Newsletter BERITA ISOPB
THE INTERNATIONAL SOCIETY FOR OIL PALM BREEDERS
PERSATUAN AHLI-AHLI PEMBIAK BAIK KELAPA SAWIT ANTARA BANGSA

VOL. 5 MARCH 1988 MEMBERS ONLY NO. 1

EDITORIAL

The causal mechanism(s) of heterosis or hybrid vigour has been a subject of controversy (and of two books) for the past three to four decades and has yet to be satisfactorily resolved. In fact, a professor of plant breeding once quipped, "If anyone can point to the cause of heterosis, he probably deserves the Nobel Prize!". Despite this, the utilisation of this phenomenon in breeding and production of hybrid seeds and planting materials has been greatly intensified both in numbers and species and even encroaching into the sacrosanct area of self-pollinated crops.

The Dominance Theory stipulates that heterosis is a consequence of the complementary effects of dominant loci. Central to this theory is that hybridity or heterozygosity is not essential for the expression of hybrid vigour and that it is possible to isolate dominant homozygotes from the segregating F_2 equal in vigour to the F_1 hybrid. The F_2 distribution also should be skewed. The theory was extended to include linkage when failure to obtain superior dominant homozygote and skewed F_2 distributions were encountered.

From such experience in his maize experiments, Hull coined the term "overdominance", to the theory originated from East and Shull. In this theory, heterozygosity or hybridity is essential for heterosis and is due to the stimulating physiological effect of divergent alleles.

The Dominance Theory appeared to have more observational and experimental support. In his survey, Williams (I think) reported that most of the reported cases of hybrid vigour, could be accounted for by the complementary - multiplicative effect of yield components e.g. high fruit number in one parent and high fruit weight in the other parent, inherited from the parents in an additive or dominance manner. There was no place for overdominance. This was the contention of Sparnaaij and van der Vossen when challenging the "Inter-Origin Effect" theory for the oil palm by the IRHO group. Evidence from quantitative genetic theory and experiments also point to the dispersion of complementary genes. i.e. Dominance Theory, as the major cause of heterosis and that overdominance and epistasis play only minor roles. Recently, the late Professor Jinks of the Birmingham, reaffirmed this from theoretical considerations and from experimental data with experimental species. He suggested that there was little evidence of geniune overdominance, and reported cases of overdominance were pseudo-overdominance brought about by linkage bias and epistasis. He further added if this is brought to the logical conclusion, it is possible to extract dominant homozygotes equal and possibly better than the F^1 hybrid. This recombinant inbred variety approach has been suggested and are being attempted for some cross-pollinated annual species, and has also been recommended for the oil palm by Dr. Lawrence when he was visiting PORIM a couple of years ago. (The feature article in this Newsletter addresses this issue). In fact Professor Jinks was suggesting using breeding methods for self-pollinated crops in cross-pollinated crops in direct opposition to the hybridists who are suggesting the other way round.

On the other hand, molecular geneticists and physiologists are rather uncomfortable with the biometrical approach, especially for traits which are far removed from the site of gene action, and have sought a molecular or biochemical approach. Indeed there have been evidence of e.g. hybrid enzymes, organelle (mitochondrial, chloroplast) complementation in heterotic hybrids. While this does not prove overdominace because overdominace does not exist at the biochemical level, it does show that hybridity or heterozygosity is associated with heterosis. Similarly the existence of polymorphic species in many natural populations has been attributed to heterozygote advantage or overdominance for fitness by population geneticists.

To the practical breeder of cross-pollinated crops the Overdominance - Dominance controversy is perhaps academic or secondary. What he's concerned with is how he can manipulate this heterotic response into his commercial seeds in the shortest time. The obvious way is by F_1 hybrid production, which produce plants not only with superior yields, but also of uniform quality and stability of performance. Why wait until the F_5 of F_6 before you know you have obtained the inbred variety equal or better than the F_1, when you can exploit the heterotic F_1 straight away? This is an important consideration when dealing especially with a perennial tree crop such as the oil palm.

Feature Article:

Recombinant Inbred Lines of Oil Palm?

1. Recombinant Inbred Lines

Though recombinant inbred lines usually mean the F_5 or F_6 families derived by selfing an F_2 of two different parental lines, the term may be applied generally to include any line that arises from recombination events in the early generations followed by fixation. This would include, for example, dihaploids, especially of F_5's anf F_3's, besides the familiar end-products of pedigree and single-seed descent breeding of self-pollinating crops.

Recent developments in biometrical genetics suggest that recombinant inbred lines which are superior to F_1 hybrids may also be obtainable in out-crossing species. Obviously, such a suggestion must contain an explanation of heterosis, the *raison d' etre* for producing hybrids, and show that the obverse phenomenon, inbreeding depression, is not an inevitable concomitant of selfing out-crossers.

