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GENOTYPE - ENVIRONMENT INTERACTION STUDIES IN PERENNIAL TREE CROPS

**Proceedings of the 1991 ISOPB International Workshop on
Genotype - Environment Interaction Studies in Perennial Tree Crops**

**12 - 13th September 1991
K.L. Hilton, Malaysia**



Organised by :

International Society for Oil Palm Breeders

with cooperation from :

Palm Oil Research Institute of Malaysia

The British Council

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(PORIM)*



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Genotype x Environment Studies in Perennial Tree Crops



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PREFACE

Genotype - Environment (GE) interactions, the differing responses of different genotypes to changes in their environment, are important to plant breeding. If such interactions are present, breeders may choose to negate them by breeding varieties of broad adaptability or exploit them by tailoring specific varieties to specific environments for maximum performance.

The biological, statistical and genetical aspects of GE interactions have been well established. Indeed GE studies are quite routine in varietal evaluation of many annual crop species. But such studies are few and sparse in tropical perennial tree crops due to an overall small research effort, the long immature period of these crops, a lengthy period of data collection and their large size. It was hence even more important that what little has been done to date should be reviewed and the work collated and discussed.



APPRECIATION

The International Society for Oil Palm Breeders (ISOPB) and the Organizing Committee of the Symposium wish to thank The British Council for sponsoring the visit of Prof. P.D.S. Caligari of the University of Reading.

We also wish to record our appreciation to Chairmen of Sessions, authors of papers and others who have given encouragement, support and assistance to the Organizing Committee of this Symposium.

Dato Dr. Hj. Abdul Halim bin Hassan
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WELCOME ADDRESS

by

Dato' Dr. Haji Abdul Halim Hassan

President,

International Society for Oil Palm Breeders

The Chairman, Palm Oil Research and Development Board, Malaysia

The Representative of The British Council,

Ladies and gentlemen.

Firstly let me rightaway thank En. Mohamad Said bin Mohamad Ali, the Chairman of the Palm Oil Research Institute of Malaysia (PORIM) for consenting to declare open this workshop. As in the past PORIM, as co-organiser, has lent considerable support to the success of this workshop.

I would also like to place on record the assistance of The British Council who have sponsored the visit of Professor Peter Caligari of the University of Reading. Special thanks to him, Prof. Manjit Kang of Louisiana State University and Prof. Yamada, presently with Universiti Pertanian Malaysia, for consenting to deliver key papers.

The International Society for Oil Palm Breeders is a relatively young organisation, being registered in Malaysia in 1983. The main aim of the Society is to advance knowledge of oil palm breeding through international cooperation. In this short period the Society has organised a number of international workshops, symposia, colloquia, courses and visits. The Society also publishes a newsletter twice a year.

Some of the workshops, symposia and colloquia are as follows, the proceedings of most of which have been published.

1985	Workshop on Oil Palm Germplasm and Utilization
1986	Colloquium on Breeding and Selection for Clonal Oil Palms
1987	Workshop on Prospects of Interspecific Hybrids
1988	Workshop on Progress in Oil Palm Breeding Populations
1989	Symposium on application of Statistics to Perennial Tree Crops Research
1989	Course on Statistics for Perennial Tree Crops Research
1990	Workshop on Yield Potential in the Oil Palm

As seen from the above the Society has been holding one or more event almost every year. This obviously would not be possible without the dedication and hard work of the various organising committee and your continued support.

I would like to close by recording our appreciation to the Chairmen of sessions, authors of papers and others who have given their assistance in the organisation of this workshop.

OPENING ADDRESS

by

En. Mohd Said Bin Mohd Ali

Chairman, Palm Oil Research and Development Board, Malaysia

Yang Berbahagia Dato' Dr. Haji Abdul Halim Hassan
President of the International Society for Oil Palm Breeders,
Representative of The British Council,
Honoured Guests & Speakers,
Ladies & Gentlemen,

I thank the ISOPB for inviting me to open this Symposium on Genotype - Environment Interaction Studies in Perennial Tree Crops. This is the second time that I have been invited to perform such a job for ISOPB. In 1989, only a few metres from here, it was the ISOPB Symposium on Application of Statistics to Perennial Tree Crops, also held in conjunction with a PORIM International Oil Palm Conference. In that Symposium, specialists deliberated on the best statistical approaches to objectively evaluate the effects of agronomic and breeding treatments in field experimentation of tropical perennial crops. This is an important and fundamental part of agricultural research and has and will contribute greatly to the development of improved agronomic practices and varieties through the years.

Today's symposium topic is an extension of the same theme using statistics as a tool in resolving an important question to growers and researchers alike: "Should the variety that has done well over there also be planted here, or vice versa, and should we in any case do it the same way?" Enmeshed in this deceptively simple question, are a host of related questions:

1. Do different varieties perform differently in different environments?; which may, to our dismay, beg the further question "how different are the varieties and environments anyway?"
2. Are there varieties which perform well in all environments i.e stable varieties, or are there likely to be varieties which perform well in certain environments, being specifically adapted or bred for such environments.
3. Do different varieties require different agronomic or management inputs such as planting density and amount and types of fertilizers for maximum production?

In attempting to answer these questions of the grower the practical breeder is confronted with many problems in the minutiae of methodology - how does one measure stability and is it a heritable trait; what sort of environments would usefully discriminate varieties and are these environments realistic; should they be a random subset or specifically chosen. And, as always, the questions of costs and efficiencies - should adaptability trials be conducted at the end of a breeding programme or at the start, two approaches with very divergent implications; and which is more efficient in a particular context, breeding for stable varieties or varieties with specific adaptation.

Three keynote speakers and 15 papers, the fare for this Symposium, will doubtless provide some answers and guidelines to these difficult questions.

Prof. Peter Caligari from the University of Reading is I am told an old familiar friend in the world of GxE. A student of the late Prof. Mather and Prof. Jinks he was in the thick of it as the genetical basis of GE was being unraveled at Birmingham. We are fortunate to have him give the keynote address this morning. And on behalf of the ISOPB and this Symposium I would like to thank the British Council for sponsoring his visit and stay in Malaysia. Prof. Manjit S. Kang from Louisiana State University, who has also been looking at GE from various angles, will speak on some of the issues in GxE interaction. By fortunate circumstances we also have Prof. Yukio Yamada of Japan, presently at Universiti Pertanian Malaysia. He will enlighten us on the analysis and interpretation of GE interactions in the context of animal breeding and husbandry, the former not all that distant from some perennial trees.

I find it particularly interesting that the 15 papers, though covering a wide range of crops - oil palms, rubber, cocoa, coconut, cassava, tea, papaya, pineapple and a forest species - all discuss the important breeding issue of GxE interactions.

With such an appealing fare, I must round up my speech, but let me first commend ISOPB for its leadership in organising this timely and useful Symposium. Timely because many of us are at the stage of agricultural development where as producers we would want to maximise profits from our agronomic inputs and as scientists, we would want to support this effort with the identification and recommendation of the best variety-agronomic input combination.

The issue of genotype-environment interaction is of interest and concern not only to oil palm scientists but to all crop scientists. Appropriately, ISOPB has extended participation to other crop scientists and I once again commend them for their leadership and vision.

I now have the pleasure to declare open the International Symposium on "Genotype x Environment Studies in Perennial Tree Crops".

GxE STUDIES IN PERENNIAL TREE CROPS:

Old, familiar friend or awkward, unwanted nuisance?

by

P.D.S. Caligari¹

ABSTRACT

Genotype environment interactions (GxE) have been recognized as existing for quite a long time, but their importance in particular circumstances and the ways of handling them are still matters of discussion. I would like to highlight four main aspects and make brief comments about each. The aspects are: Assessment, Biology, Genetics and Exploitation. I will not try to provide a balanced view of all these aspects but instead to highlight particular points concerning them in the hope that they will stimulate thought and discussion within the whole subject area of GxE. Any discussion about assessment obviously includes the statistical and analytical aspects, while under the heading of biology I will try to indicate our need to look more closely into the underlying responses, including physiological, to environmental factors. I will also try to point out the need and benefit from considering the genetical control of environmental response if we are to manipulate it efficiently and successfully. Lastly I will briefly mention the possibilities to exploit GxE, particularly in breeding programmes and suggest a way of incorporating selection for environmental response into such programmes.

