11.1 (14)	
A_t	66.6 (6)	77.2 (10)	12.9 (40)	9.9 (31)	
A_d	67.7 (8)	50.7 (12)	37.5 (15)	11.8 (16)	
19 Deli *dura*					
P	68.2 (7)	59.7 (8)	30.9 (12)	9.4 (18)	
A_t	72.0 (5)	77.8 (5)	13.8 (20)	8.4 (19)	
A_d	72.5 (5)	55.9 (10)	34.7 (14)	9.5 (14)	

of the size of the nut (shell plus kernel) in the *tenera* fruit form, where it can vary over a fairly wide range within the area occupied by the fibre mantle (see 7.1).

It is interesting to note that, although the mean P and A_d values for m for the 18 *dura* palms are considerably lower and for s considerably higher than those of the 19 Deli *dura* palms, the mean A_t values of the *dura* and the Deli *dura* palms are almost identical. This phenomenon will be discussed in Chapter 7.

The relationship between P and A values for *tenera* and *dura* (including Deli *dura*) parent palms is summarized in Table 4. P_t and A_t as well as P_d and A_d values are highly correlated for m and s and to a lesser extent for k. For fr_b P_t and A_t values are moderately correlated, but P_d and A_d values are uncorrelated. Correlation coefficients

Table 4. Coefficients of correlations between phenotypic and genotypic values of components of bunch and fruit quality.

Component	$P_t - A_t$	$P_d - A_d$	$P_d - A_t$
s. fr. w.	0.567** (n=22)	.	.
fr_b	0.577*** (n=31)	0.179 (n=30)	0.045 (n=37)
m	0.912*** (n=31)	0.872*** (n=30)	0.249 (n=37)
s	0.924*** (n=31)	0.744*** (n=30)	0.176 (n=37)
k	0.718*** (n=31)	0.584*** (n=30)	0.541*** (n=37)

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

between P_d and A_t values are very low and insignificant for all components with the exception of k.

The relation between P and A values for the above mentioned components of bunch yield and components of bunch and fruit quality is also presented in a diagrammatic way in Figs 1 to 6. Regression lines have been fitted to the scatter diagrams assuming a linear relationship between the A and P values. The correlation coefficients, which are a measure of the closeness of the linear relationship between two variables, are fairly low for a few of the components, more in particular the single-bunch weight ($r = 0.44$) and the fruit to bunch ratio for A_t and P_t values ($r = 0.58$). The assumption of a linear relationship between the A and P values and the fitting of regression lines to these data may thus, from a statistical point of view, be somewhat speculative.

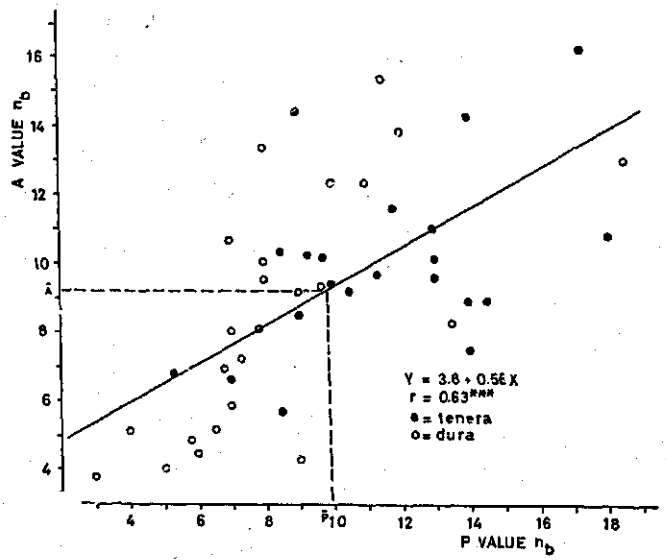

Fig. 1. Relation between phenotypic (P) and genotypic (A) values for the number of bunches (n_b) for 45 *tenera* and *dura* palms (see also Tables 1, 2 and 8).

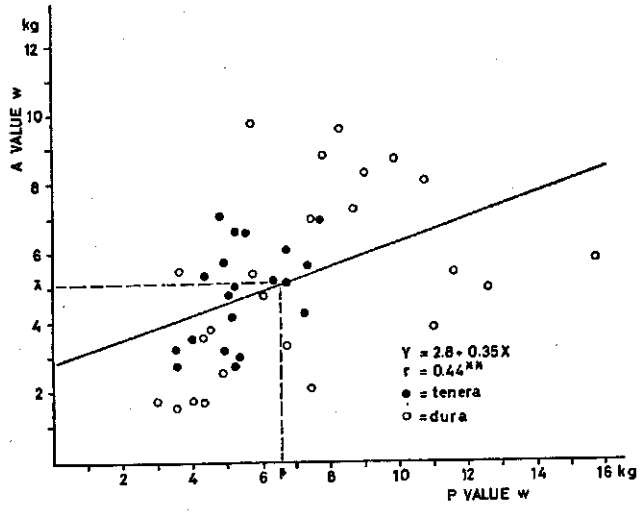

Fig. 2. Relation between phenotypic (P) and genotypic (A) values for the single-bunch weight (w) for 45 *tenera* and *dura* palms (see also Tables 1, 2 and 8).

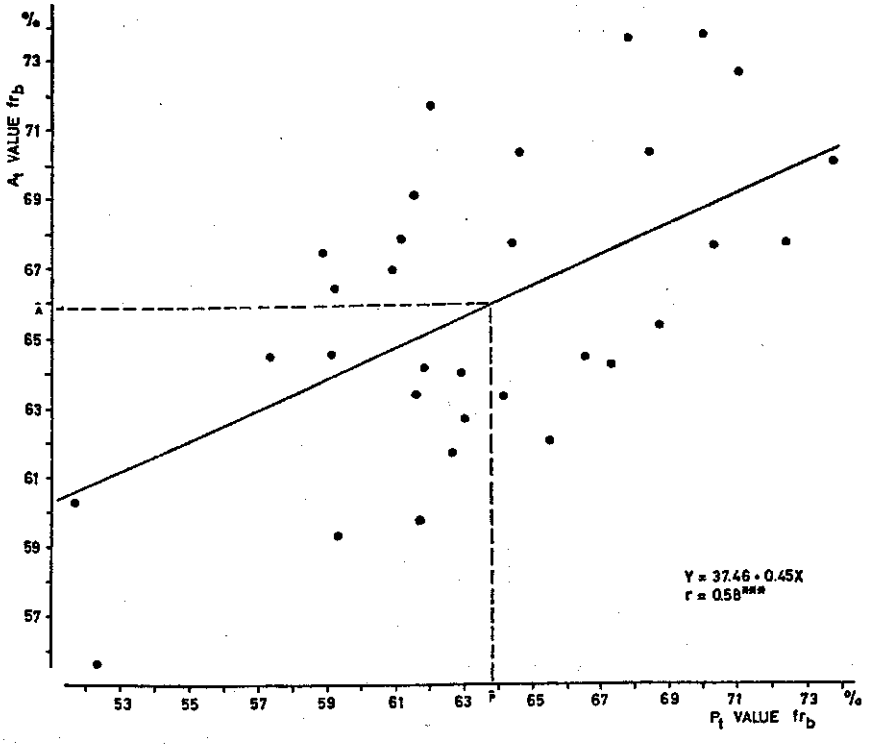

Fig. 3. Relation between phenotypic (P_t) and genotypic (A_t) values for the oil yield component fruit to bunch (fr_b) for 31 *tenera* palms (see also Tables 3, 4 and 8).

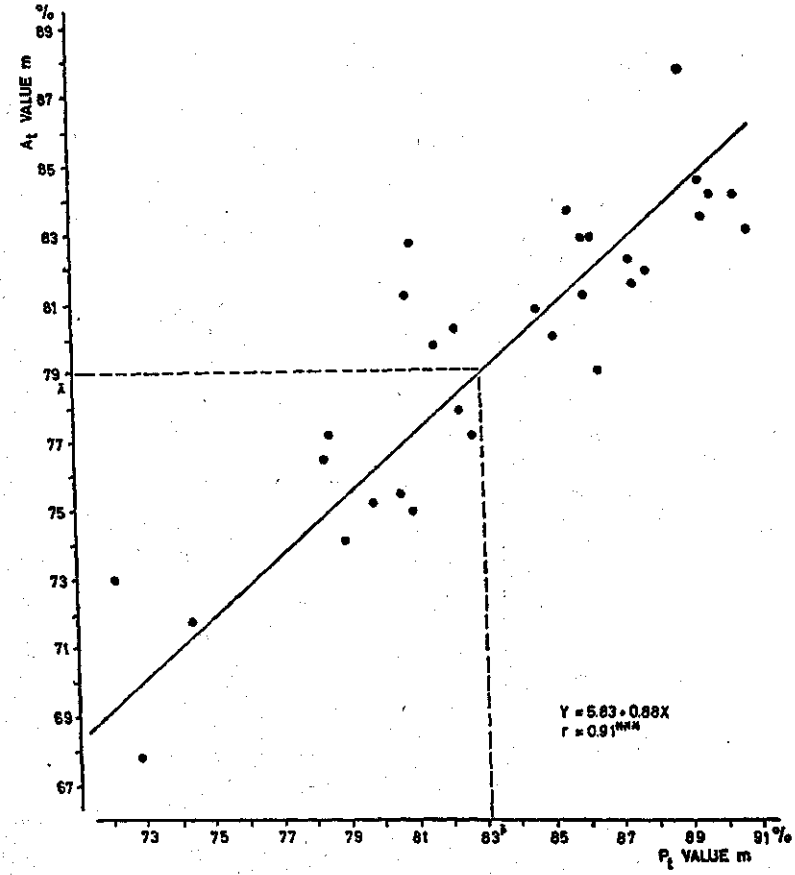

Fig. 4. Relation between phenotypic (P_t) and genotypic (A_t) values for the oil yield component mesocarp to fruit (m) for 31 *tenera* palms (see also Tables 3, 4 and 8).

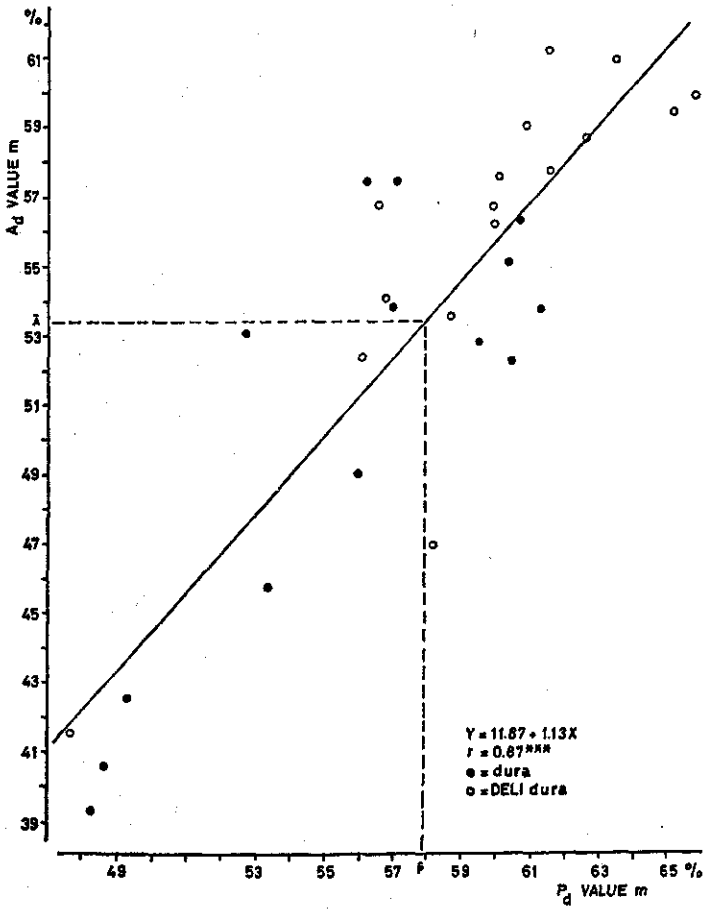

Fig. 5. Relation between phenotypic (P_d) and genotypic (A_d) values for the oil yield component mesocarp to fruit (m) for 30 *dura* palms (see also Tables 3, 4 and 8).

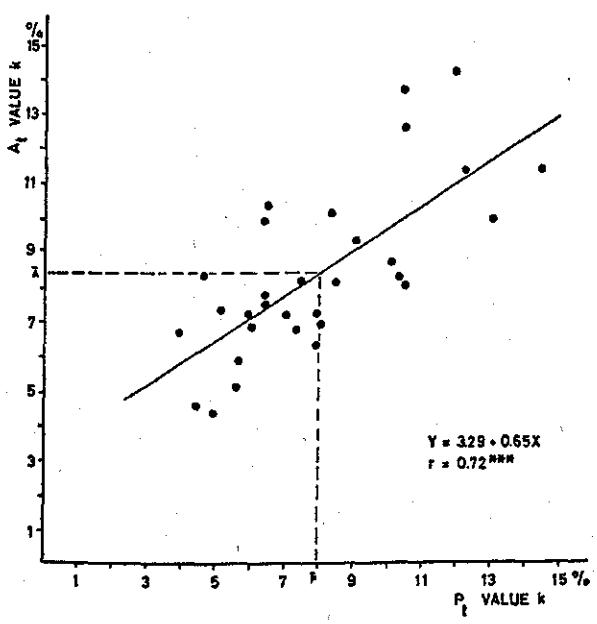

Fig. 6. Relation between phenotypic (P_t) and genotypic (A_t) values for the oil yield component kernel to to fruit (k) for 31 *tenera* palms (see also Tables 3, 4 and 8).

5 Estimates of heritability for components of oil yield

5.1 Heritability and its estimation

Heritability (in the narrow sense), h_n^2, expresses the ratio of the additive genetic variance to the total phenotypic variance of a metric character: σ_A^2 / σ_P^2. It is a very important index which enables the breeder to decide on the most efficient methods of selection in order to obtain maximum response to selection from the available breeding populations.

For the estimation of h_n^2 the regression of offspring on parent can be used. The covariance of the mean of the full-sib family and one parent or the midparent is equal to half the additive genetic variance (Falconer, 1960). The regression coefficient b for the regression of offspring on one parent is the ratio of $\frac{1}{2}\sigma_A^2$ and σ_P^2, an estimate of $\frac{1}{2} h_n^2$, and for the regression of offspring on midparent the ratio of $\frac{1}{2}\sigma_A^2$ and $\frac{1}{2}\sigma_P^2$, an estimate of h_n^2. In this case σ_P^2 is the phenotypic variance of the parents.

Estimates of h_n^2 for the components of oil yield in the oil palm from the offspring – parent regressions will be presented in 5.2. The estimates are based on the means of full-sib families and phenotypic values of the parent palms of the NIFOR breeding programme.

When additive genotypic (A) values are available, estimates of h_n^2 can also be obtained from the regression of A on P values, since $\text{cov}(A, P) = \sigma_A^2$ (Falconer, 1960). If the A values calculated in Chapter 4 are correct estimates of the actual additive genotypic values, both estimates of h_n^2 for the components of oil yield, from offspring-parent regressions (5.2) and from A–P regressions (5.3), should agree well. In both estimates the denominator of the ratio σ_A^2 / σ_P^2 will have the same magnitude, i.e. the variance of the phenotypic values of the same parent palms. However, in the h_n^2 estimates from the A–P regressions the numerator of the ratio will only be equal to σ_A^2, when the A values as calculated in Chapter 4 are indeed the additive genotypic values. Good agreement between estimates of h_n^2 from the offspring-parent regressions and from the A–P regressions would thus give additional proof of the additive nature of the genotypic variance of the components of oil yield.

5.2 Estimation of heritability from offspring - parent regressions

The means and coefficiens of variation of midparent and progeny mean values for total bunch yield and its two components for 84 *tenera* × *tenera* and *dura* × *tenera* progenies are presented in Table 5. The progeny means were adjusted for year and

Table 5. Components of bunch yield.
Phenotypic values of midparent ($\overline{P}$) and progeny means ($\overline{O}$) for 84 *tenera* × *tenera* and *dura* × *tenera* progenies, expressed as annual mean[1] per palm.

	n_b		w (kg)		Yield (kg)	
	$\overline{P}$	$\overline{O}$	$\overline{P}$	$\overline{O}$	$\overline{P}$	$\overline{O}$
Mean	10.6	9.7	6.5	5.3	62.9	49.9
Coefficient of variation (%)	22	27	26	20	22	24

1. $\overline{P}$: mean over years 1+2+3+4
$\overline{O}$: mean over years 1+2+3

field effect as described in 4.3.

The means and coefficients of variation of *tenera* (mid)parent and *tenera* progeny means of components of bunch and fruit quality for 50 *tenera* × *tenera* and 154 *dura* × *tenera* progenies are given in Table 6. Because of the apparent lack of correlation for m, the most important component of fruit quality, between *dura* palms and their *tenera* offspring (see Table 4), only the regression of *tenera* offspring on *tenera* mid-parent for the *tenera* × *tenera* crosses and the regression of *tenera* offspring on the *tenera* parent for the *dura* × *tenera* crosses are being considered here.

A summary of the estimates of h_n^2 from the regression coefficient (b) with 95% confidence limits and the level of significance of b is presented in Table 7. The regression of offspring on midparent for the two components of bunch yield and four components of bunch and fruit quality is presented diagrammatically in the Figs 7–12. The earlier remarks about fitting a regression line to pairs of data which are poorly correlated (see 4.3) also apply to some of these figures. Especially for the data on single-bunch weight the indicated regression line, although calculated from the available data, has little real meaning.

Table 6. Components of bunch and fruit quality.
Phenotypic values of *tenera* (mid)parent ($\overline{P}$) and *tenera* progeny mean ($\overline{O}$) for two sets of progenies, expressed as annual mean per palm. In brackets coefficients of variation (%).

Number and type of progenies	fr_b (%)	s. fr. w. (g)	m (%)	s (%)	k (%)	o_m (%)
50 *tenera* × *tenera*						
$\overline{P}$	63.8 (4)	8.2 (14)	84.0 (5)	8.7 (33)	7.4 (21)	46.5 (8)
$\overline{O}$	66.6 (4)	6.6 (17)	80.0 (6)	11.7 (33)	8.5 (19)	33.9 (16)
154 *dura* × *tenera*						
$\overline{P}$	64.0 (8)	7.8 (17)	84.1 (5)	8.2 (26)	7.6 (32)	46.7 (11)
$\overline{O}$	68.7 (4)	6.4 (15)	78.2 (5)	13.2 (19)	8.7 (19)	31.7 (21)

Table 7. Estimates of narrow-sense heritability from offspring-(mid)parent regressions for *tenera* components of oil yield, 95% confidence limits.

Component	*tenera* × *tenera* families			*dura* × *tenera* families		
	$\hat{h}^2_n = b$	t test b/s_b	n	$\hat{h}^2_n = 2b$	t test b/s_b	n
n_b	0.512 ± 0.212	4.83***	84			
w	0.206 ± 0.132	3.12**	84			
Total yield	0.091	n.s.	84			
fr_b	0.550 ± 0.273	4.04***	50	0.179 ± 0.163	2.15*	154
s. fr. w.	0.686 ± 0.218	8.37***	48	0.604 ± 0.208	5.70***	145
m	0.956 ± 0.177	10.99***	50	0.799 ± 0.231	6.77***	154
s	1.064 ± 0.195	11.07***	50	0.793 ± 0.163	4.84***	154
k	0.658 ± 0.252	5.78***	50	0.596 ± 0.188	6.21***	154
o_m	0.248	n.s.	34	0.230	n.s.	116

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$
n.s. not significant

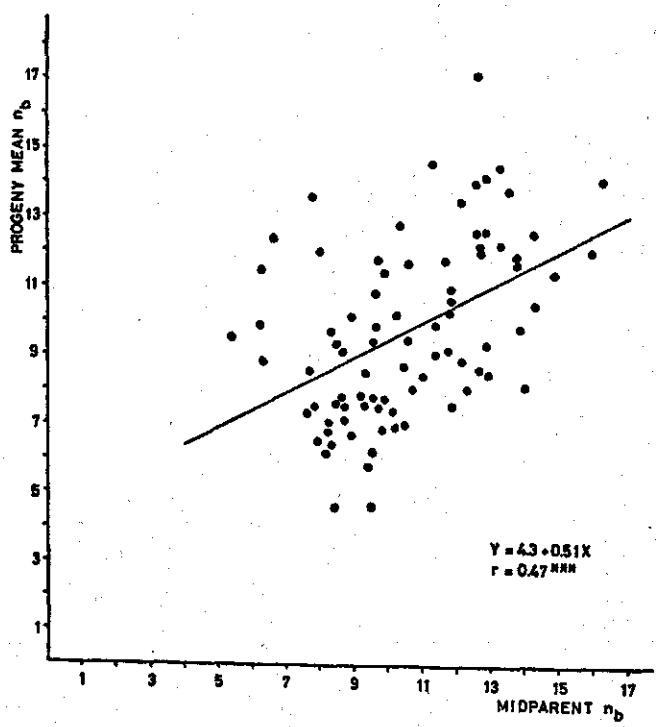

Fig. 7. Offspring-midparent regression for the oil yield component number of bunches (n_b) including 84 *tenera* × *tenera* and *tenera* × *dura* full-sib families (see also Tables 5 and 7).

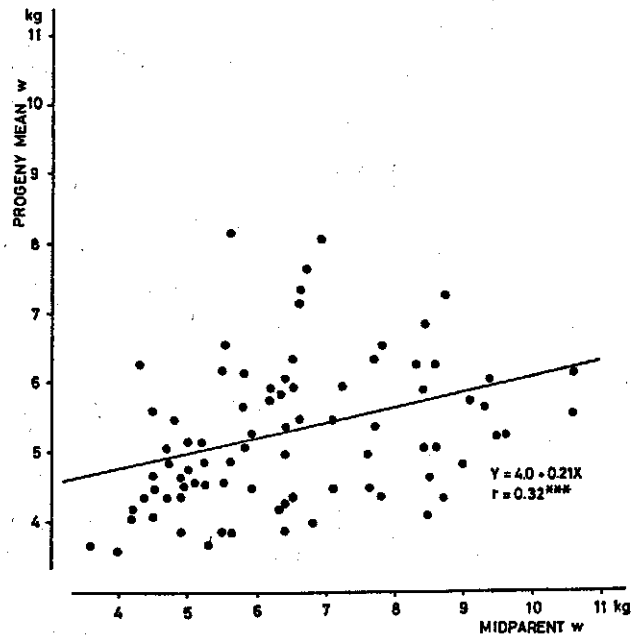

Fig. 8. Offspring-midparent regression for the oil yield component single-bunch weight (w) including 84 *tenera* × *tenera* and *tenera* × *dura* full-sib families (see also Tables 5 and 7).

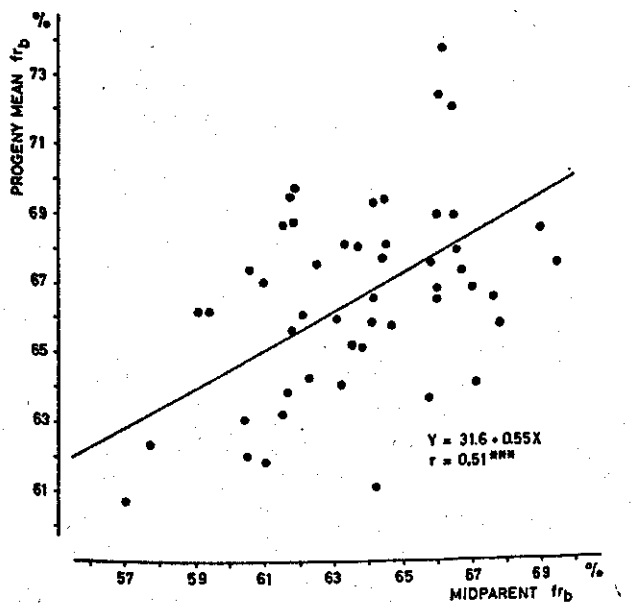

Fig. 9. Offspring-midparent regression for the oil yield component fruit to bunch (fr_b) from *tenera* values of 50 *tenera* × *tenera* full-sib families and the *tenera* midparents (see also Tables 6 and 7).