2. The Biometrical Genetics Explanation of Heterosis

Heterosis is defined as the superiority of the F_1 over the better parent, P_1 or P_2 depending on whether the increasing or decreasing expression of the character is desirable.

Using the notations of biometrical genetics the mean of each of the two inbred parental lines and of their F1 hybrid may be expressed as follows:

$P1 = m + d$ where $m = 1/2\,(P_1 + P_2)$
$P2 = m - d$ $\quad d = 1/2\,(P_1 - P_2)$
$F1 = m + h$ $\quad h = F_1 - m$

Heterosis will be observed when $h > d$, the actual magnitude being $h - d$ for positive heterosis and $h - (-d)$ or $h + d$ for negative heterosis. Since h and d are cumulative values of effects at each of k loci, where k is much larger than Mendelian numbers, heterosis would occur if the majority of loci show dominance deviations of the same sign i.e. there is net directional dominance. It follows that there will be maximum heterosis when the dominance deviations at k loci are all of the same sign (unidirectional dominance) and, conversely, none when the deviations at some loci cancel those of the opposite direction of others (ambidirectional dominance).

Where non-allelic interactions do not contribute an apparent dominance, one further condition must be met for heterosis to occur. Either there is net overdominance, or the alleles that are dominant, completely or otherwise, are dispersed between the two parents. The distinction between these two explanations of the origin of heterosis is a fundamental one. The first assumes that some genes exhibit overdominance, a property intrinsic to these genes in the heterozyous state, whereas the second, more recent argument suggests that the genes for favourable effects, distributed over both parents, become united in the heterotic F_1.

The implications are immediately obvious. If the latter were indeed true it should theoretically be possible to recover recombinant inbreds which either equal the F_1 or even surpass it, depending respectively on whether dominance is complete ($h_i = d_i$) or incomplete ($h_i < d_i$). If, however, true overdominance does exist no combination of favourable genes in recombinant homozyotes could exceed their performance in the heterozygous condition.

Clearly, the direct test of the two interpretations would be to see if superior inbred lines could, in fact, be extracted from a heterotic F_1. They have been obtained in *Nicotiana rustica*, the most extensively studied in this respect, but otherwise there have been few experiments of this sort as the theory is relatively recent and producing inbred lines takes time. Work with other sepcies is in progress.

There is also, however, an indirect test for which results from more crops are available. In the absence of significant epistasis, linkage disequilibrium and G x E interactions, estimates of D (additive variation) and H (dominance variation) may be used to derive the dominance ratio $H/D = h_i^2 / d_i^2$. In theory, this ratio is zero when there is no dominance, between zero and one for incomplete dominance, equal to unity for complete dominance and larger than unity if overdominance were present. Estimates for diverse characters in a wide range of crops have generally given values of less than unity. Moreover, even in the few exceptions where overdominance was detected it could have been spurious as the mating designs employed did not rule out epistasis and linkage disequilibrium.

Developments in biometrical genetics, meanwhile, have shown how the properties of recombinant inbred lines may be predicted from basic genetic parameters which could be estimated in the early generations. Triple test cross families provide the best estimate for this purpose and, more over, allow detection of non-allelic interactions and linkage disequilibrium. The effects of these complications on the estimates and predictions are clearly explained.

3. Inbreeding Depression

The classical explanation of inbreeding depression is that it is due to the homozygous fixation of deleterious recessive genes which in heterozygotes, are suppressed by their 'wild-type' alleles.

Theoretical arguments, supported by empirical observations, however, now suggest that inbreeding depression would only occur if there were at least some non-additive gene effects in the desired direction for the character in question. In may be easily shown, for example, that the mean value of a character completely determined by additive gene effects will not change from generation to generation. Recessive genes, deleterious in the homozyous state, may well be present but, in the modern view, as a subset of the genes determining the character.

Since selection increases

the frequency of the genes contributing to the desired effect, some of which contribute non-additively, it is not surprising that the larger the response to selection the greater is the depression upon inbreeding. This, perhaps, explains why the depression is so manifest where highly bred varieties are first selfed.

4. Recombinant Inbred Lines of Oil Palm

Returning to the title of this article we must first consider a very important character of the oil palm. Current planting materials are all monofactorial hybrids for shell thickness and, since the shell thickness gene does not appear to be a linked complex separable through recombination, inbred lines of *teneras* would be very expensive to produce; 50% of the selfs being *duras* and *pisiferas*. Furthermore, even if we do obtain superior F_5 or F_6 *tenera* lines, their multiplication to commercial quantities could only be by tissue culture. Hence, it would be prudent to first predict, using F_2 triple test cross or F_3 family information for example, the likely gains in deciding on such a costly programme. It may be noted that a secondary benefit of inbred lines, the farmer not having to pay dearly for hybrid seed, is less applicable in the oil palm as planting material cost is an insignificant fraction of total cultivation costs.

