THE ANALYSIS OF BUNCH PRODUCTION IN THE OIL PALM

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PROEFSCHRIFT
TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWKUNDE
OP GEZAG VAN DE RECTOR MAGNIFICUS IR. W. DE JONG,
HOOGLERAAR IN DE VEETEELTWETENSCHAP,
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DOOR

L. D. SPARNAAIJ

STELLINGEN

I

Een vrije uitwisseling van gegevens betreffende het landbouwkundig onderzoek tussen verschillende landen, dient gepaard te gaan met een even vrije uitwisseling van plantmateriaal.

II

Van de adviezen en het plantmateriaal door een proefstation aan de praktijk geleverd zal een beter gebruik worden gemaakt wanneer zij direct betaald worden door de belanghebbenden, in plaats van indirect via algemene heffingen op het produkt of overheids-subsidies.

III

Voor de landbouwkundig onderzoeker in de Tropen is praktische kennis van de proefveldtechniek van meer belang dan kennis van de wiskundige verwerking der proefresultaten.

IV

Onderzoek op het gebied van de produktie en de verwerking van palmwijn, als een secundaire activiteit van oliepalm-ondernemingen, kan van groot belang zijn voor de bevolking van de Afrikaanse oliepalm gebieden.

V

De sociale positie en de salariëring van landbouwkundigen in de onderontwikkelde Afrikaanse gebieden is in vele gevallen zodanig, dat te weinig inheemsen zich tot de landbouwstudie aangetrokken voelen. Als gevolg hiervan blijft er een groot gebrek bestaan aan inheemse landbouwkundigen, zonder welke een harmonische ontwikkeling van de Afrikaanse landbouw niet mogelijk is.

VI

In de overwegend agrarische Afrikaanse gebieden is uitbreiding en verbetering van de cultuur der traditionele exportgewassen van meer belang dan het bevorderen van industrialisatie.

VII

Voor de verbetering van de fabriekmatige palmolie-produktie in de natuurlijke palmwouden van Afrika is het noodzakelijk dat de fabriek de controle verkrijgt over oogst en aanvoer der vruchten.

VIII

De West-Afrikaanse gebieden, wier palmolie-produktie in hoofdzaak is gebaseerd op de wilde palmbestanden, zullen hun positie op de wereldmarkt slechts kunnen handhaven, wanneer de wilde palmen in versnelde mate door aanplanten van hoogwaardig materiaal worden vervangen.

IX

Het gebruik van verschillende lijnen of clonen voor de herhalingen van cultuurproeven is onjuist; het toepassen van verschillende cultuurmethoden in de herhalingen van een lijnen- of clonen-proefveld is daarentegen bij oriënterende toetsingen aanbevelenswaardig.

X

De veelvuldig voorkomende steriliteit bij de variëteit *pisifera* van de oliepalm berust niet op de werking van specifieke steriliteitsfactoren, maar is het gevolg van een, ten dele erfelijk bepaalde, overmatige produktie van vrouwelijke bloeiwijzen.

XI

Het is onjuist om de steriele vorm van de variëteit *pisifera* van de oliepalm uit te sluiten van het veredelingswerk. Het is waarschijnlijk dat deze vorm in zijn nakomelingschap een grotere produktiviteit en een betere vruchtsamenstelling te zien geeft dan de fertiele vorm.

XII

Het kenmerkend verschil tussen de variëteiten *dura, tenera* en *pisifera* van de oliepalm is de mate van verhouting van het parenchym weefsel binnen de beschermende vezelzone rond de kern. Bij de dura is de verhouting volkomen, bij de pisifera is zij afwezig, bij de intermediaire monohybride tenera is zij partieel.

XIII

Bij stikstofbemesting van de oliepalm dient men steeds rekening te houden met de mogelijkheid dat een eventuele verbetering in de groei en de bloei van de palmen zijn uitwerking op de produktie mist door een verschuiving van de geslachtsverhouding der bloeiwijzen naar de manlijke kant.

XIV

Het verdient aanbeveling om bemestingsadviezen aan tropische cultuurondernemingen te baseren op de verschillen tussen de resultaten van een grond- of blad-analyse van een gemiddeld monster van het betreffende terrein en de analyse-resultaten van een monster genomen in de beste delen van het zelfde terrein.

XV

Het „Little Leaf" symptoom, zoals dat in Nigeria bij de oliepalm wordt waargenomen, is het gevolg van een parasitaire aantasting van de jonge bladspeer. De vatbaarheid voor deze aantasting is in hoge mate erfelijk bepaald.

XVI

In het algemeen kunnen parasitaire wortelziekten meer effectief bestreden worden door veranderingen van het bodemmilieu in voor de parasiet ongunstige zin, dan door het kweken van resistente rassen.

SAMENVATTING

DEEL I

Over de ontwikkeling van het onderzoek met betrekking tot de oliepalm in Azië zowel als in Afrika werd een kort overzicht gegeven.

Het eigen onderzoek heeft een poging tot toetsing van enige ideeën met betrekking tot de uitwendige factoren, welke het geslacht in de bloeiwijzen der oliepalm bepalen, als uitgangspunt gekozen. Daarbij heeft zich dit werk ontwikkeld tot een algemene studie van de milieufactoren – voornamelijk die welke betrekking hebben op cultuurmaatregelen – op de geslachtsverhouding der bloeiwijzen en de overige componenten, welke de vruchttrosproduktie bepalen, zoals bladproduktie, bloemafstoting, vruchttrosmislukking en gemiddeld vruchttrosgewicht.

Het voornaamste doel van deze studie is het aantonen van de waarde van een dergelijke analyse van de vruchttrosproduktie voor de interpretatie van resultaten van veldproeven.

DEEL II

Een beschrijving van de methoden ter kwantitatieve bepaling van de verschillende componenten, die de vruchttrosproduktie bepalen, werd gegeven.

Besproken werd de wijze van uitdrukken en de statistische verwerking van de gegevens.

DEEL III

Beschreven werden de normale variaties in de componenten welke de vruchttrosproduktie bepalen als gevolg van leeftijd van de palm, grondsoort, jaargetijde, klimaat en genetisch bepaalde herkomst.

Sommige van deze gegevens zijn reeds door Broekmans gepubliceerd, doch een aanvullend onderzoek werd gedaan, voornamelijk in verband met de relatie tussen de produktiefactoren en bodemeigenschappen.

DEEL IV

Een complete analyse van de vruchttrosproduktie werd gemaakt bij een proef over verschillende methoden van aanleg van een oliepalmaanplant.

De uitkomsten laten een oogstvermeerdering zien van het object der tussenbeplanting met voedingsgewassen; de analyse der produkties hebben voornamelijk ten doel om te onderzoeken, wat de oorzaak is van dit onverwachte resultaat door de factoren welke de produktie bepalen één voor één na te gaan.

Het bleek, dat tussenbeplanting de bladproduktie sterk stimuleert in de jaren vóór de bloei. In latere jaren is de enige produktiefactor, welke gunstig door de tussenbeplanting wordt beïnvloed, de geslachtsverhouding der bloeiwijzen. Dit effect is echter beperkt tot één der zaailingfamilies en is ook duidelijk afhankelijk van het jaargetijde.

De toename in de geslachtsverhouding komt tot uiting in een toename van het aantal vruchttrossen in de objecten met tussenbeplanting van dezelfde familie in hetzelfde seizoen, hetgeen het positief eindresultaat der hogere produktie veroorzaakt.

Een bestudering der verschillende bodemfactoren heeft tot resultaat, dat het waarschijnlijk een reductie van het stikstofgehalte in de tussenbeplante objecten is, dat hier van betekenis moet worden geacht.

Deze resultaten tezamen met de ideeën van Beirnaert leiden tot een nieuwe hypothese met betrekking tot de relatie tussen geslachtsverhouding van de bloeiwijzen van de palm en de milieufactoren waarin deze verkeert.

Deel V

Een overzicht wordt gegeven van drie veldproeven welke aanvullende gegevens opleveren met betrekking tot het milieu en de factoren, welke de vruchttrosproduktie bepalen.

a. Een snoeiproef met het doel na te gaan, wat verschillen in belichting in verschillende jaargetijden tot gevolg hebben.
b. Een bemestingsproef, waarin het effect van organische en anorganische bemesting op deze factoren wordt nagegaan.
c. Een beplantingsproef gelijk aan die in deel IV besproken, doch op veel armere grond.

De gegevens uit deze proeven verkregen geven veel steun aan de hypothese in deel IV opgesteld.

Deel VI

Een bespreking wordt gegeven van de praktische betekenis der besproken resultaten.

Enige nieuwe veldproeven, met betrekking tot plantafstand, stikstofbemesting en de combinatie oliepalmen en voedingsgewassen, worden in het kort besproken.

Aandacht wordt besteed aan het belang van produktie-analyse voor de studie der palmveredeling, vooral met betrekking tot de selectie van palmen geschikt voor marginale omstandigheden, het vraagstuk der steriliteit van de pisiferapalmen en de betrekking welke bestaat tussen schaaldikte en geslachtsverhouding.

Als algemene conclusie moge gelden, dat het tegenwoordige werk van het W.A.I.F.O.R. is verbreed door de toepassing van produktie-analyse.

PREFACE—VOORWOORD

Bij de voltooiing van dit proefschrift wil ik mijn erkentelijkheid betuigen aan allen die het mij mogelijk hebben gemaakt dit resultaat te bereiken.

Hooggeleerde Coolhaas, hooggeachte promotor, Uw grote belangstelling voor het onderwerp van mijn proefschrift is voor mij steeds een stimulans geweest om deze studie, die slechts gedeeltelijk door mijn eigenlijke onderzoeksopdracht gedekt werd, tot een goed einde te brengen. Dat U tijdens Uw recente bezoek aan Nigeria zoveel waardering hebt getoond voor het werk van ons Instituut en voor mijn aandeel daarin, beschouw ik als een grote eer.

I am much indebted to the Director and the Managing Committee of the West African Institute for Oil Palm Research for their permission to pursue this study, which was only partly covered by my division's research programme, and to use the data for the preparation of a thesis.

My sincere thanks are also due to all those who have assisted in the preparation of this thesis, either by helpful discussions of controversial scientific points or by constructive criticism of the style and arrangement of the text. In this connection I wish to mention in particular Mr. C. W. S. Hartley, Director of the Institute and my colleagues Messrs. Broekmans, Bull, Whitehead and Chapas.

I also wish to express my thanks to those members of the Agronomy and Plant Breeding Divisions who have assisted me in extracting and summarizing the extensive data used in this study. I am particularly grateful to Mr. Osayi whose capable management of much of the routine work of my division was of considerable help to me during the time I was preparing this thesis.

Bij deze gelegenheid wil ik ook mijn dank betuigen aan U, hooggeleerde Dorst, voor de wijze waarop U mij hebt ingeleid in de leer der plantenveredeling, een studiegebied dat ik sinds kort ook tot het mijne heb mogen maken.

Aan Uw bemiddeling, weledelgestrenge Baumann, heb ik het te danken dat ik destijds in de gelegenheid werd gesteld mijn praktijktijd in Afrika door te brengen. De grondslag voor dit proefschrift werd reeds tijdens die reis gelegd.

CONTENTS

PART I

Introduction

The oil palm, *Elaeis guineensis* Jacq. is one of the major oil producing plants of the world, surpassing any other crop in yield of oil per acre and taking only second place in the world market as a producer of vegetable oils (Faure, 1958).

The original home of the oil palm is most likely the west coast of tropical Africa, and it occurs throughout all areas where the influence of man has caused the disappearance of the virgin tropical rain forest. The oil palm is not a forest species as it needs abundant light for its growth and production. It is most commonly found in the light secondary bush or farm land which has now largely replaced the original forest vegetation.

To what ecological association of plants the oil palm belonged originally is still a controversial question. The most recent suggestion is that it originated from the fresh water swamps along the coasts of West Africa (Waterston, 1953). It is generally accepted, however, that it is only through human activity that the oil palm has spread over such large areas. Vanderijst (1922) has put forward some interesting theories on the spread of the oil palm in central Africa, and Waterston (1953) has expressed similar views on the origin of the extensive palm groves in West Africa. Both authors agree that the rapid spread of the oil palm into new areas was intimately bound up with their penetration by man and that this introduction was intentional, involving the actual sowing of oil palm nuts around houses and in forest clearings, (Vanderijst terms this a "proto culture"). The multiplication of the species and the formation of groves must however be seen as a natural process in which man played no active part other than preventing the re-establishment of the trop cal rain forest climax in which the oil palm could not have survived.

In present days the oil palm occurs in an almost continuous belt extending from Senegal in the west through to the Belgian Congo in Central Africa. The major palm oil producing countries in this belt are Sierra Leone, the Ivory Coast, Dahomey, Nigeria, the Cameroons, the Belgian Congo and Angola. In all these countries palm oil is a vital foodstuff for the indigenous races, while in some it is also the major export product (e.g. Southern Dahomey, Eastern Nigeria) playing a dominant part in the national economy. The bulk of the oil exported is obtained by the exploitation of the semi-natural palm groves by the African farmer. Only in the Belgian Congo has the plantation industry developed rapidly; in all other West African territories the number of plantations is small and their contribution to the total oil exported is relatively unimportant.

In the middle of the nineteenth century the oil palm was introduced to the East Indies but repeated efforts of the Dutch Colonial Government to introduce it into the existing agricultural systems met with no success (Hunger, 1924). The coconut palm was the traditional source of oil in those countries and it remains so at the present day. In the second decade of the present century, however, European plantation companies began to show an interest in the oil palm and showed such confidence in the new crop that more than 6,000 acres were already planted before any plantations came into production. The optimism which led to such development has proved to be fully justified, for with the rapid spread of the plantation industry along the east coast of Sumatra and in the Malayan Peninsula, it was not long before the plantations in these two areas were exporting more palm oil than all the African countries put together. This was the situation which obtained in 1938 just before the outbreak of the Second World War (van Heurn, 1950).

The completely different development of the oil palm industry in the two main producing areas, viz. South East Asia and West Tropical Africa, is clearly reflected in the activities of the various research establishments which have grown up. Many practical problems of oil palm multiplication and planting had already been solved by the Botanical Gardens and by experienced planters in Java and Sumatra when the A.V.R.O.S. Experiment Station, at Medan, which was founded by the Planters' Association, began to work on this crop. This experiment station carried out most of its agronomic field experiments on established estates in order to solve specific questions raised by the planters. Most of the agronomic research was therefore of a very practical nature and the results were only made available to the member estates. This explains why, when the oil palm plantation industry in Sumatra was at its highest stage of development, in the years between 1930 and 1939, virtually nothing was heard of the progress of research in that area. Since the war information has been more freely available, and it is now clear that research has been directed throughout the years towards the breeding of highly productive strains. Agronomic research of a more fundamental nature has not been undertaken with the oil palm.

In the African research stations, which began work before much oil palm planting had been done, the situation was quite different. No sound basis of accumulated planters' experience was available and it therefore fell to the research organizations to carry out a great deal of simple agronomic research, covering all practical aspects of establishment, maintenance, and exploitation of oil palm plantations.

In the Belgian Congo the early work of the I.N.E.A.C. (Institut National pour l'Etude Agronomique du Congo Belge) covered such problems as germination technique, the raising of planting material in the pre-nursery and nursery, methods of establishment, and the effects of mineral and organic manures.

In the later years, the plantation industry developed rapidly and as the planters learned to establish and manage their plantations without the advice and assistance of the I.N.E.A.C., the latter's activities began to follow the same pattern as with the A.V.R.O.S. in Sumatra. Agronomic research was gradually reduced to a minimum and all efforts were directed towards an improvement in the quality and quantity of the seed supplied to the planters.

Since 1950 a more balanced research programme has again been built up, since it has become necessary to create conditions in which greatly improved strains can fully develop their high production potential.

In Nigeria and the French West African territories the foremost problem was, and still is, the improvement of the native oil palm industry which is based almost entirely on the natural palm groves, rather than on plantations. The problems have therefore been centred more on methods than on materials, i.e., they have been agronomic rather than genetic. Before any specialized research stations were established, the Agricultural Departments in the French and British West African territories were already engaged in schemes to improve the exploitation of the natural palm groves. So many technical and social difficulties were encountered however, that these early efforts usually failed.

After the war special bodies were created in Dahomey, the Ivory Coast and the French Cameroons to carry out large-scale palm grove improvement and replacement schemes, using the improved techniques developed by the French research institute, the "Institut de Recherches pour les Huiles et Oléagineux" (I.R.H.O.). These vast schemes involved the planting of many hundreds of thousands of improved seedlings, and it became imperative for the research stations to pay equal attention to agronomic and breeding problems. The former arose from the poor soil fertility and unfavourable climatic conditions in large parts of the palm belt, while the latter were brought about by the enormous consumption of seed by the various development schemes.

In Nigeria research has initially been directed more towards the improvement of planting and maintenance methods than towards the breeding of highly productive strains. At the same time, the West African Institute for Oil Palm Research has been built up and has been able to carry out a considerable amount of botanical research on the oil palm, in particular on floral biology, seed germination and nutrition.

No large-scale development of plantations or palm grove improvement schemes has so far taken place in Nigeria. Most of the improved seedlings now being issued ultimately go to small farmers and few, if any, of these palms grow up under conditions which enable them to express their inherent production capacity. Under such circumstances a preponderance of agronomic research is not unnatural. There is no doubt however that in the future the large-scale improvement and replanting of the natural palm groves will become an absolute necessity if Nigeria is to maintain its first place in the world market. The increased breeding and selection work which is necessary to meet future demands will greatly benefit from data collected in the earlier years on the biology of the palm.

The study here presented is not easily placed within the field of agronomic research discussed above. Its origin lies in the work of Beirnaert (1935) in the Belgian Congo while its practical realization is based on the extensive growth and flowering data collected from early agronomic experiments in Nigeria.

As part of the botanical work related to the breeding and selection programme of the I.N.E.A.C. in the Belgian Congo, Beirnaert made a study of the floral biology of the oil palm. In particular he studied the alternation of male and female flowering cycles, and expressed the view that this alternation is governed by both genetical and environmental factors: "il constitue l'expression de l'action du milieu sur l'aptitude héréditaire du palmier". On the strength of observations made on palms growing under different and rather exceptional conditions, he came to the conclusion that the most important environmental factor affecting flowering was the ratio between carbohydrate assimilation and mineral nutrition. An increase in this ratio would lead to an increased proportion of female inflorescences while a decrease would stimulate male flowering.

To obtain experimental proof of his theories Beirnaert started an observational experiment including about twenty rather drastic treatments such as fertilizer and trace element applications, shading, leaf pruning, excessive drainage, root pruning, etc. (Toovey, 1938). Probably due to the outbreak of the war and Beirnaert's accidental death, this experiment was never completed, and up to the present day Beirnaert's ideas have never been put to the test. Nevertheless, the results of some important agronomic experiments at Yangambi seem to support his views. This holds in particular for the classic intercropping experiment at Yangambi in which, contrary to all expectations, the yield of the palms throughout the life of the plantation proved positively correlated with the intensity of the intercropping (I.N.E.A.C., 1955). Most experiments with mineral fertilizers either failed to produce any results or indicated a yield depression by manuring (Focan, 1950).

It was suggested by the author (1951), when reporting on the experiments at Yangambi, that these peculiar results might be explained in terms of Beirnaert's hypothesis by changes in the percentage female flowering, assuming that under Yangambi conditions the factor limiting yields is the carbohydrate assimilation rather than the mineral nutrition. The ratio between these two factors would be improved by a reduced mineral nutrition due to cropping while it would be lowered by an addition of mineral fertilizers. No experimental data on flowering were available at Yangambi to test this suggestion.

In Nigeria, however, a mass of growth and flowering data was accumulated in the earlier cultural experiments (including intercropping treatments) and progeny trials, which were planted at the W.A.I.F.O.R. Main Station between 1940 and 1945. The data from the progeny trials served as a basis for Broekmans' (1957) recent investigation of the effects of climatic conditions on growth and flowering of oil palms. The data from the cultural experiments were initially used only to test the validity of Beirnaert's hypothesis. They have also provided the material for a more general study of outside influences and in particular the effects of cultural treatments on the various growth and flowering factors which are the components of bunch production.

The main object of this study has been to demonstrate the value of the analysis of bunch production for the interpretation of field experiments.