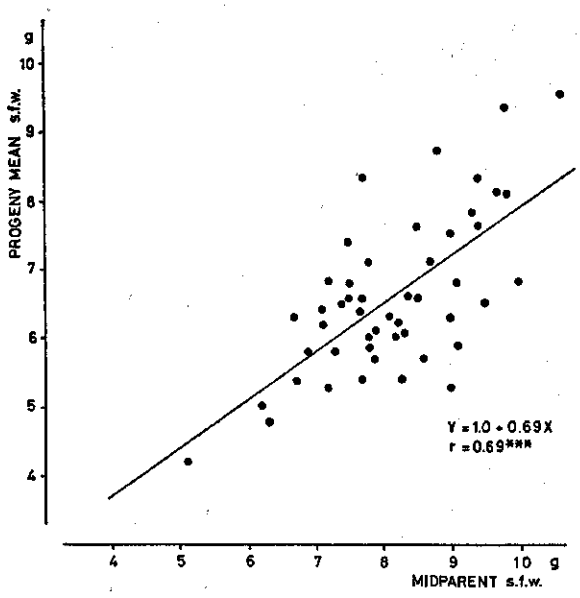

Fig. 10. Offspring-midparent regression for single-fruit weight (s. fr. w.) from *tenera* values of 48 *tenera* + *tenera* full-sib families and the *tenera* midparents (see also Tables 6 and 7).

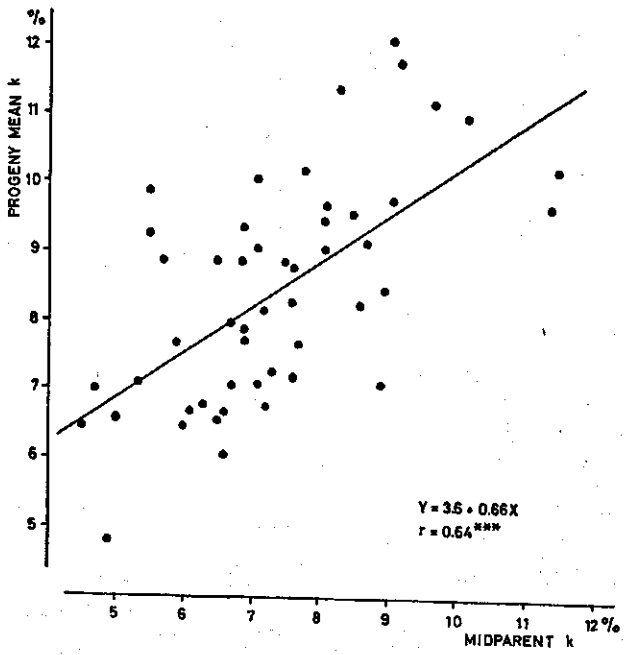

Fig. 11. Offspring-midparent regression for the oil yield component kernel to fruit (k) from *tenera* values of 50 *tenera* × *tenera* full-sib families and the *tenera* midparents (see also Tables 6 and 7).

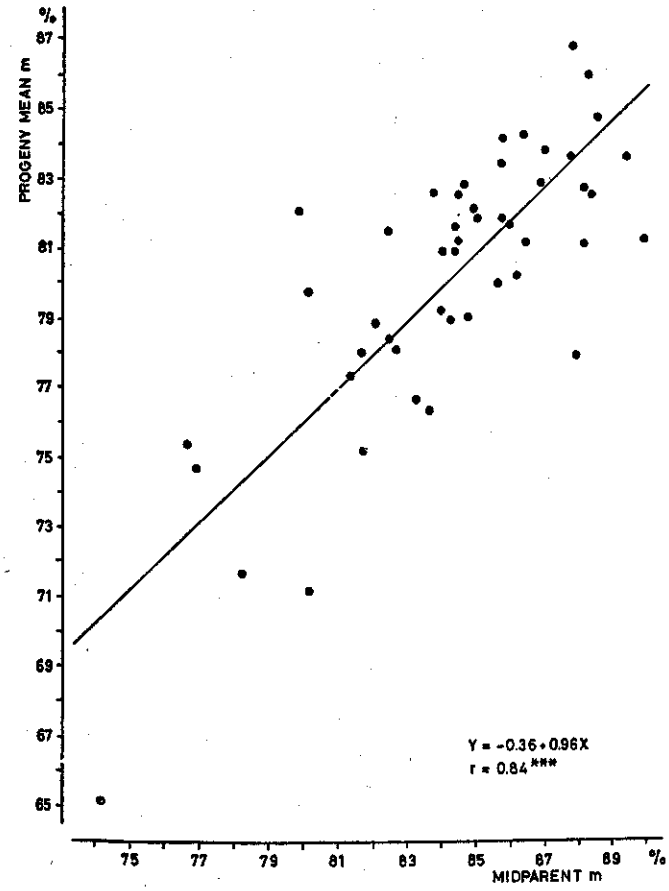

Fig. 12. Offspring-midparent regression for the oil yield component mesocarp to fruit (m) from *tenera* values of 50 *tenera* × *tenera* full-sib families and the *tenera* midparents (see also Tables 6 and 7).

5.3 Estimation of heritability from the regression of genotypic on phenotypic values

A diagrammatic presentation of the regression of A values on phenotypic values has already been given for components of bunch yield and some components of bunch and fruit quality in Figs 1 to 6.

In the calculation of A_t and A_d values for the bunch yield components, n_b and w, the mean of all *tenera* plus *dura* bunches of a full-sib family was used (see 4.2). The regression coefficients for A_t on P_t and A_d on P_d values turned out to be of the same magnitude, reason why for the estimation of h^2_n for these two bunch yield components, from the regression of A on P values, the *dura* and *tenera* values have been pooled (A_{t+d} on P_{t+d}). However, as regards to the bunch and fruit quality components (especially fr_b, m and s) h^2_n has been estimated separately from regressions of A_t on P_t, A_d on P_d and A_t on P_d, for reasons already given (see 4.3), Estimates of h^2_n for all

Table 8. Estimates of narrow-sense heritability for components of oil yield and quality from the regression of genotypic on phenotypic values based on *tenera*, *dura* or *tenera* + *dura* progeny; 95% confidence limits.

Component	Regression	n	$\hat{h}^2_n = b$	t test b/s_b
n_b	A_{t+d}–P_{t+d}	45	0.557 ± 0.210	5.34***
w	A_{t+d}–P_{t+d}	45	0.352 ± 0.220	3.23***
fr_b	A_t–P_t	31	0.447 ± 0.241	3.79***
	A_d–P_d	30	0.235	n.s.
	A_t–P_d	37	0.05	n.s.
s. fr. w.	A_t–P_t	22	0.559 ± 0.378	3.08**
m	A_t–P_t	31	0.881 ± 0.333	5.41***
	A_d–P_d	30	1.129 ± 0.438	5.28***
	A_t–P_d	37	0.323	n.s.
s	A_t–P_t	31	0.993 ± 0.376	5.40***
	A_d–P_d	30	0.976 ± 0.340	5.88***
	A_t–P_d	37	0.193	n.s.
k	A_t–P_t	31	0.653 ± 0.241	5.53***
	A_d–P_d	30	0.603 ± 0.324	3.82***
	A_t–P_d	37	0.741 ± 0.396	3.80***

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$
n.s. not significant

relevant components of yield and quality from the regression of A on P values are summarized in Table 8.

5.4 Discussion

5.4.1 Components of bunch yield

Of the two components of bunch yield the number of bunches has the higher heritability ($h^2_n = 0.512$ as compared to $h^2_n = 0.206$ for single-bunch weight, see Table 7). Heritability for total yield is extremely low and values of h^2_n are not significant for the population studied. The magnitude of these estimates is comparable to those published recently for oil palm populations in Ivory Coast as can be seen from Table 9. However, it should be realized that estimates of h^2_n may vary considerably with different populations and different environments.

From earlier studies of environmental influences on yield and its components (Broekmans, 1957c; Sparnaaij, 1960; Sparnaaij et al., 1963) it was generally inferred that the proportion of the total phenotypic variance due to additive genetic variance would be lower for number of bunches than for single-bunch weight. The first tentative

Table 9. Estimates of narrow-sense heritability for bunch yield components from offspring-parent regressions for 2 oil palm populations; 95% confidence limits.

Population	$\hat{h}^2_n$			Reference
	n_b	w	total yield	
Ivory Coast (IHRO):				
La Mé × Deli (*tenera* × *dura*)	0.50 ± 0.21	0.13 ± 0.11	·	Meunier et al. (1970)
Nigeria (NIFOR):				
tenera × *tenera* and *tenera* × *dura*	0.51 ± 0.21	0.21 ± 0.13	0.09 ± 0.20	This thesis Table 7.

estimate of h^2_n (Blaak, 1965) for single-bunch weight was relatively high (0.41). However this estimate was obtained from an offspring-parent regression whereby parents and progenies were grown under very different environments. The genotype-environment interaction may thus have unduly inflated the estimate. Blaak's (1965) estimate of h^2_n for total yield was low (0–0.23), but unfortunately no estimates for number of bunches were (or could be?) made. Consequently, Sparnaaij (1969) assumed, in the absence of further evidence, that h^2_n for number of bunches would be low.

5.4.2 Components of bunch and fruit quality

From the correlation between P and A values (Table 4) and estimates of h^2_n (Table 8) it is obvious that relevant comparisons between progenies and parents for components of bunch and fruit quality should be made only within the same fruit form (*tenera* or *dura*). Meunier et al. (1970) have not made this distinction, which may explain why their estimates for h^2_n are considerably lower than the ones presented here.

The only other published estimates of h^2_n for components of fruit and bunch quality are those given by Menendez & Blaak (NIFOR, annual report 1964). Their estimates of h^2_n for m, s and k (0.80, 0.83 and 0.61 respectively) compare quite well with those presented here in Table 8. Their estimates were based on *dura* offspring-*dura* parent and *tenera* offspring-*tenera* parent regressions in earlier generation populations of Aba and Ufuma origin.

The low values of the estimates of h^2_n for fr_b within *dura* populations or for *dura* parents and *tenera* offspring are not unexpected for a character which is known to be so much influenced by environmental factors. The fairly high value (0.44–0.55; Tables 7 and 8) within *tenera* populations, however, is rather remarkable.

5.5 Conclusions

The two sets of narrow-sense heritabilities for the components of oil yield, estimated from offspring-parent (Table 7) and A–P (Table 8) regressions, do agree well indeed, especially if the confidence limits are taken into consideration. For fr_b and the com-

ponents of fruit quality, comparisons should be made within the *tenera* values only. Both estimates of h_n^2 for single-bunch weight are low and are bound to be subject to large sampling errors: a linear relationship is hardly evident (see Figs 2 and 8). It is, therefore, not surprising that the two estimates for this component do not conform as well as for the other components of oil yield.

These results thus support the earlier conclusions made by Sparnaaij (1969) that in the breeding populations of the NIFOR substantial non-additive genetic variance is absent for all components of oil yield with the possible exception of o_m. In other words, the A values calculated in Chapter 4 are, within reasonable limits, valid estimates of the genotypic values of these components.

The components of fruit quality, except o_m (see Chapter 8), show a high to very high h_n^2 with values close to unity for m and s when estimated within the same fruit form. Selection progress for these components will thus be high when applying phenotypic mass selection within the same fruit form.

While selection progress will be very low in any method of selection for total bunch yield, continued response to selection for good genotypic values in the NIFOR oil palm population can be expected for the two components separately. The magnitude of the h_n^2 estimates for these components intimates that the response to selection should be somewhat higher for number of bunches than for single-bunch weight.

6 The importance of genetic correlations between components of oil yield to selection in the oil palm

6.1 Introduction

In oil palm breeding, improvement of oil yield is pursued by simultaneous selection of all earlier described components of oil yield. However, if maximum genetic gain is to be achieved, consideration should be given to optimum weights for each of these components to be aimed at in parent palms. The optimum weights of the components will not only depend upon (a) estimates of h_n^2, but also upon (b) estimates of the genetic correlation between components and (c) relative economic value of each component (Robinson et al., 1951). The object of the present studies is to obtain estimates of the latter two factors, from data of the NIFOR breeding populations which were also used in the two preceding chapters.

Hitherto it has been generally assumed by oil palm breeders that all components of oil yield are inherited independently (Pronk & Westenberg, 1955; Gascon et al., 1966; Sparnaaij, 1969) and the negative phenotypic correlation observed between n_b and w was thought to have an environmental cause only. In very recent studies of a Deli *dura* population carried out in Malaysia (Ooi et al., 1974) evidence was produced of a very high negative genetic correlation between the components n_b and w.

However, the Deli population is to a fairly large extent inbred (Hardon, 1970) and little additive genetic variation appears to be left in this population for these two components (Thomas et al., 1969). The Deli population would, therefore, seem unsuitable to obtain estimates of this genetic parameter. On the other hand, the NIFOR populations, which have been used to obtain estimates of the genetic parameters presented in this and the preceding chapters, include only full-sib families from crosses between unrelated parents to prevent genetic erosion as much as possible.

6.2 Causes of correlation and methods of estimation

The correlation between two metric characters can be expressed by the following parameters (Falconer, 1960): (1) *the phenotypic correlation coefficient* (r_P) which indicates the correlation between observed values, (2) *the genetic correlation coefficient* (r_A) which gives the correlation between the additive genotypic values and (3) *the environmental correlation coefficient* (r_E) which gives the correlation of environmental plus non-additive genetic effects for the two characters under consideration.

The relationship between these three parameters is given in the following equation, derived by Falconer (1960) from the definitionr of corelation coefficients and the fact

that the phenotypic covariance is the sum of the genetic and environmental covariances:

$$r_P = h_x \cdot h_y \cdot r_A + e_x \cdot e_y \cdot r_E \qquad (2)$$

where:
h_x or h_y = square root of h_n^2 of the correlated metric characters x and y, and
e_x or e_y = $\sqrt{1-h_n^2}$ for x and y respectively.

From this formula it follows that estimates of r_P alone cannot provide information on the magnitude and sign of the genetic correlation.

Estimates of genetic correlations can be obtained (1) from analyses of variance and covariance of various breeding designs (e.g. half-sib families), (2) from the offspring-parent relationship or (3) from correlated response to selection (Falconer, 1960). However, if additive genotypic (A) values of the metric characters are available, as in the case of the components of oil yield of this study, estimates of genetic correlation coefficients can, of course, be obtained directly from these data, for the reason that the genetic correlation is per definition the correlation between the additive genotypic values.

Since the A values for the components of oil yield of Chapter 4 appear to be valid and reasonably accurate estimates of the additive genotypic values (see 5.5), genetic correlations estimated from the correlation between A values should be reasonably accurate too.

6.3 The relative economic values of the components of oil yield

Before presenting the results of the estimates of correlations between the components of oil yield it will be useful to obtain estimates of the relative economic value for each of the components. The relative economic value of a component is defined as the additional profit expected from one unit increase of this component relative to that from one unit increase of another component (Hazel & Lush, 1942; Falconer, 1960).

The relation between the components of oil yield was given by Equation (1) in 2.5.

$$\text{Oil yield} = n_b \times w \times fr_b\,(m \times o_m + k \times 0.50) \qquad (1)$$

When the mean A values for each component from Tables 1 and 3 (*tenera* values of *tenera* palms) are substituted in Equation (1), total oil yield per palm per annum over the first three years of production will be:

$$\begin{aligned}\text{Oil yield} &= 9.2 \times 5.1\ (\text{kg}) \times 0.656\ (0.79 \times 0.467 + 0.085 \times 0.50)\\ &= 11.36\ \text{kg palm oil} + 1.31\ \text{kg kernel oil.}\end{aligned}$$

World market prices for palm oil and kernel oil vary considerably, but usually palm oil fetches about $\frac{2}{3}$ of the price of kernel oil. So by giving 20 economic units per kg to palm oil and 30 economic units to one kg kernel oil, above total oil yield will have a

Table 10. Estimation of relative economic values for components of oil yield in *tenera* palms. Relative economic value of w is 1. Total economic value of mean A values = 266.4 economic units.

	Components of yield and quality					
	n_b	w	fr_b	m	o_m	k
Mean A value	9.2	5.1 kg	0.66	0.79	0.47	0.08
Mean A value + standard error	12.3	7.3 kg	0.70	0.85	0.52	0.10
Marginal economic value						
in economic units	90.6	114.5	18.6	15.9	25.0	8.2
in %	34	43	7	6	9	3
Relative economic value	0.79	1	0.16	0.14	0.22	0.07

value of 266.4 economic units. For the purpose of calculating marginal economic values each single component is increased successively by a standard unit, in this case the standard error of the A value (Table 10), and the economic value of the total oil yield is calculated with the increased value of one component while keeping the other components constant. For o_m no estimates of A values are available (see 4.3), but the mean and standard error of the parental values from Table 6 were taken instead ($46.7\% \pm 5.14$). In this way six additionally different economic values were obtained. The difference between these values and 266.4 economic units is then for each component the marginal economic value if such a component is increased by a standard unit. The relative economic value of each component was determined as the ratio of its marginal economic value to that of the component with the largest marginal economic value per standard unit, in this case w. The results of the estimates are presented in Table 10.

When w is relatively high in comparison to n_b, as in the case of some Deli *dura* palms (see Table 1), the marginal economic value will become higher for n_b. For practical purposes, therefore, the relative economic values of n_b and w can be considered as equally important. The relative economic values of the components fr_b, m and o_m are respectively about 1/6, 1/7 and 1/5 of those of n_b and w, while that of k is only 1/14 of the relative economic value of n_b or w.

The major advance in selection for increased bunch quality was made after the discovery of the inheritance of the three fruit forms, The change from the *dura* to the *tenera* fruit form increases m from 56% (mean A_t value of the Deli *dura* palms in Table 3) to 79% (mean A_t value of the *tenera* palms in Table 3) and results in an increase of 30–40% in the economic value of oil yield, all other components remaining constant. This can be readily deduced from Equation (1): the total economic value is increased from 197.4 units for *dura* palms ($m = 0.56$) to 266.4 ($m = 0.79$) for *tenera* palms. However, within the same fruit form n_b and w have a relative economic value many times higher than any of the other components of oil yield.

6.4 Methods of calculating phenotypic and genetic correlations and results

The following correlation coefficients have been calculated between all possible combinations of components of oil yield, except o_m since no reliable data were available for this component. The *tenera* and *dura* palms are treated as separate populations, as has been done in the previous two chapters.

1. r_P between the phenotypic values of individual palms,
2. r_A between A_t or A_d values of respectively *tenera* and *dura* palms,
3. r_A between A_t values of *dura* palms.

The in total 86 correlation coefficients are presented in Table 11. The statistically significant genetic correlations have been italicized for easy reference. For the component single-fruit weight *tenera* r_A values could be calculated only.

Estimates of phenotypic and genetic correlations between n_b and w from pooled data of 52 *tenera* and *dura* palms were respectively $r_P = -0.590^{***}$ and $r_A = -0.584^{***}$.

In view of the high relative economic values of n_b and w, an effort was made to obtain supporting evidence of the existence of this negative genetic correlation by estimating r_A between these two components from the offspring-parent relationship and from correlated response to selection.

In the first instance an estimate of the genetic correlation between number of bunches and single-bunch weight was made from offspring-midparent covariances by applying the following formula (Reeve, 1955) to data of 25 *tenera* × *tenera* and *tenera* × *dura* full-sib families and midparents:

$$r_A = \frac{\text{cov } (x^P, y^O) + \text{cov } (y^P, x^O)}{2[\text{cov } (x^P, x^O) \cdot \text{cov } (y^P, y^O)]^{\frac{1}{2}}} \qquad (3)$$

where in this particular case: $x = n_b$ and $y = w$,
$P =$ midparent,
$O =$ offspring.

The 25 selected full-sib families are unrelated, i.e. each parent appeared in only one cross. The value obtained in this manner was $r_A = -0.738$ with $\hat{\sigma}(r_A) = 0.303$, the standard error being estimated according to Reeve (1955).

The genetic correlation was subsequently estimated from correlated response to selection in a number of parent palms and their full-sib progenies. The palms were selected for high number of bunches or high single-bunch weight, in order to obtain data on the correlated response of single-bunch weight, respectively bunch number after one generation. The genetic correlation can then be calculated from the following equation (Falconer, 1960):

$$CR_y = i \cdot \sqrt{h_x^2} \cdot \sqrt{h_y^2} \cdot \sigma(P_y) \cdot r_A \qquad (4)$$

where: CR_y = correlated response of component y,
x and y stand for number of bunches and single-bunch weight or inversely,

$$i \text{ selection intensity} = \frac{S}{\sigma(P_x)} \quad \text{whereby} \quad S = \text{selection differential and } \sigma(P_x) \text{ the phenotypic standard deviation of x in the parental population,}$$

$\sigma(P_y)$ = phenotypic standard deviation of y in the parental population.

Values obtained by this method were respectively $r_A = -0.67$ and $r_A = -0.42$.

The main criticism of the latter approach is, that selection was carried out among individuals which by themselves already represent selections from a much larger base population. Nevertheless, the estimates agree well with the earlier values and give further evidence of the existence of a fairly high negative genetic correlation between bunch number and single-bunch weight.

6.5 Discussion

6.5.1 Genetic causes of correlation between bunch yield components

The genetic cause of correlation is pleiotropy or close linkage between genes regulating the two characters (Falconer, 1960). In cotton (*Gossypium hirsutum*) negative genetic correlations do exist between economic traits, such as yield versus boll size and yield versus fibre strength, especially in populations derived from divergent crosses. Miller & Rawlings (1967) and Meredith & Bridge (1971), each working with different populations, showed how these negative genetic correlations were reduced considerably in successive generations of intermating, thus indicating that linkage was a contributing cause for the negative genetic correlation between some traits in cotton.

However, permanent negative genetic correlations between important economic traits, generally caused by pleiotropic action of polygenes, are a serious impediment to genetic improvement, even in the presence of a considerable amount of additive genetic variance (Lerner, 1958). An illustrative example is found in poultry breeding: a high negative genetic correlation exists between egg number and single-egg weight ($r_A = -0.42$ to -0.75) in lines of chickens which, for many generations, have been selected for high production (Wyatt, 1954; Hogsett & Nordskog, 1958). Lerner (1958) attributes the negative genetic correlation to pleiotropic effects of general genetic factors of physiological efficiency on the two egg production components.

The relationship between the yield components n_b and w in the oil palm appears to be analogous to that of the two egg production components of the domestic fowl, and the cause of the negative genetic correlation could thus be explained in a similar way. The 52 parent *dura* and *tenera* palms (6.4) have been selected phenotypically for high bunch yield. The negative genetic correlation between n_b and w indicates that for a number of these palms the actual yield level may already be close to a ceiling determined by genetic factors of physiological efficiency.

Table 11. Phenotypic (r_P) and genetic (r_A) correlations between components of oil yield. Upper value r_P, second value r_A within fruit form, third value r_A for *dura* palms calculated from A_t values; n ranges from 20–40 for the different correlation coefficients.

Component	w-T	w-D	fr_b-T	fr_b-D	s.fr.w.-T	m-T	m-D	s-T	s-D	k-T	k-D
n_b-T	−0.437*		−0.183		−0.151	0.078		0.098		−0.236	
	*−0.508**		−0.109		0.138	0.373		0.021		*−0.603***	
n_b-D		−0.615***		−0.135			−0.678**		0.667**		−0.314
		*−0.576****		*−0.437**			−0.117		0.029		*−0.455**
				−0.204			0.075		−0.008		−0.160
w-T			−0.212		0.092	0.079		0.028		−0.163	
			0.080		0.125	−0.308		0.113		*0.372**	
w-D				0.029			0.253		−0.284		−0.053
				*0.510**			0.372		−0.272		*−0.427**
				0.224			0.133		−0.007		−0.308
fr_b-T					−0.063	−0.352		0.144		0.568***	
					0.228	−0.207		0.055		*0.383*	
fr_b-D							0.114		0.014		−0.170
							0.213		−0.155		−0.268
							−0.192		0.302		−0.035
s. fr. w.-T						−0.373		0.151		0.259	
						−0.241		0.002		0.201	
m-T								−0.929***		−0.834***	
								*−0.922****		*−0.703****	
m-D									−0.851***		−0.555***
									*−0.958****		*−0.647****
									−0.941***		−0.832

s-T		*0.572***	
		*0.403**	
s-D			0.426*
			*0.401**
			0.594***

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

6.5.2 *Environmental factors*

In these considerations it is assumed that the genotypic values are free from environmental effects, or in other words the environment is a constant factor. In 4.2 it was explained how an effort was made to reduce environmental effects by adjusting the means of the full-sib families for between-experiment and between-year effect before genotypic values were calculated. Although in this way environmental variation has been reduced considerably, the actual genotypic values do, strictly speaking, only apply to the presently studied populations grown under environmental conditions prevalent at the NIFOR during the period 1960–1968 and only to the first three years of production. Where growing conditions are more favourable to the oil palm, as in some areas of the Ivory Coast and especially in Malaysia and Sumatra, production levels will be much higher and consequently genotypic values will be different. But also under these conditions there is a limitation to the yield potential determined by genetic factors of physiological efficiency and continuous selection pressure will result in a negative genetic correlation between the two bunch yield components.