INTRODUCTION

I must start by confessing that I have no really clear, general views about GxE in the context of Plant Breeding, either in terms of how it should be handled or viewed. I suspect this reflects somewhat loose thinking on my part but also simply the state of the subject at present. There are, therefore, no complete answers in this presentation in terms of how GxE should be handled in a plant breeding context nor is there any attempt to give a view of an idealised breeding scheme. More accurately it will simply contain a few thoughts concerning GxE interactions which might help stimulate active thought and debate.

It is possible to consider GxE interaction under four main headings and these are:

- (i) ASSESSMENT: in other words, the design of experiments, statistical assessment, particularly including the type of analysis and presentation.
- (ii) BIOLOGY: can we define more clearly environmental effects of importance; can we say anything about the physiology, etc.
- (iii) GENETICS: in other words to consider how GxE interactions are genetically controlled and determined; hence the scope for their manipulation in breeding.

and (iv) EXPLOITATION: This will clearly involve, and be reliant upon, (i), (ii) and (iii) above but will also require wider considerations, for example the use and potential range of exploitation for material emanating from a breeding programme - but for this we need to be able to breed clones with particular GxE characteristics.

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I will now briefly consider each of these in turn.

ASSESSMENT

We start with ways of assessing GxE interactions, in other words the detection, quantification and visualisation of the interactions that we are considering.

Everyone accepts that GxE interactions are taken to be the differential response of genotypes to variation in the environment. But it is necessary to be clear about what is really being considered, especially when, for instance, considering GxE in the context of breeding. Looking at the literature reveals a number of reports describing GxE but referring to a change in rank order of genotypes as the criterion for their presence. A simple graphical representation, such as that given in Figure 1 can be considered. The Figure shows a very simple situation of two genotypes and two environments. In the first case (1), everybody would agree that the environments have effects but the genotypes respond uniformly; i.e. no GxE. In the second (2), the genotypes respond differently to the environmental differences but maintain their rank order; i.e. GxE present but rank order maintained over the limited environments studied. In the last example (3) is a clear case that would be accepted by all, of GxE being exhibited. In the context of a research programme it could be suggested that for (2) a simple change of scale for the character would remove the supposed interaction. In plant breeding this is often not appropriate - farmers and growers do not generally appreciate the niceties of transformation when it comes to establishing profit margins! In other words, we must be ready when we are dealing with crop plants to face (2), if necessary. In any case, if observations were made in another environment it would clearly be possible for genotypes **A** and **B** to change their rank order.

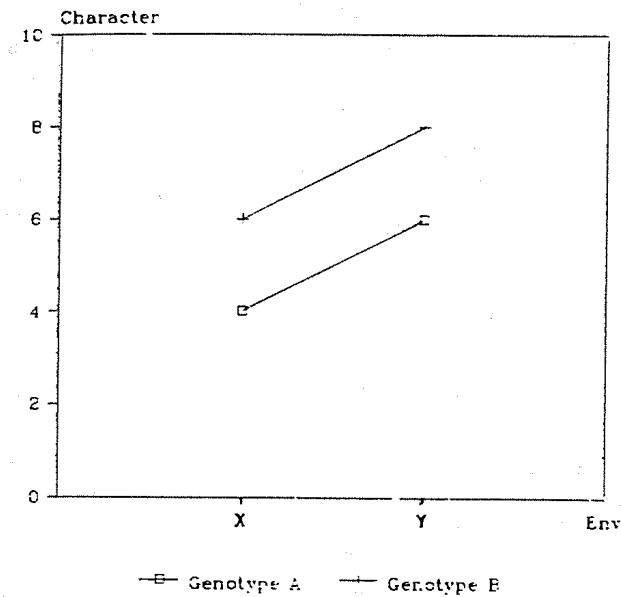
The example was chosen deliberately to have just two environments, so that there was no need to consider the question of whether to take a linear regression approach in the analysis. However, in reality the situations that are to be examined are more complex and often involve several factors such as both sites (or locations) and seasons (or years). Over the last 30 years many forms of analyses have been proposed to help in the examination and interpretation of data from such complex trials. These have included simple analyses of variance, linear regression, principal component analysis, cluster analysis, ranking, and other non-parametric tests. It is clear that, as in all situations, none of the approaches provides a universal answer but all will be useful in some circumstances.

The approach, however, that has most frequently been favoured, and often returned to, is the linear regression analysis. It has an inherent appeal, it provides a visual representation and readily provides a summarising overview - i.e. it is conceptually attractive. The approach was pioneered in 1938 by Yates and Cochran, modified in 1963 by Finlay and Wilkinson, refined by Eberhart and Russell in 1966 and given genetical credence by Perkins and Jinks in 1968. The approach is basically empirical. Who would have predicted that plotting genotype responses onto environmental effects, derived as overall line means, would give linear regressions? Why should they? What does it imply, other than additivity in a statistical sense (which we should carefully distinguish from genetical additivity)? Do the slopes measure useful parameters in terms of breeding? Are the residuals significant? If so what do they tell us?

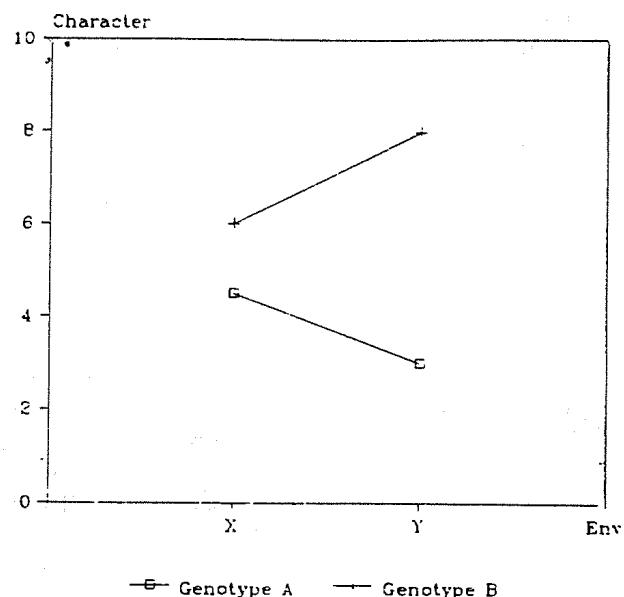
These are questions that really need to be asked. On the one hand, it is easy to be cynical and simply dismiss the approach entirely but just as easy to blindly apply textbook methods because they seem to be appropriate to our own data set (and the use of computers has made this an even more attractive path to follow). In reality, it is clear that we need to look at the objectives we have set out to achieve, design experiments on that basis (bearing in mind the biology etc of our particular species) and then analyze the data accordingly. Clearly if repeats of trials performed, as with perennials, and assessments are carried out over many years, it may well be sensible to apply the same analysis over and over again, but even so it must not be taken for granted that the same standard approach will be applicable.

FIGURE 1

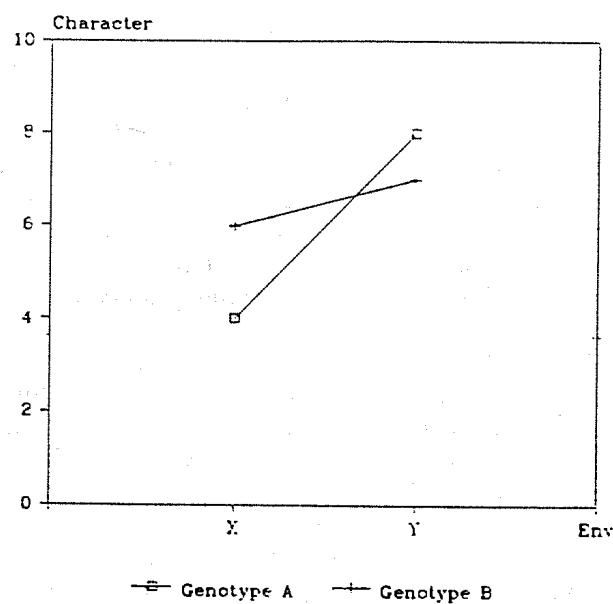
1. No interaction –
no change in rank



2. Interaction –
no change in rank



3. Interaction –
also change in rank



Three simple, theoretical examples of responses to environmental differences

BIOLOGY

So leaving the complex, intriguing and important area of assessment somewhat 'up in the air', attention can be turned to briefly consider some of the aspects of biology which are sometimes lost in a concern for getting the statistics and analyses carried out. In other words, consideration of what I have loosely called "biology". This, in fact, covers the biology of the species under study but also the environment in which it finds itself. The first question that can perhaps be asked is whether we should be using the simple mean of the trial entries as our measure of the environment? It is a biological measure, but it is a "black-box" approach to environmental variation. It is obvious that years are different in terms of many climatic factors, sites differ in terms of fertility, drainage, soil type etc, trial sites vary in management practice, aspect, etc, while plots vary in a "finer grained" way and the position of plants at an even more micro-environmental level. In some ways by posing the question we provide a partial answer. There are so many possible environmental factors the experimenter feels forced to adopt an "all encompassing" approach or risk being swamped trying to handle an infinite number of variables. This is true but is it the whole picture? Could not this also have been the cry of those who tried to handle quantitative genetics before the publications (Fisher, 1918) of Sir Ronald Fisher?