PART II

Observing and Recording the Components of Bunch Production

The ultimate aim of an agronomic research programme is to raise the yield per acre or the quality of the produce grown. In the oil palm industry the improvement of oil quality is a matter of harvesting and milling efficiency, i.e., a problem for estate managers and technologists rather than for agriculturists. The improvement of the oil content of palm fruits, on the other hand, is, so far as is known purely a genetical problem. The agronomist's task is thus reduced to increasing the weight of fruit bunches per acre by controlling the external conditions influencing yield.

Agronomic research aimed at increasing yields can be conducted along two lines. The more common approach is that of field experimentation based on experience with other crops. Such experiments are exploratory in nature, covering a wide range of treatments derived both from those used in existing agricultural practice and from the experimenter's intuition. Information gained from such experiments forms the basis for further, more detailed investigation of the effects of a narrower range of treatments.

Most experimentation on various cultural practices in oil palm cultivation has been conducted in this way, and so has some of the research on fertilizer problems, e.g., by means of large wholly exploratory factorial experiments in which the effects of the major nutrients in all possible combinations are compared.

The other approach is that of experimentation based on analytical results. It is widely used in, for example, nutritional research. Soils or leaves are analysed to determine the absolute and relative quantities of different nutrients, and the analyses are followed by field experiments designed to translate the analytical results into practical fertilizer treatments. The choice of treatments is therefore no longer empirical but is governed by a synthesis of all the information gained from the preceding analyses.

In this paper we are concerned with a form of analytical research not involving any chemical analyses but based on a study of the growth and flowering of palms growing under different environmental conditions. The bunch production under different treatments or conditions is analysed into its components in an attempt to understand how the yield differences have arisen. As a synthesis of all the information so obtained a hypothesis may then be developed which is used as the basis for subsequent field experiments.

The most important production components are:

(*a*) *Leaf production.* The number of leaves produced determines the number of inflorescence primordia laid down. Normally one such primordium is present in each leaf axil.

(*b*) *Abortion of inflorescences.* The amount of abortion of inflorescences before anthesis determines the actual number of inflorescences reaching the stage of flowering.

(*c*) *Sex of inflorescences.* The number of female inflorescences reaching the flowering stage determines the number of potential fruit bunches.

(*d*) *Survival of female inflorescences after flowering.* The survival rate determines how many of the female inflorescences reaching the stage of flowering will eventually develop into mature bunches.

(*e*) *Average bunch weight.* While the above factors determine the number of bunches eventually produced, the average bunch weight determines the final weight of bunches harvested.

The collection of accurate and continuous data on these components is costly and time-consuming and detailed observations are only justified in closely controlled experiments carried out by research establishments. It is however possible to reduce the cost of observations with only a small loss of information by adopting simplified methods, which can be used on a larger scale or in areas where staff or funds are limited.

In the present chapter both detailed and simplified methods used in the quantitative assessment of the part played by various yield components are discussed.

Leaf Production

Incremental Leaf Counts on Young Palms

If information is required on variation of growth rate with season, observations must be carried out at intervals of not more than one month. Such observations are also of value in the study of nursery and transplanting techniques, particularly where treatments which affect the supply of water to seedlings are being compared.

The last-opened leaf is marked (e.g. with a label or paper-clip or by cutting off the upper half of one or more pinnae) at the beginning of each period of observation. A month later the number of leaves opened after the one previously marked is counted and recorded and the label transferred to the youngest leaf.

Simple Determination of Total Leaf Production of Young Palms

It is not always necessary to collect leaf production data monthly. For many studies, it is sufficient to have information on the total leaf production over, say, the whole nursery period, the dry season, or the first year after planting. In such cases the following simple method may be adopted:

At the beginning of the period of observation the three youngest leaves are marked with metal labels, printed 1, 2 and 3, number 3 indicating the very youngest leaf. At the end of the period, which should be not more than one year later, the labels are traced again and all new leaves within the three labelled ones are counted and recorded. If the observation is to be continued the labels may be transferred to the three youngest leaves.

Observation of Leaf Production in Relation to Flowering

In cases where it is desired to relate the number of leaves produced to the number of inflorescences, it is necessary to have exact information on the order in which the leaves unfolded, and on the presence or absence of inflorescences in leaf axils.

The method which has been in use at W.A.I.F.O.R. for the collection of most of the data presented in the following parts may now be described.

Each palm is visited once a fortnight and any leaves which have opened since the last visit are marked with a code label consisting of any three letters. Codes for each leaf are entered into a field note book together with the date of opening of the leaf. When a leaf reaches the stage of flowering the date of opening of the inflorescence is marked against the appropriate leaf, together with the sex of the inflorescence. An example of a typical set of records is given below:

Leaf	Date opened	Inflorescence	Date opened
XOB	5.1.54	♂	8.10.54 (male inflorescence)
ATP	26.1.54	⚥	5.11.54 (hermaphrodite inflorescence)
IBI	20.2.54	+	(aborted inflorescence)
OWO	8.4.54	♀	10. 1.55 (female inflorescence)

Inflorescence Production—Abortion—Sex-Ratio

The method described in the preceding paragraph is, of course, perfectly suitable for the determination of *total inflorescence production* within any desired period of time. By simple difference between the number of leaves reaching, in a certain period, the stage at which flowers are produced and the total number of inflorescences in that same period, the amount of floral abortion can be accurately calculated.

The ratio of female and hermaphrodite inflorescences to total inflorescences (*sex-ratio*) is obtained by adding the relevant symbols for the period of time required.

The method is thus very comprehensive and allows for a study of fluctuations in leaf production rate, length of time between leaf opening and flowering, total inflorescence production, amount of floral abortion and sex-ratio.

Its main drawback is the high cost of the observations and of the clerical work involved in transcribing and summarizing the data.

While this comprehensive method is most suitable for accurate studies of variations in growth and flowering, it is too troublesome and costly to be used in ordinary field experiments.

A simpler method has therefore been developed which provides all the information usually required, at a fraction of the cost of the comprehensive method.

At the beginning of the period of observations all leaves above the one carrying a flowering inflorescence are coded systematically in the reverse order of age up to the last-opened leaves. The codes are recorded in this order in the record book, and the coding is brought up to date every two or three months. A survey of leaf and inflorescence production is held on the 1st of January, March, May, July, September and November or as near as possible to those dates. On each of these dates a metal label is tied to the leaf carrying a flowering inflorescence or, where there is no inflorescence, to the leaf of corresponding age. In each two-monthly survey the number of leaves and of male, female, and hermaphrodite inflorescences between the new metal label and the previous one is counted and recorded in the record books as follows:

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Survey	Leaf code	Leaves	♂	♀	⚥
1958	AX				
	BX				
	CX				
I	DX	4	3	—	—
	EX				
	FX				
	GX				
II	HX	4	2	1	1
	IX				
	KX				
III	LX	3	2	1	—

(The leaves immediately above the lines are those bearing the metal labels.)

The surveys are based entirely on the order of leaf production, not on the order of inflorescence production. This means that, if a leaf included in survey II does not produce an inflorescence until the period of survey III, the figures for survey II are corrected. In other words a "late" inflorescence is included in the survey to which its subtending leaf belongs.

This method provides accurate two-monthly figures for total inflorescence production, sex-ratio and abortion. No accurate information is obtained on the opening of new leaves since leaves are only counted as they reach the stage of "flowering". The coding of the leaves does not provide any additional information, but it greatly facilitates the work of the observers, reduces the number of errors and provides a means of checking observations.

An even simpler system can be adopted when one wants to collect data on sex-ratio alone. For this, it is sufficient to "harvest" and record once a month the male inflorescences which are past the stage of anthesis. The female inflorescences are counted as bunches, 5-6 months later. By comparing the number of bunches harvested in a certain period with the number of male inflorescences harvested in the corresponding period five months earlier, a fair estimate of sex-ratio is obtained. It is not more than an estimate however, as bunch failure is not taken into account. As sex-ratio is the most important yield element this method enables one to obtain a great deal of extra information from an experiment without any substantial increase in labour costs.

Bunch Failure

To determine the percentage female inflorescences not developing into ripe bunches, and to investigate the causes of any losses that occur, it is necessary to record the fate of each female inflorescence in regular observations. Such observations have not so far been carried out.

The fact that inflorescences are usually recorded by leaf and flower observers, while bunches are recorded by yield recorders quite independently of these observers, makes it difficult to combine the two records. It is, however, the intention that accurate records of bunch survival will be collected over a limited area at the W.A.I.F.O.R. Main Station in order to determine the causes of the sometimes unexpectedly high percentage of female inflorescences which are unaccounted for at harvest. This loss has so far been attributed solely to bunch failure, but it is not impossible that a considerable proportion of the "lost" bunches may be traced either to errors in yield recording or to the excessive "male-ness" of some of the hermaphrodite inflorescences. The latter are usually considered as being capable of developing into a bunch but the percentage female flowers may sometimes be so small that the whole bunch, with the male spikelets, rots or the few fruits that do develop are overlooked by the harvesters.

The figures for bunch failure which are presented in Parts II and IV can only be regarded as rough estimates obtained by comparing the total number of bunches harvested over a certain period with the total number of female and hermaphrodite inflorescences reaching anthesis in the corresponding period six months earlier.

As the period of ripening is by no means constant, such estimates are only reliable when they cover a long and continuous period. They are, therefore, unsuitable for the study of seasonal effects on bunch failure.

Bunch Yields

Yield recording is an operation which must be done with great care, since reliable yield figures constitute the basic material for the interpretation of any field experiment. There are various means of checking the accuracy of yield records but most of them have the draw-back that an error is usually detected too late to be corrected. It is therefore of great importance to make the actual operation of harvesting and recording as fool-proof as possible by insisting on weighing any bunch under the palm from which it is harvested, by surprise checks in the field and by regular surveys to check the presence and legibility of all palm labels.

At W.A.I.F.O.R. the number and weight of bunches harvested from each palm is entered in the field in special duplicate books. At the end of each month the original pages are removed, sorted out field by field and sent to the Statistics Department in Lagos where the records are transferred on to punched cards. At the end of the year the annual yield of every palm is calculated mechanically as are, by means of codes, the plot and treatment totals. This arrangement means an enormous saving of time and ensures an accuracy in additions which could seldom be attained if the work were to be done solely by clerical staff.

The disadvantage of this system, in which the records are treated mechanically outside the research station, is that an absolute uniformity in procedure is required if confusion is to be avoided. To obtain additional information afterwards, e.g. seasonal yield data, is virtually impossible. As the extraction of such data from the old harvesting books is laborious and costly, it is seldom possible to use other than annual yield data for the statistical analysis of field experiments.

In the course of the present study the importance of the interactions between the seasons and the effects of cultural treatments is indicated repeatedly, and it therefore seems advisable, at least in certain cases, to modify the mechanical treatment of the yield records to such an extent that yield summaries can be obtained at least twice a year. It is fortunate that the two main seasons of the year both last about six months, the dry season from November to April and the wet season from May to October. In most cases a single division of the year from November to October in two halves will be sufficient to demonstrate any seasonal effects.

When only annual yield data are available for a field experiment, these figures form the only basis for a statistical analysis. When, in addition to the annual yield figures, records are available on seasonal yields, or on the various production components, it is possible to carry out a statistical analysis on each set of data separately. The chance that an experiment will provide some useful information is therefore increased. In normal experimental practice it will not be necessary, however, to analyse all production components separately. In most cases it will be possible to see from a quick examination of the figures which of the components react most strongly to the treatments.

A detailed analysis of these components, summarized for each of the two main seasons separately, will generally be sufficient.

In the experiments described in the following Parts statistical treatment has in most cases been limited to the yield figures and the seasonal sex-ratio figures. The latter are chosen because sex-ratio is usually the most important individual production component. It is also a component which is apt to react to changes in environmental conditions quite differently from those of other production components (see page 29). These two facts suggest that gross environmental effects on bunch yield are not necessarily more pronounced than the effects on the individual production components. In some cases, changes in bunch yield reflect changes in sex-ratio "diluted" by opposite effects on other production components or vice versa. This "dilution" may be so pronounced that significant differences in the production components can no longer be detected from the bunch yield figures. The value of a detailed production analysis in such cases is obvious.

PART III

Variability of the Components of Bunch Production

If one wishes to study the effects of specific cultural conditions on various production components, a thorough knowledge of the normal variations in these components under the influence of age, environment, season, climate and genetic constitution is essential. In the following paragraphs these normal variations are discussed and examples are presented to illustrate their order of magnitude.

Leaf Production

The oil palm has only one apical bud from which leaf primordia are produced one by one in a regular sequence. The leaf production, i.e. the number of leaves opening in a given length of time, is determined entirely by the activity of the apical bud. As normally only one inflorescence can develop in each leaf axil it is clear that leaf production is an important yield factor. It is also an expression of the growth rate of the palm.

Age Effects

Both in the breeding experiments described by Broekmans (1957) and in the cultural experiments at W.A.I.F.O.R. a very clear effect of age on leaf production was recorded. From the time of planting the rate of leaf production increases rapidly until a maximum of roughly thirty leaves per year is reached after seven years in the field. In the following years the number of leaves produced annually gradually decreases again towards a constant level of 22-24 leaves.

In Table 1 the age effect is illustrated by the annual leaf production figures per palm in two W.A.I.F.O.R. experiments.

Table 1. Average Number of Leaves Produced per Year in Progeny Trial 6-2 W.A.I.F.O.R., 1941, and Experiment 33-2, W.A.I.F.O.R., 1940

Expt.	Age in years											
	2	3	4	5	6	7	8	9	10	11	12	13
6-2	—	—	27·2	29·5	31·4	27·8	24·8	24·0	24·5	23·3	23·3	22·8
33-2	18·3	26·5	27·1	28·7	29·0	28·1	24·7	23·3	23·3	24·2	21·3	

Soil Conditions

Marked differences in leaf production between palms in different situations, or subjected to different treatments within the same area, are only apparent in the early years of the life of the palm, i.e. in the nursery and in the first few years in the field. Once a palm is in bearing these differences disappear and leaf production becomes very uniform. Even soil fertility differences serious enough to cause differences in bunch yield of the order of 100% are scarcely reflected in leaf production figures. Leaf length, leaf area and the average life of the leaf are on the other hand strongly influenced by soil conditions. The variation in leaf production before flowering that may occur under the influence of differences in soil fertility is illustrated in Table 2. In this table the seven blocks of experiment 33-2, planted at W.A.I.F.O.R. Main Station in 1940, are considered separately. This experiment (Expt. 33-2) had been designed to compare the effects of burning the felled bush before planting and leaving it unburnt, but the experimental treatments are disregarded here as they are irrelevant to the present subject. Leaf production is shown in the years before flowering (1942-43), in the first three productive years and in the later years of production. The plots have been arranged in the order of the 1942-43 leaf production figures.

TABLE 2. AVERAGE LEAF PRODUCTION IN DIFFERENT PERIODS IN EXPERIMENT 33-2, W.A.I.F.O.R., 1940

Number of leaves per palm and per year

Block	Leaf production		
	1942-43	1944-46	1947-51
V	23·2	28·5	24·4
VII	22·9	28·3	23·9
VI	22·7	28·2	24·3
III	21·1	28·7	24·8
IV	20·6	28·6	25·0
II	19·8	27·9	24·9
I	18·0	27·0	25·1

The table shows that differences in leaf production between the blocks are considerable before flowering (1942-43), but in later years these differences rapidly disappear and are even to some extent reversed. This reversal, which is apparent in the leaf production figures for 1947-51, is purely an age effect. The palms which produced slightly more leaves in the early years are a little ahead in physiological age and are more subject to the gradual decrease in leaf production which takes place after the sixth year in the field. The correlation between 1942-43 leaf production and 1947-51 leaf production, which was calculated on the basis of individual plots, is negative and significant ($r = -0{\cdot}61^*$).

Which particular soil factors determine leaf production in the early years cannot yet be established, but it may be mentioned here that experiments at W.A.I.F.O.R. have shown that leaf production before flowering is stimulated by the application of sulphate of ammonia and farm-yard manure (*W.A.I.F.O.R., First Annual Report, 1953*, p. 74).

Climatic and Seasonal Variations

The regular alternation of a dry and a wet season, characteristic of the West African climate, induces an equally regular variation in the rate of leaf production. When the dry weather begins, in mid-November, the rate of opening of new leaves is reduced and reaches a minimum around February. As the leaf initiation within the apex of the palm continues at an undiminished rate, unexpanded leaves in a certain phase of development accumulate within the apex and central spear. With the onset of the rains these leaves, which have been retarded in development by the dry season, resume normal growth and emerge in rapid succession, causing a flush of new leaves around April or May.

There is no evidence that in a given area annual variations in total rainfall, or in the rainfall during the dry season, affect the total number of leaves produced per year (leaf initiation). The duration of the annual minimum in leaf production is, however, clearly correlated with dry season rainfall (Broekmans, 1957).

When comparing different oil palm growing areas, marked differences in *mean* annual rainfall appear to have some influence on the leaf initiation. Broekmans has found for palms of the same parentage significantly lower leaf production under the drier conditions prevailing at Ibadan (48·4 in. per year) than at Benin and Umuahia where annual rainfall is higher (71·8 and 85·3 in. per year).

Genetic Constitution

There is no doubt that leaf production is to some extent genetically determined. Consistent differences of 10-15% between progenies growing in the same field are not uncommon. The small but unmistakable differences in leaf production which exist between *dura*, *tenera* and *pisifera* palms have already been noted by Beirnaert and Vanderweyen (1941) and by Broekmans (1957). Examples of the differences which may occur between progenies can be found in Table 4 on page 28.

Floral Abortion

The abortion of oil palm inflorescences has not been seriously considered as a yield factor until recently. Broekmans' studies, however, have indicated that the number of leaves which do not produce a mature inflorescence is by no means negligible and that floral abortion is more strongly influenced by external conditions and genetic constitution than is leaf production, particularly in the early years of bearing.

Age Effects

Floral abortion is most pronounced in young palms, where inflorescence primordia in 20-30% of the leaves may be affected. In later years the amount of abortion declines steadily and, given favourable growing conditions, becomes very low. Normal values for mature palms at W.A.I.F.O.R. are of the order of 5-10% of total inflorescence primordia produced.

In Table 3 the annual abortion rate is given for a period of ten years in Experiment 33-2 at W.A.I.F.O.R. (planted 1940).

TABLE 3. AGE AND PERCENTAGE ABORTION IN EXPERIMENT 33-2, W.A.I.F.O.R., 1940

Age	4	5	6	7	8	9	10	11	12
Progeny A	23·7	24·1	19·2	17·8	11·4	17·2	11·4	4·5	6·9
Progeny B	38·1	34·9	28·4	21·3	15·0	19·6	16·7	6·3	10·5

Soil Conditions

Floral abortion may be interpreted as an adaptation by the palm to variations in available nutrient resources. As stated above, the number of leaves, and therefore the number of potential inflorescences produced per year, is not much influenced by soil variation.

The relation between abortion and soil factors cannot be clearly demonstrated as abortion is not only influenced by the nutrients actually present in the soil, but also by the number of bunches which are maturing on the palm

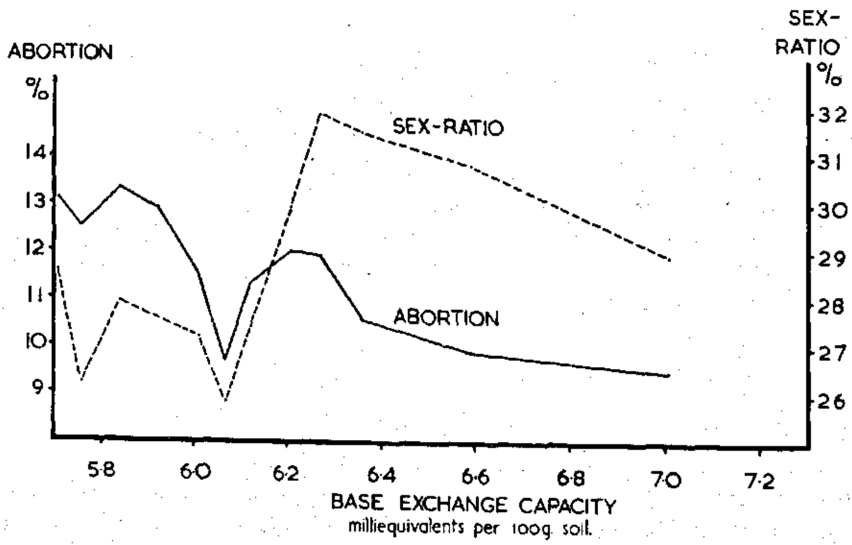


FIGURE 1. Floral abortion and sex-ratio in relation to the base exchange capacity of the soil in Experiment 33-2.

and which are competing with the developing inflorescences for nutrients. This latter number depends on various other factors such as bunch failure and sex-ratio. A much clearer relation with soil fertility is found for example when abortion is combined with bunch failure into one factor "loss of bunches" (see p. 37).