On the other hand, genotype-environment interaction may change the ranking order, or, in other words, a palm with a good genotypic value in one environment may not necessarily be ranked under the genotypically better palms in another environment. From general experience it is known that differences in relative progeny performances within West Africa are usually of minor significance, but differences between West Africa and Malaysia can be large (Sparnaaij, 1969).

6.5.3 *Genetic correlation and prediction of progeny performance*

The data presented in this chapter thus give strong evidence of the existence of a fairly high negative genetic correlation between n_b and w. This negative r_A is already incorporated in the genotypic values which have been calculated from the full-sib family means. When such A values of n_b and w for two parent palms are used to predict the mean yield of the progeny, it appears as if the two components are uncorrelated. This may have caused most oil palm breeders to believe that the components n_b and w are actually inherited independently (Pronk & Westenberg, 1955; Gascon et al., 1966; Sparnaaij, 1969).

A few examples of the good agreement between predicted and actual yield are given in the first part of Table 12. Care was taken not to include the actual yields of the seven full-sib families in the calculation of the A values of the respective parent palms. The predicted values of n_b and w for the mean of the full-sib families are the mid-parent A values, as both components are additively inherited (see 5.5). The two parents in each cross are not related by common ancestry and are in the first five examples originating from widely divergent subpopulations.

The Deli *dura* and Yangambi subpopulations are genetically very narrow populations (see 3.1 and 3.2) and all palms within these subpopulations are somewhat related by common ancestry. The degree of common ancestry can be expressed by

Table 12. Predicted and actual annual bunch yield (kg) for the first three years of production of progeny from biparental crosses between related and unrelated palms.

	Parents		F_x[1]	genotypic values $n_b \times w$		Offspring (full-sib family) $n_b \times w$ = yield	
	cross and origin ($P_1 \times P_2$)			P_1	P_2	predicted	actual
	Parents unrelated						
1	32.2612-T × 5.1295-D	Calabar × Serd. Deli[2]	0.0	16.3 × 2.8	10.7 × 7.0	13.5 × 4.9 = 66.2	13.4 × 5.0 = 67.0
2	5.368-D × 32.364-T	Serd. Deli[2] × Calabar	0.0	9.3 × 8.8	10.3 × 5.6	9,8 × 7.2 = 70.6	10.8 × 6.6 = 71.3
3	5.1225-D × 2381D-T	Serd. Deli[2] × Yangambi	0.0	5.2 × 8.7	12.6 × 5.2	8.9 × 7.0 = 61,9	9.9 × 7.1 = 69.9
4	32.3005-T × 2381D-T	Calabar × Yangambi	0.0	9.6 × 6.6	12.6 × 5.2	11.1 × 5.9 = 65.5	12.1 × 5.8 = 70.2
5	32.2612-T × 1.2229-T	Calabar × Angola	0.0	16.3 × 2.8	5.8 × 7.1	11.1 × 5.0 = 54.7	8.5 × 6.3 = 53.6
6	32.364-T × 5.1654-D	Calabar × Calabar	?	10.1 × 5.6	15.3 × 5.4	12.7 × 5.5 = 69.9	13.0 × 5.5 = 71.5
7	32.3005-T × 1.3379-T	Calabar × Calabar	?	9.7 × 6.6	9.8 × 7.3	9.8 × 7.0 = 67.8	12.0 × 6.1 = 73.3
	Parents related						
8	5.1654-D × 108.5-T	Calabar × Calabar	0.125	15.3 × 5.4	11.2 × 3.8	13.3 × 4.6 = 61.0	13.6 × 3.8 = 52.3
9	32.2612-T × 32.2005-T	Calabar × Calabar	0.125	16.3 × 2.8	9.7 × 6.6	13.0 × 4.7 = 61.1	10.5 × 4.5 = 47.3
10	5.368-D × 203.93-D	Serd. Deli[2] × Sum. Deli[3]	0.219	9.3 × 8.8	4.0 × 8.1	6.7 × 8.5 = 56.2	4.5 × 5.4 = 24.5
11	5.1295-D × 5.368-D	Serd. Deli[2] × Serd. Deli[2]	0.359	10.7 × 7.0	9.3 × 8.8	10.0 × 7.9 = 79.0	6.0 × 3.6 = 21.5
12	1.2227-D × 1.2229-T	Angola × Angola	0.500	8.1 × 8.1	5.8 × 7.1	7.0 × 7.6 = 52.8	5.8 × 5.1 = 29.6

1. F_x inbreeding coefficient for individuals in the full-sib families estimated from pedigrees according to Wright (1922).
2. Deli *dura* originating from the Serdang avenue palms 19 and 65.
3. Deli *dura* imported from the AVROS, Sumatra.

the coefficient of inbreeding, F_x (Wright, 1922; Falconer, 1960). Hardon (1970) estimates the average F_x for individuals within the Deli and Yangambi populations, of the same generation as the palms quoted in Table 12, to be 0.219–0.305 and 0.110 respectively. The two Angola palms mentioned in Table 12 are both from a selfing of one of the six original Angola palms (see 3.4) and offspring of a cross between these two palms should have an $F_x = 0.50$. The other inbreeding coefficients indicated in Table 12 are also estimated from pedigrees.

In an outbreeding plant like the oil palm, crosses between related individuals may have a deleterious effect on yield. This phenomenon, which is well known in oil palm breeding (Gascon et al., 1969; Hardon, 1970) is generally the result of physiological imbalance caused by homozygosity or genetic erosion. The examples 10–12 in Table 12 are a good illustration. The yield in all three cases is only a half to one third of that predicted from the respective A values of the parent palms and both components seem to be equally affected. Obviously, A values for n_b and w, calculated from such full-sib families, would give poor estimates of the true A values of the parents. Apart from that, the negative r_A would be expected to be close to -1.0 because of the low genetic ceiling of physiological efficiency. Any selection pressure towards increase in one of the components would be accompanied by a proportional decrease in the other component. Ooi et al. (1974) gave additional proof of the genetic erosion in the Deli *dura* subpopulation, as additive genetic variation for bunch yield and its components was shown to be very low. Besides, the genetic correlation between n_b and w in the Deli populations studied by them was estimated at $r_A = -1.0$.

In the genetically much more variable subpopulations, like the one originating from Calabar (see 3.4), the situation is different. Where parent palms are apparently unrelated, predicted and actual yields do agree well as is demonstrated by examples 6 and 7 in Table 12. The inbreeding coefficient of the originally selected palms at Calabar, from which the four parent palms of crosses 6 and 7 are descended, is not known, reason why question marks have been placed for the respective F_x values of the individuals in these two full-sib families. However, the inbreeding coefficient should be very low.

On the other hand, where palms are known, from their pedigrees, to be related, as in the case of examples 8 and 9, the actual yield is somewhat lower than expected. Similar examples could probably be given for palms of the Aba subpopulation. Unfortunately, most Aba × Aba crosses were planted after 1962 and only reliable yield records from one or two years were available, insufficient to make similar comparisons. However, even with such genetically variable subpopulations, estimates of A values from interpopulation crosses would be preferred over those estimated from within subpopulation crosses, since the exact pedigree may not always be known and, inadvertently, related palms might have been crossed with each other in the latter case.

6.5.4 *Genetic correlations between bunch yield components and other quality factors*

Other significant genetic correlations of interest between components of oil yield presented in Table 11 are those between fr_b, k and the bunch yield components n_b and w. Consequently, selection for increased bunch number will be accompanied by a relative decrease in kernel size both for *dura* and *tenera* palms – i.e. actual response to simultaneous selection for larger k values will be less than expected, while in *dura* palms this will also cause a relative decrease in fr_b. On the other hand, selection for increased bunch weight will be accompanied by a relative increase in k in *tenera* palms and a relative decrease in *dura* palms.

However, when considering the relative economic values of fr_b and especially k, which are only a fraction of n_b and w, it is clear that such a relative decrease in fr_b or k will have little effect on the total economic value of the oil yield. Apart from that, a decrease in kernel size would be accompanied by a relative increase in m due to the fairly high negative genetic correlation between these two components.

The high correlations between the fruit quality components m and s or k are not surprising, as the three ratios add up to one. It is, however, interesting to note that the absolute values of the correlation coefficients are lower between k and m, or k and s than between m and s. This indicates that the kernel size may vary, within limits, somewhat independently from the other two components (see also Chapter 7). When kernel size increases s increases too (positive r_A between k and s), since the shell has to envelop a larger kernel and actual shell thickness apparently does not decrease very much.

The components fr_b and single-fruit weight (s. fr. w.) are apparently uncorrelated. This applies also to s. fr. w. and components of fruit quality, and to s. fr. w. and the bunch yield components n_b and w. In other words, s. fr. w. does not influence the for economic yield important components and is in fact an unimportant selection factor.

From a practical point of view, it is thus mainly the negative genetic correlation between n_b and w which has to be taken into account seriously in selection and breeding, while all the other existing genetic correlations can be conveniently ignored. In the presence of the negative r_A between n_b and w, maximum progress appears to be obtained by intercrossing between widely divergent subpopulations. This will be further subject of discussion in Chapter 10.

6.5.5 *Environmental correlation*

Some consideration may be given to the presence of an environmental correlation between the two most important components, n_b and w.

An estimate of the environmental correlation (r_E) between bunch number and single-bunch weight can be obtained by substituting the earlier found values for r_P (−0.590), r_A (−0.584), h_x^2 (0.512) and h_y (0.206) in equation (2). This gives $r_E = -0.643$.

The r_E estimated in this manner is normally not purely environmental, but includes also correlation due to non-additive genetic causes (Falconer, 1960). However, since substantial non-additive genetic variation was earlier found to be absent (see 5.5), it may be assumed that the negative r_E between n_b and w is mainly caused by environmental deviations in variation. The observed negative phenotypic correlation between n_b and w is thus the result of a yield ceiling imposed by genetic as well as environmental factors, the latter being mainly climate and soil.

7 The inheritance of fruit quality components

7.1 Introduction

7.1.1 The problem of selecting dura parents

Ever since *dura* seed parents were first used on a commercial scale for the production of *tenera* (*dura* × *pisifera*) planting material, oil palm breeders have been faced with the practical problem of evaluating the *tenera* genotypic (A_t) values of *dura* palms on the basis of the phenotypic values of their fruit quality components. This is of particular importance in subpopulations consisting entirely of *dura* palms, such as the Deli *dura* subpopulation, in which no comparison with full-sib *tenera* palms can be made.

Gascon et al. (1963) found a high correlation ($r = 0.87^{***}$) between m values of full-sib *tenera* and *dura* palms when the means of 86 *dura* × *tenera* and *tenera* × *tenera* progenies were taken. The regression of *tenera* on *dura* values obtained from this study has subsequently been applied in the breeding and seed production programmes of the IRHO to select Deli *dura* palms (Noiret et al., 1966; Brédas, 1969). More recently Meunier et al. (1970) reported a correlation coefficient for the same fruit component of only 0.56^{***} for IRHO progenies, but did not comment on the apparent differences between their results and those of Gascon et al. (1963). For 104 *dura* × *tenera* progenies of the NIFOR breeding programme (NIFOR annual reports 1965–1968) the correlation coefficient was only 0.40^{***}, a value which is too low to justify the calculation of the A_t value of *dura* palms on the basis of the regression equation.

As was mentioned earlier, the phenotypic value (P_d) and *tenera* genotypic value (A_t) of *dura* palms for m and s are even less correlated and the heritabilities are low and insignificant (see Tables 4 and 8).

It follows from above that the expected response to selection for these fruit quality components, though high for *dura* parents and *dura* offspring and for *tenera* parents and *tenera* offspring, will be very low for *dura* parents and their *tenera* offspring. This is demonstrated by the data in Table 3: although the mean P_d and A_d values of the 19 Deli *dura* palms for m are considerably better than for the mean of 18 (African) *dura* palms, the difference between the respective A_t values is negligible.

7.1.2 Hypothesis on the low correlation between dura and tenera sibs

Sparnaaij (1969) explains this phenomenon by assuming that two distinctly different factors determine shell thickness in the three fruit forms *dura*, *tenera* and *pisifera*. One is Beirnaert and Vanderweyen's (1941) major gene which determines percentage lignification of the coarse fibre mantle around the kernel, i.e. 100% or no lignification in the *dura*, respectively *pisifera* fruit form and partial lignification in the *tenera*. The second factor, under influence of polygenes, determines the potential shell thickness. This is equal to actual shell in the *dura*, since 100% of the potential shell thickness is lignified. In the *tenera* the potential shell thickness is given by the actual shell plus the remaining unlignified mantle of coarse fibres around the shell (see also Fig. 13).

By measuring the shell-to-fruit ratio in the conventional way, the full potential shell is actually measured in the *dura* fruit form, but only the lignified part of it in *tenera* fruits. This may explain the poor relation between *dura* parents and their *tenera* offspring or between *dura* and *tenera* full-sibs, as regards their s value. The same is true for m which is inversely related to s (see Table 11). A good correlation within full-sib families should however exist between shell-to-fruit ratio (weight or volume) of *dura* and shell plus fibre mantle (weight or volume) of *tenera* siblings, since in that case analogous characters are measured. The main objective of the following experiments is to obtain experimental evidence in support of above hypothesis.

7.2 Methods and materials

7.2.1 Structure of the fruit

Schematic longitudinal and cross sections of a *dura* and *tenera* fruit are shown in Fig. 13. Two types of fibres are to be distinguished: (1) thin and light-coloured fibres running longitudinally and distributed evenly throughout the mesocarp of *dura* and *tenera* fruits and (2) coarser dark-coloured fibres also running longitudinally, but mostly confined to a compact fibre mantle around the shell in the *tenera* fruit. A close look at the shell structure of *dura* and *tenera* fruits reveals that the shell is also made up of these coarse fibres which, due to lignification of the fibres and the tissue in between, form a stone-hard shell. The loose ends of these fibres form a fibrous tail at the basal end of the nut (kernel plus shell).

7.2.2 Comparing methods of measuring fruit composition

A total of 25 *dura* × *tenera* and *tenera* × *tenera* progenies with 25–60 palms per progeny, all planted at the OPRC, were selected for this investigation. A representative number of fruits from ripe bunches were sampled in the same way as for the fruit samples for the usual fruit analysis.

A first series of experiments, whereby the thickness of mesocarp, fibre mantle, shell and kernel was measured with a pair of calipers at cross-section (at about A–B in

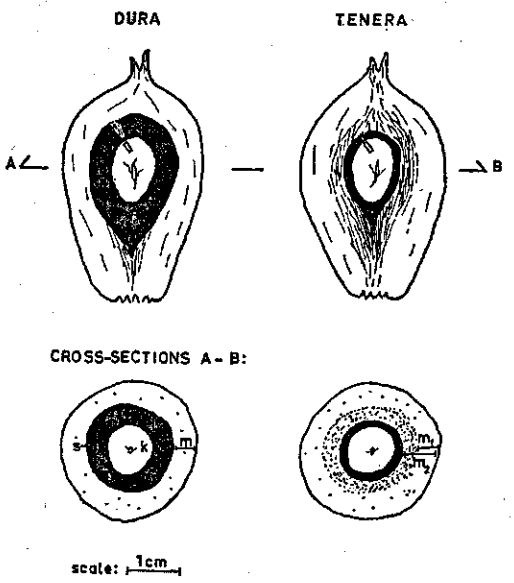

Fig. 13. Schematic longitudinal and cross sections of a *dura* and *tenera* fruit.
m = mesocarp in *dura* and mesocarp outside coarse fibre mantle in *tenera* (m_1)
m_2 = m_1 + coarse fibre mantle (f)
s = shell
k = kernel with embryo embedded in endosperm opposite germ pore

Fig. 13), did not yield the expected results. The correlation coefficient between mean shell thickness of *dura* fruits and the mean thickness of shell plus coarse fibre mantle of *tenera* fruits within progenies was only 0.20 (non-significant). Measurements at cross-section are apparently not representative of the whole fruit, especially since a large proportion of potential shell (shell in the *dura* fruits, shell plus fibres in the *tenera* fruits) is found below the kernel. This part may constitute more than 50% of the whole potential shell in some fruits.

A better approach would be to determine the weight or volume of the whole mesocarp, potential shell and kernel. Some preliminary trials showed that by careful scraping with a sharp knife the mesocarp outside the fibre mantle in *tenera* fruits (m_1 in Fig. 13) could be separated from the coarse fibre mantle. Since the specific gravity of mesocarp, fibre mantle, shell and kernel are not equal – s.g. mesocarp < 1, coarse fibre mantle > 1, shell 1.3–1.4 and kernel ≈ 1 – volumetric measurements are considered more appropriate for comparative purposes than weights. The principle of measuring the volume of irregular objects by displacement in water was applied in these experiments.

7.2.3 *Procedure for volumetric measurements*

The procedure of measuring the volume of the fruits and their components was as follows: glass bottles with extra-wide screw neck and bakelite caps are converted into volumetric flasks by fixing an inverted glass funnel, with a calibration mark at about the middle of the stem, on top of the cap of which the central part has been removed. The volume of the flask (V) is equal to the difference between the weight of the empty flask and of the flask filled to the mark with water, assuming s.g. = 1 for water. All

Table 13. Estimates of the repeatability R for single-fruit volume and ratios of fruit components from samples of 21 fruits per bunch; 19 bunches, 5–6 samples per bunch. Standard error of R estimated according to Swiger et al. (1964).

Component				
s fr. v.	m	s+f	s	k
0.85 ± 0.05	0.86 ± 0.11	0.80 ± 0.15	0.84 ± 0.12	0.93 ± 0.06

weighing was carried out with an accuracy of 0.1 g. The volume of a sample of clean undamaged fruits (14 inner and 7 outer fruits) is then determined by deducting the difference between the weights (flask + fruits) and (flask + fruit + water) from the value V. The fruits are subsequently scraped to the shell for *dura* fruits or to the coarse fibre mantle for *tenera* fruits after which the volume is determined in the manner described above. The volume of the mesocarp is the difference between the volume of whole fruits and scraped fruits. Subsequently the coarse fibre mantle of *tenera* fruits is scraped off and its volume calculated by the difference in volume between nut + fibre mantle and nut. The nuts of the *dura* and *tenera* samples are then sun-dried for a few days to facilitate cracking of the shell. The volume of the kernels is then measured; the difference between the volume of the nut and the kernel is the volume of the shell. The data are converted to ratios.

One possible point of criticism to this method is the assumption that s.g. = 1 for water, which is only true at + 4 °C. It will be less for water at ambient temperatures, usually 22–24 °C. However, since all volumes were determined by difference between the volume V and that of the objects, the actual error due to this factor must have been very small and it was, therefore, ignored in the calculations.

The most convenient sample size for these measurements was 21 (14 inner fruits and 7 outer fruits). Repeatability estimations (Falconer, 1960) with five to six samples of 21 fruits per bunch showed that this sample size was large enough to obtain sufficiently accurate estimates for the whole bunch. A summary of the results of the repeatability test is given in Table 13.

At least 3 bunches, well distributed in time, of each of 913 trees of the 25 progenies have been analysed volumetrically: 1683 *tenera* and 1453 *dura* bunches.

7.3 Results and discussion

7.3.1 The role of the fibre mantle

A summary of the results of the volumetric determinations of single-fruit volumes and the ratios of fruit quality components, i.e. means and coefficients of variation of the 25 progeny averages per fruit form, is presented in Table 14. The correlation

Table 14. Volumetric determinations of fruit quality components. Means of 25 *dura* × *tenera* and *tenera* × *tenera* full-sib families and variability between families.

Component	*tenera* bunches			*dura* bunches		
	mean	range	coeff. of var. (%)	mean	range	coeff. of var. (%)
s. fr. v. (cm^3)	9.1	5.9 – 11.8	19	11.0	7.3 – 13.8	16
m_1 (%)	72.0	63.4 – 79.8	5			
m_2 (%)	84.3	77.1 – 90.7	5			
m (%)				58.8	48.2 – 66.0	9
s+f (%)	20.4	16.4 – 25.3	12			
s (%)	8.1	5.5 – 12.0	21	31.5	26.9 – 38.7	12
k (%)	7.6	5.1 – 11.5	27	9.7	6.0 – 12.1	17

Table 15. Coefficients of correlation between *dura* and *tenera* full-sibs for the volumetric components of the fruits; 25 full-sib families.

dura	*tenera*					
	s. fr. v.	m_1	m_2	s+f	s	k
s. fr. v.	0.89***	·	·	·	·	·
m	·	0.82***	0.45*	·	·	·
s	·	·	·	0.94***	0.32	·
k	·	·	·	·	·	0.61***

* $P < 0.05$
*** $P < 0.001$

coefficients between relevant fruit components of *dura* and *tenera* full-sibs are given in Table 15. A very high positive correlation does indeed exist between shell-to-fruit (s) in the *dura* and shell + fibre mantel (s + f) in the *tenera* full-sibs. At the same time the correlation between *dura* shell and *tenera* shell is very low and insignificant. These results give thus strong experimental evidence to Sparnaaij's (1969) hypothesis that the shell in the *dura* fruit form corresponds with the shell + the fibre mantle in the *tenera* fruit form.

Not surprisingly, a very high positive correlation also exists between mesocarp-to-fruit (m) of *dura* and mesocarp outside fibre mantle (m_1) of *tenera* full sibs. On the other hand the correlation between m of *dura* and total mesocarp (m_2) of *tenera* full sibs is low and only significant for $P = 0.05$. The correlation coefficient for m in weight percentages between *dura* and *tenera* full-sibs obtained from conventional fruit and bunch analyses was for the same 25 progenies 0.54**.

A high positive correlation exists between single-fruit volume of *dura* and *tenera* full-sibs. There is also a highly significant, although considerably lower, positive cor-

relation between the respective k values.

The relation between *dura* and *tenera* full-sibs for the most interesting fruit quality components is presented diagrammatically in Figs 14–17.