Clearly there are numerous environmental factors which all join to act on the genotype in order to produce the observed phenotype. But this should not necessarily prove to be totally daunting. Clearly it may not be possible to handle all of them simultaneously, indeed it may be a distraction from a main goal if it is tried. But first it should be decided what the aims are. Secondly, if there is more than one aim, whether this implies different approaches, and thirdly, are there obvious environmental and physiological variables to be investigated and exploited? Professor Sir Kenneth Mather (pers. comm.) propounded the view that in many ways, in GxE situations, the two axes of genotype and environment should be handled similarly and with equal detail. An overall, standard analysis was a good starting point but then, by use of experimental designs the structure should be "dissected" and the underlying determinants investigated on both axes. In other words, there is a tendency to concentrate thoughts, analyses, and theorising on the genotype axis. Which genotypes are stable?, unstable", non-linear? etc. But the other axis is also amenable to similar treatment. Maybe the responses should be considered more carefully from the point of view of which environments produce what sort of variation in response, etc.

It is difficult to be specific about general biological factors as it is obvious that the factors will be dependent on the crop species, the aims for its growth and use, etc. So, by taking some very simple examples from one clonally reproduced crop, potatoes, which is certainly not a tree crop, will allow more general points to become apparent. Reviewing a number of these:- potatoes can grow in both temperate and semi-arid conditions. These give very different environments which can range from the Negev Desert to the wettest season in Britain! These could (and possibly in some circumstances probably should) be handled by a GxE approach but in other circumstances they would often be handled as specific sites, or targets, for breeding, selection or variety assessment. The results might well be viewed jointly but it would not simply be accepted that all the data were pushed together from trials in these regions and blindly used to obtain an overall and simplified answer from one single analysis.

Season can often be thought of as similar to the above. For example, in field trials run in Mediterranean countries the main growing seasons are subject to average spring and fall temperatures which are very similar but, as far as the plant is concerned the pattern of temperature is completely reversed with temperatures being near opposite extremes at each end of the growing cycle ((Nachmias *et al.*, 1988). This also applies to daylength and other environmental factors!

In addition, in commercial terms, the industry is looking for cropping in different periods of time. Potatoes are grown for very early cropping, mid-season or main crop perhaps harvested at 80, 100 and 120 days respectively (depending on area etc). Are these to be treated as one group or separately? It would be possible to treat them as one, but in reality the expectations and requirements in terms of texture and storage ability are very different; in other words consumer preference is different.

Stress tolerance/susceptibility is another aspect of a plant's response which is commonly included within various descriptions of GxE experiments/trials. Low yielding sites are often said, quite rightly, to have suffered stress. This is often true but if stress is likely to be a serious factor it should be examined in a defined way; i.e. investigating which stresses are important, how genotypes specifically respond to them and if responses to different stresses are correlated or independent. In potatoes it is possible to detail a number of stresses including: salinity, drought, flood and temperature (cold or heat). Clearly not much imagination is needed to start providing some obvious factors to study - at least initially.

Similarly, disease can be seen very much in the same way as stress is. Unless care is taken it will simply be "pooled" into an environmental effect especially if it is a disease that is not clearly visible and identified in the trials carried out.

In other words, the standard GxE analysis is useful and powerful and has a definite role to play but it should not blind us into ignoring obvious factors that should really be handled as separate entities. Some of the time it is necessary to sweep up environmental factors into our single "black-box" and handle them as one undefined mass but care should be taken not to lose sight of the need to delve within the box and identify, investigate and understand as many components as possible. It is likely that this will require the help and input from people such as physiologists, biochemists, soil scientist, meteorologists etc. It would seem that the true desire for this multidisciplinary approach, which must be essential in the longer term, has been really somewhat minimal up to present.

GENETICS

Turning attention to consideration of the genetical elements of GxE, if the environmental sensitivity of genotypes can be measured or assessed then it should be possible to study the genetics of this attribute as a character in its own right and find ways to manipulate it successfully. This element, i.e detailed genetics not simply regarding the genotypes, has been somewhat neglected; therefore the potential to manipulate stability has not been fully exploited. Highlighting just two aspects/studies may illustrate the point. The significance of the implications of the studies, perhaps because they were mainly demonstrated on *Drosophila*, have apparently not been fully utilized. The first was the unambiguous demonstration of the potential to independently adjust the mean expression of a character and its environmental sensitivity (Caligari and Mather, 1975). The experiments showed that there was the potential, at a direct genetic level, to analyse and handle the genetic determination of GxE. With *Drosophila* you can manipulate whole chromosomes as units so that it is possible to obtain any desired combination of chromosomes from two genotypes. The experiments used two inbred lines which differed for a number of characters including number (yield) of offspring produced and the response of this character to temperature.

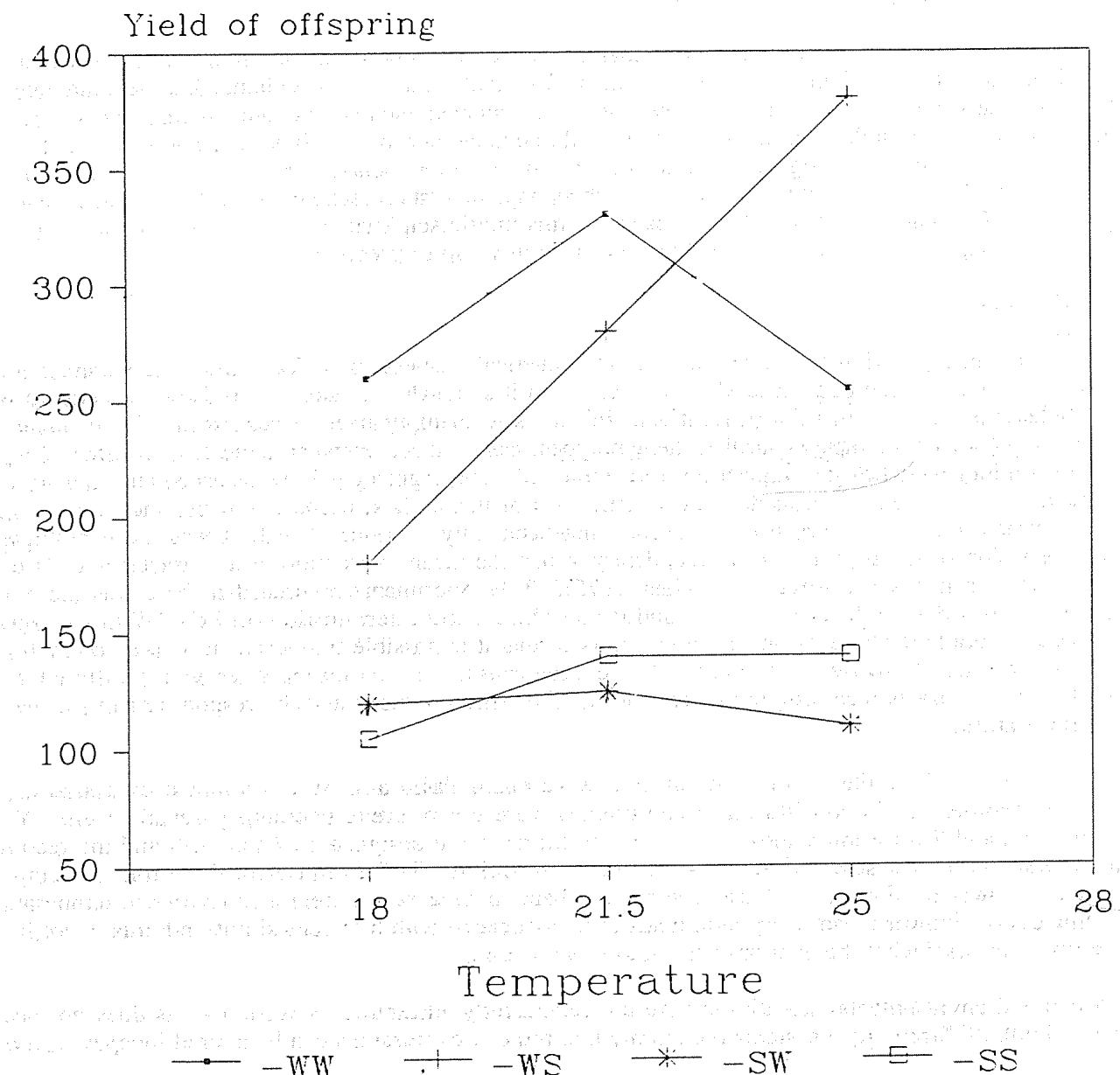
Two of the three major chromosomes were manipulated against a constant background of the X-chromosome. The two differing chromosomes were given letters denoting parental origin (W for Wellington and S for Samarkand). So the parent lines were designated -WW and -SS and the recombinants were -SW (low sensitivity) and -WS (high sensitivity). The responses of these lines to temperature are shown in Figure 2. Clearly, the recombinants have very different sensitivities to temperature. In this case the lower mean expression tends to be associated with lower sensitivity but this is not inevitably so. In brief what the experiments showed was that:

- i. Mean and environmental sensitivity were independently adjustable by selection - this does not necessarily imply different gene systems but simply that the two expressions can be altered independently.
- ii. The environmental sensitivities were independent in different characters - there was not an overall sensitivity for the genotype but it varied from character to character.

These findings were then later supported by the empirical demonstration with *Nicotiana* by Brumpton *et al.* (1977).

FIGURE 2

Yield in Drosophila Chromosome combinations



Yield of offspring in *Drosophila melanogaster* chromosome substitution lines. The one parent, Wellington, is represented by -WW (- stands for the X chromosome that is constant in this set of lines, while chromosomes II and III are shown as originating from this parent by WW). The other parent, Samarkand, is shown as -SS. The two geneotypes having the combinations of parent chromosomes are therefore designated -WS and -SW (Caligari and Mather, 1975)

The second aspect also arose from the above work and was published by Mather (1975). He showed theoretically and rather dramatically that even where initially observed responses could be fitted by a linear regression, because clear evidence of responses to different environmental factors being independent of one another had been obtained, the recombinants might be expected to be anything but linear, as is shown in Figure 3.

EXPLOITATION

Turning now to what might be considered a major focus of the symposium, and maybe the area where a clearer picture is most frequently desired, is what I have called the exploitation of GxE. The use of a rather general expression for this aspect is because it has rather wide-ranging implications. One part is of course breeding itself, but also it should help identify genotypes and environments that should be studied in more detail, for example by biochemists, physiologists, agronomists or soil scientists. Another possibility is in terms of directing growers, the advisory services, etc about where or when to plant particular types or clones, advising marketing concerns what and where to try and find suitable market places. It should also perhaps be borne in mind when considering *in situ* germplasm conservation, particularly when there is often assessment undertaken, allied to such work.

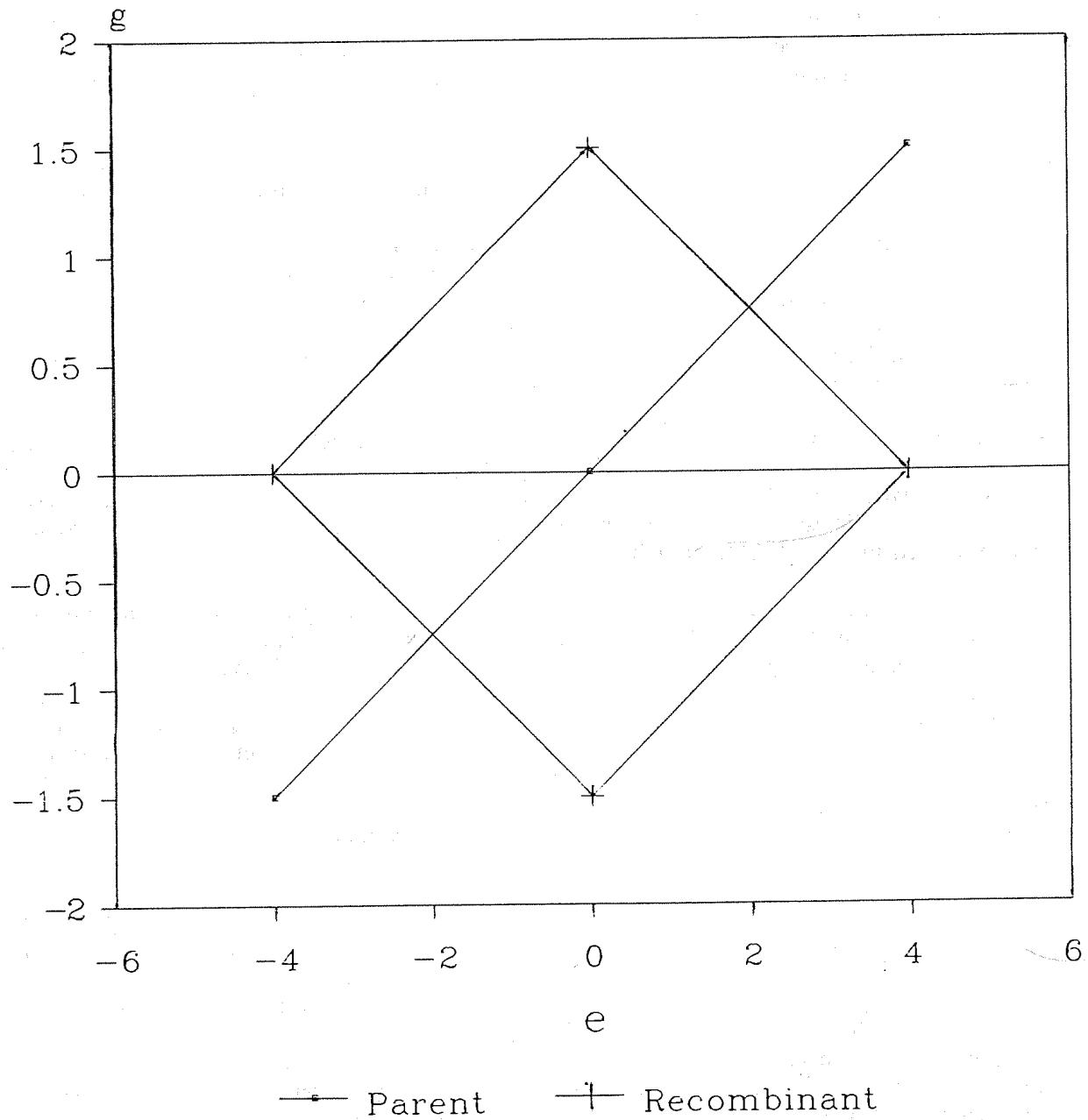
Consideration of some examples where consideration should be given in terms of GxE studies and how we carry them out, particularly perhaps with perennial crops, may be helpful. The first consideration is that of the environments that might be considered or studied. First, of course, it is necessary to ask where are the genotypes that are to be considered, supposed to be grown and under what conditions? Similarly, what genotypes are already growing in the environments of the study, what are their characters and are there obvious deficiencies? One consideration might be seasons. Even though the symposium is focusing on perennials, the point at which underlying processes take place, e.g development of flowers, as well as when harvest is expected, is extremely important. These must be major considerations, i.e. it is important to define quite clearly what is to be investigated, or produced, for what end and what market. General, loose statements about undefined situations are rarely going to lead to insights. It is essential to define the problem to whatever level is possible and then see whether it can be tackled in a practical approach.