The potential of recombinant inbred lines of *duras* in commercial planting depends on the extent to which the shell can be reduced. Examples of *duras* indistinguishable from *teneras* in shell thickness are known, but all in the thicker half of the *tenera* range. Obviously, the above proposition cannot be viable unless the gain in yield from other causes exceeds the loss due to a thicker shell.

Recombinant inbred lines aside, the method of single seed descent is, nevertheless, a convenient technique for rapidly producing inbred lines of *duras, teneras* and *pisiferas*. Some savings could be achieved by planting palms closer as one early inflorescence from each palm may be sufficient for its next generation seed. Similarly each palm could be replaced by one of its selfs, as soon as available, at the same planting point.

Rao, V. PORIM

NEWS

Commodity News

India: Palm Oil Imports

India imported 1.18 million tonnes of palm oil in 1986. 1987 import was expected to be around 1.35 million. Total oil imports for 1988 is expected to exceed 2 million tonnes.

Indonesia: Target Shortfall

Indonesia is expected to achieve half of the planned target of tripling oil palm plantation area to 1 million ha by the end of 1989. Only 7 or the 47 companies that had originally applied for new plantation licences had started operations, but a further 7 would soon be given licences. The government provides each firm with 100,000 ha under its nucleus estates scheme, where smallholders take 60% of the area and sell output to plantation companies. Land titles previously granted for 35 years could be extended for another 25 years. The new measures also entitle investors credit to develop smallholder plots while duties on imported capital goods are waived. But the new measures floundered on the high cost of bank loans, averaging 20% last year.

China: Palm Oil Imports

Palm oil imports into China have increased rapidly in recent years as a result of its open policy and rising living standards. Palm oil imports as per statistics in Singapore, Malaysia and Hong Kong were 16,000 tonnes in 1985 and 185,000 tonnes in 1986. In 1987 palm oil imports were estimated to be about 300,000 tonnes of which about 50% was used for edible purposes (mainly instant noodles) and 50% for non-edible purposes (mainly soaps).

Nigeria

Nigeria will make large quantities of high yielding and disease resistant hybrid (D x P) seeds of oil palm available between 1987 and 1990 to promote the country's palm oil production.

NIFOR is expected to produce 8 million germinated seeds.

United Kingdom: Soya Ink

The Newspaper Publishers' Association of U.K is developing and licensing a new formula for newspaper ink that uses soya bean oil as the main ingredient. Printing ink could use up to US$525 million of soya bean oil annually if tests now underway continue to look promising.

U.S.A.

Senate Amendment Bill

The U.S. Senate Agriculture Committee on October 20, 1987 has rejected the proposed amendment requiring palm, palm kernel and coconut oils to be labelled as "saturated fats" when included in processed foods. The amendment was sponsored by a senator on the grounds that it would save American tax payers US$83 million and in reducing heart disease. In opposing the amendment, the speaker for the administration cited the letter from the U.S. Trade Representative attacking the amendment as a non-tariff barrier. The bulk of soya oil consumed by the Americans was hydrogenated thereby increasing its saturated fat level and yet only tropical oils were singled out as deserving labelling. He concluded by saying that "The Administration was of the opinion that the main objective of the proposed amendment was to protect the domestic soya bean industry through legislation disguised as a health measure".

ISOPB

ISOPB with the cooperation of Marihat Research Station, is organising a one day seminar "Improvements in Oil Palm Breeding Populations" in Marihat to be followed by visits to oil palm research stations in Indonesia, from November 24 - December 1. Interested members are asvised to contact Dr. Rajanaidu, ISOPB Secretary quickly.

The proceedings at the ISOPB Workshop "Breeding and Selection for Clonal Oil Palm" are available for sale to ISOPB members at a concessional rate of M$10/- (US$4/-). Please place your orders with the ISOPB Secretary. The proceedings on the ISOPB Workshop on OxG hybrids will be a bit delayed and will be expected to be out before end of the year.

PORIM

This year has seen the exit of an invaluable scientist in the Malaysian oil palm industry - Dr. H.L. Foster - after a service extending back 15 years.

Dr. Foster was initially invited to review the results of all the fertilizer trials run by individual organizations by the consortium partners of OPGL (Oil Palm Genetics Laboratory) in 1973. The requirement was for a person experienced in the analysis of data from fertilizer trials but totally new to oil palm and thus unprejudiced by established concepts and ideas.