7.3.2 The role of the kernel

An interesting correlation is that between k and the fraction s / (s + f) in *tenera* fruits. This fraction, the degree of lignification, has a value of about 0.50 when the kernel is relatively large, and especially when the value is similar in the *tenera* and

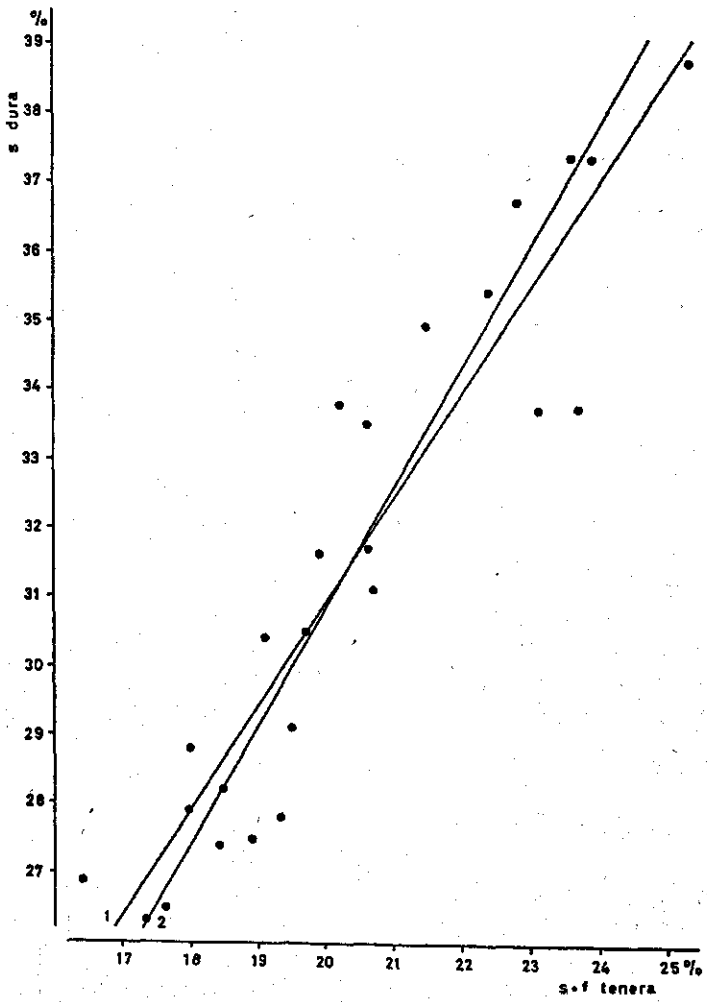

Fig. 14. Relation between shell volume (s) of *dura* and shell with fibre mantle volume (s+f) of *tenera* siblings: $r = 0.94^{***}$, $n = 25$.
Regression equations (1) $y = 0.79 + 1.51x$
(2) $x = 2.11 + 0.58y$

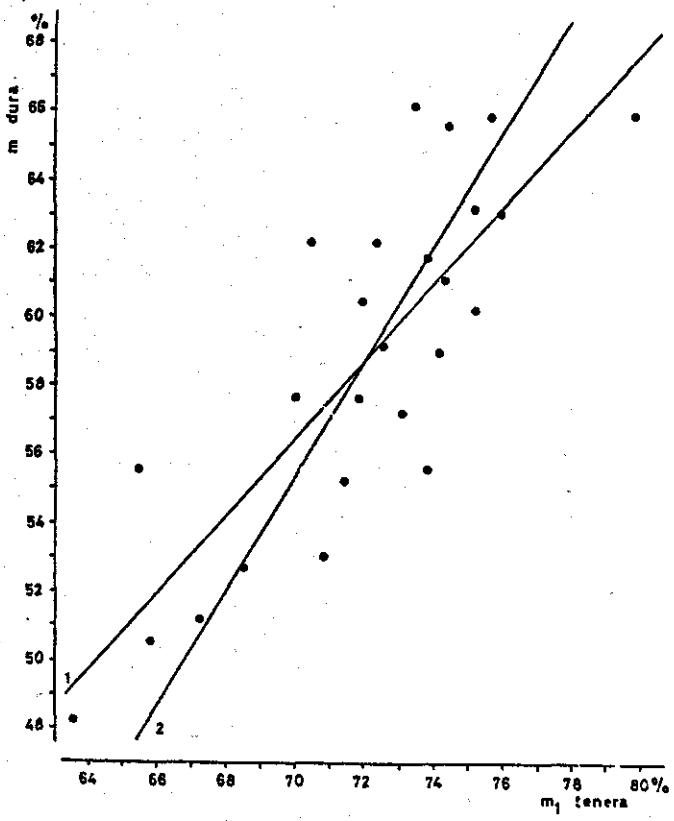

Fig. 15. Relation between mesocarp volume m of *dura* and mesocarp volume m_1 of *tenera* siblings: $r = 0.82^{***}$, $n = 25$.
Regression equations (1) $y = -22.23 + 1.13x$
(2) $x = 36.93 + 0.60y$

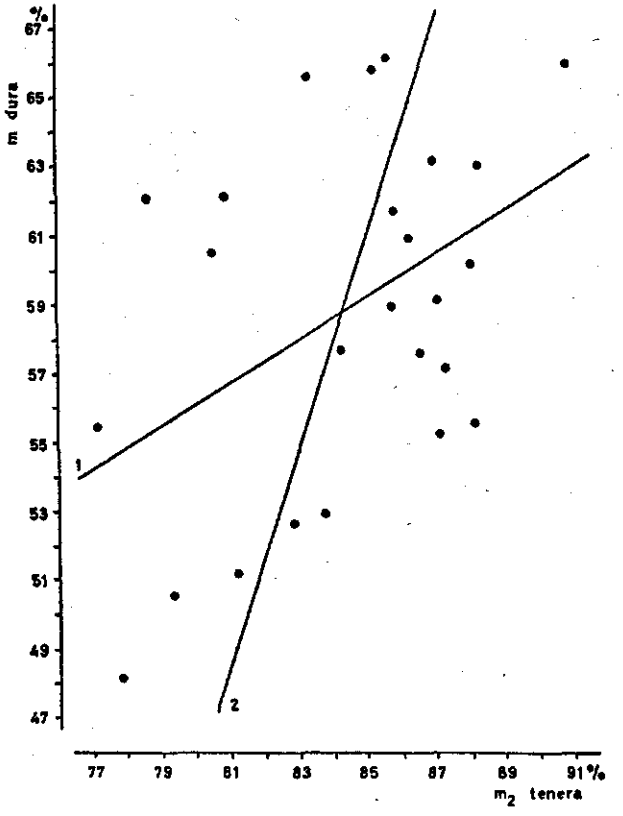

Fig. 16. Relation between mesocarp volume m of *dura* and mesocarp volume m_2 of *tenera* siblings: $r = 0.45^{*}$, $n = 25$.
Regression equations: (1) $y = 5.73 + 0.63x$
(2) $x = 65.41 + 0.32y$

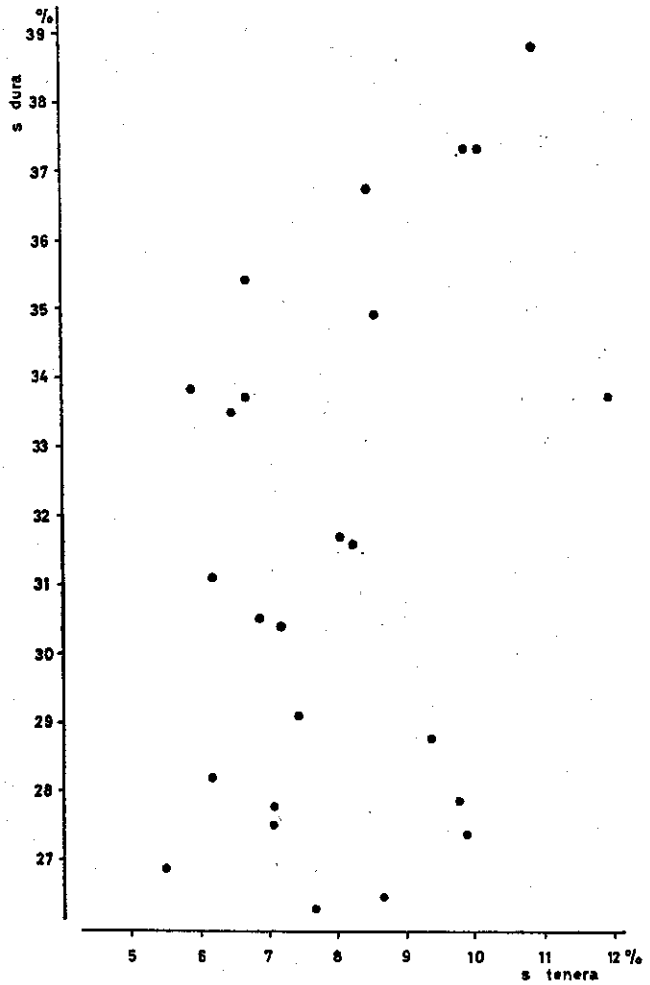

Fig. 17. Relation between shell volume (s) of *dura* and *tenera* siblings: r = 0.32, n.s.; n = 25.

dura full-sibs. The fraction is only 0.29–0.35, however, when k is relatively low and especially when k is much lower in the *tenera* than in the *dura* full-sibs. The correlation coefficient of the means of k and s / (s + f) in *tenera* fruits of the 25 progenies is 0.74***. A few demonstrative examples are given in Table 16, together with k values, for both parents. The data for the parents are from ordinary fruit and bunch analyses (weight percentages) carried out at the NIFOR.

When both parents have similar k values, the *tenera* and *dura* full sibs of their progeny will also have similar k's and the fraction s / (s + f) will be about 0.5. However, when one of the parents has a considerably lower value for k, this will apparently find its expression mainly in a lower k value for the *tenera* offspring. A lower k in

Table 16. Volumetric determinations, means of 8 *tenera* and *dura* full sibs.

Parents						*Tenera* offspring						*Dura* offspring		
cross ($P_1 \times P_2$)				k (%)[1]		m_1	m_2	s+f	s	s/(s+f)	k	m	s	k
				P_1	P_2	(%)	(%)	(%)	(%)		(%)	(%)	(%)	(%)
1.3056-T	× 32.3005-T	*tenera*	× *tenera*	5.1	7.9	73.8	88.1	20.2	5.9	0.29	6.0	55.6	33.8	10.6
5.1450-T	× 6.594-D	*tenera*	× *dura*	8.7	11.5	72.5	87.0	20.7	6.2	0.30	6.8	59.2	31.1	9.7
1.2209-D	× 38/0401-T	*dura*	× *tenera*	9.9	13.0	79.8	90.7	16.4	5.5	0.34	3.8	66.0	26.9	7.1
5.12-D	× 4.493-T	*dura*	× *tenera*	9.4	6.0	73.1	87.2	20.6	6.5	0.32	6.3	57.2	33.5	9.3
1.2227-D	× 1.2224-T	*dura*	× *tenera*	11.8	10.4	72.3	80.8	18.4	9.9	0.54	9.3	62.2	27.4	10.4
1.2229-T	× 5.1225-D	*tenera*	× *dura*	11.9	9.9	71.9	80.5	18.0	9.4	0.52	10.1	60.5	28.8	10.7
L232-T	× D22-D	*tenera*	× *dura*	7.1	6.6	74.5	83.3	17.5	8.7	0.50	8.0	65.6	26.5	7.9
A43-2-4-T	× A43-2-4-T	*tenera*	× *tenera*	14.9	14.9	65.4	77.1	23.7	12.0	0.51	10.9	55.5	33.7	10.8

1. Kernel-to-fruit ratio of the parents from ordinary fruit and bunch analysis.

tenera fruits corresponds with a lower value for s since the shell will envelop a smaller kernel and both ratios are generally of the same magnitude in *tenera* fruits, but the potential shell (s + f) is apparently not reduced in the *tenera* fruit. The fraction s / (s + f) becomes lower, but the correlation between s (*dura*) and s + f (*tenera*) within progenies remains high.

This would strongly suggest that the fraction s / (s + f) is inherently 0.5, but that the independent variation in kernel size, as explained above, can mask this.

7.3.3 Conclusions

The genetic background of the inheritance of the shell-to-fruit ratio will thus be as follows. The potential shell-to-fruit ratio is a quantitative character inherited through polygenes, while the percentage lignification of the potential shell is determined by one major gene, which causes 100% lignification if both dominant alleles are present (*dura*), 50% in the case of presence of one dominant allel (*tenera*) and no lignification when both alleles are recessive (*pisifera* fruit form). The percentage lignification in *tenera* fruits may deviate from 50% under the independent variation of kernel size.

When s / (s + f) = 0.5 in the *tenera* fruit, the correlation shell-to-fruit, (and thus also for mesocarp-to-fruit) between *dura* and *tenera* full sibs will, naturally, be high. This may well explain why Gascon et al. (1963) found a high correlation. The majority of the 86 progenies studied must have had parents with similar k values, as can be deduced from the description of the material. Only in five crosses between Yangambi and Deli material, i.e. large × small kernel, the ratio s / (s + f) will have been lower. On the other hand the 96 crosses studied by Meunier et al. (1970) include 23 Yangambi × Deli crosses, reason why they found a considerably lower correlation. Additional evidence could be obtained from the 104 NIFOR *dura* × *tenera* progenies. The correlation coefficient between the m values of *dura* and *tenera* full sibs increases from 0.40 to 0.74, when a number of progenies of which the parents are contrasting in their k values are left out.

For the oil palm breeder the practical implication of the nature of the inheritance of shell-to-fruit ratio, the most important component of fruit quality, is that for *dura* palms the A_t value of this component can only be obtained by sib-selection (from the mean of the *tenera* full sibs) or by progeny testing in *dura* × *tenera* crosses.

8 Variability and heritability of oil and dry-fibre content in the mesocarp of mature oil palm fruits

8.1 Introduction

8.1.1 Variability

The relative economic value of the fruit quality component oil-to-mesocarp (o_m) is higher than that of any of the other fruit quality components (see Table 10). The variation found in present-day breeding populations is considerable and individual palm values for the o_m value may range from 40 to 60%. It is thus an important selection factor. However, from the estimates of heritability for components of oil yield in Table 7 and from those given by Meunier et al. (1970) it appears that h_n^2 for this component is low and insignificant. This may, to a certain extent, be the result of using in the estimation data from trees in the first year of production, when the o_m value can be extremely low and variable. Such low values apparently do not bear any relation to the inherent oil content of mature palms. Somewhat higher values of h_n^2 will thus be obtained when this 'age effect' is eliminated by excluding bunches from very young palms. Besides this, other non-genetic causes of variance are of considerable magnitude (Sparnaaij, 1969) so that h_n^2 for o_m will never be high.

From this it follows that multiple measurements are required over a considerable period of time to obtain reliable estimates of genotypic values. Direct oil content determinations of a representative sample of fruits from a bunch either by Soxhlet extraction (Blaak et al., 1963) or by the 'oléomètre' (Servant et al., 1963), although accurate, are very labour and capital intensive. Consequently, in large selection programmes such as that of the NIFOR or the IRHO where 50–100 samples may have to be determined per day, the total capital layout for oil determination alone is very high.

8.1.2 Relations between oil, water and fibre in the mesocarp

The mesocarp of oil palm fruits is made up of the three components: oil, water and dry matter, the latter mainly consisting of fibres. Vanderweyen et al. (1947) concluded from studies carried out at Yangambi that the dry-fibre content has a fairly constant value, about 16% of the fresh mesocarp. This was later confirmed by Desassis (1955a, b) in Dahomey (IRHO), who also suggested that dry-matter content was independent of the degree of maturity of the fruits, and by Chapas et al. (1957) in Nigeria (NIFOR). A fairly simple indirect method of oil content determination could thus be applied by

determining the water content only and by calculating the oil content from the equation:

$$o_m = 84 - w_m \quad (5)$$

where: o_m = % oil to mesocarp,
w_m = % water to mesocarp.

Apparently, these studies have been carried out with material of very limited variability. More extensive studies carried out in Nigeria (NIFOR) revealed that there existed considerable variation of the dry-matter content due to genetic and environmental causes of variance (NIFOR annual report, 1962; Blaak et al., 1963), thus raising some doubts about the reliability of the indirect method.

8.2 Object of the experiments

If the genetic proportion of the total variance observed for the dry-fibre content is high, considerably higher than for the oil content, it should be possible to make reliable estimates of the progeny mean fibre-to-mesocarp ratio by a limited number of direct analyses by Soxhlet extraction. The oil content of subsequent samples can then be estimated by a modified indirect method by substituting this mean fibre content and the measured water content in the following equation:

$$o_m = 100 - f_m - w_m \quad (6)$$

where: f_m = % fibre (= dry matter) to mesocarp.

The main object of the following experiments has been to obtain estimates of heritability of o_m and f_m and additional information about optimal sampling techniques.

8.3 Methods and materials

A total of 411 *tenera* and 305 *dura* palms, representing 29 different full-sib families, of which 12 were planted in 1961, 10 in 1964, 4 in 1966 and 3 in 1967, all at the OPRC, were repeatedly sampled during the period January 1970 to July 1971.

For the water, oil and fibre content determinations the NIFOR procedure (Blaak et al., 1963) was followed with some modifications.

A preliminary test showed that detached fruits lose weight due to evaporation of the water in the mesocarp at a rate of 2–3% per 24 hours, while scraped mesocarp loses weight even more rapidly. The weight of the fresh mesocarp was, therefore, calculated from the difference of the weight of the fruit sample taken from the bunch on the day of harvesting and the weight of the nuts a few hours after removing the mesocarp. A delay of several days between weighing the fresh fruit and depulping by scraping is unavoidable when many samples have to be processed, but this does not affect the oil quantity (Blaak et al., 1964), After scraping, all mesocarp of the fruit

sample is collected carefully and transferred to a Killner jar.

Moisture content of the fresh mesocarp is determined from the difference between fresh and dry weight after 24 hours drying in an oven at 105 °C. About 25 g dry mesocarp is minced in a household mincer, re-dried for 24 hours at 105 °C, then left to cool in a desiccator after which duplicate 5 g samples are transferred to filter paper containers plugged with cottonwool. Since minced dry mesocarp is very hygroscopic, the containers with 5 g samples are returned to the oven to dry another hour at 105 °C after which they are left to cool in a desiccator, then weighed and placed in the 600-ml Soxhlet extractor which can contain 24 samples. Petroleum ether (specific boiling point 60–82 °C) was used as solvent for the oil extraction.

Some trials showed that after about 4 hours over 91% and after 10 hours more than 98% of the oil had been extracted. Little was gained by longer extraction and the extraction period was, therefore, fixed at 11 hours. In this way it was possible to extract 24 duplicate samples per day with one Soxhlet apparatus, the duplicate samples being extracted in different runs.

After completion of the extraction period, all samples are removed, left to dry on the laboratory bench to remove excess petroleum ether, then dried 24 h at 105 °C, cooled to room temperature in a desiccator and weighed. The oil quantity is equal to the difference in weight between the dry mesocarp sample before and after oil extraction and the value is converted to % oil of fresh mesocarp, In over 95% of all cases the difference in percentage oil in the fresh mesocarp between the duplicate samples was less than 2%.

Repeatability estimations with five 21-fruit samples per bunch for 16 bunches, each from a different palm have indicated that a sample of 21 fruits is adequately representative for the whole bunch (see also 7.2). A summary of the repeatability test is given in Table 17.

Table 17. Estimates of the repeatability R for the ratios water to fresh mesocarp, oil to fresh mesocarp and fibre to fresh mesocarp from samples of 21 fruits per bunch; 16 bunches, 5 samples per bunch. Standard error of R estimated according to Swiger et al. (1964).

Component		
w_m	o_m	f_m
0.95 ± 0.02	0.93 ± 0.03	0.95 ± 0.02

8.4 Results and discussion

8.4.1 Influence of degree of maturity of the fruit

To obtain information about the changes in oil, water and dry-fibre content of the mesocarp during the last stage of maturation, samples of 21 fruits were taken at intervals of four to five days from 36 days before (day −36) to 4 days after (day + 4) optimal maturity from 20 bunches harvested on different trees. The results of three bunches with equal o_m value at maturity are presented diagrammatically in Fig. 18. Since the water content decreases proportionally with the increase in oil content, only the percentages oil and dry fibre in the fresh mesocarp are given. These data confirm the earlier results published by Dessassis (1955b): while the oil content increases rapidly during the last 25–30 days of maturation, the dry fibre content remains fairly constant. On day + 4 the majority of the fruits have become detached and a drecrease in fresh weight of the mesocarp due to evaporation, especially at the base of the fruits, may bring about the observed slight increase in oil content.

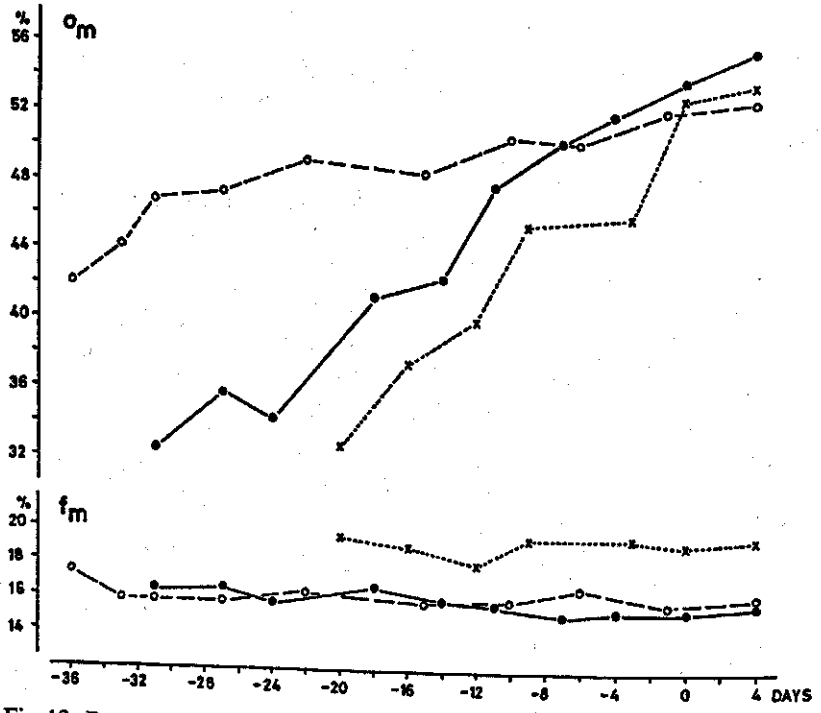

Fig. 18. Progression in oil (o_m) and fibre (f_m) content of the fresh mesocarp from 36 days before to 4 days after optimal maturity of 3 palms in Expt 851.

Symbol	Palm
●——●	851.53-T
○----○	851.607-D
×.....×	851.381-D

The data also emphasize the importance of harvesting the bunches at optimal maturity. The practice of harvesting slightly underripe bunches, as applied at the NIFOR in order to obtain good estimates of the fruit-to-bunch ratio, may be the cause of high non-genetic variation in the o_m value.

The increase of the oil content during maturation is different from palm to palm as is shown in Fig. 18: from day −14 to day 0 the order of importance of the three palms is changed twice and especially for palm 851.381D the oil determination of a slightly unripe bunch would highly underestimate its ultimate oil content. Slightly unripe bunches were, therefore, as much as possible excluded from oil determinations.

8.4.2 Seasonal variation

Another important aspect is the seasonal variation in oil and fibre content which was observed at the NIFOR (NIFOR annual report 1962; Blaak et al., 1963). This was confirmed at the OPRC in Ghana as can be seen from Fig. 19 in which mean

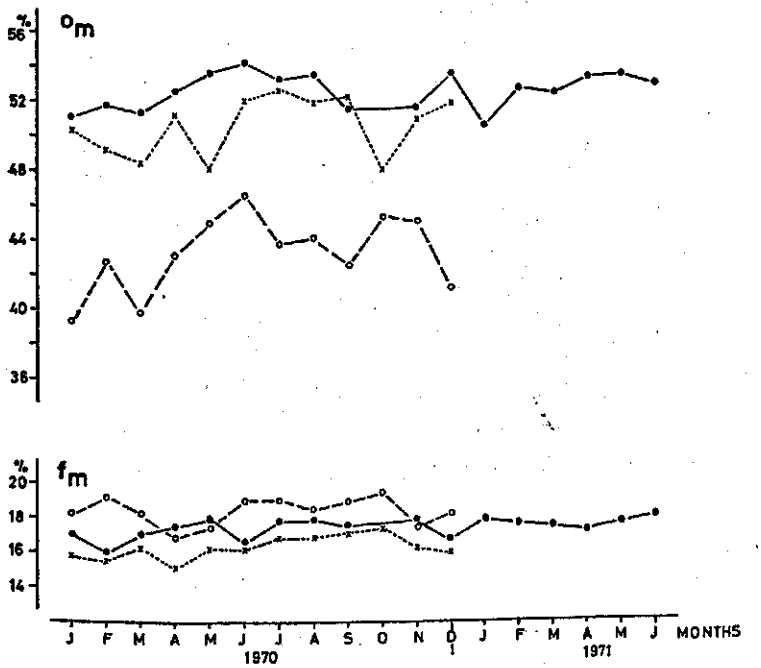

Fig. 19. Seasonal variation in the mean oil (o_m) and fibre (f_m) content of the fresh mesocarp of *tenera* bunches of 3 progenies.
Mean content and standard error over the whole period per progeny:

Symbol	Progeny	o_m (%)	f_m (%)
●——●	1.2227-D × 1.2224-T	52.5 ± 1.03	17.4 ± 0.54
○——○	1.53-D × 32/0401-T	43.0 ± 2.25	18.4 ± 0.77
×.....×	1.3056-T × 32.3005-T	50.6 ± 1.69	16.3 ± 0.64

tenera progeny values of o_m and f_m have been plotted per month for three different progenies, one for a period of 18 months, the other two for one full year. The monthly variation within progenies is considerable for both components, but the three progeny means are clearly distinct. This indicates that reliable progeny means can only be obtained, especially for o_m, from a large number of determinations which cover at least one full year (excluding small bunches from palms in the first year of production).