The strong positive correlation which exists between abortion and sex-ratio (see p. 26) is another important factor which masks to a large extent any direct relationship that may exist between abortion and soil fertility. In Figure 1 it is shown for example how the apparent negative relationship between abortion and base exchange capacity (a rough measure of soil fertility within the experiment) is upset by the positive correlation with sex-ratio.

Seasonal and Climatic Conditions

The optimum conditions for floral abortion occur in the dry season (December to March) when the supply of moisture is limited and the number of ripening bunches on the palms is maximal. If an inflorescence aborts, it usually does so four to five months before it would normally open. The effect of abortion on the number of inflorescences which reach anthesis is therefore most pronounced around June-July. Annual variations in percentage abortion are correlated with the intensity of the dry season and with the sex-ratio. Numerical examples and graphs illustrating seasonal and climatic effects on the amount of abortion are presented by Broekmans (1957) and will not be repeated here.

Genetic Differences

Floral abortion is to a large extent dependent on the genetic constitution of the palm. Broekmans has already drawn attention to the differences in abortion between the three main forms *dura*, *tenera* and *pisifera*. While there is little difference between *dura* and *tenera* (abortion in *dura* usually being a little higher), the *pisifera* shows a very much lower abortion due probably to the absence of ripening bunches.

When comparing different progenies as a whole pronounced differences in abortion may be found. In Table 4 this is illustrated for the thirteen progenies of Experiment 6-2.

The most conspicuous feature of these figures is the absence of a negative correlation between abortion and average yield. It would appear that average yield is higher in progenies with a higher percentage floral abortion, quite contrary to what one would expect. (The coefficient of correlation between abortion and yield is +0·489, but is not significant.) This may be explained by the strong positive correlation (r=0·756**) between sex-ratio and abortion and the predominant effect of sex-ratio on yield. This correlation is much more clearly demonstrated by the data from this progeny trial than by the data from Expt. 33-2 (Figure 1), because the confusing effects of soil fertility have been eliminated.

Beirnaert supports his views on the relation between environment and flowering with the results of counts of inflorescences and floral primordia on some palms growing under abnormal conditions. He does not, however, present any conclusive evidence for the correctness of his hypothesis. Furthermore, his examples only relate to cases where the assimilatory activity of the palm is affected (changes in A). What interests the agronomist more, however, is whether changes in the mineral nutrition "N" have a direct effect on the sex-ratio as is implied in Beirnaert's hypothesis. When considering this point it must be remembered that mineral nutrition and assimilation are not independent processes. A change in "N" can only be expected to affect the A/N ratio when A is limited by conditions other than the mineral nutrition. It has been suggested by several authors (Fickendey and Blommendaal, 1929; Ferrand, 1950) that this is the case in most African oil palm areas where

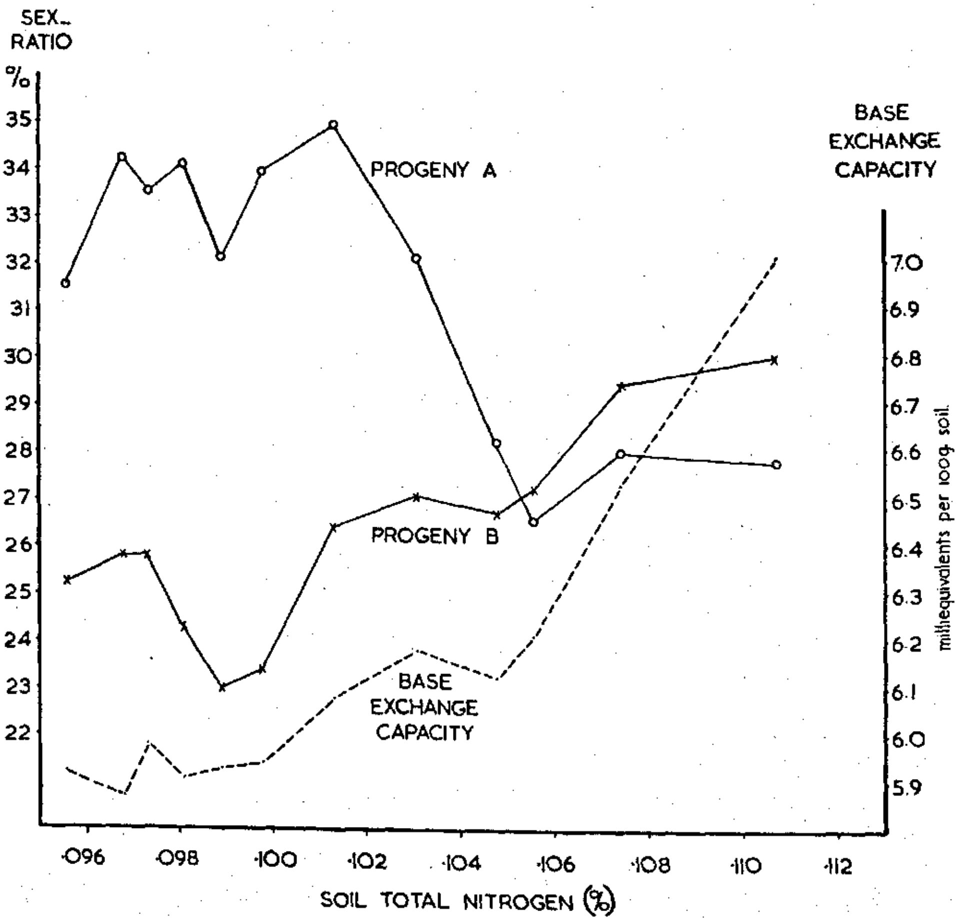


FIGURE 2. Sex-ratio in relation to soil total nitrogen for the two progenies of Experiment 33-2. Figures for base exchange capacity have been plotted for each point of the sex-ratio and nitrogen curve to demonstrate the combined effect of nitrogen and base exchange capacity on the sex-ratio.

carbohydrate assimilation is limited by the amount of available sunlight, particularly during the wet season. Applying Beirnaert's hypothesis one inevitably arrives at the rather unexpected conclusion that an increase in mineral nutrition may under such conditions lead to a decrease in sex-ratio or that a reduction in mineral nutrition may increase sex-ratio.

The relations between soil factors and sex-ratio in Experiment 33-2 have been examined in the light of Beirnaert's suggestions and have shown at least one thing quite clearly: it cannot be said that an increase in mineral nutrition leads to a decrease in sex-ratio. In fact it could be shown that for one of the progenies planted in Expt. 33-2 the base exchange capacity which can be taken as a rough index of soil fertility within the area, was positively and

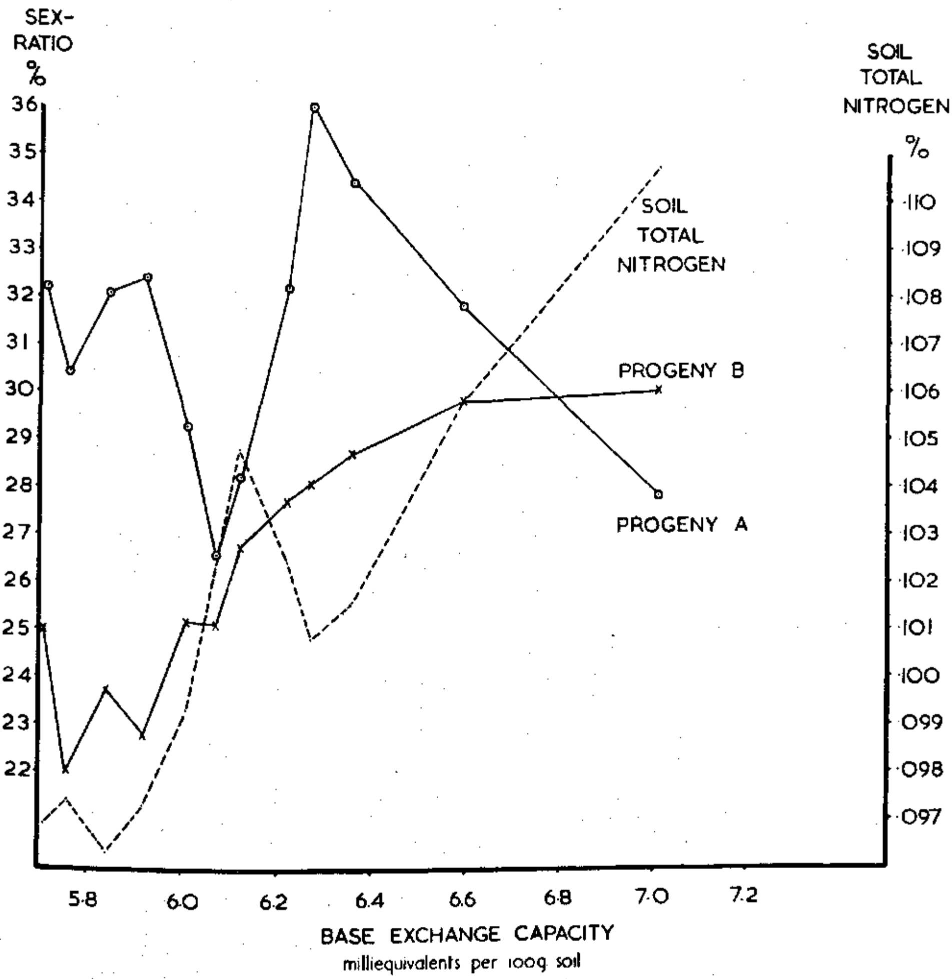


FIGURE 3. Sex-ratio in relation to base exchange capacity for the two progenies of Experiment 33-2. Figures for soil total nitrogen have been plotted for each point of the sex-ratio and B.E.C. curve to demonstrate the combined effect of nitrogen and B.E.C. on sex-ratio.

significantly correlated with the sex-ratio (r=+0·64*). Of all the other soil factors examined none were significantly correlated with sex-ratio, but the figures for total nitrogen are presented here because there is a suggestion that some progenies may have their sex-ratio adversely affected by increasing soil total nitrogen. There is a negative correlation between total nitrogen and sex-ratio in progeny A but it just misses significance at P=0·05.

The relevant data are presented as running totals of three plots in Table 6 and in Figures 2 and 3. It would appear that the progenies react differently

TABLE 6. SEX-RATIO IN RELATION TO TOTAL NITROGEN CONTENT OF THE SOIL AND BASE EXCHANGE CAPACITY. EXPERIMENT 33-2, W.A.I.F.O.R., 1940

Total nitrogen in % and B.E.C. in m.e. per 100 gm. soil (averages of analyses in 1941, 1945 and 1951). Sex-ratio for the period July 1947-June 1953

(a) Plots arranged according to total nitrogen content	Total Nitrogen	B.E.C.	Sex-ratio	
			Progeny A	Progeny B
	%	*m.e.*	%	%
14- 8-11	0·0956	5·92	31·5	25·2
8-11- 7	0·0968	5·87	34·2	25·8
11- 7- 4	0·0973	5·98	33·5	25·8
7- 4- 9	0·0981	5·91	34·1	24·3
4- 9- 6	0·0989	5·93	32·1	23·0
9- 6- 3	0·0997	5·94	33·9	23·4
6- 3- 5	0·1013	6·08	34·9	26·4
3- 5-10	0·1031	6·18	32·1	27·1
5-10- 1	0·1048	6·12	28·2	26·7
10- 1-12	0·1056	6·21	26·6	27·2
1-12- 2	0·1074	6·53	28·0	29·4
12- 2-13	0·1107	7·01	27·8	30·0

(b) Plots arranged according to B.E.C.	B.E.C.	Total Nitrogen	Sex-ratio	
			Progeny A	Progeny B
	m.e.	%	%	%
7- 6-14	5·71	0·0969	32·2	25·0
6-14- 9	5·76	0·0974	30·4	22·0
14- 9- 8	5·84	0·0963	32·1	23·7
9- 8-11	5·92	0·0973	32·4	22·8
8-11-10	6·01	0·0993	29·3	25·2
11-10- 1	6·07	0·1023	26·6	25·1
10- 1- 5	6·12	0·1048	28·2	26·7
1- 5- 4	6·21	0·1024	32·1	27·7
5- 4- 3	6·27	0·1008	36·0	28·1
4- 3-12	6·36	0·1016	34·4	28·7
3-12- 2	6·59	0·1058	31·8	29·8
12- 2-13	7·01	0·1107	27·8	30·0

to soil factors, though the differences observed are relative rather than absolute.

The same two progenies A and B are also represented in another experiment, 33-1, planted in the same year and adjacent to Expt. 33-2. As the data from these two experiments are unique in that they combine the analyses of a number of soil factors and growth and flowering figures collected over a long period, the data from Experiment 33-1 are also presented here in a graphical form (Figure 4), in the same way as those of Expt. 33-2. The general level of fertility is lower in Expt. 33-1 and it is of interest to record that the level of nitrogen in the soil appears to reach an optimum around 0·072% below which there is a sharp decline in sex-ratio of progeny A. Base exchange capacity has no longer any clear influence on either progeny A or B in these less fertile plots, but there are indications that the individual bases are of some importance: magnesium in the case of progeny A and potassium in the case of progeny B. Neither of these apparent relationships is statistically significant but they are of sufficient interest, as a basis for possible future studies, to be recorded here.

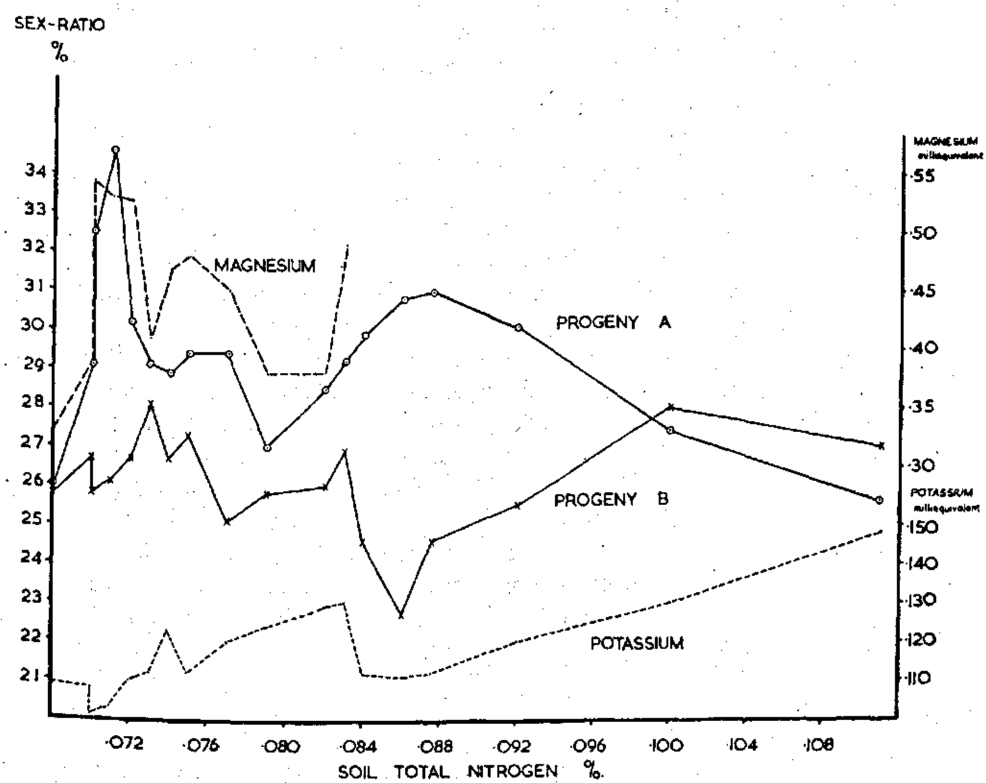


FIGURE 4. Sex-ratio in relation to soil total nitrogen for Experiment 33-1. Figures for potassium and magnesium have been plotted for each point of the sex-ratio and nitrogen curve to demonstrate the combined effect of nitrogen and magnesium on progeny A and of nitrogen and potassium on progeny B.

It may be concluded from the above data that Beirnaert's suggestions as regards the relations between sex-ratio and soil fertility cannot be accepted in their general sense. There are indications, however, that an increase in the supply of at least one of the major nutrients, nitrogen, may adversely affect the sex-ratio.

Seasonal and Climatic Conditions

Broekmans (1957) has recently published a very thorough study of the variations in sex-ratio under the influence of rainfall, sunshine and the change of seasons. In this section only his more important conclusions will be incorporated while readers are referred to the original work for examples and a more detailed treatment of the subject.

Under Nigerian conditions, monthly variations in the sex-ratio of inflorescences show a pronounced seasonal trend. The proportion of female inflorescences reaches a maximum in February or March and a minimum around October. These fluctuations are most pronounced in young palms, where maxima of 60-70% may be followed by minima as low as 10%. As the palms grow older the fluctuations become less pronounced.

Seasonal variations in sex-ratio reflect the seasonal changes in climatic and soil conditions two years earlier. According to Broekmans, the average time between sex differentiation and anthesis is two years. The dry season, with its abundant sunshine, favours female flowering and the wet season, with its long spells of overcast skies, favours male flowering. The seasonal fluctuations in sex-ratio may thus be interpreted in terms of Beirnaert's ideas.

Annual variations in sex-ratio can be traced to conditions *within* the dry or wet season two years previous to the year of yield. In the dry season, for example, the limiting factor is no longer sunlight but water, as is indicated by a strong correlation between November-April (dry season) rainfall, and both the maximum and the average sex-ratio two years later. Broekmans (1957) calculated significant correlation coefficients of more than 0·7 in two different experiments over 8-9 year periods. In the wet season sunshine is the limiting factor in most instances and it is likely that there exists a positive correlation between sunshine in the wet season and sex-ratio. Sufficient data are not yet available, however, to present reliable correlation coefficients. The amount of rainfall during the wet season may also exercise an indirect effect, through leaching of nutrients. In particular the nitrogen status of the soil is known to be affected by heavy rainfall.

Genetic Constitution

There is a considerable variation in sex-ratio between individual palms, between progenies, and between different varieties. Of most interest genetically is the relation between sex-ratio and the fruit form of the oil palm. Beirnaert and Vanderweyen (1941) and Broekmans (1957) have presented conclusive evidence that the average sex-ratio is highest in *pisifera* palms, lowest in *dura* and intermediate in *tenera.*

Broekmans gives the following example:

	Planted	Period of observation	Sex-ratio in dura	tenera	pisifera
			%	%	%
Experiment 1-1	1939	1943-49	27·9	31·1	45·7
Experiment 6-2	1941	1945-56	29·4	31·4	—

Another remarkable difference in sex-ratio level is that between imported Deli palms and local Nigerian palms.

Broekmans' average figures for mature palms in the Deli Trial (Expt. 5-1) are:

Malayan Deli	20·4%
Nigerian palms	33·5%

Even more pronounced differences have been found in Sierra Leone where the figures shown in Table 7 were collected (unpublished data, Agricultural Dept., Sierra Leone):

TABLE 7. SEX-RATIO OF PALMS OF DIFFERENT ORIGIN AT NJALA, SIERRA LEONE

Years after planting	Introductions			Local origins		
	Angola	Deli	Nigerian	Kawei	Henoi	Kpolei
5	52·6	5·4				
6	62·5	13·7				
7	66·6	15·4		45·5	55·5	33·3
8	43·5	12·0		47·6	83·3	58·8
9	43·5	9·7	47·6	45·5	71·4	55·5
10	43·5	7·9	27·8	30·3	52·6	31·2
11	40·0	—	31·2	18·9	45·5	27·0

Variations in sex-ratio between the thirteen progenies compared in Experiment 6-2 are shown in Table 4. The variations in this experiment, ranging from 19·6% to 33·2%, are by no means extreme. The table nevertheless clearly illustrates that *sex-ratio is the most important single factor determining the relative yields of the progenies.* Variations in abortion are of a secondary nature, as appears from the clear positive correlation between sex-ratio and abortion. Floral abortion keeps the number of inflorescences within the limits of the palms' bearing capacity. As female inflorescences cause a much heavier drain on the palms' resources than male inflorescences, a higher sex-ratio may be expected to lead to a higher degree of abortion.