On this theme, it does seem obvious that a more rigorous approach is required when it comes to the environmental aspects. It is often possible to read statements in papers saying "this year was much wetter/ drier/ hotter/ colder/ later/ earlier/ etc as well as the soil is heavier/ lighter/ freer draining/ compactable/ etc". This may be satisfactory but should it not be possible to quantify these somewhat more even if only in terms of the biological response of the characters in question in the species being handled? Taking years as an example: the type of year must be a vital consideration in trying to judge GxE in a perennial crop. But are there distributions of expression over reasonable periods of time? How do others judge these statements about the type of year their experiment is run in. Should they rely on the general impressions of people round them, the commercial growers, even the newspapers, the television, etc?

Would it not be logical to start to think constructively about the environmental aspects? The potential for trying to get much closer collaboration with, for example, agrometeorologists must be explored more constructively. In the interim period, and perhaps for a longer time, would it be possible to start thinking of trying to produce comprehensive distributions of expression for characters over sites and years? This would open the possibility of starting to judge at least where the year or general geographic area lay in terms of its likely frequency of re-occurrence, in other words, in relation to general distribution of expression. Clearly if a reasonable body of data were collected it could be treated as giving a continuous distribution. The major problem with this is of course that most of the data that are collected are subject to many other variables and so cannot, straightforwardly be used either to construct such a distribution or to be judged on it. This is a problem but one I suspect that there are a number of solutions to (although others more used to handling these types of situations will probably have some even better ideas). One is to use as large a body, of as widely representative sets of data as possible to try and build such a picture and, at the same time, to judge for example, the effect of the year, on a similarly wide basis. Given collaboration amongst a group of widely dispersed interested

FIGURE 3

GxE Response to 2 Factors Parent & possible recombinant



Theoretical responses of a parental genotype and a possible recombinant assuming independent responses to different environmental factors (Mather, 1975)

parties, it would be perfectly possible to build such body of data. It would have limitations. Yield continuously increases over time but it could nevertheless provide a baseline against which to make statements.

To continue this theme - it would be sensible to try to and obtain a clearer idea for the relative importance of some of the more obvious variables, for instance year and site. Looking through the literature the answers vary considerably. All possible suggestions are made for the importance of the environmental factors. Some suggest site can be the major variable, more point to year and many the interaction of the two. If a more defined and wider ranging approach was adopted it would be possible to start to answer this question in terms of particular crops, at least within some defined limits. This is in many ways, coming back to the point that Professor Sir Kenneth Mather raised. Is the environmental axis being handled sensibly? It is sensible to deal in terms of the expression of the character; although it is an obvious way to proceed perhaps it can be done more constructively and more analytically. If plant breeding and subsequent exploitation are to progress, this seems essential.

It would be possible to spend some time dealing with a number of possibilities, particularly perhaps in terms of breeding. For example, is selection in a poor environment the best way to achieve stable genotypes? When should we breed for general varieties and when specialist ones in terms of their environmental range? How early in a breeding programme should there be trials at more than one site? In commercial assessment and statutory trials how many sites and seasons should be tested? These questions should form part of a wider discussion. But these question have already been recognized and people are aware of them. What would, therefore, seem more profitable is to present a somewhat different approach.

A different approach to GxE has been advocated by Brown (1988) who takes two ideas and combines them into one approach. He first takes the idea of a distribution of environments and combines this with the idea of predictions arising from this distribution (in other words a similar approach to that of cross prediction advocated in genetical terms by Jinks, Pooni *et al.* (e.g Jinks and Pooni, 1976; Pooni and Jinks, 1978) and reported extensively by others (e.g Simpson and Snape, 1979; Tapsell and Thomas, 1983; Thomas and Tapsell, 1983; Brown and Caligari, 1989; Brown and Caligari, 1987; Caligari, Powell and Jinks, 1985; Caligari and Brown, 1986; Powell, Caligari, McNicol and Jinks, 1985) - an approach of a very considerable practical application in breeding and which has not yet been fully appreciated). Considering many breeding programmes, large bodies of data are already collected concerning genotypes (clones) over a number of years and when this is superimposed on trials at a number of sites it produces a large sample of "environments". In the potato breeding programme at the Scottish Crop Research Institute, for example, we would commonly run trials of relatively advanced clones at two sites in one year, at seven in the next and 11 in the one after, prior to submission for official trials, giving 20 "environments" in all (Brown, 1988). Now what Brown argued in his paper was that if these are regarded as a random set of environments then it is possible to use a similar approach to cross prediction but in terms of environments.

In other words, if a genotype is raised in a number of environments that are considered to be a random sample then taking a single genotype - *i* - we can ask: What is the probability of genotype *i* exceeding a particular target value - *T*? In fact, we can simply use the following probability integral: when predictions are for values greater than target:

$$f_{\infty}^T f(X_i) dX_i$$

and when the predictions are for values less than the target,

$$f_{-\infty}^T f(X_i) dX_i$$

The probability density function $f(X_i)$ will be determined by the mean expression of genotype *i* and the environmental variance of this *ith* genotype. The value of *T* can be set at any level desired but

which might, for example be related to the behaviour of controls or the best clones within the material tested. If it is assumed that the probability function is normally distributed then the probability can be obtained as:

$$\frac{T-X}{\sigma}$$

or

$$\frac{X-T}{\sigma}$$

It is therefore, easy to compare the genotypes under test by examining the probabilities of exceeding the targets that have been set; in other words looking for those genotypes which show the highest proportion of environments in which they exceeded the target. The data can still be examined to see in which environments particular genotypes do well or poorly but it does give the desirable feature of using all the data for each genotype. In addition, just as for cross prediction, environmental prediction can be extended to combine results from a number of characters taken together - simply by including the covariance between characters as part of the multivariate function.

This approach appeared to work well when tested on a sample of genotypes over two years (Brown, 1988). It does, however, need to be tested much more widely and in a range of situations. Nevertheless, it does effectively combine mean and stability into one value to be assessed and, even more, allows a number of different characters or traits, along with their stabilities, to be simultaneously included into a single value. The approach can, in fact, be further extended if samples of progenies were used to provide multi-site trials at a very early stage of the breeding programme. This would seem to offer an extremely powerful selection system which included GxE as an integral component at a very early stage of a breeding programme.

In summary, consideration has been given to assessment, biology, genetics and exploitation and in some cases it has perhaps merely been a statement of the obvious. Nevertheless it may provide sufficient stimulus (or anger) to encourage others to contribute actively. That the symposium is being held, is testimony to a feeling that GxE is an area that needs more attention. However, many will wonder whether GxE is an "Old, familiar friend or just a awkward, unwanted nuisance that somehow has to be dealt with". On balance it is an area which still needs considerable work. It is an area that can easily be dominated by statistics, which while being an essential element, must be seen as a tool rather than an end in itself. If viewed in a more integrated way GxE is an area which perhaps needs some interesting new insights but which could provide some fascinating opportunities.

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GENOTYPE- ENVIRONMENT INTERACTION (GE) STUDIES IN OIL PALM (*Elaeis guineensis*) PROGENIES

by

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ABSTRACT

This paper describes the results of genotype-environment studies in two experiments. Experiment 1 consisted of 33 bips tested at 6 sites and in the second experiment 50 Nigerian open - pollinated families were evaluated at 3 sites. In Experiment 1, the mean yield (FFB) ranged from 85 kg P¹ Yr⁻¹ at Kudat to 184.4 kg at Carey Island. The pooled data over the sites showed significant genotype-environment interaction for yield, bunch number and average bunch weight. The stability of the progenies were studied by regression analysis and coefficient of variation (C.V). Progeny x Year interaction was also investigated but it was largely absent. Heritability estimates for yield (FFB), bunch number (BNo) and average bunch weight (ABWT) were 0.04, 0.10 and 0.04 respectively.