The choice fell on Dr. Foster because of his extensive experience on fertilizer trials on field crops in Uganda. He was therefore appointed Senior Research Fellow in MARDI funded by ODA (Overseas Development Administration of U.K.).

His first tour of duty lasted until 1976 during which time he extensively analysed data from 34 NPKMg trials. On completion of this task, he returned to the UK to rest and recover for a year waiting further calls to duty. MARDY (Malaysian Agricultural Development and Research Institute) engaged him to work on fertilizer trials on field crops in 1977.

In 1981, he joined PORIM as a Senior Research Fellow and for the next years went about analysing and examining all the available fertilizer trials in Malaysia, to determine the yield potential and fertilzier requirements for the various oil palm growing areas. His job was almost done, when he terminated his position in March, 1988 and took up his new assignment in Papua New Guinea as the Director of the Oil Palm Research Association.

Dr. Ian E. Henson joined PORIM as a Senior Research Fellow in March. His job is to look into photosynthesis and productivity of the oil palm.

Curriculum Vitae	Year
BSc - Botany - University of Durham UK	1971
PhD - Botany - University College of Wales Aberystwyth UK *(Flowering and Plant Hormones)*	1974
Post- Doctoral Fellow Department of Botany University of Glasgow UK *(Root nodules and plant hormones)*	1974-77
Employed at: Plant Breeding Institute, Cambridge UK including oversea work at ICRISAT, Hyderbad, India *(Abscrsic acid, water relations of pearl millet and rice)*	1978-84
CSIRO Western Australian Laboratories, Perth, Australia *(Water relations of lupins and wheat)*	1985-87

REFERENCES OF INTEREST

THE EFFECT OF PALM AGE AND PLANTING DENSITY ON THE PARTITIONING OF ASSIMILATES IN OIL PALM (ELAEIS GUINEENSIS)

By C.J. BREURE

Dami Oil Palm Research Station, Kimbe,
West New Britain, Papua New Guinea

(Accepted 23 April 1987)

SUMMARY

Yield and growth records from an oil palm planting density experiment, comparing 56, 110, 148 and 186 palms ha^{-1} and a progeny experiment, planted at 115 and 143 palms ha^{-1}, were used to estimate the partitioning of assimilates into those used for structural dry matter (DM) production, and those used for growth and maintenance respiration.

Gross photosynthetic assimilation (A) for closed canopies was estimated from absorbed photosynthetically active radiation (PAR), derived from actual sunshine hours, and the assimilation-light tesponse curve, to be 128 t CH_2O ha^{-1} year^{-1}. A for non-closed canopies was calculated by correcting for the degree of light transmission, which in turn was estimated from recorded leaf area index values (L), i.e. the total leaf area per unit ground area.

Forty-eight percent of gross assimilation was used for DM pro-

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duction, about half of this being lost in growth respiration. The remaining 52% was lost in maintenance respiration. These losses appeared to level off before crown expansion was completed, and since trunk biomass continued to increase, maintenance respiration per unit biomass (R) decreased with age.

An increase in planting density reduced the assimilates available for bunch DM, had little effect on those for vegetative growth, but strongly reduced maintenance respiration and, since biomass was little affected, reduce R. Assimilates for bunch DM ha-1 reached a maximum at L = 5.6.

The observed trends in R as a function of palm age and planting density merit further study.

THE EFFECT OF DIFFERENT PLANTING DENSITIES ON YIELD TRENDS IN OIL PALM

By C.J. BREURE

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(Accepted 3 March 1987)

SUMMARY

Sixteen years' yield and growth data from an oil palm planting experiment, comparing 56, 110, 148 and 186 palms ha-1, and additional records from a progeny experiment, were used to study the effect of palm age and planting density on carbohydrates incorporated in total above ground dry matter production per palm (TDMc) and its components: fruit bunch yield (Yc) and vegetative growth (VDMc). The canopy efficiency (e), the amount of carbohydrate incorporated in dry matter production per unit of absorbed radiation per hectare, decreased from the fifth to eighth year then levelled off, but increased once crown expansion was completed. The decrease in e paralleled the expansion of the intercepting leaf surface, and might therefore be linked to an increase in maintenance respiration losses. These losses were apparently not compensated for by an increase in photosynthetic production. The subsequent increase in e in older palms appears to have been due to improved light distribution as a result of an increase in light penetration. The effects of changing levels of light interception and distribution on e were more pronounced at higher density, and resulted in marked differences in changes to TDMc with age between densities. Corresponding differences occurred with Yc, so that the optimum density for current yield decreased until 12 to 13 years from planting, then markedly increased. These findings are discussed in relation to the measures which might be used to increase yield per unit area.