8.4.3 Differences between tenera and dura fruit forms

Averages of the mean values for the 29 progenies under study computed from about 1500 *tenera* and 1050 *dura* bunches harvested during the period January 1970–July 1971 are presented in Table 18. One 21-fruit sample was taken of each *dura* bunch and two of each *tenera* bunch. One of the *tenera* fruit samples was used to determine oil and fibre in the mesocarp outside the fibre mantle $o(m_1)$ and $f(m_1)$, while from the other samples these components were determined in the whole mesocarp: $o(m_2)$ and $f(m_2)$.

Tests of significance of the differences between *dura* and *tenera* full sibs for oil and dry-fibre to mesocarp for 21 *dura* × *tenera* and *tenera* × *tenera* progenies as well as their correlation coefficients are summarized in Table 19.

While the difference in dry-fibre content is highly significant when $f(m_2)$ of *tenera* palms is compared to f_m of the *dura* full sibs, this difference is insignificant for the mesocarp outside the coarse fibre mantle ($f(m_1)$) of the *tenera* and f_m of the *dura* full sibs. This forms additional evidence of the actual relation, regarding m and s values, between *dura* and *tenera* full sibs shown in Chapter 7. The dry-fibre content of the coarse fibre mantle, determined in fruits of a number of *tenera* bunches, is much higher, ranging from 21–31%. This explains why the dry-fibre content taken over the whole mesocarp of *tenera* fruits is generally higher than for *dura* fruits. On the other hand, oil content in the coarse fibre mantle is generally not higher than 12–20%. It is, therefore, not surprising that, although $o(m_1)$ of *tenera* palms is significantly higher than o_m in *dura* full sibs, $o(m_2)$ is somewhat lower ($P < 0.05$). The correlation between *dura* and *tenera* full sibs is very high in all cases.

Table 18. Mean ratios (%) oil to fresh mesocarp and fibre to fresh mesocarp of 29 full-sib families.

	tenera fruits				*dura* fruits	
	$o(m_1)$	$o(m_2)$	$f(m_1)$	$f(m_2)$	o_m	f_m
Mean	52.6	48.7	15.0	16.8	49.8	15.3
Coeff. of var. (%)	4	5	5	5	5	4
Range	47.3 – 56.7	42.0 – 52.3	14.1 – 17.2	15.3 – 19.0	44.2 – 55.6	14.4 – 16.6

Table 19. Relationship[1] between *tenera* and *dura* full sibs for oil and dry fibre content of mesocarp; 21 full-sib families.

dura	*tenera*			
	$o(m_1)$	$o(m_2)$	$f(m_1)$	$f(m_2)$
o_m				
$\bar{d}$	2.15	-1.89	·	·
r	0.91***	0.88***	·	·
t	2.98**	2.75*	·	·
f_m				
$\bar{d}$	·	·	-0.38	1.51
r	·	·	0.78***	0.67***
t	·	·	1.25 n.s.	4.22***

1. $\bar{d}$ = mean difference between *tenera* and *dura* full sibs (%)
r = correlation coefficient
t = $\bar{d}/s_{\bar{d}}$, test of significance of $\bar{d}$ (Snedecor & Cochran, 1968).
* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$
n.s. not significant

8.4.4 Heritability estimations

Estimates of the proportion of genetic variance to total variance (heritability in the wide sense) for the o_m and f_m values were made from estimates s_b^2 and s_w^2 of the components of variance between and within progeny (σ_b^2 and σ_w^2 respectively) from an analysis of variance for biparental progenies (Falconer, 1960; Mather & Jinks, 1971), in this case the *tenera* palms of 15 full-sib families of the progeny trials 851 (1961) and 852 (1964) at Kade, Ghana. The estimates of the components σ_b^2 and σ_w^2 have the expectations:

$$Es_b^2 = \tfrac{1}{2}\sigma_A^2 + \tfrac{1}{4}\sigma_D^2 + \sigma_{EC}^2 \qquad (7)$$

and

$$Es_w^2 = \tfrac{1}{2}\sigma_A^2 + \tfrac{3}{4}\sigma_D^2 + \sigma_E^2 \qquad (8)$$

where: σ_A^2 = component of genetic variance due to additive effects
σ_D^2 = component of genetic variance due to dominance effects
σ_{EC}^2 = component of variance due to common environment of the families
σ_E^2 = component of variance due to general environmental causes (= error variance).

The heritability in the wide sense is equivalent to:

$$h_w^2 = (\sigma_A^2 + \tfrac{1}{2}\sigma_D^2) : (\sigma_A^2 + \sigma_D^2 + \sigma) \quad (9)$$

and can be estimated from the components of variance between and within progeny, provided the component of variance due to common environment of the families (σ_{EC}^2) is negligible:

$$h_w^2 = \frac{2\,\sigma_b^2}{\sigma_b^2 + \sigma_w^2} \quad (10)$$

However, above expectations involve the following assumptions (Lerner, 1958; Cockerham, 1963): (1) normal diploid Mendelian inheritance, (2) not more than two alleles at many loci and small effects of allelic substitutions, (3) no inbreeding, (4) no linkage, (5) no epistasis, (6) no genotype-environment interaction. Assumption (1) is most likely to be valid in the case of the oil palm (Thomas et al., 1969) and also (2) should be acceptable for the two quantitative characters studied here. Crosses between somewhat related parents could not always be avoided completely, since otherwise the number of full-sib families would become very low. The assumptions (4)–(6) cannot be tested in the breeding design utilized here. Besides, the low number of full-sib families and of palms per family (see Table 20) does not allow for very accurate estimations. It is thus realized that below interpretation of the components of variance is only a tentative approach.

Estimates of h_w^2 from the 15 progenies together and from 6 progenies in Experiment 851 and 9 in Experiment 852 separately for oil and dry fibre content of *tenera* mesocarp are given in Table 20. It is remarkable how the high value of h_w^2 for oil content obtained when all 15 progenies are pooled, drops to a low value when only progenies of the same experiment are considered in the analysis of variance. On the other hand the values of h_w^2 for dry-fibre content remain of the same magnitude. Expt 851 was planted in 1961 and Expt 852 in 1964. Besides, the production level in Expt 851 is considerably higher than in Expt 852, mainly due to differences in water availability in the soil during the dry season (see Chapter 9). This difference between the experiments has apparently produced a high σ_{EC}^2 for the oil content ratio, reason why the

Table 20. Estimates of wide-sense heritability and standard error for oil-to-mesocarp and fibre-to-mesocarp ratios of *tenera* fruits.

Number of progenies	n_0[a]	$\hat{h}_w^2$[a]	
		o_m	f_m
15 (Expts 851, 852)	15.4	0.98 ± 0.25	0.88 ± 0.24
6 (Expt 851)	17.0	0.31 ± 0.21	0.95 ± 0.38
9 (Expt 852)	12.8	0.30 ± 0.23	0.72 ± 0.31

a. n_0 = weighted number of palms per progeny according to Snedecor & Cochran (1968).

estimate for h_w^2 is highly inflated and formula (10) is not applicable. The magnitude of σ_{EC}^2 is reduced considerably when only progenies of the same experiment are included in the analysis of variance with the result that the estimate of h_w^2 is much lower and probably much closer to its actual value. The component σ_{EC}^2 is apparently low for the dry-fibre content, since estimates for h_w^2 are high in each of the three analyses of variance.

For reasons given above not too much value should be attached to the actual values of h_w^2 obtained. Nevertheless, there is substantial evidence that the genetic proportion of the total variance observed is likely to be much higher for f_m than for o_m.

8.4.5 Repeatability estimations

Information on the magnitude of h_w^2 for bunch and fruit quality components can also be obtained from components of variance within palm (σ_w^2) and between palms (σ_b^2). The component σ_b^2 has σ_{EC}^2 in its expectation. This component σ_{EC}^2 is the between-palm variance due to persistent environmental differences such as water availability and fertility of the soil. The ratio of σ_b^2 to $\sigma_b^2 + \sigma_w^2$, called the repeatability R of the character, may thus estimate the upper limit of h_w^2 (Falconer, 1960).

Estimates of R for the ratios oil and dry fibre to mesocarp for 37 *tenera* palms (7 bunches per palm) in Expt 851 and again for 29 *tenera* palms (6 bunches per palm) in Expt 852 are presented in Table 21. Estimates of R for the other important bunch and fruit quality components, from which accurate estimates of h_n^2 are available (Table 7), have been included in that table for easy comparison. The estimates of R for fr_b are based on the usual spikelet sample per bunch; for the fruit quality components 21-fruit samples were taken. Harvesting dates of the bunches covered as much as possible one full year.

Again R appears to be considerably higher for f_m than for o_m. The value of R for m and k could be expected to be high, in view of the high heritability h_n^2 of these components (see Tables 7 and 8).

Table 21. Estimates of the repeatability R for components of bunch and fruit quality of *tenera* palms from 2 experiments. Standard error of R estimated according to Swiger et al. (1964).

Component	Expt 851	Expt 852
o_m	0.46 ± 0.10 (N=37, n=7)[1]	0.52 ± 0.09 (N=29, n=6)
f_m	0.73 ± 0.06 (N=37, n=7)	0.71 ± 0.07 (N=29, n=6)
fr_b	0.17 ± 0.06 (N=36, n=8)	–
m	0.90 ± 0.02 (N=36, n=8)	–
k	0.82 ± 0.04 (N=36, n=8)	–

1. N = number of palms, n = number of bunches per palm.

There is good reason to assume that the σ^2_D will be of minor importance for f_m and o_m, as it is for the other fruit quality components.

Tentative estimates of h^2_n, based on all available data from above described experiments, may then be 0.25–0.40 for o_m and 0.60–0.80 for f_m.

This should, of course, be verified by more reliable estimates obtained from offspring-parent regressions or by intra-class correlations from full-sib and half-sib families or other suitable designs. At the time of the above described studies suitable populations were not available for such estimates.

8.5 Practical implications for routine determinations of mesocarp oil content

A practical implication of above results is that it is justified to apply an indirect and consequently less expensive method of estimating oil to mesocarp, using equation (6), provided the progeny mean value of the dry-fibre content is first determined from a limited number of direct analyses. The stage of ripeness of the bunches used to determine the dry-fibre content is, within limits, less important that that of bunches for direct oil analysis (see Fig. 18). The dry-fibre content is also less affected by the 'age effect' and provided the very first small bunches are excluded, the bunches harvested in the first year of production can be used to estimate the mean fibre-to-mesocarp ratio of a full-sib family by direct analysis of a few bunches per month per family. These values are then used in the second year of production to estimate the oil content of the mesocarp by the modified indirect method, taking care to sample fully ripe bunches only. The water content can be accurately measured from all mesocarp of a 21-fruit sample. This procedure should yield reliable estimates of A values for oil to mesocarp at a reasonable cost.

The direct determination of the fibre content can be done by Soxhlet extraction, for which a single sample of 5 g water-free finely minced mesocarp appears to be adequate, or by a cold extraction method, developed by Blaak (1970), which he claims to be less expensive.

9 Water stress: an important cause of environmental variance for growth and bunch production in the oil palm in West Africa

9.1 Introduction

9.1.1 Physiological effects

The photosynthetic activity of the heliophile oil palm is at its maximum only under conditions of bright sunshine and optimum rate of transpiration, i.e. when water availability is unrestricted. Cuticular transpiration in the oil palm is negligible and transpiration is regulated effectively by the movement of the semi-xeromorphic stomata which are only found on the abaxial surface of the leaflets (Rees, 1961). Wormer and Ochs (1959) found a direct relation between rate of transpiration and stomatal aperture as measured by the infiltration technique described in 9.2. The stomatal aperture and thus transpiration decreases progressively as water stress in the palm increases, but a saturation of the leaf tissues of over 90% at midday is maintained until close to the wilting point (Ochs, 1963). The oil palm is in this way able to survive prolonged periods of water stress, though, obviously, growth and production are seriously restricted. The whole metabolism of the plant comes to a gradual standstill and sunshine received during such periods of water stress will be ineffective for photosynthesis.

9.1.2 Seasonal variation

In West Africa there is a main period of water deficit, usually between November and March, coinciding with high insolation. The extent of the period of actual water stress in the palm during that period is the main yield limiting factor. An exploratory irrigation trial carried out in the Ivory Coast (Desmarest, 1967) has indicated that, by maintaining soil moisture at field capacity, oil palm yield levels in West Africa can be brought close to those of Malaysia and Sumatra, where periods of water deficit are generally of minor importance or totally absent, when soil moisture is maintained at field capacity. The mean annual water deficit computed from monthly water balances is a useful parameter to delineate in broad terms areas climatically favourable for oil palm production in West Africa (Olivin, 1968; van der Vossen, 1969b).

9.1.3 Effective sunshine and water stress

The second important yield limiting environmental factor is total hours of sunshine. Total insolation at Sassandra in the Ivory Coast near the actual site of the irrigation trial is more than 2200 h/a (Desmarest, 1967), approaching values obtained in Malaysia and Sumatra. However, in many areas suitable for oil palm cultivation in West Africa total of hours of sunshine per annum is considerably lower and more variable (Hartley, 1967). The parameter effective sunshine (E.S.) takes both factors, water availability and sunshine hours, into account. Sparnaaij et al. (1963) found a high correlation between mean annual yield of a mature oil palm field and E.S. for corresponding periods 28–30 months earlier (see also 2.3).

The nutrient status of the oil palm can also be a yield limiting factor, but Ruer (1966) and van der Vossen (1970) demonstrated that the correlation between leaf potassium or phosphorus content and yield was high and significant only in years with corresponding E.S. exceeding 1600 h/a.

Besides its application in agronomic research, the parameter E.S. also enables the breeder to make corrections for between-year effect when the results of progeny trials of different age are to be compared.

9.1.4 Variations due to soil type and topography

Sparnaaij et al. (1963) estimated available water at field capacity to be about 1.2 mm/cm soil for soils at the NIFOR. In contrast to the free draining and uniform sandy soils at the NIFOR and the IRHO (see Hartley, 1967 for soil descriptions) the major upland soils at the OPRC are clay to silty clay soils, derived from pre-Cambrian phyllites, with frequent to abundant ironstone concretions and quartz gravels in the subsoil. Only the colluvial soils at the lower slopes are free from gravels (see Obeng, 1959, for a description of soils near Kade).

Even within one progeny trial there frequently exists a considerable variation in soil series having widely different water-holding capacities, resulting in large differences in the duration of periods of water stress. This was thought to be the major cause of large environmental between-block and sometimes even within-plot variances in bunch production observed particularly in a progeny trial, Expt 851, planted in September, 1961.

Expt 851 was thus considered an ideal object to study the effect of varying periods of water stress on bunch yield and its components and some growth parameters. The stomatal aperture test was used to estimate accurately the actual period of water stress in individual palms.

9.2 Methods and materials

9.2.1 Measurement of the stomatal aperture

Stomatal aperture was measured using an infiltration technique with aqueous isopropanol solutions as described by Wormer & Ochs (1959), Rees (1961) and Ochs (1963). Twelve solutions were prepared with increasing surface tension, solution No. 1 being 100% isopropanol and solution No. 12 only 45% isopropanol. Penetration of these solutions through the stomata on the abaxial surface of the leaflets of the oil palm can be observed as the appearance of scattered dark spots of intercellular flooding. A droplet of each solution, starting with No. 1, is applied to the leaf surface, and the number of the solution which is just able to infiltrate into the stomata is an index of the stomatal aperture. When even solution No. 1 is unable to penetrate, the stomata are considered closed and transpiration rate of the palm will be negligible.

The stomatal aperture is uniform over the whole leaf surface except for the area close to the midrib where they tend to open more widely. Preliminary experiments showed that the stomatal aperture does not vary much between leaflets of the same leaf or between leaves of the same palm, except for the very young leaves (less and more variable aperture). The stomata of the oil palm are also much less light and temperature sensitive than those of e.g. the groundnut or coffee (Wormer & Ochs, 1959; Wormer 1965).

For the purpose of standardization, two leaflets of Leaf 17, which is at about the midcrown of the palm, were sampled. Since Leaf 17 of a 8–10 year old palm is beyond normal reaching distance, a hooked knife attached to a pole was used to cut the two leaflets from Leaf 17. This is permissible as the stomata of a leaflet start to close about five minutes after severing it from the leaf (Wormer & Ochs, 1959). The solutions were applied to both leaflets and the mean of the two readings taken as the index of stomatal aperture for the palm.

Typical daily curves of stomatal movement have been presented by Rees (1961) and Ochs (1963) and these have been confirmed by observations on individual palms in Expt 851. The largest differences between palms with or without water stress are observed between 13.00 and 15.00 h. Sampling was, therefore, carried out in the field during this period. One team of two recorders could sample 25–30 palms in the course of these two hours. Stomatal aperture was determined at weekly intervals on each of 115 palms between November 1968 and April 1969 and on each of 132 different palms between November 1969 and April 1970.

9.2.2 Application in a field experiment

The 12 progenies in Expt 851 have been planted according to a complete randomized block design, in four replications with 12 palms per plot. The experiment is on a gentle slope covering a catena of soil series, starting from sedentary upland soils in block 4 to colluvial soils in blocks 2 and 3, the latter bordering on alluvial valley

bottom soils which are water-logged during the greater part of the year.

The yield was recorded in the usual way from the first year of production in 1965. In May 1971 leaf length, number of leaflets and leaf area of Leaf 17, estimated according to a method developed by Hardon et al. (1969), were determined of six central palms in each of the 48 plots. In an adult oil palm plantation the number of leaves per palm is kept fairly constant because of harvesting and pruning practices. The mean number of leaves per palm in Expt 851 varied between 32–36 and no significant progeny effect on number of leaves could be detected. Hardon et al. (1969) showed that a good estimate of mean leaf area could be obtained by measuring the area of one leaf at midcrown and leaf area of Leaf 17 is considered a valid index of leafiness of a mature palm.

Leaf samples were taken in 1969 from a representative number of palms and sent to the NIFOR for foliar analysis. The nutrient status of all the palms was satisfactory (see van der Vossen, 1970, table 12) and could thus not be a factor limiting yield.

9.3 Results

9.3.1 Data on stomatal aperture

Progression of stomatal aperture during the dry season varied indeed widely between palms. The readings of the stomatal test were converted into number of dry days as follows. If the index for a palm was 8 or higher at a particular moment, the 7 preceding days were counted as wet i.e. water stress of that palm was low. The 7 preceding days were counted as dry days when the index was 7 or lower. Index 8 was taken as the critical value, since at that index of stomatal aperture transpiration rate of the palm is reduced to about 50% (Ochs, 1963).

The progression of stomatal aperture for the period November 1968 to April 1969 for palms with respectively 0, 35 and 91 'dry days' is presented diagrammatically in Fig. 20, together with weekly rainfall for corresponding periods. Stomatal movement of the palm with 91 dry days, which is situated on the upper slope where soils are very concretionary, closely follows the rainfall pattern, indicating that the water holding capacity of that particular soil is low. The palm with 0 dry days is planted on a colluvial soil close to the valley bottom. Water storage capacity of this soil is apparently high. The palms in that area of the experiment may also benefit from seepage water coming from the upper slope as well as from a fairly high groundwater table, as they are bordering on the valley bottom swamp.

9.3.2 Yield of palms in relation to water stress

Yield progression graphs for palms with four different dry-day regimes are presented in Fig. 21. Each graph represents the mean of about 20 palms. Cumulative yield over six years is for the palms with 0–7 dry days (1968/69 dry season) almost

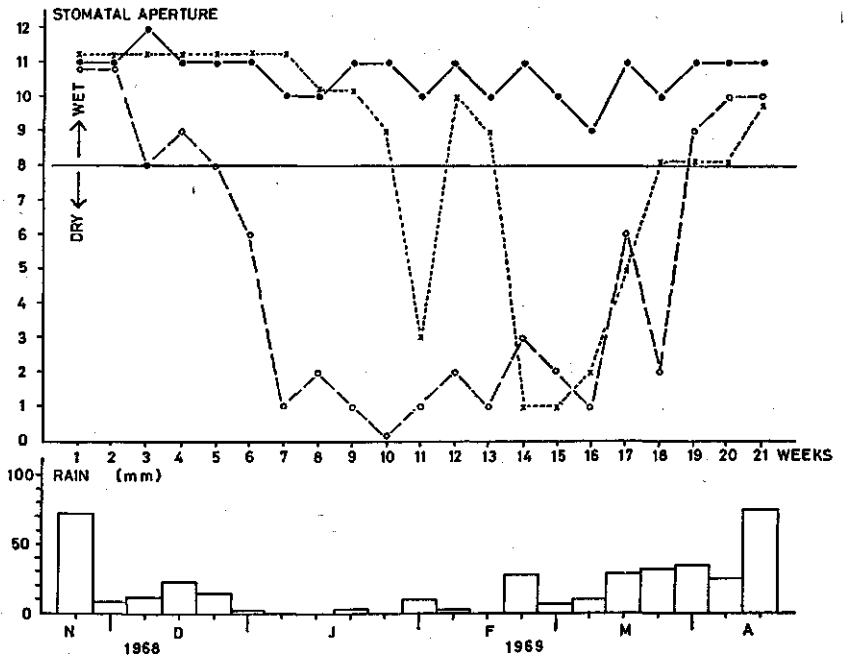

Fig. 20. Progression of stomatal aperture (index 0–12) for 3 palms during the 1968/69 dry season in Expt. 851. Weekly rainfall data are presented in lower histogram.

Symbol	No. of dry days
●——●	0
O----------O	91
×.....×	35

three times that for the palms with 84 or more dry days: 87 versus 31 t/ha.

Progeny means for bunch yield and its two components, growth parameters of Leaf 17 and leaf area index (LAI) for 9 progenies are given in Table 22. Three other progenies in Expt 851 are actually samples of commercial D × P material and thus not full-sib families as the other nine, reason why they have been left out. There are statistically significant differences between the progenies for all characters except leaf length. An analysis of variance of mean number of dry days per plot showed that there was no significant progeny effect on stomatal aperture.

The correlation between cumulative yield for the first 4 years (1965–68) and number of dry days measured in 1968–69 for 115 individual palms was negative and highly significant: $r = -0.68^{***}$. The correlation coefficient increased to $r = -0.71^{***}$ when yields were corrected for progeny effect. The latter correlation is presented diagrammatically in Fig. 22. The correlation between number of bunches (1965–68) and number of dry days (1968–69) was $r = -0.68^{***}$. The coefficient of correlation between cumulative yields of the first 5 years (1965–69) and number of dry days measured in 1969–70 for 133 palms was $r = -0.64^{***}$. The correlation coefficient was somewhat lower ($r = -0.58^{***}$) for the 115 earlier mentioned palms, when

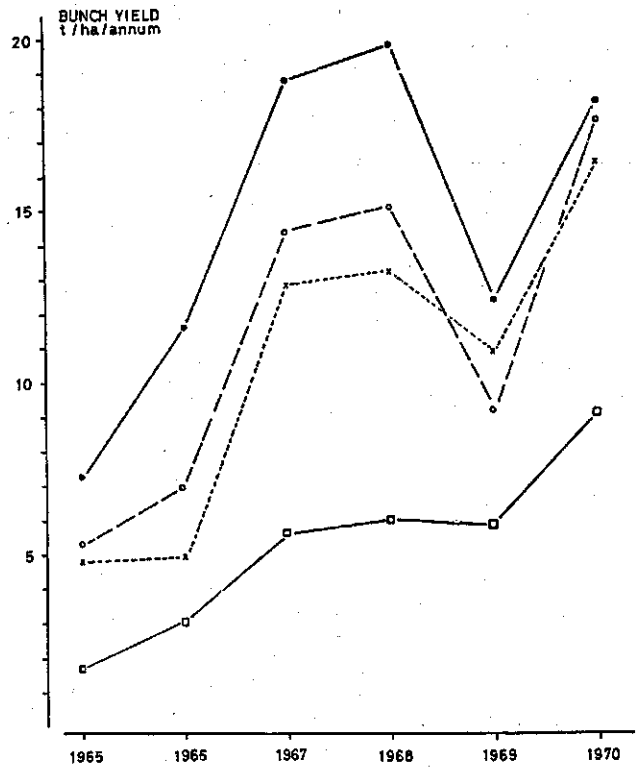

Fig. 21. Yield progression for palms in Expt 851 with different number of dry days as measured in the 1968/69 dry season by the stomatal aperture test (means of 20 palms).