Bunch Failure

Not all female or hermaphrodite inflorescences that reach the stage of anthesis develop into ripe bunches. There is always a certain loss, due to premature rotting of bunches. In mature plantations and on good soils the incidence of bunch failure is of no practical importance, but in young palms or in poorer areas there may be a considerable difference between the numbers of female and hermaphrodite inflorescences counted and the number of fruit bunches harvested.

Age Effects

In young palms, with their high sex-ratio and relatively high proportion of hermaphrodite and andromorphous inflorescences, bunch survival is usually poor. In later years, when the sex-ratio declines and only normal inflorescences are produced, the majority of the bunches reach maturity. The bunch survival figures for the first six years of production in Experiment 33-2 are shown in Table 8. In the later years (1951-53) harvesting was incomplete and no reliable figures are available.

Table 8. Bunch Survival in Relation to Age in Experiment 33-2, W.A.I.F.O.R., 1940

Bunch survival as percentage female+hermaphrodite inflorescences reaching maturity. Number of inflorescences and yield per palm

Period	Female+ hermaphr. infl.	Bunch survival	No. of bunches	Average bunch wt.	Total weight of bunches
Progeny A	%	%		*lb.*	*lb.*
1944-45	10·7	53·8	5·7	5·4	31
1945-46	10·9	65·9	7·2	7·8	56
1946-47	10·3	77·8	8·0	12·6	101
1947-48	10·4	73·2	7·6	13·6	103
1948-49	8·9	80·6	7·2	17·7	128
1949-50	7·7	85·2	6·6	18·2	120
Progeny B					
1944-45	8·9	44·9	4·0	7·3	29
1945-46	8·7	64·0	5·3	11·7	62
1946-47	6·7	90·4	6·0	17·9	108
1947-48	6·8	87·4	5·8	20·0	116
1948-49	7·2	87·8	6·4	20·9	133
1949-50	6·2	92·6	5·7	22·5	128

Soil Conditions

Bunch failure is a yield regulating factor like floral abortion. Both reduce the potential number of bunches to an actual number of bunches which is likely to be in keeping with the available nutrient resources. As these effects occur at different stages of bunch development, they are to some extent complementary. This is illustrated in Table 9 where the total loss of bunches through abortion and bunch failure has been calculated for individual plots of Experiment 33-2. For this calculation it has been assumed that abortion affects male and female inflorescences to an equal extent.

It must be mentioned again that the actual values for bunch failure in Table 9 are too high, owing to incomplete harvesting, but they nevertheless illustrate quite clearly the negative correlation between the loss of bunches (through abortion and bunch failure) and base exchange capacity. (r= −0·71**).

TABLE 9. LOSS OF POTENTIAL FRUIT BUNCHES THROUGH ABORTION AND BUNCH FAILURE IN RELATION TO BASE EXCHANGE CAPACITY AND SEX-RATIO. EXPERIMENT 33-2, W.A.I.F.O.R., 1940

Base exchange capacity in m.e. per 100 gm. soil. Average yield and flowering data for the period 1948-53 (yield) or July 1947-June 1953 (flowering)

	B.E.C.	Sex-ratio	Abortion rate	Bunch failure	Total loss of infl.	No. of Bunches per year	Average bunch weight
Non-burnt plots	*m.e.*	%	%	%	%	*No.*	*lb.*
7	5·63	31·9	12·1	29	37·6	5·0	22
6	5·72	26·9	10·8	28	35·8	4·3	23
11	6·02	25·9	8·8	31	37·1	4·1	21
10	6·03	23·6	9·6	28	34·9	3·8	21
1	6·18	27·9	10·7	14	23·2	5·2	25
12	6·43	29·2	9·8	19	27·0	5·0	25
2	7·00	28·8	9·5	14	22·2	5·4	26
Burnt plots							
14	5·77	26·9	13·0	15	26·0	4·8	26
9	5·78	27·2	13·8	22	32·8	5·5	18
8	5.97	32·2	16·0	18	31·1	3·9	22
5	6·18	30·7	13·7	18	29·3	5·5	22
4	6·30	31·0	11·6	20	29·3	5·4	24
3	6·33	34·4	10·4	16	24·8	6·1	24
13	7·58	28·6	12·2	12	22·7	5·5	25

N.B.—Figures for Base Exchange Capacity are the averages for samplings in 1941, 1945 and 1951.

Seasonal and Climatic Conditions

When considering seasonal and annual fluctuations in bunch survival in a given area, it must be borne in mind that the survival or failure of a bunch depends primarily on pollination and fruit setting, and therefore on the weather conditions during and after the period of anthesis. At the same time, however, the correlation with abortion, determined by weather conditions in the preceding dry season, must not be overlooked. In short, one may postulate that bunch survival in any one year will be high when climatic conditions in that same year have been favourable for pollination and fruit setting and the number of bunches has already been reduced by abortion at an earlier stage. Survival will be poorest when weather conditions are unfavourable and few or none of the inflorescences have been lost by abortion. It has not yet been possible to confirm these apparent interactions with accurate experimental data.

Genetic Constitution

Figures for bunch survival for the thirteen progenies in Experiment 6-2 would seem to indicate that bunch failure is not a factor of importance in oil palm breeding and selection. The degree of bunch survival in the best progenies is no better than that in the poorest yielding ones. This is illustrated in Table 4.

It should be mentioned in this context that the *pisifera* palm, which usually has an exceptionally high sex-ratio but low abortion, often suffers from 100% bunch failure.

Average Bunch Weight

Average bunch weight is as variable a yield factor as the number of bunches. Its variability is, however, largely of a secondary nature, since average bunch weight is mainly determined by bunch number with which it is negatively correlated. The direct effects of environment are less pronounced than in the case of bunch number.

Age Effects

The rapid increase in bunch weight with increasing age of the palm is shown in Table 8. This increase is continuous throughout the economic life of a plantation although the rate of increase is slower in later years. In the first years of production bunches of 5-10 lb. or even less are normal, while a fully grown smooth-stemmed palm of 30 years or more often produces bunches of between 50 and 100 lb. in weight.

Soil Conditions

Soil conditions influence the average weight of the bunches both directly and indirectly via the number of bunches and the percentage bunch failure. This latter relation can be explained as follows:

(*a*) Conditions which lead to a high percentage of bunch failure will also affect the percentage normal fruits in the surviving bunches.

(*b*) Bunch failure is less efficient as a correcting factor than abortion, as more nutrients are required to bring a bunch to the stage where it "fails" than to bring it to the stage of abortion. A failed bunch will therefore affect the average bunch weight more than an aborted bunch. Some relevant figures are shown in Table 9.

Seasonal and Climatic Conditions

Since average bunch weight is partly determined by the number of spikelets and flowers per spikelet, which are differentiated more than two years before anthesis, and partly by the effectiveness of pollination and fruit setting, it is clear that climatic and seasonal effects are difficult to interpret. There are marked seasonal variations in average bunch weight with a maximum around May and with minima around February and July, but the exact relationship between average bunch weight and preceding weather conditions is not yet clear.

Annual variations are largely determined by the numbers of bunches produced and by age effects. No sound information is available regarding the direct effect of annual climatic variations on bunch weight.

Genetic Constitution

When the thirteen progenies of Experiment 6-2 (see Table 4) are compared, the average bunch weight appears to be a factor of secondary importance. The productivity of a progeny is primarily determined by the number of bunches it bears, while the average bunch weight is responsible merely for secondary trends in the relationship between total yield and bunch number. For example, the relatively unsatisfactory yields of the progenies with the highest number of bunches (i.e. above six), are due to a fall in average bunch weight which is disproportionate to the rise in bunch number.

The differences between *dura* and *tenera* palms as regards bunch weight are in accordance with the differences in sex-ratio mentioned earlier: the *dura* produces fewer but heavier bunches than the *tenera*. Most of the Deli strains imported into West Africa are characterized by a low number of very heavy bunches.

PART IV

An Example of a Complete Analysis of Bunch Production

An account is given in the following paragraphs of the results of a cultural experiment laid down at the W.A.I.F.O.R. Main Station, near Benin, in 1940. The details of this experiment and the basic yield data have been presented by the author in a paper on mixed cropping in oil palm cultivation (Sparnaaij, 1957). The purpose of this section is to illustrate how additional useful information can be gained by a more thorough treatment of the yield figures, and by a study of the available growth and flowering data.

Experimental Details

The experiment was planted in June 1940 on an area cleared from high forest by burning. The palms were planted with bare roots at a triangular spacing of 29 ft. The experimental area is divided into twenty-five plots of sixteen palms each, arranged in a 5×5 Latin square layout. Single guard rows separate all plots. Each plot is divided into two subplots of eight palms so as to compare the progenies of two different *dura* palms selected at Aba. The progenies were obtained by selfing and are therefore entirely *dura* in fruit form. Identical progenies were planted in the Burning versus Non-Burning Experiment 33-2 which has provided so much of the material for Part III.

The five establishment treatments compared in the experiment were:

Treatment A. Intercropping with food crops in the first two years after planting. This treatment represents the two-year cropping cycle normal for Benin Province, but in the experiment cropping was carried out between the young oil palms. Yams formed the main crop and were interplanted with other crops such as cowpea, maize and okro (*Hibiscus esculentus*) at wide spacing. The land was allowed to revert to a weed or leguminous cover after the last crop had been harvested.

Treatment B. Intercropping to exhaustion. This treatment has no practical importance but was introduced to determine the period for which food crops could profitably be grown between normally-spaced palms, and the effects of continued cropping on palm yields. Yams, maize and cassava were grown until the canopy of the palms had closed, after which the only possible crop was cocoyams (Colocasia and Xanthosoma spec.). After the last cocoyams had been harvested in 1952 the land was left to revert to a natural cover.

Treatment C. Natural cover, regularly maintained. Normal low weed cover was encouraged from the beginning and maintained by regular cutlassing;

this represents the control treatment. Together with treatment E, it is a standard method of establishment and maintenance for commercial plantations.

Treatment D. Natural cover, neglected. In this treatment the least possible care was given to the natural cover, which was cut back only once a year. This state of affairs is very commonly found in local palm plantings. The cover was cut annually at the end of the rains. In the early years it often reached a height of 10-12 ft. before it was slashed.

Treatment E. Leguminous cover, regularly maintained. A leguminous cover was sown consisting of a *Calopogonium-Pueraria* mixture. *Pueraria* became dominant after the first year.

Before an analysis of bunch production was undertaken, the following information was already available:

(*a*) All factors of soil fertility, which were determined at various stages (1941, 1945, 1951 and 1956), were more adversely affected by intercropping treatments than by the control.

(*b*) The yields of the intercropped plots were as good as, and in the early years significantly better than, the yields of the control plots.

These results were apparently contradictory which was an additional reason for carrying out the detailed analysis described in the following paragraphs. At the same time it was hoped that the analysis would provide a basis for further research, by confirming or amending the theoretical explanation suggested for the intercropping effects observed in the Belgian Congo experiment (see p. 14).

Soil Analysis in the Experimental Plots

Composite soil samples, comprising ten cores, were taken in each plot of the experiment in 1941, 1945, 1951 and 1956. These samples have been subjected to detailed analyses, the earlier ones in Ibadan (Kowal, 1954), the last series at W.A.I.F.O.R. (Kowal and Tinker, 1959). A summary of the analytical results is presented in Table 10.

The figures up to 1951 were summarized and analysed statistically by Kowal (1954). The following is a quotation from his discussion of the treatment effects:

"The experiment succeeded primarily to illustrate a remarkable loss of soil fertility under conditions of continuous intercropping (treatment B). Under this rather drastic treatment the soil organic matter content was reduced by approximately 17% of its original level during eleven years of intercropping. In consequence a loss of approximately 10% in base exchange capacity, 21% of total nitrogen, 33% of exchangeable potash, 35% of exchangeable magnesium and 29% of exchangeable sodium has occurred, as compared with the original level of soil factors.

TABLE 10. ESTABLISHMENT EXPERIMENT 33-1, W.A.I.F.O.R., MAIN STATION, 1940
Average results of analyses of soil samples taken in 1941, 1945, 1951 and 1956.
Level of sampling 0-6 in.

Soil factor	Year of Sampling	Treatments				
		A Two years' inter-cropping	B Inter-cropping to exhaustion	C Weed-cover slashed regularly	D Weed-cover neglected	E Legu-minous cover
Soil reaction pH in water	1941 1945 1951 1956	5·69 5·82 5·75 5·75	5·80 6·13 5·67 5·70	6·20 6·69 6·04 6·00	5·97 6·41 5·90 5·90	5·86 5·91 5·48 5·60
Base exchange capacity m.e. per 100 g. soil	1941 1945 1951 1956	5·10 4·85 5·39 5·27	5·02 5·10 4·96 5·78	5·78 6·24 6·76 6·14	5·60 5·88 5·60 5·98	4·94 5·18 4·86 5·62
Total exchangeable bases m.e. per 100 g. soil	1941 1945 1951 1956	3·56 3·21 3·61 3·11	3·60 3·72 3·38 3·72	4·70 5·14 5·28 4·34	4·36 4·70 4·08 4·00	3·48 3·64 2·96 3·28
Percentage total nitrogen	1941 1945 1951 1956	0·079 0·078 0·072 0·070	0·080 0·080 0·066 0·068	0·080 0·090 0·100 0·075	0·090 0·089 0·105 0·079	0·083 0·080 0·090 0·074
Percentage organic carbon	1941 1945 1951 1956	0·834 0·936 0·904 1·050	0·856 0·948 0·750 0·970	1·066 1·077 1·066 1·040	1·062 1·070 0·994 1·090	0·920 0·967 0·916 1·070
Exchangeable calcium m.e. per 100 g. soil	1941 1945 1951 1956	3·10 2·90 3·39 3·24	3·28 3·66 3·12 3·33	4·26 5·16 4·88 3·86	4·10 4·10 4·08 3·84	3·22 3·82 2·78 3·25
Exchangeable potassium m.e. per 100 g. soil	1941 1945 1951 1956	0·103 0·114 0·100 0·052	0·125 0·119 0·084 0·060	0·135 0·184 0·112 0·062	0·102 0·155 0·140 0·076	0·121 0·129 0·116 0·072
Exchangeable magsium m.e. per 100 g. soil	1941 1945 1951 1956	0·75 0·69 0·62 0·43	0·85 0·70 0·55 0·48	0·83 0·90 0·75 0·71	0·75 0·83 0·75 0·70	0·80 0·80 0·58 0·42
Exchangeable sodium m.e. per 100 g. soil	1941 1945 1951 1956	0·27 0·30 0·21 0·09	0·27 0·22 0·19 0·12	0·34 0·26 0·25 0·14	0·26 0·22 0·25 0·15	0·29 0·29 0·25 0·11

"In contrast to this rather drastic treatment, bush covers (treatments C and D) had an advantage, during the whole of the experimental period to date, over the remaining treatments under test. . . . Treatments A and E can be regarded as intermediate in their effects on soil fertility."

The original levels of the soil factors in the plots under treatment B, referred to by Kowal, are those determined in 1940 before clearing and burning. Those figures are not reproduced here as they are very unreliable, being based on one sample per plot only. The above figures for percentage loss can therefore only be regarded as estimates. They nevertheless show quite convincingly that continuous cropping has *not* improved soil fertility.

The last set of soil samples, which were taken long after the experimental treatments had ceased, showed a tendency for all plots to assume an equal nutrient status although treatments C and D maintain their superiority in all the usual indices of soil fertility.

Bunch Yields

Regular yield recording commenced in January, 1945, i.e. 4½ years after planting, and still continues. The annual yield figures are presented in Table 11.

TABLE 11. YIELD OF FRUIT BUNCHES PER ACRE IN ESTABLISHMENT EXPERIMENT 33-1, W.A.I.F.O.R., MAIN STATION, 1940

Year	A Two years' intercropping	B Intercropping to exhaustion	C Weed cover slashed regularly	D Weed cover slashed once a year	E Leguminous cover
	lb.	*lb.*	*lb.*	*lb.*	*lb.*
1945	2,434	2,711	1,991	1,961	1,984
1946	4,412	5,340	4,215	2,747	4,262
Sub Total	6,846	8,051	6,206	4,708	6,246
1947	7,047	7,364	7,049	5,393	6,584
1948	6,520	6,909	7,108	5,178	6,972
1949	7,601	8,688	7,628	6,073	7,363
1950	6,065	4,736	6,009	5,342	6,840
1951	4,418	5,016	3,471	2,948	4,064
1952	5,615	5,992	6,841	5,561	6,496
1953	10,357	10,196	7,555	7,502	10,302
1954	7,627	7,613	6,101	6,269	6,882
1955	8,923	10,738	8,408	9,614	8,493
Sub Total	64,173	67,252	60,170	53,880	63,996
1956	7,441	8,106	9,499	8,537	9,245
1957	9,467	7,949	9,963	9,238	9,354
1958	6,063	6,124	5,232	6,128	6,290
Sub Total	22,971	22,179	24,694	23,903	24,889
Grand Total	93,990	97,482	91,070	82,491	95,131

The differences between the treatments were statistically significant only in the first two years of harvesting. In these two years the palms subjected to continous intercropping (B) yielded 29% more than the mean of the palms in the two control treatments C and E (significant at 5%).

In the third year of harvesting (1947) this difference became much smaller and stayed at an average of 8% (non significant) for a period of nine years.

From 1956 onwards the intercropped plots began to lag behind the other treatments. The difference over the last three years was 7% in favour of the two control treatments.

Over the fourteen-year period as a whole the continuously cropped plots have yielded 5% more than those of the other treatments. Although this difference is non-significant, it remains quite remarkable that there has been

TABLE 12. NUMBER OF BUNCHES PER PALM IN ESTABLISHMENT EXPERIMENT 33-1 W.A.I.F.O.R., MAIN STATION, 1940

Year	A Two years' intercropping	B Intercropping to exhaustion	C Weed cover slashed regularly	D Weed cover slashed once a year	E Leguminous cover
1945	6·14	6·38	5·54	5·95	5·75
1946	7·80	8·72	7·34	5·26	7·79
Sub Total	13·94	15·10	12·88	11·21	13·54
1947	7·36	7·15	7·31	6·25	6·81
1948	6·55	6·80	6·85	5·62	6·71
1949	6·94	7·65	6·69	5·76	6·81
1950	5·19	3·96	5·14	4·69	5·78
1951	2·84	2·96	2·40	1·86	2·58
1952	2·70	2·72	3·02	2·54	2·84
1953	5·20	4·84	3·64	3·71	4·90
1954	3·99	3·76	3·12	3·05	3·38
1955	4·28	5·15	4·00	4·46	4·09
Sub Total	45·05	44·99	42·17	37·94	43·90
1956	3·55	3·80	4·16	3·92	4·15
1957	4·36	3·56	4·34	4·12	4·16
1958	2·74	2·71	2·25	2·65	2·69
Sub Total	10·65	10·07	10·75	10·69	12·00
Grand Total	69·64	70·16	65·80	59·84	69·44

no significant depression of yields in view of the considerable reductions of soil fertility under intercropping.

As a first step in the further analysis of these results, gross bunch yields may be split into two components, viz., number of bunches and average bunch weight. The average annual values for number of bunches are shown in Table 12 those for average bunch weight in Table 13.

TABLE 13. AVERAGE BUNCH WEIGHT IN ESTABLISHMENT EXPERIMENT 33-1, W.A.I.F.O.R., MAIN STATION, 1940

Year	A Two years' intercropping	B Intercropping to exhaustion	C Weed cover slashed regularly	D Weed cover slashed once a year	E Leguminous cover
	lb.	*lb.*	*lb.*	*lb.*	*lb.*
1945	6·7	7·1	6·0	5·5	5·8
1946	9·4	10·2	9·6	8·7	9·1
Average	8·0	8·6	7·8	7·1	7·4
1947	16·1	16·9	16·3	14·5	16·2
1948	16·7	17·1	17·4	15·4	17·4
1949	18·4	19·0	19·1	17·6	18·1
1950	19·6	20·1	19·6	19·1	19·8
1951	26·1	28·4	24·2	26·5	26·4
1952	34·8	36·8	37·9	36·7	38·3
1953	33·4	35·3	34·8	33·8	35·2
1954	32·0	33·9	32·7	34·4	34·2
1955	34·8	34·7	35·0	35·9	34·6
Average	25·8	26·9	26·3	26·0	26·7
1956	35·0	35·7	38·2	36·4	37·2
1957	36·3	37·3	38·4	37·4	37·6
1958	37·0	37·8	38·9	38·7	39·1
Average	36·1	36·9	38·5	37·5	38·0
Overall Average	25·4	26·4	26·3	25·8	26·4

A comparison of the two tables indicates that, considering the period 1945-55, the bunch number rather than the average bunch weight is responsible for the good yields of the continuously intercropped plots. While the plots of treatment B have produced 6·8% more bunches than the plots of the two control treatments, the difference in average bunch weight is only 2·2%.