In Experiment 2, the mean yield (FFB) ranged from 148 kg P¹ Yr⁻¹ at Kluang to 173 kg at Klang. The analysis of data pooled over sites showed significant GxE interaction for FFB and BNo and not for ABWT. The h² estimates for FFB, BNo and ABWT were 0.66, 0.40 and 0.86. These were much higher than those estimated in Experiment 1. The contribution of GxE interaction towards the total genetic variation was rather low in both the experiments.

INTRODUCTION

It is well known that genotypes differ in their response to changes in the environment such as rainfall, soil, agronomic practices etc. Previously it was thought that GE was a nuisance and attempts were made to minimise it by scale transformation. At present, a number of methods are being used to detect and quantify the level of GE. Yates and Cochran (1938) had shown that it was possible to detect and measure the level of GE without any reference to genetical implications. Eberhart and Russell (1966) partitioned GE into the linear response of genotypes to environment and the remainder interaction as the deviation from the linear regression. Perkins and Jinks (1968) refined the technique by fitting a model which specified the contribution of genetic, environmental and GE to generation means and variances.

A number of GE studies in oil palm had been reported (Rosenquist, 1982; Obisesan and Fatunla, 1983; Rajanaidu *et al*, 1983; Rajanaidu *et al* 1985; Ong *et al* 1986; Lee *et al* 1987; Yong and Chan, 1990 and Rajanaidu *et al* 1990). Rosenquist (1982) indicated the absence of GE by studying the ranking of DxP hybrids at two sites. It is to be noted that no change in the ranking of progenies at these sites does not preclude the presence of GE. Of the eight papers reported on GE in oil palm, 3 papers covered oil palm progenies observed at 2 locations (Rosenquist 1982; Lee *et al* 1987; Yong *et al* 1990). With the genotypes observed at 2 locations, it is not possible to regress genotypes over environment; especially to partition the GE into linear and non-linear responses. Obesesan and Fatunla (1983), Lee *et al* (1987) and Yong *et al* (1990) have also studied the yield stability of progenies over the years.

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This paper describes the detection and quantification of GE in two experiments. The stability of the progenies were studied by using regression analysis (b) and coefficient of variation (C.V.). The level of GE contribution towards the total genetic variation was calculated using variance components of the analysis of variance (ANOVA).

MATERIALS AND METHODS

Experiment 1

Experiment 1 describes the performance of 33 DxP (*Dura x Pisifera*) progenies planted at six sites located in Peninsular Malaysia and Sabah. The DxP progenies were derived from crosses between Deli *duras* (females) and *pisiferas* of AVROS, Serdang 27B, Lever LN, Serdang 29.36 and Lever Cameroons (LC). The parental palms were selected from the Sabah Breeding Programme (Rajanaidu *et al* 1985).

The trials at these 6 sites were laid down in January-September 1981. The details of the experiment are given in *Table 1*. The soil types ranged from coastal clay to riverine alluvium and the planting density from 136-148 palms ha⁻¹. The progenies were arranged in a completely randomised design (CRD) with two blocks per site and 5 palms per family per block. The rainfall in these sites varied between 1800-3500 mm per annum. The site at 0.815 (Kudat) had a distinct dry period. The yield (fresh fruit bunches) records were accumulated from 1984-1987 at trials 0.822, 0.831, 0.827, 0.811 and 1984-1989 at 0.815 and 0.817. For GE analysis only the common 4 years (1984-1987) were considered.

Table 1. Information on the trial sites and experimental designs

Trial No.	0.811	0.815	0.817
Date of Planting	January 1981	June 1981	June 1981
Location	Ulu Dusun, Sandakan	Pinawantai, Kudat	Lumadan, Beaufort
Soil type	Riverine Alluvium	Sandy loam	Riverine Alluvial
Density (ha ⁻¹)	148	148	148
Design	CRD	CRD	CRD
Plot size	5 palms per family per block	5 palms per family per block	5 palms per family per block
No of blocks	2	2	2
Yield recording	1984-1987	1984-1987	1984-1988
Rainfall	3169 mm (1971-1988)	2049 mm (1982-1989)	3580 mm (1982-1989)
No of rainy days	-	102	156

Table 1. (contd.)

Trial No	0.822	0.827	0.831
Date of Planting	Sept. 1981	March 1981	Sept. 1981
Location	Jendarata Est.	Carey Island	Sg. Buloh Est.
Soil type	Coastal clay	Carey series	Coastal Clay (Selangor series)
Density (ha ⁻¹)	148	138	136
Design	CRD	CRD	CRD
Plot size	5 per palms family per block	5 palms per lock family per block	5 palms per family per block
No of blocks	2	2	2
Yield recording	1984-1987	1984-1987	1984-1987
Rainfall	1800 mm (1969-1988)	1935 mm (1980-1989)	1848 mm (1980-1989)

In the ANOVA, all the items were considered random because the results of Experiment 1 and 2 will be used to make a general statement on GE in oil palm. The outline of the ANOVA is given in Appendix 1. The expected mean squares were used to estimate heritability (h^2) for fresh fruit bunches (FFB), bunch number (BNO) and average bunch weight (ABWT) and magnitude of genotype x environment interaction (GE). Progeny x Year interaction was investigated by considering the annual yields and progenies. The FFB, BNO and ABWT were expressed on a per palm basis.

A simple regression analysis was carried out to study the stability of progenies. The regression method was compared to coefficient of variation of the progenies (C.V.).

Experiment 2

This experiment consists of 50 open-pollinated families derived from samples collected in Nigeria in 1973. The families were tested at 3 sites i.e Kluang (0.152), Klang (0.803) and Teluk Intan (0.802). The trials at three sites were laid down in September, 1976. The details of Experiment 2 are given in *Table 2*. The soil types are inland sedentary, coastal alluvial and peat. The planting density varied from 136-148 palms ha^{-1} and the rainfall from 1539 to 1985 mm/yr. The standard yield parameters were collected from 1982-1985.

Table 2. Information on the trial sites and experimental designs

Trial No.	Site	Location	Soil type	Density palm ha^{-1}	Av. Annual rainfall (mm)
0.152	Site 1	Kluang	Inland sedentary	148	1985
0.803	Site 2	Klang	Coastal alluvial	136	1981
0.802	Site 3	Jendarata, Teluk Intan	Peat	148	1539

Table 2 (contd)

Trial No.	Site	Location	Design	Plot size	No of Blocks	Yield Recording
0.152	Site 1	Kluang	CRD	6Palm/family/ block	2	1982-1985
0.803	Site 2	Klang	CRD	6 palm/family/ block	2	1982-1985
0.802	Site 3	Jendarata, Teluk Intan	CRD	6 palm/family/ block	2	1982-1985

ANOVA and regression analysis were carried out to study the stability of the progenies. Heritability estimates were computed for economic traits and these were compared with the DxP populations of Experiment 1.

RESULTS AND DISCUSSION

Experiment 1

Table 3 shows the overall performance of 33 families at each site. At Kudat (0.815) the mean yield was much lower than other sites where the mean yield ranged from 140-184 kg FFB per palm per

year. The lower yield at Kudat could be attributed to a distinct dry period and this is reflected in lower bunch production. At Sg. Buluh (0.831), the bunch number was rather high i.e 18.13 bunches per palm per year but the bunch weight was the lowest and hence the overall yield was 141 kg FFB per palm per year.

Table 3. Mean performance for FFB, B.NO and ABWT at each site (84-87)

Trial		FFB	BNO	ABWT
0.811	(Ulu Dusun) (U.D)	140.9	11.2	11.8
0.815	(Kudat) (K.D)	85.1	8.7	10.2
0.817	(Beaufort) (B.F)	140.9	11.4	11.6
0.822	(Jendarata) (J.R)	163.4	16.1	10.7
0.827	(Carey) (C.I)	184.4	20.1	10.0
0.831	(Sg. Buluh) (S.B)	141.2	18.1	9.1
Overall mean		142.7	14.3	10.6
CV		31.1	27.3	24.9

ANOVA carried out for FFB, BNO and ABWT at each site of Experiment 1 are given in *Tables 4-6*. For FFB, there was no significant difference between progenies at four out of the six sites, indicating lack of genetic variation for FFB at the four sites. Similar pattern emerged for BNO and ABWT. The sites 0.822 and 0.827 showed lower C.V. for FFB, BNO and ABWT (i.e 17-18%) when compared to the sites 0.811, 0.815 and 0.817 where the C.V.s for FFB were in the range of 36-47%. These C.V.s were computed on an individual palm basis.