Symbol	No. of dry days	Cumulative yield 1965–70 (t/ha)
●——●	0– 7	87
○----○	28– 35	69
×.....×	56– 63	63
□——□	84–105	31

cumulative yields of the first 6 years (1965–70) were compared to number of dry days (1968–69). Coefficients of correlation between yield and its components, growth parameters of Leaf 17 and number of 'dry days' for 111 individual palms are given in Table 23.

9.4 Discussion: effect of water stress on bunch yield and its components

In oil palm fields in West Africa planted with high yielding progenies at convential plant densities (148 palms/ha), competition for light starts about 6–7 years after field planting, when the leaves begin to overlap. Increased competition for light (reduced E.S.) affects in first instance the sex ratio which in turn determines the yield

Table 22. Progeny mean for yield and its components, growth parameters of leaf 17 and leaf area index (LAI) for 9 progenies planted in 1961. Expt 851.

Progeny	Yield components[1]			Leaf 17 parameters[2]			LAI[2]
	n_b	w	annual yield (t/ha)	area (m^2)	number of leaflets	length (m)	
1	11.4	8.4	14.3	10.29	333	5.18	4.85
2	9.1	6.4	8.7	8.28	327	4.67	3.90
3	6.2	10.7	10.1	9.10	332	4.71	4.29
4	8.4	8.7	10.9	9.50	336	4.99	4.48
5	10.1	8.3	12.5	9.23	333	4.92	4.35
9	7.3	10.0	10.6	8.82	311	5.11	4.16
10	7.6	8.7	10.1	8.93	325	4.90	4.21
11	7.4	9.3	10.2	8.68	339	4.97	4.09
12	10.7	6.2	10.0	8.03	352	4.99	3.78
Mean	8.8	8.5	11.0	8.98	332	4.94	4.19
Least significant difference (5%)	2.8	2.9	2.7	1.12	15	n.s.	0.52

1. Mean 1965–1970.
2. Measured in 1971.

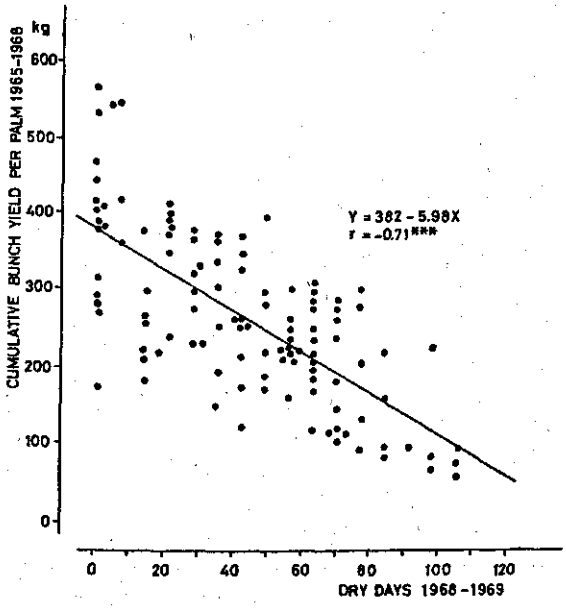

Fig. 22. Relation between cumulative yield per palm (1965–68) and number of dry days as measured by the stomatal aperture test in the dry season 1968–69 for 115 palms in Expt 851.

Table 23. Coefficients of correlation between yield components, growth parameters of Leaf 17 and number of dry days as measured by the stomatal aperture test in progeny trial 851, planted 1961 (n = 111).

	(2)	(3)	(4)	(5)	(7)
(1) n_b 1965–70	–0.38***	0.62***	0.18	0.20*	–0.49***
(2) w 1965–70		0.40***	0.15	0.36***	–0.19
(3) Total yield 1965–70			0.28**	0.51***	–0.58***
(4) Number of leaflets Leaf 17				0.67***	–0.13
(5) Area Leaf 17					–0.31**
(6) Length Leaf 17					–0.44***
(7) Dry days 1968–69					

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

component number of bunches (n_b). Since the sex ratio is defined about 2½ years before harvesting (Broekmans, 1957c), the start of light competition will be reflected in the yield 8½–9½ years after planting. The effect of competition for light is clearly demonstrated by the upper three graphs in Fig. 21. Growth of the palms with 84 or more dry days per year is much slower and competition for light may start for these palms only in the 9th or 10th year after planting. The unfavourable climatic conditions during 1966–67 may have aggravated the decline in yield in 1969. Actually, in most other oil palm experiments in Ghana (van der Vossen, OPRC annual reports 1969–70) the 1969 yields were below average. During the first four years of production the extent of the period of water stress in the dry season is the main yield limiting factor, while in the following years competition for light becomes a second increasingly important factor. This may well explain why the correlation between the number of dry days and cumulative yields over the first four years are somewhat higher than between the number of dry days and the yield over the first six years of production.

Of the two components of bunch yield it is again the number of bunches which is mainly affected by increased periods of water stress, as can be seen from the correlations between bunch number and number of dry days ($r = -0.49^{***}$) and between single-bunch weight and number of dry days ($r = -0.19$ N.S.) in Table 23. This agrees with earlier conclusions by Broekmans (1957c) and Sparnaaij et al. (1963) that a reduction in the total carbohydrate assimilation, due to periods of water stress causing a decrease in E.S., primarily affects the sex ratio, which is the main factor determining number of bunches. Only under extreme conditions of water stress the single-bunch weight will be affected also.

These results seem somewhat contradictory to the heritability estimates for both components: h_n^2 is considerably higher for number of bunches than for single-bunch weight (see Tables 7 and 8). However, these estimates of heritability were based on the performance of full-sib families and parents grown at the NIFOR where soils are

much more uniform and between-palms variation in duration of water stress will be small. Actually, heritability in the wide sense, estimated from components of variance between and within progeny in Expt 851, were for total bunch yield $h_w^2 = 0.12$, for number of bunches $h_w^2 = 0.34$ and for single-bunch weight $h_w^2 = 0.24$. Here again it is realized that the interpretation of the genetic components of variance is only a tentative approach, since some of the assumptions (see 8.4) made when estimating genetic variances from a biparental progeny design could not be tested. The fairly good agreement (similar trend) of these estimates with those of Tables 7 and 8 can be explained by the fact that the variation in number of dry days was largely confounded with blocks. The variance ratio for block effect was significant at $P < 0.001$ for total bunch weight and number of bunches and significant at $P < 0.05$ for single bunch weight. The greater part of the variation due to number of dry days could thus be removed from the total phenotypic variance by deducting the variance due to block effect from the total sum of squares.

9.5 Discussion: effect of water stress on growth

The rather low negative correlation ($r = -0.31^{***}$) between leaf area and number of dry days, see Table 23, intimates that leaf area is somewhat less affected by water stress, and thus by reduced carbohydrate assimilation, than total yield. Number of leaflets is apparently totally unaffected by water stress ($r = -0.13$, not significant) On the other hand, leaf length was 5.15 m for palms with 0–7 dry days against 4.45 m for palms with more than 70 dry days and the correlation between leaf length and number of dry days ($r = -0.44^{***}$) was higher than the correlation between leaf area and number of dry days. This effect of water availability on leaf length was also reported by Desmarest (1967) for his irrigation trial. So under favourable growth conditions one may expect longer leaves and somewhat longer and broader leaflets (higher leaf area) but no increase in number of leaflets.

The mean stem height was for palms in block 3, where mean number of dry days in 1968/69 was 22 days, 2.50–3.00 m against 1.80–2.20 m for palms in block 4 where mean number of dry days was 58. Under West African conditions dry weight of stem and rhachides may account for over 88% of total vegetative dry matter for 10-year old palms (Rees & Tinker, 1963). Circumstances at the time of measuring did not allow a full growth analysis, but the leaf length and stem height data from Expt 851, although admittedly rather rough indices for vegetative dry matter production, intimate that vegetative dry matter production is also strongly influenced by the annual period of water stress in the palm. On the other hand, Corley et al. (1971a, 1971b) concluded from an analysis of growth in Malaysia that vegetative growth is fairly constant and only when this has reached a certain level would excess dry matter be utilized for bunch production. The present data, obtained under suboptimal and more variable environmental conditions, do not support this conclusion. The environmental variance component is considerable for both vegetative growth and bunch production. The threshold value of vegetative dry-matter production before excess dry matter is

utilized for bunch production is apparently much lower than suggested by the results obtained in Malaysia.

9.6 Discussion: relationship between bunch yield and growth parameters

Although the other correlation coefficients presented in Table 23 are strictly speaking not related directly to the main subject of this chapter, it may be appropriate to make some comments at this stage.

Hardon et al. (1969) showed that a fairly high correlation existed between leaf area and total yield and this could be confirmed by the data from Expt 851 ($r = 0.51^{***}$, Table 23). Both factors also depend on number of dry days, but calculation of the partial correlation, keeping dry days constant, ($r_{35.7} = 0.43$) indicated that the larger part of the correlation is inherent to leaf area and yield alone. From the two bunch yield components single-bunch weight shows a higher correlation ($r = 0.36^{***}$) with leaf area than number of bunches ($r = 0.20^{*}$). This led Hardon et al. (1969) to suggest that there could be an ontogenetic relationship between number of leaflets per leaf and number of spikelets per bunch, as the latter is an important bunch-weight determining factor (see also Thomas et al., 1970). However, no evidence for this hypothesis could be found from the present data, since number of leaflets and single-bunch weight were uncorrelated ($r = 0.15$). On the other hand de Berchoux and Gascon (1965) found within four out of seven full-sib progenies a significant but rather low correlation ($r = 0.21^{*} - 0.44^{**}$) between leaflet number and single-bunch weight.

Statistically significant progeny differences were found for leaf area and leaflet number, but not for leaf length (see Table 22). Tentative estimates for the wide-sense heritability gave a higher value for number of leaflets ($h_w^2 = 0.38$) than for leaf area ($h_w^2 = 0.17$). Hardon et al. (1972) concluded from estimates of genetic variances of growth parameters in Malaysia that heritability of leaf area was generally low, but did not give heritability estimates for number of leaflets. It should be recalled here also that leaf area and number of dry days are negatively correlated, while number of leaflets and number of dry days are uncorrelated, suggesting that for number of leaflets the environmental component of variance is low.

Leaf area strongly depends on number of leaflets ($r = 0.67^{***}$, Table 23) but also on leaf length ($r = 0.68^{***}$, calculated from 36 plot means of 6 palms), but the number of leaflets depends apparently much less on leaf length ($r = 0.37^{*}$, $n = 36$). In other words, when leaf length increases, due to favourable environmental factors, leaf area increases too. This must be due mainly to an increase in length and width of the leaflets, since number of leaflets does not increase appreciably.

Although it was not possible, in the absence of detailed growth analysis data, to estimate net assimilation rate, it was tempting to calculate a kind of 'net economic assimilation rate' expressed as fresh bunch weight in kg per m^2 leaf area per year. The mean value of this parameter for 36 plots of 6 palms for the years 1968–70 varied from 0.17 to 0.40. There were no statistically significant differences between progeny

means. On the other hand, the correlation between this parameter and number of dry days was negative and highly significant : r = −0.60***. Hardon et al. (1972) found that the heritability for the net assimilation rate was low compared to other growth parameters.

9.7 Practical implications

9.7.1 Lay out of field experiments

In areas where soil factors are so variable as at the OPRC in Ghana, it will be essential to lay out experiments in such a manner that variation in available water in the soil is as much as possible confounded with block effect. Variation in the extent of the period of water stress has been shown to be the main cause of environmental variance of individual palms for bunch production. A detailed soil survey map is of great help to plan field experiments correctly in advance, as water holding capacity largely depends on the texture of the soil series. Once the palms are well established, an accurate map of the variation in extent of the period of water stress, or number of dry days, can be prepared from stomatal aperture data of a number of palms. Corrections for bunch yield can then be made, if within-block or even within-plot variation of number of dry days is still considerable. This will enhance the precision of estimating the treatment effect in agronomic experiments as well as in progeny trials, as the error variance component will be reduced. At the same time such information is of great help to within-progeny selection for seed palms and parents for further breeding.

9.7.2 Yield corrections and predictions

In the preceding paragraphs the stomatal aperture test was described as a very useful tool to determine the variation in the extent of the period of water stress between palms of the same field. The parameter effective sunshine, on the other hand, makes it possible to predict future yield levels and to make corrections for between-year effect when comparing progeny trials planted in different years. The start and extent of the period of water stress is in the latter case estimated by assuming a potential evapotranspiration of 100–112 mm per month (Chapas & Rees, 1964) and total available water in the upper 100 cm of soil (effective rooting depth of mature oil palms) at field capacity to be about 120 mm (Sparnaaij et al., 1963) for the sandy soils at the NIFOR. However, the amount of available water varies considerably at the OPRC along with different soil series. The stomatal aperture test measures the extent of the period of water stress directly, but it would be too expensive to apply this test every year with the purpose of calculating the annual E.S. The stomatal aperture test can, however, be used to estimate the maximum amount of available water for different soil series, provided mature oil palms are available. Studies on effective rooting depth on sandy as well as clayish and concretionary soils carried out in Ghana (van der Vossen, OPRC annual report 1970) have indicated that the effective rooting depth of palms 10 years

old or older is 100–120 cm, irrespective of soil type. Only in very concretionary and gravelly soils, usually found at the summit of the hills, rooting was somewhat shallower. Ruer (1967) showed convincingly that the primary roots descending vertically down to greater depths are mainly functioning to give a firm anchorage and play little or no part in the absorption of water. Applying this to Expt 851 indicated 50 mm available water for the top 120 cm in the sedentary soils of the upper slope (palms with >84 dry days in Figure 21) against 200 mm for the colluvial soils (palms with 28–35 dry days in Fig. 21).

The palms with 0–7 dry days in Fig. 21 apparently benefitted from a high groundwater table and could thus not be used to estimate available water at field capacity for those soils. Once these values for available water are known, annual E.S. can be calculated for palms on different soils in the usual way and yield predictions can be made.

9.7.3 Moisture conservation

Elimination of the period of water stress in West Africa by irrigation, though very effective as shown by Desmarest (1967), does not (yet) seem feasible on a large scale for economic reasons. However, a reduction in the period of water stress can be effected by conserving as much as possible the available water in the soil through cultural measures. Ochs (1963) describes methods of 'dry farming' between the palms in Dahomey by keeping the soil completely bare during the main dry season, while Bachy & Regaud (1968) reported the highly beneficial effect on yield of complete mulching of palms in a field in Cameroon. The first method would induce serious problems of soil erosion in most oil palm areas in Ghana, because of topography and type of soils, while the second method poses a serious fire hazard in an oil palm field during very dry weather. It is standard practice to establish a leguminous cover crop (in Ghana mainly *Pueraria phaseoloides*) in between the palms at the time of planting. This cover crop effectively controls soil erosion and noxious weeds (grasses), while it improves simultaneously the organic matter content of the topsoil. However, this cover crop is very competitive to the palms as regards the available water in the soil, especially during the early years when the canopy is not yet closed.

An experiment was started in 1966 to investigate whether checking of the growth of the cover crop by very low brushing in the dry season would give an improved conservation of the available water in the soil and thus have a beneficial effect on growth and production of palms. A summary of the results for the first two years of production is given in Table 24. The mean increase in bunch production in the low-brushed plots compared to normally maintained plots was 35% in 1969 and 22% in 1970. The stomatal aperture test, however, indicated that in two of the five replications the amount of available water in the soil was higher in normal-brushed than in the low-brushed plots due to edaphic differences, thus compensating for the higher transpiration of the cover crop in these plots. Differences in yield between the two treatments in these two replications were in fact negligible, reason why the overall treat-

Table 24. The effect of checking the growth of the cover crop in the dry season on bunch yield (t/ha) of young palms. Experiment 853-2, planted in 1966.

Treatment	1969	1970
Normal brushing	1.92	5.33
Low brushing	2.59	6.52
Least significant difference (5%)	0.47	1.21

ment effect in the experiment was only significant at $P = 0.1$. However, in the remaining three replications the increase in yield for 1970 because of low brushing was more than 36%. This again demonstrates how the stomatal aperture test can provide useful information for a correct interpretation of the results. For this experiment it appears that the positive effect of low brushing on yield is much more pronounced than is suggested by the analysis of variance of the data.

10 Practical implications for oil palm selection

10.1 Conclusions from preceding studies

10.1.1 Summary of conclusions

Some of the points emerging from the foregoing studies have important consequences for oil palm breeding. It will, therefore, be useful to summarize the main conclusions before discussing in greater detail methods of selection which should lead to increased selection progress.

1. The genotypic component of variance for all components of oil yield mainly consists of additive variance in the NIFOR breeding populations studied (Chapters 4 and 5). The estimation of genotypic values of these components for individual palms from sets of full-sib family means, as proposed by Sparnaaij (1969) and applied in Chapter 4, is therefore justified.
2. For the components number of bunches (n_b) and single-bunch weight (w), estimates of A values should be obtained from the first three years of production. Such estimates are free of the effects of competition for light between palms which usually starts in the fourth year of production (4.3). This emphasizes also high production at an early age, a factor of great importance in a perennial plantation crop such as the oil palm.
3. In contrast to what has been generally assumed, a fairly high *negative* genetic correlation ($r_A = -0.58$) does exist between the two most important components n_b and w (Chapter 6). This negative r_A becomes even higher when the parents are related. The consequence of a negative r_A between two characters is that response to selection is much less than would be expected from the respective heritability estimates, when selection is applied to both simultaneously (Falconer, 1960). Better selection progress for higher bunch yield appears to be obtained by intercrossing between individual palms of widely divergent subpopulations.
4. The relative economic value is many times higher for the components n_b and w than for the other components (see Table 10). The oil-to-mesocarp ratio (o_m) is the third in the order of importance of the components. In oil palm breeding programmes priority should thus be given to the improvement of these three components of oil yield. So far, there has been a general tendency in oil palm breeding to put more effort into selection for bunch quality components.
5. Oil-to-mesocarp (o_m) is a component with a fairly low heritability ($h_n^2 = 0.20$–0.40) and multiple measurements are required over at least one year to obtain reliable estimates of A values for o_m from the mean of full-sib families (Chapter 8). On the

other hand, the dry-fibre content of the mesocarp (f_m) was shown to have a considerably higher heritability ($h_n^2 = 0.60–0.80$). This opens the possibility of substituting direct methods of oil content determinations, presently applied at most oil palm selection centres, by a much less expensive and relatively simple 'modified indirect' method as described in Chapter 8. Whatever method is applied, it is essential for oil to mesocarp determinations that only fully ripe bunches are sampled.

6. The observed narrow-sense heritabilities of the components of oil yield (see Tables 7 and 8) imply that for the components ratio mesocarp or shell to fruit (m or s) the phenotypic value of a *tenera* palm (P_t) is by itself a good estimate of its genotypic *tenera* value (A_t). For these components there will be little gain in accuracy by estimating A_t values from full-sib family means, as it will be for the other components.

7. The nature of the inheritance of m and s (Chapter 7) implies that the phenotypic value for those components in a *dura* palm (P_d) gives a poor estimate of its genotypic *tenera* value (A_t). The A_t value of a *dura* palm can only be obtained from the mean of its *tenera* full sibs or from the mean of the *tenera* palms in a full-sib family of a *dura* × *tenera* cross. For the components m or s only the A_t value of a *dura* palm is relevant in present day oil palm breeding and seed production programmes.

8. The results of the repeatability estimations, presented in Tables 13, 17 and 21, indicate that a 21-fruit sample (7 outer and 14 inner fruits) is large enough to determine accurately all fruit quality components of a bunch (m, s, k, o_m). The 500 g sample (50–100 fruits) usually taken at the NIFOR thus seems unnecessarily large.

9. The stomatal aperture test described in Chapter 9 is a very sensitive and accurate method of estimating the exact extent of the period of water stress in the oil palm during the dry season. The high negative correlation ($r = -0.71$) between the length of the period of water stress and cumulative yield over the first four years of production of individual palms implies that water stress is the main factor of environmental variation in the oil palm during the early years of production in West Africa. The stomatal aperture test may thus find application in breeding as well as agronomic field experiments as a method to estimate the magnitude of the environmental variance due to variation in periods of water stress, mainly caused by differences in the water holding capacity of different soils. This is of practical importance in areas (like in Ghana) where soil factors vary considerably within short distances.

10. The stomatal aperture test can also be used to estimate the water holding capacity of the soils on which oil palms are grown and thus increase the accuracy of estimating effective sunshine hours, an important parameter to predict future yields of mature oil palm fields (Sparnaaij et al., 1963) and also to make corrections for between-year effect when comparing the yield performances of progeny trials of different age (9.7).

11. Vegetative dry-matter production in the oil palm is also considerably influenced by the extent of periods of water stress (9.5).

12. Intensive repressing of the growth of the leguminous cover crop during the dry season, especially at the beginning of it, can be an efficient method of water conservation in young oil palm fields. This may result in higher and more reliable figures for bunch yield (9.7) during the first three years of production on which estimates of

genotypic values for bunch yield components are based.

10.1.2 Limitations

Estimates of genetic parameters are not only a property of the particular character under study, but also of the population from which these parameters have been derived and of the environmental circumstance to which the population has been subjected (Falconer, 1960). Generalization of some of the above conclusions are, therefore, only valid when the structure of the population is similar to those of the NIFOR breeding populations and when the environmental conditions are comparable.

For example, Thomas and Hardon (1969) found additive genetic variation to be virtually absent for the two most important components of oil yield, n_b and w, in Deli *dura* populations grown in Malaysia. On the other hand, results reported in 9.5 intimate that under more variable environmental conditions in West Africa estimates of h_n^2 for vegetative dry-matter production will be considerably lower than the value for h_n^2 found for this character by Hardon et al. (1972) in Malaysia.

10.2 Selection for bunch yield and maintenance of additive genetic variability

10.2.1 The principle of intercrossing genetically diverse populations

The negative genetic correlation observed between the two bunch yield components, n_b and w, indicates the existence of a genetic ceiling of physiological efficiency (6.5). By intercrossing genetically very diverse palms, this ceiling will be raised because of accumulation of genes of general physiological efficiency in the offspring. Only in such crosses does the genotype of a palm achieve its full expression. Estimates of genotypic values for the components of bunch yield should, therefore, be restricted to yield data from crosses of this kind (see 6.5).

Palms selected from two different subpopulations are more likely to be genetically diverse than when they are selected within the same subpopulations. This principle has, in fact, already been applied in the NIFOR breeding programme: the majority of the crosses have been made between palms of different subpopulations (Sparnaaij et al., 1963). In the IRHO breeding programme this principle has been carried to the extreme by restricting all breeding work mainly to the Deli, Yangambi and La Mé subpopulations (Meunier & Gascon, 1972). Examples of interpopulation crosses were presented in Table 12 (crosses 1–4 in particular).

Some of the subpopulations available to the oil palm breeders, like the Deli and Yangambi populations, are genetically very narrow. Although the initial results of the interpopulation crosses, in particular between Deli and Yangambi palms, were very positive (Gascon et al., 1964, 1966), further selection progress for higher bunch yield cannot be expected, because little additive genotypic variance appears to be left in these populations (Thomas & Hardon, 1969; Hardon, 1970).

On the other hand, the Calabar, Aba and Ufuma subpopulations are genetically

much more variable. This has already been illustrated for the Calabar population by crosses 6 and 7 in Table 12 (see also 5.6). The Calabar palms 5.1654-D and 32.3005-T are both very good yielders – respectively 82.6 kg and 64 kg bunch yield per annum, averaged over the first three years of production – and both have also good A values for the bunch yield components (as estimated from interpopulation crosses). The progeny performance of these two palms in crosses 6 and 7 (Table 12) is excellent, indicating that in both crosses the two parent palms are genetically very diverse. However, in a widely spaced perennial plant like the oil palm, a high selection intensity is necessary in view of the large area of land required for progeny testing. Consequently, the actual number of different genotypes contributing to the next breeding generation is comparatively small and additive genetic variability will decrease in subsequent generations, even in these highly variable subpopulations. In the present generation of the Calabar population some palms are already related and, when crossed with each other, will show disappointing progeny performance (see crosses 8 and 9 in Table 12).

It follows from above that the basic principles in oil palm breeding programmes should continue to be:

1. maintaining genetically diverse subpopulations;
2. employing only interpopulation crosses for the estimation of A values for the components of bunch yield, as well as for seed production.