Considering the individual years, it appears that this small difference in bunch weight in favour of intercropping is very consistent during the first seven years of production. In later years this difference is no longer found. It would appear that this effect of intercropping on bunch weight is a result of the slightly advanced development of the palms subjected to this treatment. In the following pages these differences in development (physiological age) will be further discussed.

The difference in number of bunches in favour of intercropping are more important than the differences in bunch weight, but very inconsistent from year to year. This may be regarded as a first indication that climatic conditions have an important effect on the relative yield of palms subjected to different treatments.

Leaf Production

Regular leaf counts on all experimental palms began in 1942 and were continued until 1952. In Table 14 the average leaf production per year is shown for the three years before harvesting commenced and for two further periods of four years when the palms were in production.

Table 14. Average Leaf Production per Year and per Treatment: Establishment Experiment 33-1, W.A.I.F.O.R., Main Station, 1940

	Progeny A					Progeny B				
	A	B	C	D	E	A	B	C	D	E
1942	24·5	24·2	20·9	18·7	22·1	24·2	24·7	21·6	20·1	21·1
1943	28·2	28·5	28·3	25·1	27·0	27·8	27·8	26·6	24·9	25·4
1944	30·8	30·5	30·4	28·4	29·3	28·9	28·9	28·8	28·7	28·4
1942-44	83·5	83·2	79·6	72·2	78·4	80·9	81·4	77·0	73·7	74·9
1945	30·8	29·8	30·1	27·3	29·8	28·9	29·3	28·3	26·5	29·3
1946	29·6	30·5	29·4	29·1	31·5	31·6	27·5	26·9	27·0	30·0
1947	28·3	28·7	29·1	28·3	27·9	26·3	27·1	26·7	26·4	27·5
1948	24·6	24·6	25·9	25·3	24·7	23·0	23·4	23·0	23·5	23·0
1945-48	113·3	113·6	114·5	110·0	113·9	109·8	107·3	104·9	103·4	109·8
1949	22·3	23·7	23·3	22·5	21·8	21·8	21·6	20·9	21·6	22·2
1950	22·4	23·1	22·7	21·5	22·3	21·6	21·8	20·9	21·5	22·1
1951	23·6	23·4	22·8	23·3	22·5	22·0	21·7	21·5	22·6	21·8
1952	24·4	23·8	25·0	24·3	24·8	23·7	23·4	22·8	23·1	23·6
1949-52	92·7	94·0	93·8	91·6	91·4	89·1	88·5	86·1	88·8	89·7
Total	289·5	290·8	287·9	273·8	283·7	279·8	278·6	268·0	265·9	274·4

In the early years (1942-44) the differences in favour of the intercropping treatments A and B are statistically significant. It can therefore be concluded that these treatments have stimulated leaf production which is one of the most reliable indices of growth and development. Once the palms are in production the differences in leaf production disappear completely, except in the area of Treatment D. The differences in total leaf production are maintained, however. It follows that the intercropped plots continue to be a little ahead of the other plots in development and degree of maturity. This must be borne in mind when considering the effects of the treatments on other yield factors, particularly in the early years of production.

TABLE 15. INFLORESCENCE ABORTION IN THE ESTABLISHMENT EXPERIMENT 33-1, W.A.I.F.O.R., MAIN STATION, 1940

(*a*) *First three years of production* (1944-46)

Treatment	Progeny A				Progeny B				Overall % Abortion
	Leaves 1943-45	Inflorescences 1944-46	Aborted inflorescences		Leaves 1943-45	Inflorescences 1944-46	Aborted inflorescences		
	No.	*No.*	*No.*	%	*No.*	*No.*	*No.*	%	%
A	89·9	62·2	27·6	30·8	85·6	62·8	22·8	26·6	28·7
B	88·8	63·5	25·3	28·5	86·0	62·2	23·8	27·7	28·1
C	88·8	63·1	25·7	28·9	83·7	61·4	22·3	26·7	27·8
D	80·8	59·4	21·4	26·5	80·1	59·8	20·3	25·3	25·9
E	86·1	59·5	26·6	30·9	83·1	61·1	22·0	26·5	28·7

(*b*) *Years* 1947-52

Treatment	Progeny A				Progeny B				Overall % Abortion
	Leaves Mar. '46-Feb. '52	Inflorescences 1947-52	Aborted inflorescences		Leaves Mar. '46-Feb. '52	Inflorescences 1947-52	Aborted inflorescences		
	No.	*No.*	*No.*	%	*No.*	*No.*	*No.*	%	%
A	151·3	132·3	19·0	12·6	145·1	124·8	20·3	14·0	13·3
B	153·0	129·7	23·3	15·2	142·6	122·6	20·0	14·0	14·6
C	153·5	131·3	22·2	14·5	139·6	121·6	18·0	12·9	13·7
D	149·4	125·3	24·1	16·2	142·1	130·1	12·0	8·4	12·3
E	150·8	133·2	17·6	11·7	146·1	127·8	18·3	12·5	12·1

The differences between the two progenies are very consistently in favour of progeny A. There is however no evidence of any statistical interaction between progenies and treatments.

INFLORESCENCE ABORTION

It has become clear from the preceding section that leaf production under the different treatments is almost equal and cannot be expected to cause any differences in yields. As a next step in the analysis, the floral abortion in the different treatments is compared. The relevant figures are grouped in Table 15.

Although one would expect that the intercropped plots, being physiologically older than the control plots, would have the least abortion, no evidence *(c) Whole period of observations*

Treatment	Progeny A				Progeny B				Overall % Abortion
	Leaves 1943-51	Inflorescences 1944-52	Aborted inflorescences		Leaves 1943-51	Inflorescences 1944-52	Aborted inflorescences		
	No.	*No.*	*No.*	%	*No.*	*No.*	*No.*	%	%
A	241·1	194·5	46·6	19·3	230·7	186·0	44·7	19·4	19·4
B	241·8	193·2	48·6	20·1	228·6	184·7	43·9	19·2	19·6
C	242·3	194·4	47·9	19·8	223·3	183·0	40·3	18·0	18·9
D	230·2	184·7	45·5	19·8	222·2	189·9	32·3	14·5	17·2
E	236·9	192·7	44·2	18·6	229·2	188·9	40·3	17·6	18·1

of such an age effect is found, not even in the early years of bearing. In the later years the continuously intercropped palms, in spite of their advanced development, actually abort a higher percentage of their inflorescences than any other treatment. The differences between intercropping and control treatments are not significant however and in any case it must be borne in mind that differences in abortion may also have arisen indirectly from changes in sex-ratio. This, however, does not affect the most important conclusion, viz. that the good yields of the intercropped palms are *not* a result of a decrease in floral abortion. In fact the total number of inflorescences reaching anthesis is lower in the continuously cropped plots than in any other treatment, as appears from section *b.* of Table 15.

Sex-Ratio

The influence of the treatments on the sex of the inflorescences produced is shown in Table 16. It must be remembered that the effect of any treatment or climatic condition on sex-ratio is in fact an effect on sex differentiation two years before flowering. The early years (1944-46) and the later years of production (1947-52) are considered separately and the data have been compiled separately for the whole years and for the periods of low and high sex-ratio. The former period, which covers about half the year, coincides more or less with the rainy season while the period of high sex-ratio coincides with the dry season. The great differences in average sex-ratio in the two seasons is attributed to the effects of wet season and dry season conditions two years earlier on sex-differentiation (see p. 34). The actual periods of low sex-ratio in the individual years were as listed below. These periods cover the six or less months in which sex-ratio was below the year's average in both progenies.

1944	January-June*	1949	July-November
1945	May-October	1950	July-November
1946	July-November	1951	June-October
1947	July-November	1952	May-October
1948	June-November		

*N.B. In young palms the period between sex-differentiation and anthesis is shorter.

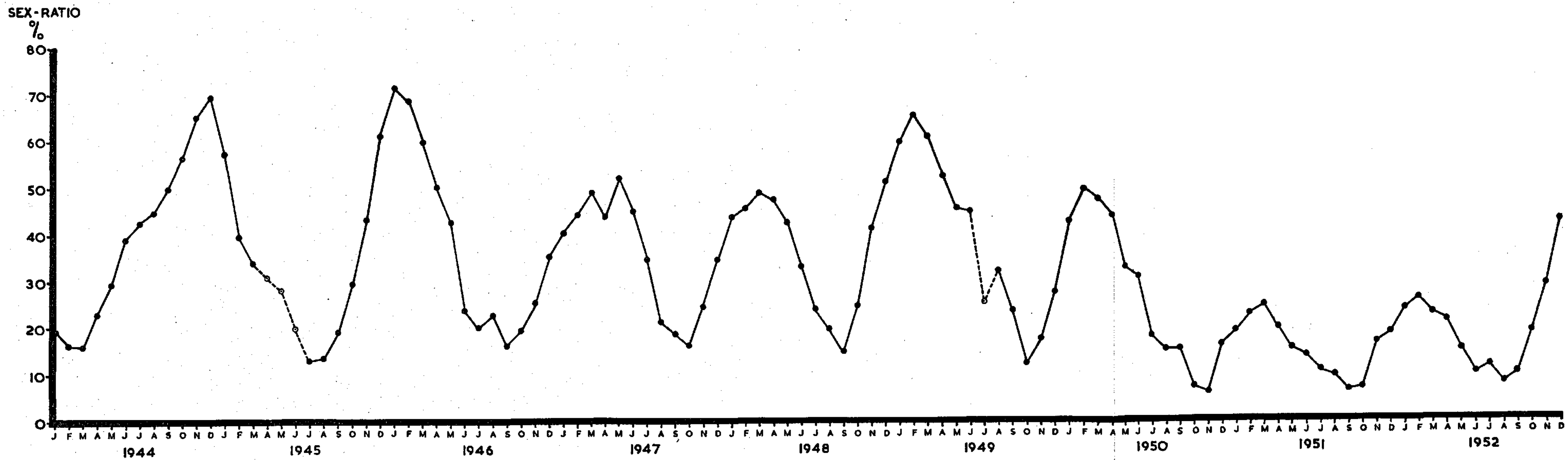


FIGURE 5. Monthly sex-ratio values for Experiment 33-1, averaged over the two progenies, for the period 1944-52.

In Figure 5 the monthly sex-ratio values for the whole period 1944-52 are shown graphically; they are averaged over the two progenies.

TABLE 16. SEX-RATIO IN THE ESTABLISHMENT EXPERIMENT 33-1, W.A.I.F.O.R., MAIN STATION, 1940

Average number of inflorescences and the number of female and hermaphrodite inflorescences produced during the period 1944 to 1952

I PERIOD 1944-46

Treatment	Progeny A			Progeny B		
	Total infl.	Fem. + herm. infl.	S.R.	Total infl.	Fem. + herm. infl.	S.R.
A	62·2	27·6	44·5	62·8	20·7	32·8
B	63·5	30·1	47·5	62·2	17·8	28·6
C	63·1	30·0	47·4	61·4	16·0	26·0
D	59·4	26·9	45·3	59·8	19·9	33·3
E	59·5	31·0	52·1	61·1	18·2	29·8

II PERIOD 1947-52

Treatment	Progeny A			Progeny B		
	Total infl.	Fem. + herm. infl.	S.R.	Fem. + Total infl.	herm. infl.	S.R.
A	132·3	37·3	28·2	124·8	34·2	27·4
B	129·7	40·4	31·2	122·6	29·6	24·1
C	131·3	37·6	28·6	121·6	31·6	26·0
D	125·3	33·1	26·4	130·1	31·9	24·5
E	133·2	38·1	28·6	127·8	34·2	26·8

The differences between progenies, both in female and hermaphrodite inflorescences and in sex-ratio, are highly significant (P=0·01).

The overall differences between the treatments (Table 16) are small but the results suggest that the good yield of palms of progeny A in plots of treatment B is due to a high sex-ratio. This high sex-ratio is not apparent in progeny B. If the analysis of the components of yield were to be halted at this point, the only possible conclusion would be that there is no consistent effect of the treatments on sex-ratio. Further analysis shows that this conclusion is incorrect. In Table 17 separate figures are presented for the two main sex-ratio periods, the period of low sex-ratio (inflorescences which reached the stage of sex differentiation in the wet season) and the period of high sex-ratio (sex determined in the dry season).

TABLE 17. SEASONAL INFLORESCENCE PRODUCTION IN ESTABLISHMENT EXPERIMENT 33-1, W.A.I.F.O.R., MAIN STATION, 1940

Production of inflorescences during seasons of low sex-ratio and seasons of high sex-ratio

I PERIOD 1944-46

(*a*) *Seasons of low sex-ratio*

Treatment	Progeny A			Progeny B		
	Total infl.	Fem.+ herm. infl.	S.R.	Total infl.	Fem.+ herm. infl.	S.R.
A	25·7	7·0	27·0	26·8	3·1	11·6
B	27·0	10·8	39·8**	25·8	3·4	13·2
C	25·8	7·9	30·6	27·9	3·1	11·0
D	26·0	8·2	31·4	29·1	4·6	15·8
E	20·0	6·0	29·8	28·3	3·3	11·8

** The difference in sex-ratio between treatment B and the average of the other treatments is highly significant (P=0·01) for progeny A. There is a very highly significant difference between the sex-ratio for the two progenies, averaged over the treatments (P=0·001).

(*b*) *Seasons of high sex-ratio*

Treatment	Progeny A			Progeny B		
	Total infl.	Fem.+ herm. infl.	S.R.	Total infl.	Fem.+ herm. infl.	S.R.
A	36·5	20·6	56·4	36·0	17·6	48·9
B	36·5	19·9	52·9	36·4	14·4	39·6
C	37·3	22·1	59·2	33·5	12·9	38·5
D	33·4	18·7	56·0	30·7	15·3	49·8
E	39·5	25·0	63·3	32·8	14·9	45·4

There is a very highly significant (P=0·001) difference between the sex-ratio for the two progenies, averaged over the treatments.

II Period 1947-52

(a) Seasons of low sex-ratio

Treatment	Progeny A			Progeny B		
	Total infl.	Fem.+ herm. infl.	S.R.	Total infl.	Fem.+ herm. infl.	S.R.
A	60·4	10·0	16·6	61·6	9·3	15·1
B	61·0	14·1	23·4**	61·0	9·4	15·4
C	60·1	9·1	15·1	59·1	8·6	14·6
D	59·6	10·5	17·6	61·2	8·8	14·4
E	60·3	9·8	16·2	64·4	10·6	16·5

**The differences in sex-ratio between treatment B and the average of the other treatments is highly significant (P=0·01) for progeny A. There is a significant interaction between treatments and progenies (P=0·05).

(b) Seasons of high sex-ratio

Treatment	Progeny A			Progeny B		
	Total infl.	Fem.+ herm. infl.	S.R.	Total infl.	Fem.+ herm. infl.	S.R.
A	71·9	27·3	38·0	63·2	24·9	39·4
B	68·7	26·3	38·3	61·6	20·2	32·8
C	71·2	28·5	40·0	62·5	23·0	36·8
D	65·7	22·6	34·4	68·9	23·1	33·5
E	72·9	28·3	38·8	63·4	23·6	37·2

These data show that the favourable effect of continuous intercropping is limited to the seasons of low sex-ratio and to progeny A. In the seasons of high sex-ratio the effect of continuous intercropping on sex-ratio is, if anything, negative, in particular in progeny B.

The next question to be answered is whether the positive effect of continuous intercropping on sex-ratio in progeny A could be held responsible for the positive effect of intercropping on yield. It has been established that this effect on sex-ratio is limited to the wet season flowering only. Any effect of intercropping, via sex-ratio, on yield must therefore be limited to the dry season. In Table 18 the annual yield figures have been split into two six-monthly totals, one corresponding with the periods of low sex-ratio (dry season yields) and one with the periods of high sex-ratio (wet season yields). The actual periods chosen for the individual years are six months later than those listed on p. 48 (six months being the average time between flowering and harvesting).

TABLE 18. SEASONAL YIELDS IN THE ESTABLISHMENT EXPERIMENT, W.A.I.F.O.R., MAIN STATION, 1940

Wet and dry season yields 1948-53 per palm

	Wet season yields (Dry season flowering)				Dry season yields (Wet season flowering)			
	Progeny A		Progeny B		Progeny A		Progeny B	
Treatment	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
A	19·2	396·6	17·8	446·1	10·4	237·3	10·7	257·8
B	17·6	396·7	15·0	395·2	14·2	310·8	11·0	294·9
C	19·1	389·3	16·6	437·9	10·6	246·4	8·6	211·5
D	13·4	273·6	13·6	412·0	12·2	264·2	8·6	205·8
E	20·1	448·3	16·2	392·2	10·1	243·2	12·2	296·2

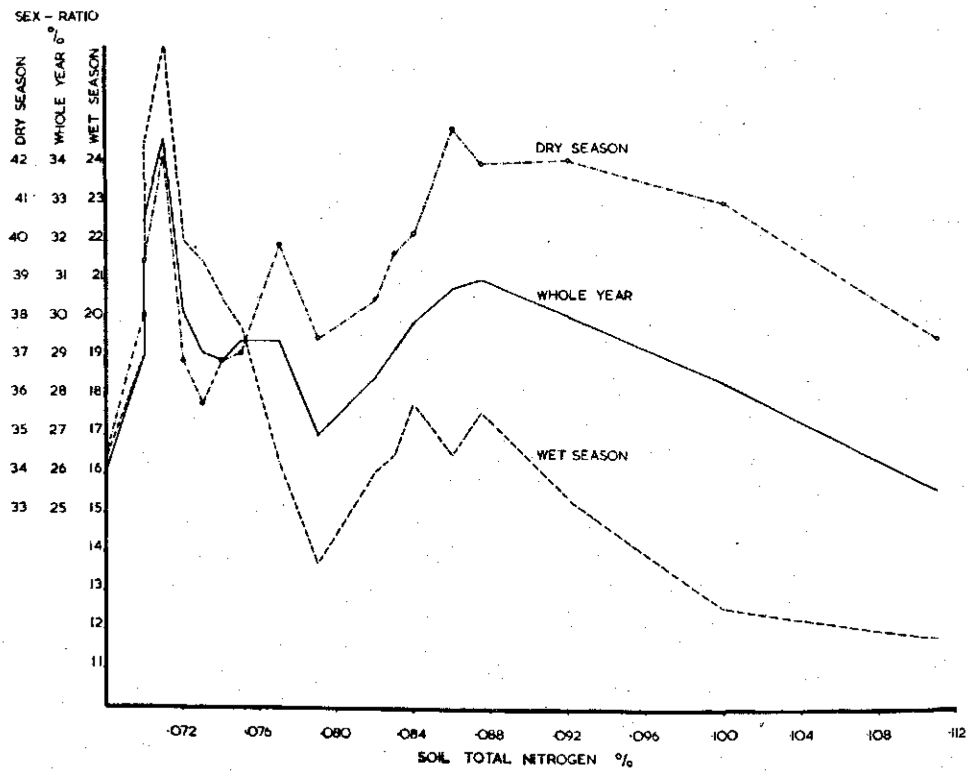


FIGURE 6. Sex-ratio in relation to soil total nitrogen in Experiment 33-1 for progeny A. Separate curves are drawn for the whole year, the dry season and the wet season.

The figures do indeed show that the higher yield in the continuously cropped plots is solely due to a higher number of bunches in the dry season and is clearest in progeny A. These findings, together with the absence of any positive effect of intercropping on leaf production, abortion and, as we shall see later, bunch failure, make it certain that the effect of continuous cropping on yield, observed in experiment 33-1, is the result of an increase of sex-ratio in the wet season, in particular in progeny A.