Table 4. ANOVA for FFB at each site (84-87)¹⁾

Source	df	0.811(U.D) ms	0.815(K.D) ms	0.817(B.F) ms
Progeny (P)	32	5086.5(NS)	1067.0(NS)	6318.3(NS)
Reps (R)	1	254187.8	3148.9	99470.2
P x R	32	4761.2(NS)	821.3(NS)	5427.8*
Within seedlings	185	4455.9	957.6(264)	3577.4(264)
Mean		140.9	85.1	141.0
CV		47.4	36.4	42.4
Rainfall (mm)		3169	2049	3580

1) Figures in the parenthesis are degrees of freedom

Table 4 (contd)

Source	df	0.822(J.R) ms	0.827(C.I) ms	0.831(S.B) ms
Progeny (P)	32	1312.9*	3786.6**	748.1(NS)
Reps (R)	1	4079.3	3451.0	3684.2
P x R	32	800.9(NS)	1853.8**	903.4(NS)
Within seedlings	185	878.6(226)	1081.5(246)	1317.6(241)
Mean		163.4	184.4	141.2
CV		18.2	17.8	25.7
Rainfall (mm)		1800	1935	1848

1) Figures in the parenthesis are degrees of freedom

Table 5. ANOVA for Bunch No at each site (84-87)

Source	df	0.811(U.D) ms	0.815(K.D) ms	0.817(B.F) ms
Progeny (P)	32	33.2(NS)	12.6(NS)	27.08(NS)
Reps (R)	1	918.0	91.3	273.9
P x R	32	29.3*	9.0	24.9(NS)
Within seedlings	185	19.4	8.9(264)	20.6(264)
Mean		11.2	8.7	11.4
CV		39.3	34.48	39.7

Table 5 (contd)

Source	df	0.822(J.R) ms	0.827(C.I) ms	0.831(S.B) ms
Progeny (P)	32	25.84(NS)	61.5**	13.48(NS)
Reps (R)	1	0.16	18.3	0.7
P x R	32	11.85(NS)	14.3(NS)	14.4(NS)
Within seedlings	185	9.64(226)	14.0(264)	19.0
Mean		16.14	20.1	18.1
CV		19.2	18.6	24.1

Table 6. ANOVA for ABWT at each site (84-87)

Source	df	0.811(U.D) ms	0.815(K.D) ms	0.817(B.F) ms
Progeny (P)	32	24.4(NS)	6.18(NS)	12.3*
Reps (R)	1	620.1	1.8	123.5
P x R	32	13.2	8.3(NS)	8.2(NS)
Within seedlings	185	18.2	7.8	6.8
Mean		11.8	10.2	11.6
CV		36.3	27.4	22.4

Table 6 (contd)

Source	df	0.822(J.R) ms	0.827(C.I) ms	0.831(S.B) ms
Progeny (P)	32	5.1*	11.1**	2.8(NS)
Reps (R)	1	6.3	0.7	26.3
P x R	32	3.6(NS)	4.5(NS)	3.3(NS)
Within seedlings	185	3.0	3.4	4.6
Mean		10.7	10.0	9.1
CV		16.3	18.4	23.7

ANOVA for the pooled data is given in *Table 7*. There were significant differences for the items FFB, BNO and ABWT at progeny and progeny x site interaction items.

Table 7. Pooled ANOVA for FFB, BNO and ABWT (84-87)

Source	df	ABWT ms	BNO ms	FFB ms
Progeny (P)	32	16.5**	65.2**	4360.7*
Sites (S)	5	304.4	5806.2	316386.0
Reps/Site (R)	6	160.4	258.8	72881.0
P x S	160	9.3*	22.1*	2889.1*
P x R	192	6.8(NS)	17.4**	2428.1**
Seedlings	1426	6.9	15.1	1966.1
Mean		10.5	14.3	142.7
CV		24.9	27.3	31.1

Table 8 shows that the bulk of the variation was confined to the variation within seedlings item (σ^2_w). The progeny item (σ^2_p) contributed about 2-5% and family x site interaction (σ^2_{ps}) about 2-4% towards the total variation. The h^2 estimates for FFB, BNO and ABWT were 0.04, .10 and .04 respectively. The material used in this trial was a wide range of Deli *duras* and *pisiferas* of Sabah Breeding Programme (Rajanaidu *et al.*, 1992). The low h^2 estimates and interaction items (PxS) were rather unexpected.

Table 8. Estimates of variance components for GE and h^2 for FFB, BNO and ABWT

Items	FFB	BNO	ABWT
$\sigma^2_w(\%)$	91	89	94
$\sigma^2_{pb}(\%)$	5	3	-
$\sigma^2_{ps}(\%)$	2	3	4
$\sigma^2_p(\%)$	2	5	2
h^2	0.04	0.10	0.04
mean	142.4	14.3	10.5

Using the FFB values recorded at each site, ANOVA was carried out to investigate Progeny x Year (PxY) interaction (Table 9). In general, the PxY interaction was absent except at site 0.822 where it was significant at 5% level. Studies by Obisesan and Fatunla (1983) had shown the presence of PxY for FFB, BNO and ABWT.

Table 9. Progeny x Year interaction at each site

Source	df	ms	0.817	0.815	0.822	
			df	ms	df	
Progeny (P)	52	18208.6**	51	5747.7**	52	4981.8(10%)NS
Year (Y)	4	1068246.0	4	814082.3	3	1384519.0
REP/Site (R)	5	173501.9	5	3091.9	4	16976.2
P x Y	208	4781.7(NS)	204	2265.7(NS)	156	3866.3*
P x R	260	6530.1**	255	2569.1(NS)	208	3185.8(NS)
Seedlings	2045	5466.9	2010	2570.8	1412	3216.5
	(85-89)		(85-89)		(84-87)	
Mean		151.16		98.5		161.3
CV		48.91		51.7		35.1

Table 9 (contd)

Source	df	0.827 ms	df	0.831 ms
Progeny (P)	42	16748.1**	46	4678.8**
Year (Y)	3	915686.8	3	400772.3
Rep/Site (R)	4	7634.8	4	13528.7
P x Y	126	25599.9(NS)	138	1692.8(NS)
P x R	168	2905.1**	184	2169.9(NS)
Seedlings	1288 (85-89)	2557.4	1388 (84-87)	2541.9
Mean		185.2		140.5
CV		27.3		35.8

The relationship between the mean performance of a progeny and its sensitivity (**b**) to the environment are shown for FFB, BNO and ABWT in Figure 1, Figure 2 and Figure 3 respectively. In the case of FFB, there were progenies with high yield and showing both low and high sensitivity. For example progeny 1823 is high yielding and **b** < 1, whereas, progeny 2075 is high yielding and the **b** > 1. Similar trend was noted for the trait bunch number. The ABWT showed the opposite trend. The high yielding progenies had lower bunch weight and **b** < 1. In the case of progenies 1897 and 1823, FFB was most sensitive to environment and the ABWT was the least. The coefficient of variation (C.V.) and progeny means for FFB, BNO and ABWT are given in Figures 4, 5 and 6 respectively. The high yielding progenies 1823 and 1897 showed C.V close to 40% for FFB and BNO. The ABWT had shown lower level of C.V indicating stability of this trait over environments. The correlation between C.V and **b** was studied and it was found that for FFB, there was significant correlation between C.V. and **b** but not for BNO and ABWT. (Table 10).

Table 10. Correlation between Regression Coefficient (b) and C.V.