10.2.2 Introduction and use of new germ plasm

In practically all oil palm selection programmes there is now an impelling need to re-establish new, genetically highly variable subpopulations. The importance of this has been acknowledged in a few recent publications on oil palm breeding (Hardon, 1970; Sparnaaij, 1972; Ooi et al., 1974 (in press).

Genetic variability should in the first instance be sought in new introductions from centres of high genetic diversity, notably eastern Nigeria and western Cameroon. At the NIFOR a fairly comprehensive stock of oil palm germ plasm, collected in 1962–1963 in eastern Nigeria, is already present (NIFOR annual report 1965). However, it has become a matter of urgency to carry out large scale systematic prospections and collect as much breeding stock as possible from within the centres of high genetic diversity for the oil palm, i.e. the semi-wild palm groves, before irreplaceable oil palm germ plasm is lost. Zeven (1967) concluded from his studies that the palm groves in eastern Nigeria are deteriorating rapidly due to the progressive conversion of groves to farm land, to the continuous felling of oil palms for wine tapping, or just to the replacement of grove palms by regular oil palm plantations established from improved seed. The danger of losing valuable germ plasm due to the retrogression of centres of genetic diversity is, of course, a matter of serious concern for many other crops. Meyer (1968) expressed similar fears for the centre of genetic diversity for *Coffea arabica*, which is situated in the south-western highlands of Ethiopia.

Palms originating from the same location or palm grove in the centres of high genetic diversity are assumed to share a similar gene pool and can thus be considered

to constitute one subpopulation. Subsequent selection and breeding work will be facilitated considerably, if such subpopulations are maintained as separate populations right from the start.

Individual tree selection for bunch yield and its components can be carried out after the third year of production. This will be about the seventh to eight year after collections of the new material have been introduced: i.e. two years from seed to field planting, two to three years to first production and another three years yield recording.

10.2.3 Individual selection by means of a selection index

Interpopulation crosses are most successful when subpopulations are very divergent in the two bunch yield components, as was illustrated by Sparnaaij (1969) with a numerical example. As with the presently distinguished subpopulations, some of the new ones may be characterized by producing a relatively low number of heavy bunches (type I subpopulation) and others by a high number of relatively small bunches (type II). These characteristics may be accentuated by selecting primarily for high single-bunch weight in type I subpopulations and for high bunch number in subpopulations of type II. A *selection index* based on the two bunch yield components may here increase the response to selection.

The general formula for the selection index is given by:

$$I = \sum_{i=1}^{n} b_i X_i \qquad (11)$$

where: b_i = partial regression coefficient of the yield A value on the phenotypic value of the i^{th} trait.

When only two traits are involved the selection index can be reduced to its simplest form as suggested by Falconer (1960):

$$I = P_x + WP_y \qquad (12)$$

where in this case: P_x = phenotypic value of n_b of a palm
P_y = phenotypic value of w of a palm
W = weighing factor = ratio of the two partial regression coefficients.

The weighing factor W can be expressed in terms of phenotypic variances and narrow-sense heritabilities for both traits (σ_x^2 and σ_y^2, resp. h_x^2 and h_y^2), phenotypic and genetic correlations between the two traits (r_P resp. r_A) and relative economic value (w_e) of one trait to the other (Falconer, 1960):

$$W = \frac{\sigma_x^2 \, \mathrm{cov}(HY) - \mathrm{cov}(HX)\,\mathrm{cov}(XY)}{\sigma_y^2 \, \mathrm{cov}(HX) - \mathrm{cov}(HY)\,\mathrm{cov}(XY)} \qquad (13)$$

where: $\mathrm{cov}\,(HX) = h_x^2 \, \sigma_x^2 + w_e \, r_A \, h_x \, h_y \, \sigma_x \, \sigma_y$

$\mathrm{cov}\,(HY) = w_e \, h_y^2 \, \sigma_y^2 + r_A \, h_x \, h_y \, \sigma_x \, \sigma_y$

$\mathrm{cov}\,(XY) = r_P \, \sigma_x \, \sigma_y$

The application of individual selection by means of a selection index in the subpopulations can best be illustrated by a numerical example. Two hypothetical subpopulations have the following characteristics as regards bunch yield and its two components over the first three years of production:

Population 1 (type I): $\bar{n}_b = 6$, $\bar{w} = 9$, mean yield per annum ca. 54 kg; $\sigma_{n_b} = 3.0$ and $\sigma_w = 4.5$; $r_P = -0.59$; the linear regression equation for w on n_b is $w = 14.31 - 0.885\, n_b$.

Population 2 (type II): $\bar{n}_b = 10$, $\bar{w} = 5.4$, mean yield per annum ca. 54 kg; $\sigma_{n_b} = 5.0$ and $\sigma_w = 2.7$; $r_P = -0.59$; the linear regression equation for n_b on w is $n_b = 15.90 - 1.093\, w$.

By assuming a relative economic value of w to n_b of 2.00 in Population 1 and 0.50 in Population 2, selection for an increase in single-bunch weight will be accentuated in the first and an increase in bunch number in the second population. The genetic properties of the two characters are taken to be similar to those of the already studied NIFOR breeding populations: h_n^2 (n_b) = 0.512 and h_n^2 (w) = 0.206 (Table 7); $r_A = -0.584$ (6.4).

By substituting all above values in equation (13) and substituting the resulting W's in equation (12), the following selection indices are obtained:

Population 1: $I = n_b + 1.343\, w$

Population 2: $I = n_b + 0.669\, w$

Each subpopulation will, of course, have its specific selection index, but above examples demonstrate how in a type I subpopulation the selection index will effect selection pressure for high total yield and heavy bunches and in a type II subpopulation for high yield and high number of bunches. The response to selection by means of the above proposed selection index is expected to compare favourably with individual selection for high bunch yield and its components by truncation, since in the selection index the genetic properties of the bunch yield components are taken into consideration.

The main criticism to index selection, as applied here, will be that the magnitude of the genetic parameters used to construct the index are estimated from the present NIFOR breeding populations, which are not identical to the new populations to which the selection index will be applied. However, it is very unlikely that these will vary all that much from population to population, provided the environmental conditions in which the new populations are grown are similar.

Palms selected in this manner within the different subpopulations will then form the parents of a breeding programme of which the outlines will be discussed in 10.6.

In the subsequent cycle of selection and breeding, crosses are made between subpopulations of the same type – type I × type I and type II × type II – using as parents the best palms as indicated by the selection index. The purpose of such crosses is to maintain a high level of genetic variability. Another advantage is that from this stage onwards one can proceed with family selection and only the best palms out of the best families are used as parents for another cycle of interpopulation test crosses between type I and type II subpopulations. Such intercrossing of subpopulations of the same type should also be extended to include the standard subpopulations, i.e. Deli, Yangambi, Calabar, Aba, etc. populations, to take advantage of the favourable characteristics already present in these populations. In other words, the best Deli palms should be crossed with the best palms of new type I subpopulations, while some of the best Calabar or Aba palms should be crossed to palms of new type II subpopulations.

10.3 Selecting for bunch and fruit quality

In selection programmes of all oil-palm selection centres, bunch and fruit quality analysis work constitutes an important cost factor in terms of equipment and labour. With the conclusions as stated in points 4, 5, 6, 7 and 8 of 10.1 in mind, important savings in costs can be made by restricting all bunch analyses to *tenera* bunches and emphasizing oil analysis rather than physical fruit quality analysis, in view of the comparatively high relative economic value of the oil-to-mesocarp ratio (Table 10).

This will also imply that in new subpopulations as much as possible only *tenera* palms should be selected to facilitate simultaneous selection of all oil yield components. In the subsequent cycle, when family selection will be applied, *dura* palms can also be selected if these are excelling in bunch yield, since the A_t values for the fruit quality components can be reliably estimated from the mean of the full-sib *tenera* palms.

A short outline of the proposed revised bunch analysis follows below:

A sample of 21 fruits is taken from *tenera* bunches on the same day or at the latest the next morning after harvesting and subsequently weighed. The *tenera* bunches may have been harvested from *tenera* palms of recently introduced new subpopulations, or from *tenera* × *tenera* and *tenera* × *dura* crosses. This sample is then analysed to determine the dry-fibre content (direct extraction) or oil content (modified indirect method) of the mesocarp, whatever required, in the manner described in Chapter 8. This procedure will also automatically produce information on the value of m from the ratio of total fresh mesocarp to total fruit weight of the 21-fruit sample. If required, the nuts of the sample can be cracked in the usual way and kernels weighed to obtain k. The fruit-to-bunch ratio (fr_b) is obtained from a sample of spikelets as described by Blaak et al. (1963).

Bunches harvested during the first year of production (excluding the very first bunches) will be used to determine not only the fruit quality components m, s and k but also fibre-to-mesocarp (f_m). Three to four bunches analysed per *tenera* palm in this first year should be adequate to obtain reliable individual palm data for new subpopulations. When determining progeny averages of bunch and fruit quality components for test crosses, it will also be preferable to sample three or four bunches of each *tenera* palm in a *tenera* × *tenera* or *tenera* × *dura* cross, rather than to take 15 bunches at random per progeny each month as has been the practice at the NIFOR (Blaak et al., 1963). In both types of crosses 50% of the palms will be *tenera* palms and, with about 60 palms per cross, four bunches analysed of each *tenera* palm means, in fact, that fewer bunches are to be analysed per cross ($30 \times 4 = 120$ against $15 \times 12 = 180$).

Bunches harvested from the second year of production onwards are used to determine oil to mesocarp (o_m) by the modified indirect method. At this stage it is essential to analyse fully mature bunches only (10.1, point 7) and to analyse bunches harvested at different times of the year to even out seasonal variations in mesocarp oil content. As regards fr_b, more reliable data are likely to be obtained from bunches harvested from the second year of harvesting onwards.

All data on bunch and fruit quality components, for individual palms or progeny means, can thus be collected before the end of the third year of production, when also data on the bunch yield components become available.

10.4 The relation between early and mature bunch yield: plant density - progeny trials

The best estimates of genotypic values for the components of bunch yield are obtained from the first three to four years of production, when the disturbing influence of light competition is still negligible (Sparnaaij, 1969; see also 4.3). All selection fields should, therefore, be planted at a spacing in which competition for light between palms does not affect the first three years of production, under most West African conditions about 9m triangular spacing, to obtain spacing independent estimates of A values for the two bunch yield components.

Restricting selection for bunch yield and its components to the early years is, however, of only limited value in predicting the yield performance for older palms. Sparnaaij (1969) showed how especially palms with high A values for bunch number (i.e. high sex ratio) are affected by the increasing competition for light between palms in mature plantations and, therefore, suggested that continued high production could best be obtained by a combination of a medium bunch number with a high single bunch weight. This can be achieved by interpopulation crosses between type I and type II subpopulations. However, there is likely to be a strong interaction between genotype and spacing.

Information about genotype-spacing interactions can be obtained by planting all *dura* × *tenera* and *tenera* × *tenera* test crosses (i.e. type I × type II interpopulation

crosses) in the four-row planting system of the NIFOR (Sparnaaij et al., 1963), in which every fifth north-south row is left unplanted. The greater the difference between the mature yields of the palms in the two outer rows (i.e. low plant density, less light competition) and the two inner rows (i.e. 9 × 9 m full plant density), the wider will be the spacing required for such a cross for optimum production at maturity. However, this system requires 25% more land for the test crosses and additional labour to check the growth of the leguminous cover crop in the fifth rows. It has been observed at the NIFOR that the benefit of less light competition can easily be nullified by increased competition for soil moisture between the cover crop and the palms in the two outer rows (Sparnaaij, personal communication). Besides, the optimal combination of genotype and spacing will also depend upon other environmental conditions.

An alternative way to determine genotype-spacing interactions would be to plant all progeny trials at one standard spacing and determine the A values for the components of bunch yield from the first three years of production. At the same time a number of plant density – progeny trials should be established in the major areas of oil palm cultivation served by the breeding centre to obtain information about the optimal combination of genotype and spacing for each area, required to assure a continued high production level in mature plantations.

The progenies included in such a trial should all have a high production potential but be very divergent in the bunch yield components, i.e. a range should be covered from a high bunch number (accompanied by a medium single-bunch weight) to a fairly low bunch number (with a high single-bunch weight). Such progenies can be obtained by interpopulation crosses, selecting as parents palms with known A values for the bunch yield components. Since optimal plant density decreases with age of the palms, the trials should also include a variation in plant density with age.

A plant density-progeny trial of such a type was planted at the OPRC in Ghana in 1970 (van der Vossen, OPRC annual report 1970). This experiment compares in a latin square design five different plant densities (palms/ha) as follows:

No.	First 6 years	Final density
1.	203 (hexagonal)	102 (triangular)
2.	228 (hexagonal)	114 (triangular)
3.	259 (hexagonal)	129 (triangular)
4.	295 (hexagonal)	148 (triangular)
5.	148 (triangular)	148 (standard spacing)

Each main plot, which covers 0.41 ha (excluding guardrows), contains in subplots 6 *dura* × *pisifera* progenies of different bunch yield composition, i.e. with widely different ratios between n_b and w. By double density in the early years better use will be made of the available land (high leaf area index) resulting in a higher production per ha right from the first year of production. There is also an improved utilization of the available water in the soil for oil palm growth and production because of the better coverage of the ground with palms. Less water will be lost due to transpiration of the cover crop. Higher density will induce earlier light competition between palms,

but it depends mainly on the mean length of water stress period how soon the leaves will start to overlap (see Chapter 9: high negative correlation between leaf length and number of dry days).

In view of the increased cost of establishment for double density planting, at least three years production at double density are thought to be required to make the system profitable. The plant densities of Treatments 2 or 3 are, therefore, likely to be more suitable at the OPRC than those in Treatment 4, since under the environmental conditions prevalent at that station the canopy starts to close about 6–7 years after planting at a plant density of only 148 palms/ha. Such high plant densities may be more suitable for drier areas where growth will be slower, while the low densities of Treatment 1 should give good results in areas where the annual period of water stress is short.

There is likely to be a considerable genotype-density interaction. The right combination of bunch yield components for each situation can be deduced from the performance of the progenies. This provides a basis for choosing the optimal spacing for the area concerned and the type of progeny to be planted. Commerical planting material can be produced by crossing parent palms, which have A values equivalent to the parent palms of the best progeny in the experiment.

Some evidence of the positive effect of lower than usual plant density in a mature plantation on bunch yield is available from two exploratory thinning experiments started in Ghana in 1967 in two oil-palm fields of 4 ha planted in 1957–1958. Systematic thinning from 148 p/ha to 100 p/ha resulted in a statistically significant increase in bunch yield per palm from 2–3 years after thinning onwards (van der Vossen, OPRC annual report 1970). In one experiment yield increased from 59 kg ($n_b = 4.4$; $w = 13.4$) to 77 kg ($n_b = 5.4$; $w = 14.2$) per palm for 1970, and in the other experiment from 62 kg ($n_b = 5.1$; $w = 11.9$) to 84 kg ($n_b = 7.0$; $w = 12.0$) per palm. In these experiments the increase in yield per palm did not compensate entirely for the lower density and, consequently, bunch yield per ha is somewhat less, However, the plant material consisted of early extension work seed (*dura* × *tenera* and *dura* × *pisifera*) issued by the NIFOR around 1955. In modern high yielding progenies the effect is expected to be much more pronounced, leading to even higher yields per ha at lower densities.

10.5 Growth analysis and selection for bunch yield

Hardon et al. (1969) and Corley et al. (1971b) developed methods of estimating growth parameters, like leaf area and leaf area index (LAI), vegetative dry matter production (VDM), crop growth rate (CGR) and net assimilation rate (NAR) from nondestructive measurements and showed that under Malaysian conditions significant progeny differences existed for most of the growth parameters. It was pointed out by these authors that the highest yielders in a heterogenous population may also be the most competitive (high VDM) and that a population consisting of mainly such highly competitive palms obtained by selection may not be suitable to obtain

high (mature) yields under normal plant densities. They produced some evidence that phenotypic selection for yield was accompanied by higher values for VDM.

On the other hand, selection for a high bunch index (BI), i.e. the ratio of bunch yield (Y) expressed as dry matter over total dry-matter production (BI = Y/(Y + VDM) resulted also in higher bunch yield but at the same time in a considerably lower value for VDM.

It seems, therefore, important to incorporate BI selection in oil palm selection programmes. It should be applied to those individual palms or families which have already been selected on the basis of the first three years yield records, in order to select for genotypes which combine high bunch yield with a comparatively low VDM production. This way of tandem selection has the added advantage that the labour intensive growth analysis is restricted to promising selections only.

Whether inclusion of BI selection will increase selection progress, depends on the amount of additive genetic variance present for VDM, one of the two parameters determining BI. Hardon et al. (1972) obtained fairly high heritability estimates for VDM (h_n^2 = 0.41–0.65) but these were obtained under the optimal and uniform environmental conditions prevailing in Malaysia. In 9.5 some evidence was produced that under West African conditions h_n^2 is much lower. There is thus an apparent need for similar growth analysis work to be carried out under West African conditions. At the NIFOR as well as the OPRC there are sufficient suitable progeny trials available for accurate estimation of additive genetic variances of these growth parameters.

10.6 Outlines of an oil palm breeding programme

The main conclusions reached in the previous paragraphs of this chapter can be used to introduce further refinements into current oil palm breeding programmes, assuring continued selection progress. In this final paragraph general outlines will be presented of such a modified breeding programme. A schematic presentation of the proposed modified breeding programme is given in Fig. 23.

New subpopulations, introduced from centres of high genetic diversity for the oil palm, are presumed to be already available. These form together with the earlier 'standard' subpopulations (Deli, Calabar, Aba, Yangambi, etc.) the base populations for the first cycle of the breeding programme. Individual selection for oil yield components is carried out in the new subpopulations during the first three years of production (year 1+2+3), while only *tenera* palms are considered to facilitate simultaneous selection for bunch yield as well as fruit quality components (see 10.3). A selection index, as proposed in 10.2 for the bunch yield components is expected to increase selection efficiency. A distinction is made between subpopulations of type I (high single-bunch weight) and type II (high bunch number). In the 'standard' subpopulations selection is mainly based on genotypic value for the components of oil yield, since such values are already available for a number of palms form the previous breeding programme. In that case *dura* palms can also be selected, for the reason that A_t values for the fruit quality components (in particular m) are known.

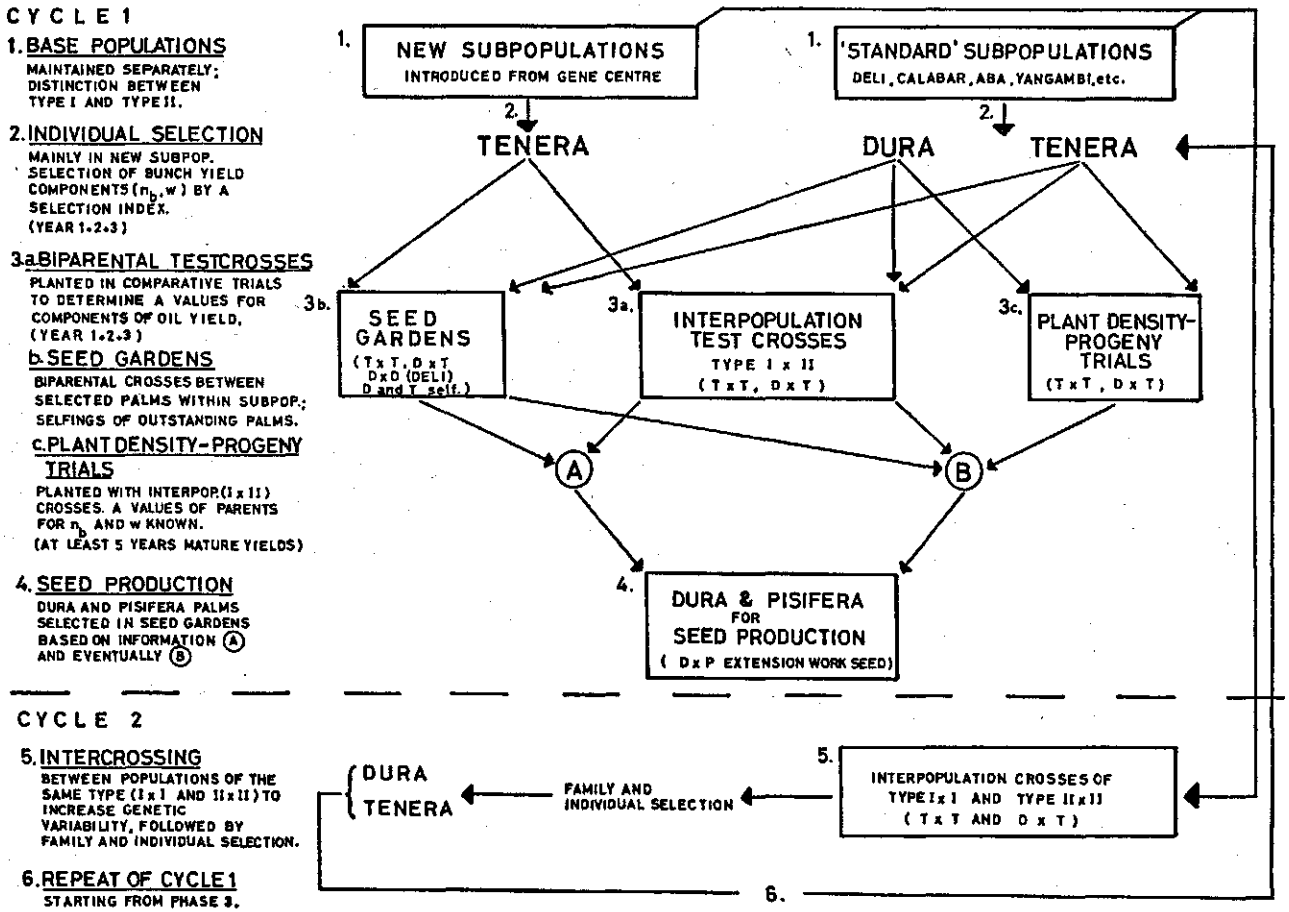

Fig. 23. Schematic presentation of a proposed modified oil palm breeding programme.

Progenitors for the first cycle of the breeding programme are thus *tenera* palms selected from the new subpopulations and *tenera* as well as *dura* palms from the 'standard' subpopulations.

The programme of biparental test crosses to determine A values for the components of oil yield (for palms of new subpopulations) and the establishment of seed gardens (3a and 3b in Fig. 23) is carried out in a similar way as outlined by Sparnaaij (1969) and requires, therefore, little further comment. A new aspect is that all test crosses are restricted to type I × type II interpopulation crosses. Seed gardens are established from crosses between pairs of palms within the same subpopulation in addition to a number of selfings of the very best progenitors. The test crosses are planted out in comparative trials, preferably at one spacing (see 10.4). Simultaneously, a number of plant density-progeny trials, of a design as described in 10.4, are to be planted in various areas.

Until data are becoming available from these plant density-progeny trials (at the earliest 11 years after planting, since at least five years mature yield data are required), selection of parent palms for seed production (legitimate seed from *dura* × *pisifera* crosses) is based on information obtained from the test crosses and some within family selection in the seed gardens (path A in Fig. 23). The number of seed trees to be selected depends primarily on seed requirements. Eventually, commercial planting material with a combination of bunch yield components optimally suited for a particular area and the for such an area recommended plant density system can be produced by taking the information obtained from the plant density-progeny trials into account as well (path B in Fig. 23).

The second cycle of selection and breeding is started by intercrossing between populations of the same type, (i.e. I × I and II × II) as discussed in 10.2, to increase genetic variability by recombination of genes. Such (biparental) crosses should not be restricted to the very best selections, i.e. the progenitors of the first breeding cycle, but include as many palms as possible. The distinction between type I and II subpopulations continues to be made, but the number of subpopulations will be reduced and each subpopulation consists of full-sib families. After applying family selection and individual selection within the best families, carried out during the first three years of production, a number of *dura* and *tenera* palms will be chosen to form the progenitors of a new cycle of breeding and seed production, repeating the same procedures of making test crosses and establishing seed gardens and plant density-progeny trials, as applied in the first cycle (see Fig. 23).

Oil palm breeding demands long term planning. Already the first cycle of above sketched selection programme will require 20–25 years before the full returns will become available to the oil palm industry.