The last question that remains to be solved is why intercropping should have a favourable effect on wet season sex-ratio and hence on dry season yield. As all soil factors are adversely affected, it would seem that only a negative correlation between one or more of the soil factors and sex-ratio in the wet season (or dry season number of bunches) could explain the favourable intercropping effect. It is therefore of interest to look once more at the relationships between soil factors and sex-ratio, briefly discussed in Part III (for the *same* two progenies), but this time with particular regard to the wet season sex-ratio. The major results of this investigation are presented in Figures 6, 7 and 8. The plots were arranged in the order of magnitude of the soil factor concerned and, as the plot to plot variations were considerable,

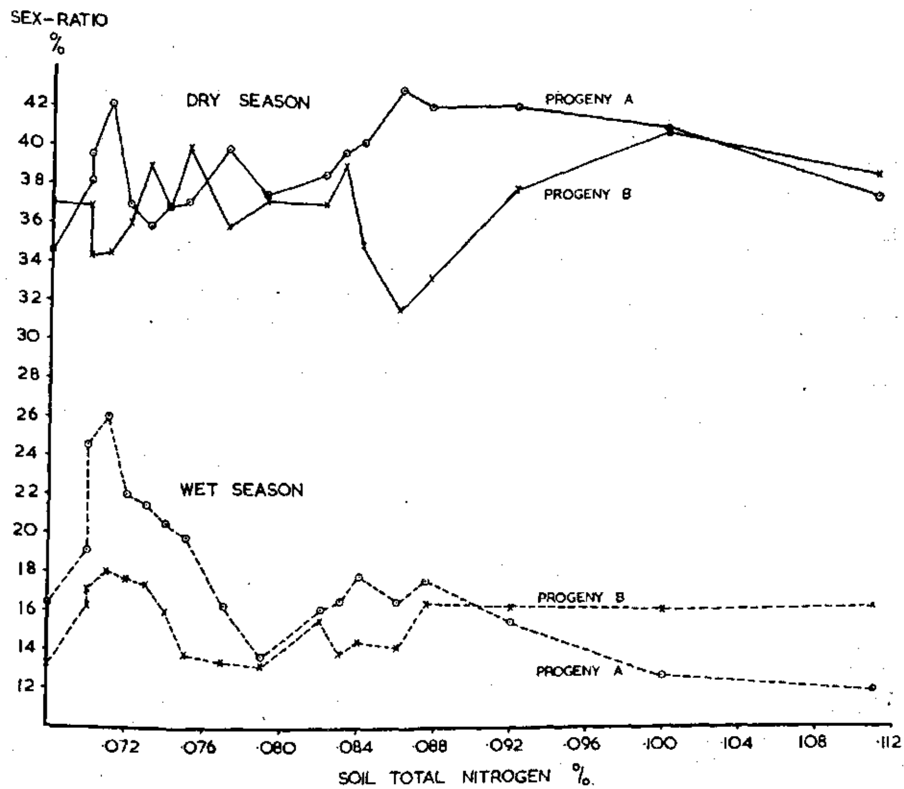


FIGURE 7. Sex-ratio in relation to soil total nitrogen in Experiment 33-1 for the two progenies and for the two seasons.

running means of three plots were calculated to determine the points for the curves. The plots of treatment D, natural cover slashed once a year, have been omitted from these calculations because they are not directly comparable with the other treatments. The high cover which was allowed to grow up in the plots of this treatment not only affects soil conditions but the whole environment in which the palms are growing.

It may be recalled here that in Part III there were some suggestions of an adverse effect of high soil nitrogen on sex-ratio, in particular in progeny A. Such a relationship might well be responsible for the effect on sex-ratio of continuous intercropping, which has itself been shown to reduce soil nitrogen. The fact that the apparent negative correlation between soil nitrogen and sex-ratio is again limited to the wet season and to progeny A, as is illustrated in Figures 6 and 7, would seem to support this suggestion. The correlation is however not quite significant unless the three lowest N plots which are probably sub-optimal are disregarded. A more definite result is obtained when the number of bunches in the dry season is considered. The negative correlation with soil nitrogen illustrated in Figure 8 was found to be statistically significant. ($r = -0{\cdot}445^*$)

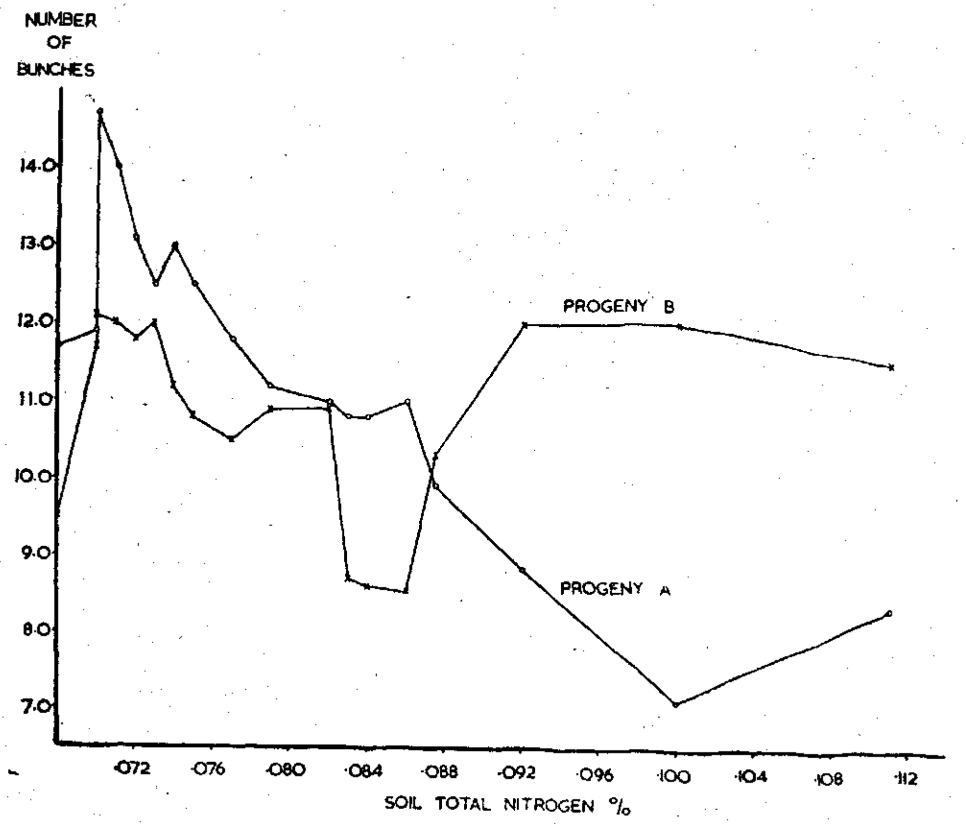


FIGURE 8. Number of bunches produced in the dry season in relation to soil total nitrogen for the two progenies of Experiment 33-1.

Bunch Failure

As has been stated before, the amount of bunch failure is a yield factor of a secondary nature, being usually determined by the number of bunches developing in relation to soil fertility conditions. It is also known that it decreases rapidly with advancing age of the palm. These two relationships are clearly demonstrated in Table 19.

In the early years the continuously cropped plots show the lowest figure for bunch failure, in spite of the relatively high number of female inflorescences and the reduction of soil fertility under this treatment.

Table 19. Bunch Failure in the Establishment Experiment 33-1, W.A.I.F.O.R., Main Station, 1940

Percentage bunch failure 1945-53

	A	B	C	D	E
(a) Early years (flowering 1944-46)					
Progeny A ..	26·6	22·2	21·9	34·0	30·0
Progeny B ..	31·4	14·7	29·2	33·6	34·9
Average	29·0	18·5	25·6	33·8	32·4
(b) Later years (flowering 1947-52)					
Progeny A ..	14·9	14·8	11·6	15·0	14·0
Progeny B ..	9·6	6·3	9·2	20·2	10·2
Average	12·2	10·5	10·4	17·6	12·1

At the same time the loss of inflorescences through bunch failure is highest in palms of treatment D (neglected maintenance) although the total number of inflorescences is very low and soil fertility is unaffected. It is clear that at this stage *physiological age* is the major factor determining bunch failure. The leaf production figures, presented on p. 46, have shown clearly that treatment B is the most advanced and treatment D the most retarded in development at this stage of the experiment.

In later years, when these differences in development are minimal, the usual relationship between bunch failure and number of female inflorescences becomes apparent (cf. Tables 19 and 16), except for treatment D which maintains a very high percentage of bunch failure. It is likely that the failure of so many bunches in the palms subjected to this treatment is a direct result of abnormal environmental conditions. It is possible that uncontrolled bush cover interferes seriously with the movement of pollen and thus reduces pollination and fruit setting.

Interpretation of the Data Provided by the Analysis of Bunch Production

The analysis of bunch production in this Establishment Experiment is now complete and has provided the following additional information:

(1) Leaf production, percentage abortion, percentage bunch failure and average bunch weight are not improved under conditions of continuous cropping, except in the early years when a slight age effect is apparent.

(2) The sex-ratio in the wet season of progeny A under continuous cropping is significantly higher than the average sex-ratio of the other treatments. This increase in sex-ratio is responsible for an increase in number of bunches in the dry season, and consequently for the observed overall yield difference.

(3) There are indications that these effects of intercropping may be explained by a negative correlation between soil total nitrogen and sex-ratio.

It has already been mentioned in Part I that, on the basis of Beirnaert's theories, it could be expected that the favourable effects of intercropping, observed both in the Belgian Congo and Nigeria, were caused by a change in sex-ratio under the influence of a reduction in "mineral nutrition". The analysis of bunch production in the Establishment Experiment at the W.A.I.F.O.R. Main Station has lent some support to this suggestion but has shown at the same time that the relationships are by no means as simple as was originally assumed. It has been demonstrated (*a*) that in the early years the effect of intercropping on the physiological age of the palm is more important than the effect on sex-ratio, (*b*) that the different "minerals" in the soil have very different effects on sex-ratio and that "mineral nutrition" cannot therefore be considered as one single factor, (*c*) that the genetical constitution of the palm to a large extent determines its reaction to intercropping and (*d*) that the effect of intercropping is markedly seasonal under West African conditions.

The following hypothesis on the influence of external conditions on sex-ratio has now been developed from the above facts.

The ratio between male and female inflorescences in the oil palm is influenced by the ratio between carbohydrates and nitrogen in its tissues. An increase in carbohydrate assimilation relative to nitrogen absorption will increase the percentage of female inflorescences while increases in nitrogen supply relative to assimilation will stimulate male flowering. This relation exists only, however, if photosynthetic activity is limited by other environmental factors, such as light intensity, water supply or mineral nutrition. When, for example, inadequate light is restricting photosynthesis, an increase in nitrogen supply will decrease the ratio of carbohydrates to nitrogen, which will in turn lead to a higher proportion of male flowers. Similarly it follows that when the sex-ratio is low, owing to poor light conditions, a reduction in nitrogen uptake will improve the sex-ratio.

It is likely that in many parts of Africa inadequate light is the primary factor limiting oil palm yields, in particular during the rainy season, and effects of cultural treatments on yields will therefore often be determined by their effect on the ratio between photosynthesis and nitrogen supply.

The fact that, under such conditions, intercropping is not detrimental to yield can perhaps be explained by the reduction in nitrogen supply caused by cropping, leading to an increase in sex-ratio.

This hypothesis is by no means proven by the data set out above, and it is clear that it can only be investigated fully by detailed physiological work. Before using the hypothesis as a basis for further work it is therefore of importance to examine some of its implications, which have not been considered in the preceding analysis.

The hypothesis implies, amongst other things, that:

(*a*) a variation in light intensity only (within certain limits) must have an effect on sex-ratio opposite to the effect attributed to a variation in nitrogen supply under constant light conditions;

(*b*) the effects of variations in light intensity or nitrogen supply should be most pronounced at the end of the rainy season when the carbohydrates in the plant are likely to be at their lowest level;

(*c*) when or where a factor other than light (e.g. water, availability of mineral nutrients) is limiting carbohydrate assimilation, variations in this factor, rather than variations in light intensity will influence the sex-ratio.

To test the correctness of these implications relevant data from two other experiments were examined and one new experiment was carried out. This work will be described in Part V.

PART V

Additional Experimental Data on the Relationship between Bunch Production and Environment

In this Part three experiments will be reviewed which provide additional information on the relationship between environment and the elements of bunch production.

(*a*) A Pruning Experiment to test the effects of variations in light intensity in different seasons.

(*b*) A manurial Experiment testing the effects of applications of organic manure (bunch refuse) or fertilizers at two different seasons.

(*c*) An Establishment Experiment similar to the one reviewed in Part IV but planted on a very much poorer soil.

The data provided by these experiments serve to strengthen the hypothesis developed in Part IV.

The Observational Pruning Experiment

Beirnaert (1935) has already mentioned some examples of the effects of reduced light intensity or reduced assimilatory capacity on sex-ratio. He had observed that palms growing under shade, stripped by weaver birds or badly affected by *Helminthosporium*, were generally very low in sex-ratio. These observations were in fact the only (published) basis of his ideas on the effects of environment on sex-ratio. As we have seen, the observations from the W.A.I.F.O.R. intercropping experiment support Beirnaert's views but still do not supply any direct evidence that light intensity is one of the major factors determining sex-ratio. To obtain further evidence on this point, an experiment was carried out at W.A.I.F.O.R. in which the amount of light falling on closely spaced palms was increased in various degrees by pruning one or more of the surrounding palms.

The experimental area consisted of a number of progeny rows planted in 1941 at a spacing of 14½×25 ft., i.e. double the normal density of 29 ft. triangular.

A proportion of the palms was severely pruned in 1952, 1953 and 1954 in such a pattern that the non-pruned palms could be divided into four groups, constituting the experimental treatments:

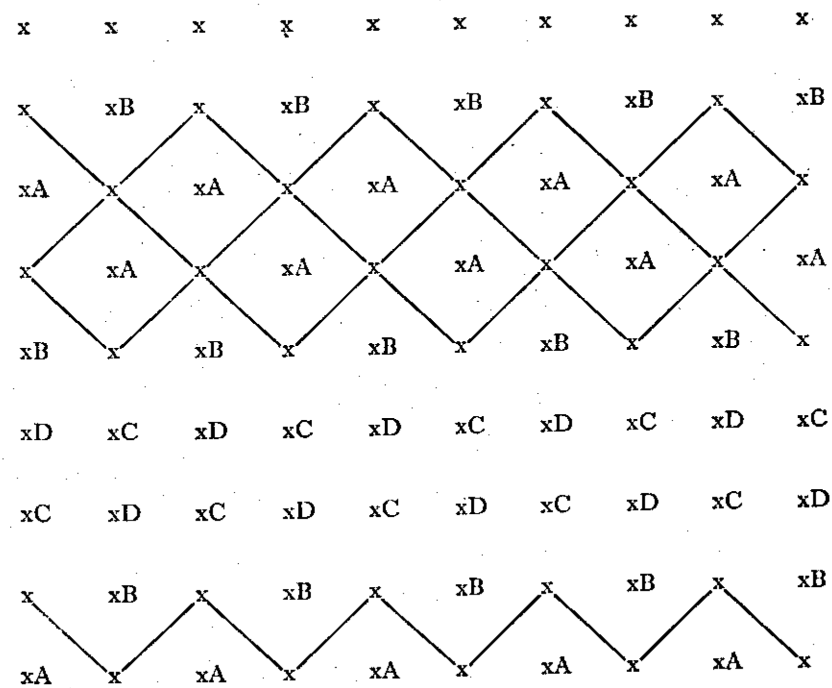
A. Palms surrounded by 4 pruned palms.

B. Palms adjacent to 3 pruned palms.

C. Palms adjacent to 1 pruned palm.

D. Control—palms surrounded by unpruned palms only.

The pattern of pruning was as follows:



The experimental area was divided into three sections in which the pruning was carried out at three different times of the year:

I. December (beginning of dry season)
II. April (beginning of wet season)
III. August (middle of wet season)

In each section twenty-four palms have been chosen for each treatment.

The actual dates of pruning were as follows:

Section I. Dec. 1952—Dec. 1953—Dec. 1954—Jan. 1956
Section II. April 1953—April 1954—April 1955—April 1956
Section III. Aug. 1953—Aug. 1954—April 1955—Aug. 1956

The pruning in Section III in 1955 was carried out four months early by mistake.

Individual yield records are available from 1946 onwards. The average yields per treatment and per palm since 1951 (i.e. two years before the first pruning) are shown in Table 20.

TABLE 20. OBSERVATIONAL PRUNING EXPERIMENT 1-15, W.A.I.F.O.R. MAIN STATION: EFFECT OF PRUNING SURROUNDING PALMS

Weight of bunches per palm in lb.

Treatments	1951	1952	1953	1954	1955	1956
Block I. *Pruning in December*	*lb.*	*lb.*	*lb.*	*lb.*	*lb.*	*lb.*
A Surrounded by 4 pruned palms	18·7	19·4	65·5	65·5	144·1	137·7
B " " 3 " "	21·7	16·8	40·1	53·2	101·3	66·3
C " " 1 " palm	40·5	22·3	50·5	47·4	81·9	67·9
D " " 0 " "	24·8	29·3	45·3	34·0	62·8	52·2
Block II. *Pruning in April*						
A Surrounded by 4 pruned palms	16·8	8·1	36·0	43·1	103·1	99·5
B " " 3 " "	29·4	29·8	28·1	37·0	68·6	75·4
C " " 1 " palm	12·3	18·6	17·8	25·9	43·7	23·0
D " " 0 " "	23·7	24·8	37·1	25·1	51·2	39·2
Block III. *Pruning in August* (Pruned in April in 1955 in error.)						
A Surrounded by 4 pruned palms	18·0	23·2	33·4	32·1	78·0	99·2
B " " 3 " "	16·8	24·2	36·9	35·3	55·5	48·5
C " " 1 " palm	30·9	23·2	50·1	30·3	48·0	62·9
D " " 0 " "	21·1	24·3	36·7	22·4	45·7	28·4
Average						
A Surrounded by 4 pruned palms	17·8	16·9	44·6	46·9	108·4	112·1
B " " 3 " "	22·6	23·6	35·0	41·8	75·1	63·4
C " " 1 " palm	27·9	21·4	37·5	34·5	57·9	51·3
D " " 0 " "	23·2	26·1	39·7	27·2	53·2	39·9

The yield increases in palms receiving the highest light increment are quite spectacular: 100% in 1955 and nearly 200% in 1956. Although the systematic layout makes statistical analysis impossible, there can be no doubt that these differences are real, and the probability that they result from increases in light intensity is very high. Effects of pruning on competition for soil nutrients cannot be excluded but the differences are such that they are unlikely to result from increases in mineral uptake, particularly as the experimental area was free from deficiency symptoms.

The treatments have affected both the number and the weight of bunches produced. The most pronounced effect on number of bunches was observed in the block pruned in December while the greatest increase in average bunch weight occurred in the block pruned in August. This is illustrated in Table 21 for the years 1955 and 1956.

TABLE 21. YIELDS PER PALM IN 1955 AND 1956 IN THE OBSERVATIONAL PRUNING EXPERIMENT 1-15, W.A.I.F.O.R. MAIN STATION: EFFECT OF PRUNING SURROUNDING PALMS

Number and average weight of bunches per palm

Treatments	1955		1956	
	No.	Av. Wt.	No.	Av. Wt.
		lb.		*lb.*
Block I. *Pruning in December*				
A Surrounded by 4 pruned palms ..	4·9	23·3	4·6	29·7
B ,, ,, 3 ,, ,, ..	3·8	26·4	2·2	28·8
C ,, ,, 1 ,, palm ..	3·5	23·4	2·3	28·7
D ,, ,, 0 ,, ,, ..	2·4	26·4	1·8	29·9
Block II. *Pruning in April*				
A Surrounded by 4 pruned palms ..	3·9	26·6	3·3	26·6
B ,, ,, 3 ,, ,, ..	3·2	22·6	3·1	23·4
C ,, ,, 1 ,, palm ..	2·3	21·0	1·2	18·2
D ,, ,, 0 ,, ,, ..	2·8	18·1	1·8	21·3
Block III. *Pruning in August* (Pruned in April 1955 in error.)				
A Surrounded by 4 pruned palms ..	2·6	30·2	3·2	30·0
B ,, ,, 3 ,, ,, ..	2·0	27·8	2·0	22·3
C ,, ,, 1 ,, palm ..	2·2	21·3	2·4	25·6
D ,, ,, 0 ,, ,, ..	2·2	20·7	1·5	18·6

Growth and Flowering

In the years 1954, 1955 and 1956 growth and flowering observations were made on palms subjected to the various treatments. These observations have made it possible to investigate how the increase in yield under reduced shade has arisen.

In Table 22 leaf production, sex-ratio and percentage abortion for July 1954-June 1955 and July 1955-June 1956 are tabulated. These two periods correspond with the two years for which yield figures are given in Table 21.

These figures show that leaf production is only slightly improved following an increase in light intensity. The differences are of the order of 3 to 10%.

The effects of the treatments on floral abortion are very striking. In block III the percentage abortion in palms receiving the greatest light increment (treatment A) dropped to about one-quarter of the abortion found in control palms.