In the meantime optimal use should be made of the results of selection programmes, such as the one initiated at the NIFOR in 1957 (Sparnaaij et al., 1963). Thereby, interpopulation crosses (type I × II) should be emphasized and only material used with known A values for the components of oil yield as foundation stock for *dura* and

pisifera palms for seed production. Such plant material should by now completely replace the extension work seed issued so far, which is produced mainly from crosses between phenotypically selected *dura* and *pisifera* palms.

Summary

The oil palm has the highest production potential of all oil bearing crops and its economic importance is rapidly increasing in many countries in Asia, Africa, Central and South America. Prospects of further improvement of the oil yield by breeding are favourable, especially if one considers that present plant material is the result of only two or three generations of selection, generally starting from genetically narrow base populations.

Selection procedures are to a great extent limited because the oil palm is an outbreeding perennial plant for which no practical method of asexual propagation has yet been developed. The common selection procedures applied are individual selection and progeny testing to determine genotypic values for a number of components of oil yield, viz.: number of fruit bunches per palm per year (n_b), single-bunch weight (w), fruit to bunch (fr_b), mesocarp to fruit (m), shell to fruit (s), kernel to fruit (k) and oil to mesocarp (o_m).

The main object of the present studies has been to contribute to a better understanding of the variability and inheritance of the components of oil yield and to indicate methods of selection which should result in maximum genetic improvement per unit of time and effort expended. The studies are based on published data of the breeding programme of the Nigerian Institute for Oil Palm Research (NIFOR, annual reports 1951–1968) and on the results of a number of experiments carried out at the Oil Palm Research Centre in Ghana during the period 1965–1971.

The general introduction to oil palm breeding in Chapter 2 and outlines of the breeding programmes of the most important oil palm selection centres in Africa and Asia given in Chapter 3 serve as a background of easy reference for the subsequent chapters.

Genotypic values for the components of oil yield, actually additive genotypic values and denoted with symbol A, for a number of individual parent palms were estimated from sets of full-sib family means according to a method proposed by Sparnaaij (1969). The full-sib family means were derived from data of the NIFOR breeding programme (NIFOR annual reports 1964–1968). There was good agreement between values of the narrow-sense heritabilities (h_n^2) for each component of oil yield estimated from the regression of A on phenotypic values and from offspring-(mid)parent regressions. In other words, the genotypic component of variance for the components of oil yield mainly consists of additive variance in the studied NIFOR breeding populations and the calculated A values are, within reasonable limits, valid estimates of the genotypic values of these oil yield components.

The following values for h_n^2 were obtained:
- Bunch yield components for *tenera* and *dura* parents and offspring: 0.51–0.55 (n_b) and 0.21–0.35 (w).
- Bunch and fruit quality components for *tenera* parents and their *tenera* offspring: 0.45–0.55 (fr_b), 0.80–0.95 (m), 0.79–1.00 (s) and 0.60–0.66 (k).
- Bunch and fruit quality for *dura* parents and their *dura* offspring: 0.24 (fr_b), 1.00 (m), 0.98 (s) and 0.60 (k).
- Bunch and fruit quality components for *dura* parents and *tenera* offspring: 0.05–0.18 (fr_b), 0.32 (m), 0.19 (s) and 0.74 (k).

The genotypic (A) values were also used to estimate genetic correlations – per definition the correlation between A values (Falconer, 1960) – between components of oil yield. In contrast to what has been generally assumed, a fairly high negative genetic correlation was found to exist between the components n_b and w (over the first three years of production). Estimates of r_A between these two yield components, from offspring-midparent covariances and from correlated response to selection, agreed well with the first estimate. In the presence of such a substantial negative r_A between n_b and w, which is attributed to pleiotropic effects of general genetic factors of physiological efficiency, maximum selection progress appears to be obtained by intercrossing individual palms of widely divergent subpopulations. Significant correlations between other oil yield components are shown to be of little consequence for oil palm selection.

A detailed study on the nature of the inheritance of the three fruit quality components has been made in an effort to explain the reason for the poor relation between the phenotypic values of *dura* and *tenera* full-sibs or *dura* palms and their mean *tenera* offspring (low h_n^2) as regards the components m and s. Experimental evidence is produced of Sparnaaij's (1969) hypothesis that two different factors determine shell to fruit (s) and thus also mesocarp to fruit (m), viz. potential shell thickness and percentage lignification of this potential shell. From the results of the present study it is concluded that the potential shell-to-fruit ratio is a quantitative character inherited through polygenes, while the percentage lignification is determined by one major gene which causes 100% lignification if both dominant alleles are present (*dura*), 50% in the case of presence of one dominant allel (*tenera*) and no lignification when both alleles are recessive (*pisifera* fruit form). The 50% lignification in *tenera* fruits may appear to be less due to variation in kernel size. Only the genotypic *tenera* value of a *dura* palm for the components m and s is of relevance in present day selection and seed production programmes. This *tenera* value of *dura* palms can only be obtained from the mean of *tenera* full sibs or from the mean of *tenera* palms in an F_1 of a *dura* × *tenera* cross. On the other hand, the phenotypic value of a *tenera* palm for the components m and s is by itself a reliable estimate of its genotypic value (high h_n^2 for m and s).

The ratio oil to mesocarp (o_m) is an important component of oil yield. However, it was found that data for this component obtained from bunches harvested during the first year of production, as published by the NIFOR (NIFOR annual reports 1964–

1968), bear little relation to the inherent o_m values. These data could, therefore, not be used to obtain reliable estimates of h_n^2 for this component.

Investigations into the variability and heritability of the three components of the mesocarp of oil palm fruits – oil (o_m), water (w_m) and dry matter or fibre (f_m) – have led to the following conclusion. The ratio o_m is a component with a fairly low heritability ($h_n^2 = 0.20–0.40$) and multiple measurements are required over at least one full year (excluding the first year of production) to obtain reliable estimates of genotypic values from the means of full-sib families. On the other hand, the dry-fybre content (f_m) has a considerably higher heritability ($h_n^2 = 0.60–0.80$) and it is also less dependent on age of the palms and ripeness of the bunch. This offers the possibility of substituting the capital intensive direct methods of determining oil to mesocarp (Soxhlet extraction, or extraction with the 'oléomètre' as used by the IRHO) by a much less expensive and relatively simple 'modified indirect' method. This method involves the determination of f_m from a limited number of bunches (stage of ripeness less important) applying direct extraction methods followed by the determination of only the water content of the mesocarp (w_m) of a large number of bunches (only fully ripe bunches from the second year of production onwards). The component o_m is then calculated from the equation: $o_m = 100 - f_m - w_m$.

A number of experiments have been carried out to investigate the effect of different periods of water stress on bunch yield and its two components, as well as on vegetative growth of the oil palm. The stomatal aperture test, using an infiltration technique with aqueous isopropanol solutions, proved to be a very sensitive and accurate method of estimating the exact extent of the period of water stress in oil palms during the dry season. In one field experiment, where soil factors varied considerably, a high negative correlation ($r = -0.71$) was found between the annual period of water stress, as measured by the stomatal aperture test, and bunch yield of individual palms cumulatively over the first four years of production. Significant negative correlations between various growth parameters and the length of the period of water stress intimate that for vegetative dry-matter production the proportion of the environmental variance to total phenotypic variance is also considerable under West African growth conditions. Practical applications of the stomatal aperture test in oil palm selection and agronomic research are indicated.

In conclusion, the implications of the results of these studies in oil palm selection are discussed in greater detail. Continued selection progress for oil yield, more in particular bunch yield, will require the re-establishment of new, genetically highly variable and very divergent subpopulations resulting from systematic germ plasm collections in the centres of high genetic diversity. A proposed selection index including the bunch yield components n_b and w may increase response to individual selection initially to be carried out within these subpopulations. Divergency between subpopulations as regards the bunch yield components n_b and w should be enhanced by emphasizing selection for high w combined with high total bunch yield in certain populations (type I) and high n_b with total bunch yield in others (type II). For the estimation of genotypic (A) values of the components n_b and w as well as for seed

production only type I × type II interpopulation crosses should be made.

Improved methods of selection for bunch and fruit quality components (fr_b, m, s, k and o_m) are discussed. All bunch analysis work can be restricted to *tenera* bunches harvested during the first two to three years of production.

The best estimates of A values for the components n_b and w are obtained from the first three to four years of production, when the disturbing influence of competition for light between palms is still negligible. However, such values are as such of limited value in predicting the yield performance for older palms. The relation between early and mature bunch yield in the oil palm is discussed. The best solution appears to be to plant all progeny trials at one standard spacing (e.g. 9 × 9 m triangular) at the main selection station in order to determine the A values for the components n_b and w (and also the other oil yield components) from the first three years of production. At the same time a number of plant density-progeny trials, of which the design is given, should be planted in the major areas of oil palm cultivation served by the breeding centre. This will provide information about the optimum combination of bunch yield components and spacing for each area, assuring a continued high production level in mature plantations.

Possibilities of incorporating growth analysis in an oil palm selection programme are briefly discussed.

Outlines of a modified oil palm breeding programme are given (see Fig. 23).

Samenvatting

Naar een doeltreffender selectie op de olie-opbrengst bij de oliepalm (Elaeis guineensis Jacquin)

Van alle olie en vet leverende gewassen heeft de oliepalm het grootste opbrengstpotentieel. Het belang van de oliepalmcultuur neemt de laatste jaren in een groot aantal landen in Azië, Afrika en Zuid- en Midden-Amerika aanzienlijk toe. Het plantmateriaal dat nu algemeen gebruikt wordt is het resultaat van slechts twee of drie generaties selectiewerk, waarbij vaak is uitgegaan van genetisch nogal enge basispopulaties. Vooruitzichten voor verdere verhoging van de olie-opbrengst door middel van veredeling zijn gunstig.

Veredelingsmethoden worden bepaald door het feit dat de oliepalm een meerjarig en kruisbestuivend gewas is zonder de mogelijkheid (tot nu toe) van vegetatieve vermeerdering. Fenotypische selectie op individuele basis gevolgd door paarsgewijze kruisingen en toetsing van de F_1 nakomelingen (full-sib families) ter verkrijging van genotypische waarden voor een aantal opbrengstcomponenten zijn de voor de hand liggende methoden, De belangrijkste componenten van de olie-opbrengst zijn: aantal vruchttrossen per jaar per palm (n_b), gemiddeld trosgewicht (w), vruchtgewicht over trosgewicht (fr_b), de gehalten aan vruchtvlees (m), schaal (s) en zaad (k) in de vrucht en het oliegehalte van het vruchtvlees (o_m).

Het doel van de onderhavige studie was het verkrijgen van een beter inzicht in de variabiliteit en vererving (heritability) van bovengenoemde componenten en vervolgens het aangeven van doeltreffender methoden van veredeling in de oliepalm. De studie is gebaseerd op de resultaten van het veredelingsprogramma van de NIFOR in Nigeria (zoals gepubliceerd in de jaarrapporten) en een aantal laboratorium- en veldproeven uitgevoerd in de jaren 1965–1971 op de OPRC in Ghana.

Alle noodzakelijke achtergrondinformatie over taxonomie, bloembiologie en selectiemethoden in de oliepalm, alsmede over de veredelingsprogramma's van de belangrijkste selectiecentra in Afrika en Azië is samengevat in de hoofdstukken twee en drie.

Voor een aantal ouderpalmen van het NIFOR veredelingsprogramma zijn de genotypische waarden van elk van de olie-opbrengst componenten berekend, waarbij gebruik is gemaakt van de gemiddelde waarden van de full-sib nakomelingen van paarsgewijze kruisingen, zoals deze zijn gepubliceerd in de NIFOR jaarrapporten. Deze genotypische waarden, in feite additief-genotypische waarden waarvoor het symbool A is gebruikt, zijn berekend volgens een methode zoals voorgesteld door Sparnaaij (1969). Schattingen van h_n^2 voor elk van de componenten, verkregen door middel van de regressie van A op fenotypische ouderwaarden en van nakomelingen – ouder regressies, kwamen goed overeen. Daaruit kan geconcludeerd worden dat, tenminste in de bestudeerde NIFOR veredelingspopulatie, voor elk van de olie-opbrengst compo-

nenten de genotypische variantiecomponent voornamelijk bestaat uit additieve variantie. De gevolgde methode van berekening van de A waarden is dus juist en redelijk nauwkeurig.

De volgende schattingen voor h_n^2 werden verkregen:
- Voor n_b: 0,51–0,55 en w: 0,21–0,35; waarbij ouders en nakomelingen bestaan uit *dura* en *tenera* palmen.
- Voor fr_b: 0,45–0,55; m: 0,80–0,95; s: 0,79–1,00; en k: 0,60–0,66; binnen de *tenera* vruchtvorm (d.w.z. *tenera* ouders en nakomelingen).
- Voor fr_b: 0,24; m: 1,00; s: 0,98; en k: 0,60; binnen de *dura* vruchtvorm.
- Echter voor *dura* ouders en hun *tenera* nakomelingen was h_n^2 slechts: voor fr_b: 0,05; m: 0,32; s: 0,19; voor k bleef de waarde evenwel van gelijke grootte nl. $h_n^2 = 0{,}74$.

De berekende genotypische waarden werden vervolgens gebruikt ter verkrijging van schattingen van genetische correlaties – per definitie de correlatie tussen A-waarden (Falconer, 1960) – tussen de verschillende olie-opbrengstcomponenten. Tegen de algemene verwachting in kon een nogal hoge negatieve genetische correlatie worden vastgesteld tussen de componenten n_b an w, waarbij uitsluitend de eerste drie produktiejaren in aanmerking werden genomen. Met het oog op de belangrijke consequenties van een dergelijke negatieve r_A tussen de twee belangrijkste olie-opbrengstcomponenten voor de selectie werd ter bevestiging dezelfde genetische correlatie vervolgens geschat middels een nakomelingen-ouders covariantie-analyse tussen ouders en nakomelingen en via de gecorreleerde selectie respons van n_b t.o.v. w en andersom. Er bleek een goede overeenkomst tussen de verschillende schattingen. De negatieve genetische correlatie tussen n_b en w is toe te schrijven aan de pleiotropische werking van algemene genetische factoren verantwoordelijk voor de stofwisselingsefficiëntie. In de aanwezigheid van deze negatieve r_A tussen n_b en w zullen de beste vorderingen in selectie voor een hogere vruchttrosopbrengst in kg worden verkregen via interpopulatiekruisingen, waarbij de subpopulaties zo divergent mogelijk dienen te zijn. Er werden ook andere significante r_A's tussen de verschillende componenten van de olieopbrengst gevonden, maar deze bleken van weinig belang te zijn voor de selectie.

De vererving van de componenten van de vruchtkwaliteit (m, s en k) was het onderwerp van een gedetailleerde studie. In het algemeen bestaat er namelijk geen verband tussen het mesocarp- of schaalgehalte van *dura* en *tenera* vruchten van full-sib palmen en is de h_n^2 van deze eigenschappen bijzonder laag, wanneer *dura* ouders worden vergeleken met hun *tenera* nakomelingen. De door Sparnaaij (1969) opgestelde hypothese ter verklaring van deze schijnbare ongerijmdheid kon worden bevestigd door de proefresultaten. Het schaalgehalte (en dus ook het mesocarpgehalte) van een oliepalmvrucht wordt bepaald door twee verschillende factoren: de potentiële schaaldikte en daarnaast het percentage lignificatie van deze potentiële schaal. De conclusie is, dat de potentiële schaaldikte een kwantitatief-genetische eigenschap is. Daarentegen wordt het percentage lignificatie bepaald door een enkel gen met intermediaire werking, waarbij het homozygoot dominante genotype gelijk is aan 100% lignificatie zoals in de *dura* vruchtvorm, de heterozygoot gelijk aan 50% lignificatie zoals in de *tenera* vruchtvorm en het homozygoot recessieve genotype gelijk aan afwezigheid van

enige lignificatie zoals in de *pisifera* vruchtvorm. Variatie in zaadgrootte kan de eigenlijke 50% lignificatie in de *tenera* vruchtvorm maskeren. Slechts de genotypische *tenera*-waarde (A_t) van een *dura* palm voor wat betreft het mesocarp- of schaalgehalte is in de tegenwoordige selectie- en zaadproductieprogramma's van praktische waarde. Deze kan verkregen worden via een sib-analyse of uit het gemiddelde van de *tenera*-nakomelingschap. Daarentegen geeft de fenotypische waarde van een *tenera* palm een nauwkeurige schatting van zijn genotypische waarde voor deze eigenschappen (zeer hoge h_n^2 voor m en s).

Het oliegehalte van het vruchtvlees is een belangrijke selectiefactor. Het bleek echter, dat de analysecijfers van dit oliegehalte van vruchttrossen geoogst in het eerste jaar van produktie, zoals gepubliceerd in de NIFOR jaarverslagen, niet bruikbaar waren voor het bepalen van genotypische waarden of schattingen van h_n^2. Nader onderzoek, middels een groot aantal analyses van het oliegehalte, naar de variabiliteit en vererving van de drie componenten waaruit het vruchtvlees bestaat – olie (o_m), water (w_m) en droge stof of vezels (f_m) – heeft tot de volgende conclusie geleid. Het oliegehalte van het vruchtvlees is een factor met een lage waarde voor h_n^2 (0,20–0,40) en voor het verkrijgen van betrouwbare gegevens over de genotypische waarde van een ouderpalm, zoals bepaald via toetskruisingen, is een groot aantal analyses over tenminste een volledig jaar (met uitzondering van het eerste jaar van produktie) noodzakelijk. Daarentegen heeft het droge-stofgehalte een aanzienlijk hogere heritability ($h_n^2 = 0{,}60–0{,}80$), waarbij ook nog is gebleken dat het droge-stofgehalte minder beinvloed wordt door de leeftijd van de palm, het seizoen of de rijpheid van de vruchttros. Hiervan kan gebruik gemaakt worden om de nogal dure directe bepalingen van het oliegehalte (Soxhlet-extractie of extractie met de door de IRHO gebruikte 'oléomètre') te vervangen door een veel eenvoudiger 'gewijzigde indirecte methode'. Het inherente vezelgehalte van een full-sib nakomelingschap dient dan eerst bepaald te worden door middel van een beperkt aantal directe extracties (leeftijd van de palmen en rijpheid van de vruchttros minder belangrijk). Daarna kan het analysewerk beperkt worden tot bepalingen van het vochtgehalte van het vruchtvlees, waarbij zonder grote moeilijkheden een groot aantal trossen kan worden geanalyseerd. Hierbij is het juiste stadium van rijpheid van de vruchttros essentieel en kunnen bovendien geen eerstejaars vruchttrossen gebruikt worden. Het oliegehalte wordt dan berekend uit de vergelijking: $o_m = 100 - f_m - w_m$ (%).

Een aantal veldproeven werden uitgevoerd om nadere gegevens te verzamelen over de invloed van variërende perioden van watertekort in de oliepalm op de oogst, de twee componenten n_b en w, als ook de vegetatieve groei. Het bleek dat de periode van watertekort in de oliepalm zeer nauwkeurig bepaald kan worden aan de hand van metingen van de opening van de huidmondjes, de z.g. 'stomatal aperture test'. Hierbij werd gebruik gemaakt van een infiltratietechniek met een serie isopropanoloplossingen. In een veldproef, waar op korte afstand aanzienlijke verschillen optraden in bodemgesteldheid, werd een hoge negatieve correlatie ($r = -0{,}71$) gevonden tussen de gemeten periode van watertekort in de palm in het droge seizoen en het totale trosgewicht per palm over de eerste vier produktiejaren. Significante negatieve correlaties

werden ook gevonden tussen de lengte van de periode van watertekort en verschillende parameters van de vegetatieve groei van de oliepalm. Op deze wijze kon worden aangetoond dat, tenminste onder Westafrikaanse milieu-omstandigheden, ook de vegetatieve groei in de oliepalm aanzienlijk wordt beïnvloed door het milieu. Enkele voorbeelden worden gegeven van praktische toepassingsmogelijkheden van de 'stomatal aperture test' ter verkrijging van een juiste interpretatie van de resultaten van veldproeven met oliepalm.

In het laatste hoofdstuk wordt ingegaan op de consequenties van de verkregen resultaten voor de oliepalmveredeling. De nadruk wordt gelegd op het belang van het instandhouden en uitbreiden van genetisch variabele en divergente subpopulaties. Dit is vooral van belang voor de selectie op hogere vruchttrosopbrengsten. Daarvoor zullen regelmatig explorations van de genencentra van de oliepalm moeten plaatsvinden. Een selectie-index met n_b en w als componenten wordt voorgesteld om de respons van individuele selectie, als eerste stap uit te voeren in de nieuwe subpopulaties, te vergroten. Hierbij wordt een onderscheid gemaakt in subpopulaties waarbij vooral de component w uitspringt (type I) en een tweede type subpopulaties, die gekarakteriseerd worden door een hoog aantal trossen (type II). Dit onderscheid moet dan door selectie met behulp van de index geaccentueerd worden. Voor het bepalen van genotypische waarden evenals voor de uiteindelijke zaadproduktie dienen alleen kruisingen gemaakt te worden tussen palmen van verschillende typen subpopulaties.

Aanzienlijke vereenvoudigingen kunnen worden gemaakt in de selectiemethoden voor de tros- en vruchtkwaliteitsfactoren (fr_b, m, s, k en o_m). Daarbij kan al het selectiewerk beperkt worden tot trossen van *tenera*-palmen geoogst gedurende de eerste twee à drie produktiejaren.

De beste schattingen van de genotypische waarden voor de componenten n_b en w worden verkregen uit resultaten van de eerste drie à vier produktiejaren, omdat dan de lichtconcurrentie tussen de palmen nog verwaarloosbaar is. Dergelijke schattingen zijn echter slechts van beperkte waarde bij het voorspellen van het produktieniveau van oudere palmen. Als oplossing van dit probleem wordt voorgesteld alle toetskruisingen, die noodzakelijk zijn voor het schatten van de genotypische waarden van de ouderpalmen, uit te planten op het hoofdproefstation in een standaard plantverband (gewoonlijk 9 × 9 m driehoeksverband). Tegelijkertijd worden dan een aantal speciale 'plant density-progeny trials', waarvan de details worden besproken, uitgeplant in de verschillende gebieden die gewoonlijk het plantmateriaal van het proefstation betrekken. Deze proeven geven de uiteindelijke informatie over de voor elk gebied optimale combinatie van genotype en plantafstand, die noodzakelijk is om ook in oudere aanplanten een hoge produktie te garanderen.

Een korte beschouwing is gewijd aan de mogelijkheden van toepassing van verschillende groeimetingen in de oliepalmselectie.

Voorstellen van een gewijzigd veredelingsplan voor de oliepalm worden besproken en schematisch weergegeven in Fig. 23.

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Symbols and abbrevations

A	genotypic value
A_d	genotypic value based on *dura* progeny only
A_t	genotypic value based on *tenera* progeny only
A_{t+d}	genotypic value based on *tenera* and *dura* progeny
BI	bunch index = bunch dry matter over total dry matter
CGR	crop growth rate
-D	*dura*
E.S.	effective sunshine
f	fibre mantle-to-fruit ratio
f_m	fibre-to-fresh mesocarp ratio
$f(m_1)$	fibre-to-fresh mesocarp outside fibre mantle
$f(m_2)$	fibre-to-fresh mesocarp including fibre mantle
fr_b	fruit-to-bunch ratio
h_n^2	narrow-sense heritability
h_w^2	wide-sense heritability
k	kernel-to-fruit ratio
LAI	leaf area index
m	mesocarp-to-fruit ratio
m_1	mesocarp outside fibre mantle
m_2	mesocarp including fibre mantle
NAR	net assimilation rate
n_b	number of bunches per palm per year
o_m	oil-to-mesocarp ratio
$o(m_1)$	oil-to-mesocarp outside fibre mantle
$o(m_2)$	oil-to-mesocarp including fibre mantle
P	phenotypic value
P_t	phenotypic value of *tenera*
P_d	phenotypic value of *dura*
-P	*pisifera*
r_A	coefficient of correlation between the additive genotypic values
r_E	coefficient of correlation between the values of environmental plus non-additive genetic effects
r_P	coefficient of correlation between observed values
s	shell-to-fruit ratio
s. fr. v.	single-fruit volume
s. fr. w.	single-fruit weight
-T	*tenera*
VDM	vegetative dry-matter production
w	mean single-bunch weight per palm
w_m	water-to-fresh mesocarp ratio