There is also an important rise in sex-ratio in Block I, pruned in December. In the other two blocks the rise in sex-ratio, although clear, is less and yield increases can be attributed mainly to reduced abortion.

The experimental palms in Block I (December pruning) received a greater

TABLE 22. AVERAGE LEAF PRODUCTION PER PALM, SEX-RATIO AND PERCENTAGE ABORTION IN THE OBSERVATIONAL PRUNING EXPERIMENT 1-15, W.A.I.F.O.R., MAIN STATION

Treatment	July '54-June '55			July '55-June '56		
	Leaves	Sex-ratio	Abortion	Leaves	Sex-ratio	Abortion
	No.	%	%	*No.*	%	%
Block I. *Pruning in December*						
A Surrounded by 4 pruned palms	22·0	25·5	12·7	22·2	26·3	12·1
B ,, ,, 3 ,, ,,	21·6	18·5	12·5	22·2	14·1	23·4
C ,, ,, 1 ,, palm	20·8	19·4	18·3	20·7	15·3	21·2
D ,, ,, 0 ,, ,,	20·8	14·6	17·8	20·6	13·7	25·7
Block II. *Pruning in April*						
A Surrounded by 4 pruned palms	19·9	23·1	21·6	20·7	28·5	27·1
B ,, ,, 3 ,, ,,	18·8	22·5	31·4	18·9	24·1	27·0
C ,, ,, 1 .. palm	20·0	22·7	34·0	19·0	19·5	37·0
D ,, ,, 0 ,, ,,	19·5	22·4	40·5	18·8	21·1	42·3
Block III. *Pruning in August*						
A Surrounded by 4 pruned palms	22·0	14·6	6·8	21·5	20·0	11·6
B ,, ,, 3 ,, ,,	21·9	12·3	11·0	21·4	14·6	19·6
C ,, ,, 1 ,, palm	20·8	15·8	17·8	20·7	16·9	25·6
D ,, ,, 0 ,, ,,	20·4	19·1	35·8	20·2	15·0	34·1

light increment than those in the other blocks because (*a*) there is more sunshine in the months December-March than in any other period of the year and (*b*) leaf production is at a minimum in this period and the pruned palms will therefore need a longer time to regain crowns of normal size and so begin to shade neighbouring palms. This may explain why the rise in sex-ratio is most important and most prolonged in Block I.

Although treatments were not randomized and statistical analysis could not therefore be carried out, this experiment has left little doubt that there is a direct relationship between the amount of light available to the palm and its sex-ratio. To prove the existence of such a relationship was not, however, the sole purpose of the experiment. It was also hoped to collect some accurate information on the duration of the time lag between the applications of treatments and the appearance of effects on the various yield components, in particular on sex-ratio.

The exact time of appearance of increases in *average bunch weight* cannot be determined accurately as the yield figures are only available as annual totals. The average bunch weight figures for 1953 in Block I show nonetheless, that an increase has taken place within the first year after the treatment was applied.

Block I, first pruned December 1952

Average bunch weight	*1952*	*1953*
Treatment A	20	21
„ B	19	16
„ C	24	17
„ D	23	17

Reduced *abortion* is observed in all three blocks from the beginning of the flowering observations in January 1954. As the first pruning in block III was only done in August 1953, this means that the pruning has influenced the number of inflorescences within 5-6 months after it was carried out. As the inflorescences pass the critical stage at which abortion usually occurs about five months before anthesis, this indicates that the pruning of adjoining palms has an immediate influence on abortion. This immediate reaction of the palms to the pruning of surrounding palms provides the strongest indication that the pruning effect is in fact a light effect.

Effects on *sex-ratio* appear after a delay of 19-20 months. This is illustrated in Table 23 in which sex-ratio figures for treatment A are compared with those for the control treatment D for two-monthly periods. The figures cover the period July 1954-June 1956, i.e. the period corresponding with the 1955+1956 yield data presented in Table 21.

TABLE 23. AVERAGE SEX-RATIO FIGURES FOR SIX TWO-MONTHLY PERIODS IN THE OBSERVATIONAL PRUNING EXPERIMENT 1-15, W.A.I.F.O.R., MAIN STATION

Average for the two years 1954/55 and 1955/56

Treatment	July-Aug.	Sept.-Oct.	Nov.-Dec.	Jan.-Feb.	Mar.-Apr.	May-June
	%	%	%	%	%	%
Block I. *Pruning in December*						
A. Palms surrounded by 4 pruned palms	*9·3*	*24·0*	35·2	26·6	16·6	10·9
D. „ „ „ 0 „ „	*4·1*	*16·6*	23·6	20·1	17·0	8·7
Block II. *Pruning in April*						
A. Palms surrounded by 4 pruned palms	12·6	13·0	*29·1*	*41·0*	34·4	14·0
D. „ „ „ 0 „ „	14·8	12·3	*18·9*	*33·0*	34·4	26·9
Block III. *Pruning in August*						
A. Palms surrounded by 4 pruned palms	3·1	18·6	28·4	14·6	*14·1*	*6·6*
D. „ „ „ 0 „ „	5·8	14·5	28·6	21·1	*9·2*	*6·4*

Pruning was carried out in such a way that palms surrounded by pruned palms enjoyed improved light conditions for a period of roughly four months (if necessary surrounding palms were pruned back slightly again after two months). In each of the three blocks of the experiment the period of four months has been traced in which the greatest relative difference between treatments can be found. These periods, for which the sex-ratio figures are in italics in Table 23, can be taken to correspond with the pruning periods.

The fact that the reaction to December pruning is most clear in July-August, the reaction to April pruning in November-December and the reaction to August pruning in March-April can only mean that the time lag between the treatment and its effect on sex-ratio, i.e. the maximum time lag between sex differentiation and anthesis, is 19-20 months. This conclusion cannot be generally applied however. The experimental palms are growing under conditions of close spacing, which may well influence the speed of inflorescence development, or the stage of sex-differentiation. The accurate determination in this experiment of 19-20 months as the period between sex-differentiation and anthesis has some general importance however. It can be deduced that the period of minimal sex-ratio, which in this area is about July, is determined 19-20 months earlier around November-December, i.e. after the end of the wet season, while the period of maximal sex-ratio, around December, is determined by conditions in April-May, i.e. after the dry season during a transition period of heavy showers and bright sunshine.

General application of this deduction would suggest that under Nigerian conditions this time lag between sex-differentiation and flowering in any area can be determined by counting the number of months between April or November and the months of highest or lowest sex-ratio in the second year following.

It may be concluded that the results of this observational trial lend support to the hypothesis in two of its implications: (*a*) that an increase in light intensity has a positive effect on sex-ratio, and (*b*) that an increase in light intensity is most effective when it occurs at the end of the wet season.

The Bunch Refuse Experiment

The production analysis of the Establishment Experiment 33-1 has suggested that sex-ratio may be negatively correlated with total nitrogen in the soil, particularly in the wet season. In the hypothesis put forward in Part IV the seasonal trend in the nitrogen effect has been attributed to the strong fluctuations in the amount of sunlight within the year. It was suggested that in the dry season, when sunlight is abundant, variations in nitrogen supply could have but little effect on the ratio between carbohydrates and nitrogen in the palm, but in the wet season when carbohydrate assimilation may well be restricted any rise in nitrogen content would decrease the carbohydrate/nitrogen ratio and consequently the sex-ratio.

This interpretation implies that under certain conditions (depending on climate and the genetic constitution of the palm) a difference in the effects of nitrogen manuring may be expected according to the time of the year in which nitrogen is applied. An experiment at W.A.I.F.O.R. Main Station in which bunch refuse and a fertilizer mixture, including nitrogen, have been applied annually, either in April or in October, since 1949, has provided some information which lends support to the suggested seasonal effect of nitrogen application on sex-ratio.

The Bunch Refuse Experiment 3-3 was originally designed to compare various methods of returning bunch refuse to the plantation either alone, as an organic manure or as ash, or in combination with fertilizers. The following treatments were compared in a single replicate of a 2^5 confounded factorial layout, comprising four blocks of eight plots with sixteen palms per plot:

Factor	Level 0	Level 1
R	No bunch refuse	½ cwt. bunch refuse per palm
M	Broadcast around the base	Applied in lines between the palms
T	Applied in April	Applied in October
B	Refuse not burnt	Refuse burnt and applied as ash
F	No fertilizer added	3 lb. N.P.K. mixture (1:1:1) added

The area was planted in 1947 and the first applications were made in 1949. In 1956 the dose of fertilizer mixture was increased to 12 lb. per annum and the dose of bunch refuse to 4 cwt. per annum as the original doses were evidently too small to maintain the important treatment effects observed in the early years.

Analyses of yield data from this experiment have been considerably complicated by the presence of dummy treatments. Eight plots receive no treatment at all and four treatments are duplicated. One treatment effect was large enough however to attain statistical significance in each of the years so far analysed (1952-57) in spite of the unsatisfactory design and the very high coefficient of variability (ranging from 44% in 1952 to 15% in 1957). During the first four years of production the yield of plots receiving bunch refuse+fertilizers in April was nearly double the yield of plots receiving the same treatment in October. In later years the difference has become smaller but has remained statistically significant. Relevant yield figures are presented in Table 24.

An explanation for this pronounced time effect, which accords well with the sex-ratio hypothesis, immediately suggests itself:

The fertilizer mixture increases the nitrogen content of the soil and thereby reduces the sex-ratio, in particular when the application takes place at the end of the wet season. When the fertilizer mixture is applied at the end of the dry season, the negative N effect on sex-ratio is weaker and the favourable action of the other fertilizers predominates. The role of the bunch refuse is less clear. It seems to intensify the effect of the fertilizers without exercising an effect of its own.

It was decided to test the correctness of this interpretation by means of an analysis of bunch production, as this might confirm one of the more important practical implications of the sex-ratio hypothesis: viz. that fertilizer applications, especially those including nitrogen, might under certain conditions lead to a decrease in sex-ratio and consequently to a decrease in yield.

Regular flowering observations were carried out from the beginning of 1955 and are continuing to date. The summarized results for the years 1955-57 are shown in Table 25. For this summary the less important factors, method of application and burning of bunch refuse, were disreagrded.

TABLE 24. EFFECT OF FERTILIZER AND TIME OF APPLICATION IN THE BUNCH REFUSE EXPERIMENT 3-3, W.A.I.F.O.R., MAIN STATION, 1947

Yield of fruit bunches per acre per annum

Ferti-lizer	Time of application	Bunch refuse				No bunch refuse			
		1951-1954	1955	1956	1957	1951-1954	1955	1956	1957
		lb.	*lb.*	*lb.*	*lb.*	*lb.*	*lb.*	*lb.*	*lb.*
Ferti-lizer	April	3,827*	11,983*	7,854*	9,358*	3,385	10,540	7,310	9,216
	October	2,013	7,585	5,202	7,407	2,882	10,322	6,239	7,913
	Mean	2,925	9,784	6,528	8,382	3,134	10,431	6,774	8,564
Nil	April	3,153	9,672	6,913	8,329	—	—	—	—
	October	2,911	8,745	6,519	8,365	—	—	—	—
	Mean	3,032	9,208	6,716	8,347	3,167	8,815	6,003	6,437
	Mean	2,976	9,496	6,622	8,364	3,150	9,623	6,389	7,500

* The difference between times of application of bunch refuse + fertilizer is statistically significant (P=0·05).

TABLE 25. LEAF PRODUCTION, SEX-RATIO AND PERCENTAGE ABORTION: BUNCH REFUSE EXPERIMENT 3-3, W.A.I.F.O.R., MAIN STATION, 1947

Average for the period 1955-57

Treatment		Av. No. of leaves	% Sex-ratio	% Abortion
Control	(8 plots)	23·5	30·6	8·2
Bunch refuse in April	(4 plots)	24·3	34·1	9·1
Bunch refuse in October	(4 plots)	24·6	34·7	7·2
Fertilizer in April	(4 plots)	24·7	33·9	7·7
Fertilizer in October	(4 plots)	25·2	27·3	7·0
Fert. + bunch refuse in April	(4 plots)	24·6	33·5	6·9
Fert. + bunch refuse in October	(4 plots)	24·3	31·9	8·0

The figures show a considerably lower sex-ratio in the "October" plots than in the "April" plots but there is one confusing factor. In contrast to the yield figures the differences in sex-ratio between times of application are much more pronounced in the plots without bunch refuse than in the plots which have received both fertilizer and bunch refuse. This would indicate that the significant effect on yield of time of application of bunch refuse+fertilizer are not primarily sex-ratio effects but are caused rather by such factors as changes in bunch survival and average bunch weight.

The differences in sex-ratio are not significant, but there are further indications that the important difference observed between the plots which received fertilizers in April or October are true "time of application" effects. It may be seen, for example, from Table 26 that the depression of sex-ratio in the "October" plots is most pronounced between September and March, i.e. the period of flowering which corresponds with the period of sex-differentiation immediately after an application. Similarly it appears that there is a depression of sex-ratio in the "April" plots between March and August.

TABLE 26. SEX-RATIO FOR TWO-MONTHLY PERIODS. BUNCH REFUSE EXPERIMENT 3-3, W.A.I.F.O.R. MAIN STATION, 1947

Averages for 1955-57

Treatment (disregarding bunch refuse)		Jan.-Feb.	Mar.-Apr.	May-June	July-Aug.	Sept.-Oct.	Nov.-Dec.
Control: no fertilizer	(16 plots)	45·9	44·8	29·3	22·6	20·9	31·9
Fertilizer in April	(8 plots)	48·6	42·5	30·8	21·8	23·2	33·7
Fertilizer in October	(8 plots)	41·9	40·0	29·4	20·6	18·8	28·4

The depressive action of the October fertilizer application appears to last longer than that of the April application. This may be explained by the fact that the fertilizer is not leached out of the soil until after the dry season, while the April applications are usually followed by heavy rainfall within a few months.

The bunch refuse experiment has not yielded any conclusive evidence that nitrogen application in October depresses the sex-ratio. It has however shown that a depression of sex-ratio in the October plots is one of the factors contributing to the significant differences in yield between April and October applications of bunch refuse and fertilizer. This depression is most pronounced in the period of the year corresponding with the months immediately following an application. We cannot yet exclude the possibility that this sex-ratio effect is due to chance. We can however say that if it is a real effect it is probably attributable to nitrogen. Potassium is, if anything, positively related with sex-ratio and phosphate has so far been largely ineffective under W.A.I.F.O.R. conditions.

It can thus be concluded that the trends observed in this experiment agree well with the hypothesis but clearly need more confirmation in experiments specially designed for the purpose. Some such experiments have already been started and are discussed in Part VI.

THE ESTABLISHMENT EXPERIMENT, NKWELE

In the sex-ratio hypothesis it has been postulated that a decrease in soil nitrogen has a favourable effect on sex-ratio when the carbohydrate assimilation is limited by environmental factors. So far only the factor light intensity has been discussed in this connection. The hypothesis implies that when other environmental factors, such as water supply or mineral nutrition, are limiting, variations in these factors rather than in light intensity may be expected to influence the sex-ratio and its relations with soil nitrogen. The factor water supply has already been discussed by Broekmans (1957). In the driest months of the year this factor definitely limits carbohydrate assimilation but, as available nitrogen in the soil is always at a low level in these months, it is unlikely that intercropping could exercise much influence on the nitrogen uptake. It is of more interest to consider what happens when soil fertility becomes a limiting factor. This situation may be expected in poor areas, towards the beginning of the wet season when water supply and light intensity are both optimal. It would follow from the hypothesis that under such circumstances intercropping may have an unfavourable effect on sex-ratio.

An Establishment Experiment, planted in 1943 on very poor land at Nkwele in Eastern Nigeria, can provide some relevant information on this point. The experiment has been described extensively in an earlier paper on mixed cropping (Sparnaaij, 1957) and only a brief description of layout and yield data will be given here.

Four treatments were compared in two replicates of a 4×4 Latin square. The treatments were:

A. Control. Leguminous cover, regularly slashed.

B. Natural cover, slashed at end of rains only. This treatment is comparable with treatment D in the Establishment Experiment at the W.A.I.F.O.R. Main Station (Part IV).

C. Intercropping every fourth year. The land was cropped with yams and maize followed by cassava in 1943-44 and in 1947-48. As the yields of the foodcrops were very low in the second cropping cycle, no further cropping was attempted.

D. Continuous intercropping with manuring. This treatment represents "compound farming", i.e. farming near to the homestead. The land is cropped continuously with maize, yams and cocoyams and was manured with 4 tons of farm-yard manure in 1944, 1946 and 1948, the last time combined with an application of 15 lb. incinerator ash per palm.

In the early years the palms in the cropped plots showed much better growth than those in the A or B plots as is shown by the leaf production figures in Table 27.

TABLE 27. LEAF PRODUCTION IN ESTABLISHMENT EXPERIMENT 704-1, NKWELE, 1943

Number of leaves per palm per year

Treatment	1945	1946	1947
A. Leguminous cover, regularly slashed	16·4	21·6	26·1
B. Natural cover, slashed once annually	13·5	18·3	23·9
C. Intercropping every fourth year	18·9	21·6	27·9
D. Continuous intercropping with manuring ..	24·4	29·2	30·3

The low average level of leaf production as compared with the Main Station experiment reflects the great difference in soil fertility between the two areas. The yields of the food crops, too, remained far below those obtained at Benin.

The yield figures, presented in Table 28, reflect the early differences in leaf production. During the first three years of bearing the continuously intercropped plots yielded more than twice as much as the control plots, a difference which is highly significant.

TABLE 28. ANNYAL YIELDS IN ESTABLISHMENT EXPERIMENT 704-1, NKWELE, 1943

Yield of fruit bunches in lb. per acre

Year	A Control	B Natural cover slashed annually	C Intercropping every four years	D Continuous intercropping with manuring
	lb.	*lb.*	*lb.*	*lb.*
1948	1,621	1,019	2,542	4,485
1949	2,626	1,943	4,097	5,962
1950	2,343	1,548	1,017	3,417
1948-50	6,590	4,510	7,656	***13,864
1951	3,126	2,330	2,153	2,917
1952	3,382	3,095	3,466	4,308
1953	4,685	3,795	3,460	4,168
1951-53	11,393	9,220	9,070	11,393
1954	2,949	2,763	1,955	2,611
1955	4,921	4,223	3,600	4,035
1956	3,558	2,568	2,987	3,136
1954-56	11,428	9,554	8,542	9,782
1957	3,072	2,535	2,083	2,938
1958	3,364	3,060	2,645	3,033
Total	35,847	28,879	30,005	41,010

***The difference between treatments A and D is very highly significant (P=0·001).

In later years this difference disappears completely and then, from 1953, becomes negative.

These data on leaf production and bunch yield indicate (*a*) that intercropping, although initially having a pronounced positive effect, is an exhaustive treatment, and (*b*) that the intercropping effect is, in part, an "age" effect, particularly in poor areas. What the figures cannot show is whether the remarkable effect on flowering, which was observed in the Main Station experiment, is also operative in this very much poorer area.

Unfortunately no data on flowering were collected prior to 1955 and complete records are only available for 1956. These few data nevertheless demonstrate clearly a positive effect of intercropping on the sex-ratio in the wet season and a negative effect in the later part of the dry season. The relative number of inflorescences flowering in the wet season is so low, and the depressive effect of cropping on dry season sex-ratio and on the other production components so pronounced, that the overall effect of intercropping is to reduce yield. It can therefore be concluded that at Nkwele the major limiting factor is soil fertility (whether relating to the chemical or the physical status of the soil), but that in the wet season light is limited to an extent where sex-ratio is depressed, particularly in the more fertile (i.e. not intercropped) plots. Table 29 illustrates these seasonal influences.

TABLE 29. GROWTH AND FLOWERING DURING 1956 IN ESTABLISHMENT EXPERIMENT 704-1, NKWELE, 1943

Number of leaves per palm, sex-ratio and abortion percentage

Treatment	Whole year			Sex ratio					
	Leaves	Sex-ratio	Abortion	Jan.-* Feb.	Mar.-Apr.	May-June	July-Aug.	Sept.-Oct.	Nov.-Dec.
		%	%	%	%	%	%	%	%
A	20·9	16·8	15·4	41·6	29·7	10·2	5·2	12·4	2·6
B	20·3	15·6	21·5	33·5	28·3	17·9	12·8	7·4	3·0
C	19·2	15·1	24·3	31·1	34·4	10·4	8·1	9·9	4·0
D	18·7	15·4	20·7	23·4	26·4	31·0	10·7	15·8	4·3

* Period of highest sex-ratio; sex determined at the end of dry season two years earlier, see page 64.

The season of low sex-ratio lasts longer in this area than in Benin, viz. from May to December. Nevertheless only 32% of the total number of female and hermaphrodite inflorescences opening in 1956 were produced in these eight months in control plots. In treatment D however, the percentage was much higher: 53%.

The results of the production analysis in this experiment thus seem to confirm one of the implications of the sex-ratio hypothesis, viz. that when soil fertility is limiting carbohydrate assimilation, as is likely to be the case in poor areas at the end of the wet season, intercropping has an adverse effect on sex-ratio.

The experiments described in Parts IV and V were not designed to allow for a detailed analysis of bunch production. It is not surprising, therefore, that the analyses have not led to absolutely conclusive results. Their great importance lies however in the fact that they have provided much new information on the relationships between the environment and the production of the palms.

While the yield figures from these experiments led only to a number of inexplicable and even contradictory conclusions, which could not be used as a basis for further work, the results of the detailed production analyses have opened a wide field for further research both in agronomy and in oil palm breeding. Such further research based on the theoretical conclusions of the production analyses will be reviewed in Part VI.

PART VI

Discussion of Practical Considerations and Further Research

The purpose of this final part is to illustrate how the results of the production analyses, presented in Parts IV and V, have influenced plantation practice and have transformed a largely exploratory research programme into an analytical one.

Plantation Practices

The positive effect of intercropping on yield in Experiment 33-1 and the depressive effect of October manuring in Experiment 3-3 have made it clear that the highest yields are not always obtained under the highest soil fertility conditions and that there may be important interactions between cultural measures and season. It is not surprising that in both cases the sex-ratio was found to be responsible for these unexpected effects. There is no reason, after all, why a monoecious plant such as the oil palm should necessarily react to improved fertility conditions by an increase in the proportion of female flowers rather than of male flowers.

We have seen, in fact, that while there are soil fertility factors, such as base exchange capacity, which in certain cases have a favourable effect on the sex-ratio, there are others, such as nitrogen, which seem to have a depressing effect upon it, in particular in the wet season. It is clear that fertilizer practice will have to be adapted to our knowledge of such relations. Great care with nitrogen applications would appear necessary, in particular as regards the timing of the application. At the W.A.I.F.O.R. Main Station for example, sulphate of ammonia is applied as a rule in the months of March, April and May only. Applications in other months are only permitted on an experimental basis. This measure merely constitutes a safeguard against possible negative effects of later applications on sex-ratio. A more positive application of the same principle may lead to a system of combined fertilizer and cultural treatments, aimed at reducing the nitrogen status of the soil in the wet season and increasing it in the dry season. The problem of planting distance is also involved, as a wider spacing with better access of sunlight to the palms is likely to raise the sex-ratio and to reduce or even eliminate any depressive effect of nitrogen.

These considerations have been taken into account in the designing of certain agronomic field experiments, dealing with widely different problems, which have been laid down recently in West Africa. Some examples are given below.

One of the most urgent questions being investigated is that of nitrogen manuring. This is covered by two experiments, one on mature palms and one on newly-planted palms. The former experiment compares four methods of nitrogen application with a control treatment. These methods are single heavy applications of sulphate of ammonia in April or in October, the same quantity applied in six doses throughout the wet season, and an application of the same amount of nitrogen in the form of urea in two doses in April and October.

While this simple experiment on mature palms is intended solely to provide an early answer to the practical question of the desirability of nitrogen manuring and its timing, the newly planted Experiment 33-9 has a more comprehensive design. It can be regarded as a repetition, in a more satisfactory form, of the Bunch Refuse Experiment (3-3) described in Part IV but with the possibility of separating the nitrogen effect from the effects of the other fertilizers. The factors time of application (April, October and April+October), addition of bunch refuse, and presence or absence of nitrogen in the fertilizer mixture are tested in a factorial layout. It is expected that this experiment will provide more reliable and more complete information on the interactions of these factors than could be obtained from the earlier Bunch Refuse Experiment.

The problems of intercropping and fertilizer application and their interactions are being fully investigated in the Planting and Farming Experiments, laid down at the W.A.I.F.O.R. Main Station and at the Substation in Abak in Eastern Nigeria in 1957 (W.A.I.F.O.R., 1957). The primary aim of these experiments is to investigate the possibility of planting palms with food crops on a more permanent basis, by adopting special spacings and by applying fertilizers to counteract the loss of fertility through cropping. In the experiments, the cultivation of food crops is carried out both during the establishment of the plantation and on a regular rotational basis between widely spaced rows of palms. In addition to these practical problems the experiment is designed to provide information on more fundamental questions, such as the interactions between intercropping (reduced fertility), manuring (increased mineral nutrition) and its timing, and spacing (variations in light supply and in root space per palm). A dry season cultivation has been incorporated to simulate the effect of cropping, i.e. the soil is kept more or less bare in the dry season with vegetation increasing in the wet season. The special spacings adopted are half and two-thirds density and they have been derived from the normal spacing by omitting every third and fourth row or every third row only. In the twin rows, so obtained, all palms receive as much light as outside row palms in ordinary plantings. It is therefore very likely that the yield per acre will be more than half or two-thirds of that obtained under normal spacing. The one or two row wide strips between the twin rows of palms are used for a more or less permanent system of farming. In the two-thirds density this farming cannot go on for very long, but it is nevertheless expected that both the arable crops and the palms will benefit from this system; the former because they have their own uninterrupted space and are suffering less from shade than under a system of prolonged intercropping among normally spaced palms, the latter because they receive more light and are subjected to a lesser extent to exhaustion of the soil immediately around them. This system can therefore be regarded as one of extended establishment intercropping. Food crops are grown for a longer period than is normal (or desirable) in establishment intercropping, but ultimately the land may carry palms only, which may well produce as much per acre as a normally established plantation.

The half-density spacing, on the other hand, is intended to make a permanent combination of palms and arable farming possible.

In the experiment the ordinary system of establishment intercropping for two years is also tested again, both in the normal and the twin-row spacings. A direct comparison of the effects of cropping within the rows of palms (for two years) or outside the rows of palms (for a longer period) is thus made possible.

One trial which has directly resulted from the production analysis described in Parts IV and V has been started recently. This trial is not primarily concerned with practical cultural treatments but rather with unnaturally drastic changes in the palm's environment. The exaggerated treatments, necessary to effect these changes, are intended to alter the growth and flowering to such an extent that the general inferences from earlier experiments, on the relations between flowering and environment, can be subjected to a more conclusive test.

The following six treatments are compared.

A. Control.

B. Reducing the number of active leaves to two-thirds of its normal number by repeated light pruning.

C. Heavy nitrogen dressing, combined with bunch refuse.

D. A combination of treatments B and C.

E. Opening a trench around the palms with a radius of 7 ft., a depth of 3 ft. and a width of 1 ft.

F. Trenching as in treatment E combined with light pruning (as in B) of the *surrounding* palms.

Additional dressings of sulphate of magnesium and of sulphate of potash are given to palms in treatments C, D, E and F, treatments which might otherwise induce deficiencies of K and Mg, thus confusing the effects of the main treatments.

It will be seen from the choice of treatments that they are intended to effect changes in the relative intensity of photosynthetic activity and mineral (in particular nitrogen) nutrition. The two extreme treatments are D, in which the assimilatory capacity is reduced by leaf pruning and the nitrogen nutrition is increased by heavy applications of sulphate of ammonia, and treatment F, in which the photosynthetic activity is likely to be increased by increased light intensity while the root activity is reduced by trenching. The other treatments are intermediate in their influence on the ratio between assimilatory activity and mineral nutrition. The conditions brought about by the treatments will be maintained for a period of one year; at the end of this period pruning and fertilizer application will be stopped and the trenches will be allowed to fill up again.

The experiment has been laid down on the plots of three progenies in a progeny trial planted in 1941. This has made it possible to test the effects of the treatments in palms with normal flowering habits (progeny I) palms with a very low sex-ratio (progeny II) and palms with a very high sex-ratio (progeny III).

Oil Palm Breeding

The amount of oil produced per acre is determined by the total weight of fruit bunches and the percentage oil to bunch. For the oil palm breeder the method of selecting for bunch yield does not present many problems, as the recording of palm yields and the selection of the most productive progenies and individuals is a relatively simple matter. The improvement of fruit and bunch quality, on the other hand, is a much more laborious undertaking which requires a great deal of analytical and clerical work. It is also known that the variations in bunch yield are much more extreme than the variations in fruit and bunch quality. While, in any sizeable field, palms can be found which are yielding 100-200% more than the field average, the maximum differences that can be expected in percentage oil to bunch are of the order of 50% only, within each fruit form, i.e. *dura* or *tenera*. Even if allowance is made for the effects of soil heterogeneity in the selection fields, it may well be expected that a selection on the basis of yields would lead to more spectacular results than selection on the basis of fruit and bunch composition.

The yield of the oil palm is however so much influenced by external factors, such as soil fertility and climate, that the value of palms selected primarily on yield is very uncertain, in particular when their seed is to be planted in areas which differ in soil and climate from the selection station. Fruit and bunch composition, on the other hand, are more independent of external conditions and can be used with more confidence as a basis of selection.

Selection on yield is of course particularly difficult when individual palms are compared but even when progenies are compared, in properly randomized trials, yield standards are set fairly low and the progenies for seed production (or breeding) are chosen mainly on fruit and bunch composition. More severe yield standards are only likely to be effective where the seed produced is planted locally. A progeny of exceptional productivity (i.e. giving proof of an exceptionally high production potential) may of course be chosen for further breeding, even when fruit and bunch composition are below average, but it would not be selected for extension work seed production.

It follows from the above that national or regional research institutes tend to concentrate in the first place on the improvement of fruit composition while in the selection fields of commercial plantation companies emphasis will be laid more on bunch yield. This situation has often led to disappointments and to the, sometimes justified, opinion among planters that their own planting material, however crudely selected, is preferable to the seed from a research institute.

The application of analysis of bunch production in breeding work may well change this picture fundamentally. It has been demonstrated in the preceding parts of this paper that the various production components are differenlty affected by changes in environment. It may therefore be expected that areas with conditions which adversely affect one or more production components, say leaf production or sex-ratio, should only be planted with palms in which these components are relatively high. So far only one factor has been recognized as being important for the adaptability of palms to marginal conditions (marginal as regards soil fertility, water or light), viz. the sex-ratio. Broekmans (1957) has already drawn attention to the better adaptability of progenies with a high sex-ratio to semi-arid conditions. The remarkable difference between the two progenies compared in the Burning versus Non-Burning Experiment 33-2 and in the Establishment Experiment 33-1 at the Main Station is an example of better adaptability to poor soil conditions of a progeny with a higher sex-ratio.

An example of the importance of a high sex-ratio under conditions of poor light intensity has been provided in a large Spacing Experiment at the W.A.I.F.O.R. Main Station (Expt. 22-1). In this experiment, which was planted in 1945, eight spacings are compared in twelve replications. Each replication has been planted with the selfed progeny of one *dura* palm and it is therefore possible to compare the reaction of palms of different genetic constitution to the planting density. Four triangular spacings were included in this experiment (21 ft., 25 ft., 30 ft. and 42 ft.). The differences between the progenies are so large that one is inclined to believe that the choice of a spacing for any planting should be determined in the first place by the characteristics of the planting material available.

In general a spacing of 21 ft. triangular has proved too dense but there is one progeny which continues to produce at a very high level under this spacing. While the yield per acre for 21 ft. triangular, averaged over all progenies, has dropped to 62% of the control (30 ft. triangular) in 1958 this one progeny still yields 16% more than the control. Here again it proved to be an exceptionally high sex-ratio which gave the progeny its ability to thrive under these adverse conditions. Such an ability may prove of great importance in future palm-grove improvement work where young palms will have to be planted in the shade of old wild palms.

Some general recommendations may be derived from our present knowledge of the relationships between progenies (or any other group of more or less uniform genetical constitution) and cultural treatments.

In the first place, agronomic experiments should be planted with seedlings grown from a representative mixture of seeds rather than with one or more known progenies. The results of the Establishment Experiment, described in Part IV, leave no doubt that more reliable results of more general applicability would have been obtained if a mixture of seed had been planted, instead of the two progenies which have shown such different reactions to the treatments. The same comment applies to the spacing experiment. Because each block has a different progeny and because there is a remarkable interaction between treatments and progenies the experimental error is greatly increased.

Progeny trials, on the other hand, should be planted at two different spacings and if possible cover different treatments or conditions in the different blocks in order to increase their general applicability. This is of particular importance for selection stations serving large areas, covering a wide range of conditions.

Introduction of selected palms into any new area should be preceded by a local test of some known progenies, to determine the type of palm most suitable to the local conditions. In such progeny trials it will be of particular interest to analyse the production and to compare the results with those obtained from the same progenies at the selection station. This procedure will indicate the major differences between oil palm growth and flowering in the two areas and the general characteristics of palms suitable for the new area. It has to be recognized, however, that the carrying out of such a programme, prior to introduction, makes the process of selection, breeding, testing and issue, a very long one. Until such accurate data on growth and flowering are available it is advisable, in any marginal areas, to plant only palms with a known high sex-ratio. To select progenies with a high sex-ratio it is of course not necessary to collect accurate data on flowering. It is sufficient to select those with a relatively high number of bunches.

There is a further problem in oil palm breeding which may benefit from the analysis of growth and flowering: the selection of the *pisifera* parent for the *dura*×*pisifera* cross. This cross is the most important source of seed as it produces a progeny composed entirely of *tenera* palms. The *pisifera* parents may be completely abortive ("sterile"), when only the male inflorescences develop normally; partially abortive, when some ripe fruits are produced occasionally; or fertile, when both male and female inflorescences reach maturity. The selection of abortive *pisifera* palms on the basis of yield or fruit composition is impossible and it is in any case not always certain whether an abortive palm is a *dura*, a *tenera* or a *pisifera*.

This makes it understandable why most oil palm breeders prefer to use, whenever possible, the relatively rare fertile *pisifera* palms, which have a measurable production and fruit composition, are of unquestionable fruit form, and are unlikely to pass on undesirable sterility factors to their progenies.

In view of the importance of the *pisifera*, a study of the nature of sterility and fertility in *pisifera* palms is urgently required. It is in this study that an analysis of growth and flowering is likely to play a predominant role. There are indications, for example, that sterility is not governed directly by genetical factors, as many workers believe (de Poerck, 1950; Henry & Gascon, 1950), but is simply a reaction by the palm to the very high sex-ratio and the low percentage inflorescence abortion (before anthesis) usually found in the "sterile" *pisifera* palm. This unusual combination of characteristics (high sex-ratio and low abortion) is responsible for the excessive number of female inflorescences commonly observed on "sterile" *pisifera* palms. The possibility that the "sterility" of the *pisifera* is in fact a form of bunch rot induced by excessive female flowering cannot be dismissed without serious investigation. Confirmation of this causal relation would necessitate a review of breeding policy. The sterile *pisifera* would no longer be considered as a carrier of undesirable sterility factors, but as a source of "high sex-ratio" factors which are often very desirable.

The results of the experiments discussed in Parts IV and V have demonstrated that it is possible to change the sex-ratio of a palm by cultural measures. If the relation between sex-ratio and sterility, postulated above, is a true one, then it must be possible to influence the sterility of the *pisifera* by cultural treatments. Investigations into these possible relations between sterility and environment have already been initiated. The analysis of growth and flowering will form an essential part of them.

A third genetical problem relating to the study of growth and flowering is the apparent relationship between sex-ratio and shell thickness. It has already been mentioned (p. 35) that the thick shelled *dura* palm has a lower sex-ratio than the thin shelled *tenera* palm, while the shell-less *pisifera* has usually a very high sex-ratio. There are, however, also indications that, within certain progenies, shell thickness is negatively correlated with sex-ratio.

In one progeny, planted at the W.A.I.F.O.R. Main Station and comprising 105 palms, the following relations were found between percentage shell in the fruit and sex-ratio.

Percentage shell	28-33—	Sex-ratio	56·0%
„ „	34-39—	„	54·9%
„ „	40-48—	„	49·1%

The 10% of the palms with lowest percentage shell had a sex-ratio of 63·9%. The 10% of the palms with highest percentage shell had a sex-ratio of 40·9%.

Considerably more data, relating to shell thickness rather than to percentage shell, will have to be collected before the existence of such a relation can be conclusively established. This work is of more than academic interest as it has some bearing on important practical problems in oil palm selection, e.g. the positive correlation between shell thickness and fruit to bunch ratio. Although this correlation is usually attributed to the higher density of the thick-shelled fruits, there are also indications that differences in the degree of fruit setting, in favour of the thick-shelled fruits, are partly responsible for the correlation. It would be interesting to know whether there are any relations between the shell thickness and the sex-ratio on the one hand and the sex-ratio and the degree of fruit-setting on the other hand.

The relationship between these three factors has recently gained added importance by the discovery that fertile *pisifera* palms appear to be related to *tenera* palms with exceptionally thick shells. It might therefore be suggested that poor fruit setting, sometimes leading to partial or complete bunch failure, and "sterility" are similar phenomena, being most serious when sex-ratio is high or shells are thin and being virtually absent when sex-ratio is low or shells are thick. In the *pisifera* palm the shell has not developed, but factors for shell thickness are nevertheless present and seem to influence the degree of fertility considerably.

This problem, which is at present being investigated at W.A.I.F.O.R., may well prove to be of great importance for the future of oil palm breeding.

The range of problems being studied on the basis of the results of only a few production analyses, make it clear that production analysis is of much more than incidental importance. It not only increases the value of the experiments to which it is applied but also provides a basis for further research. The scope of the present research work at W.A.I.F.O.R. on the agronomy and the breeding of the oil palm has been widened considerably by the application of production analysis.

SUMMARY

Part I

A brief outline is given of the development of oil palm research in Asia and Africa, as a background to the work described in this paper. The present study started as an attempt to test some suggestions by Beirnaert on the external influences determining sex in the oil palm. It has developed into a more general study of environmental effects, in particular the effects of cultural treatments, on sex-ratio and the other components of bunch production: leaf production, floral abortion, bunch failure and average bunch weight. The main object of this paper is to demonstrate the value of such analyses of bunch production for interpreting the results of field experiments.

Part II

A description is given of methods used in the quantitative assessment of the different components of bunch production. The problems connected with the summarizing and the statistical analysis of the data are discussed.

Part III

Normal variations in the components of bunch production under the influence of age, soil, season, climate and genetic constitution are described. Some of the data have already been published by Broekman but additional information is provided, in particular on the relationship between the production components and soil factors.

Part IV

As an example of a complete analysis of bunch production an account is given of the results of an experiment on various methods of establishment.

The yield figures indicate a positive, and in the early years significant effect of one treatment, continuous intercropping. The production analysis is intended primarily to investigate what is the origin of this unexpected result by examining, one by one, the separate production components.

It is shown that intercropping greatly stimulates leaf production in the years before flowering. In the later years the only production component which is favourably influenced by intercropping is the sex-ratio. This effect is however limited to one progeny and is markedly seasonal. This increase in sex-ratio is responsible for an increase in number of bunches in the intercropped plots in the same progeny and the same season, resulting in the positive overall effect of intercropping on yield.

A study of the various soil factors has shown that it is likely that the effect of intercropping results from a reduction in soil nitrogen. These findings together with Beirnaert's ideas lead to a new hypothesis on the relationship between the sex-ratio of the palm and its environment.

Part V

Three experiments are reviewed which provide additional information on the relationships between environment and the components of bunch production.

(*a*) A Pruning Experiment to test the effects of variations in light intensity in different seasons.

(*b*) A Manurial Experiment testing the effects of applications of organic manure (bunch refuse) or fertilizers at two different seasons.

(*c*) An Establishment Experiment similar to the one reviewed in Part IV but planted on a very much poorer soil.

The data provided by these experiments lend much support to the hypothesis developed in Part IV.

Part VI

The practical implications for oil palm plantation practice of the results of the above study are discussed. Some new agronomic experiments based on these results are briefly described, covering such problems as spacing, nitrogen application and the combination of palms and food crops.

Attention is drawn to the importance of production analysis for the study of breeding problems such as the selection of palms suitable for marginal conditions, the sterility of the *pisifera* palm and the relationships between shell-thickness and sex-ratio.

It is concluded that the scope of the present research work at W.A.I.F.O.R. has been widened considerably by the application of production analysis.

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