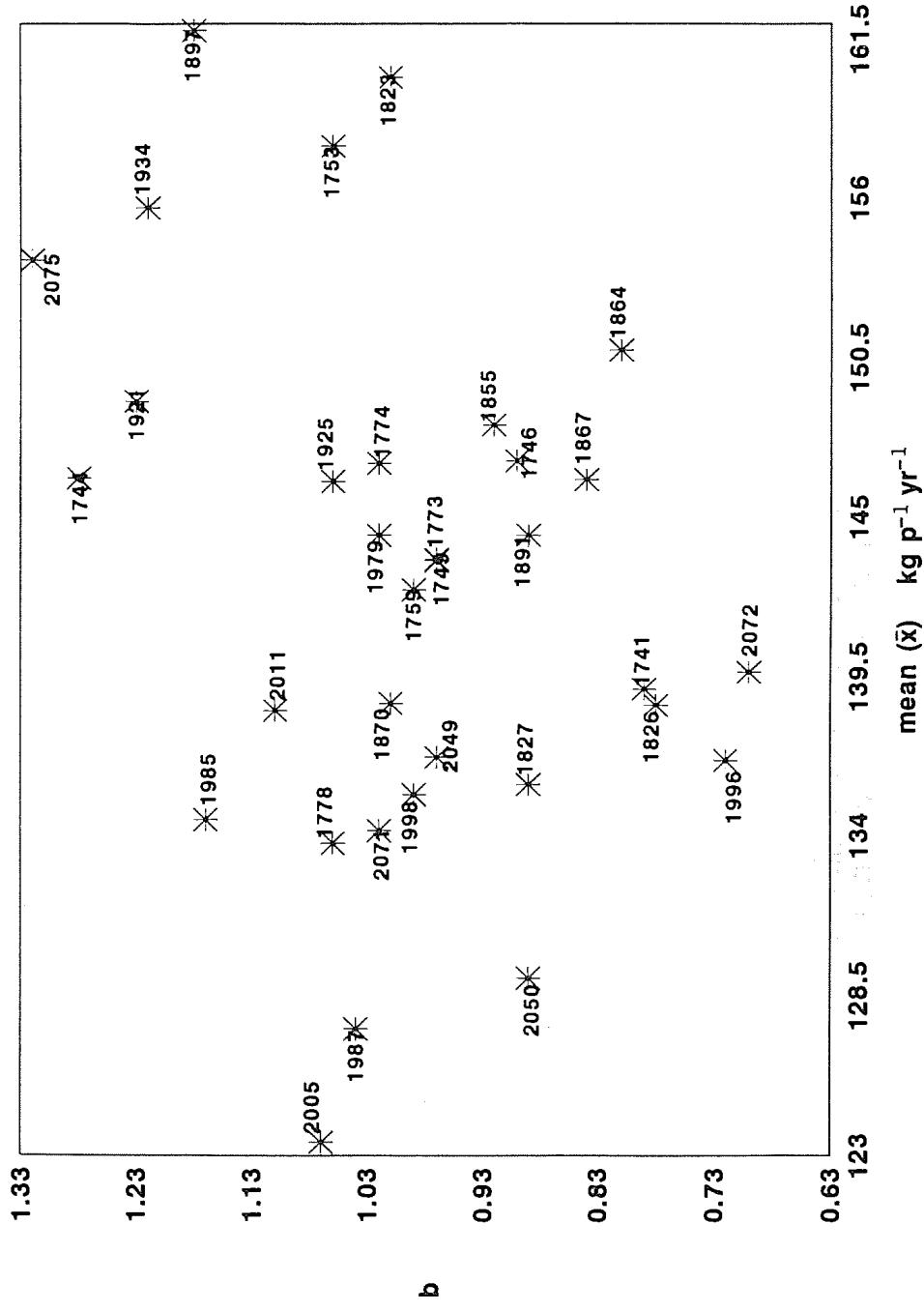
	df	Value
FFB	33	0.45**
Bunch No.	33	0.14NS
Av. Bunch Wt.	33	0.33NS

The trials 0.822, 0.827 and 0.831 were analysed for oil/palm/year, kernel/palm/year and bunch analysis components (Tables 11 and 12). The main traits oil/palm/year and kernel/palm/year had not shown significant GE. In the case of bunch analysis, fruit to bunch ratio (F/B), mesocarp to fruit ratio (M/F) and shell to fruit ratio (S/F) had shown significant GE. However, the main economic traits oil to bunch ratio (O/B) and kernel to bunch ratio (K/B) had not shown any significant differences.

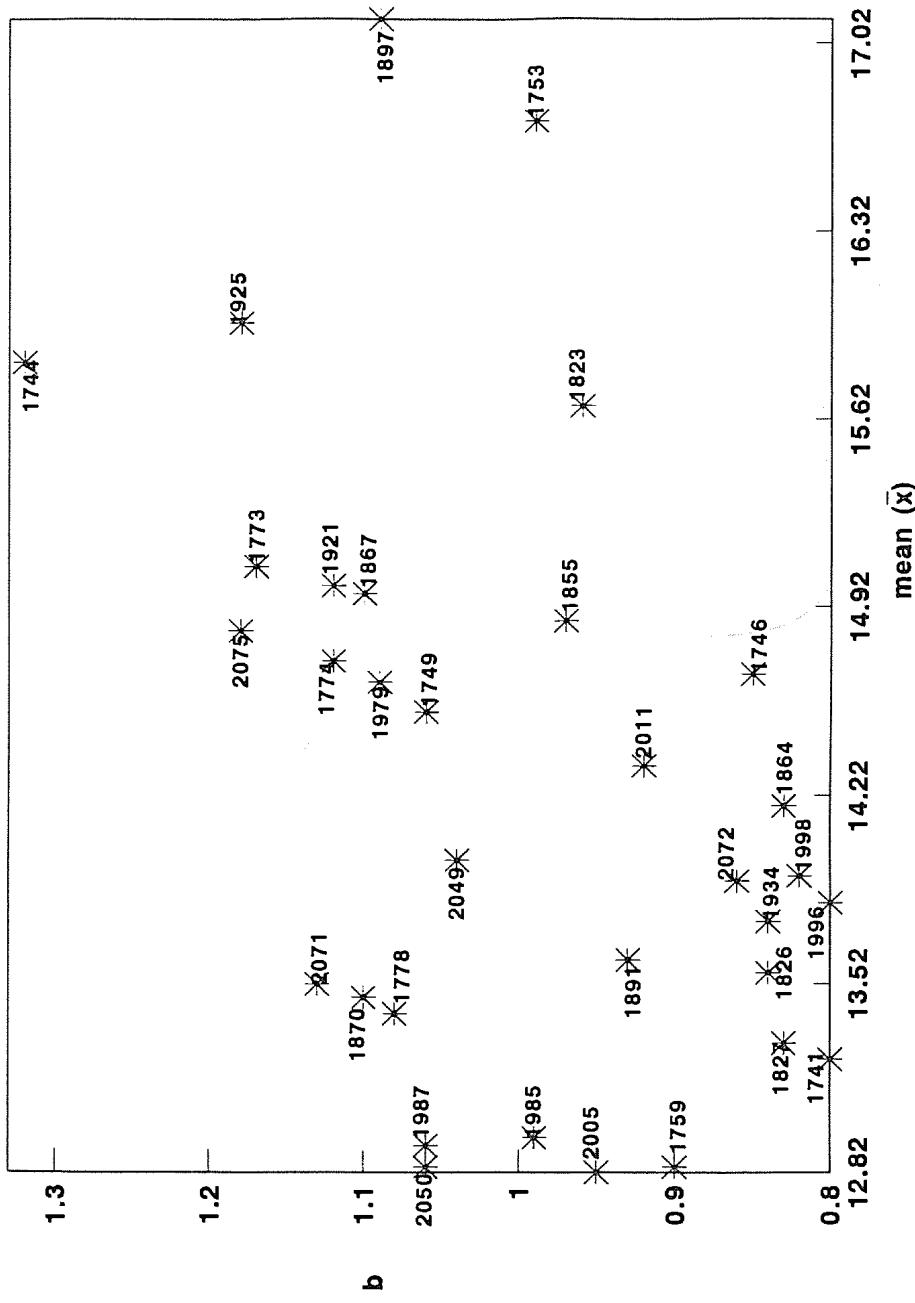
Table 11. ANOVA for Oil/Palm/Yr and Kernel/Palm/Yr at Sites 0.822, 0.827 and 0.831

Items	df	O/P/Yr ms	K/P/Yr ms
Progeny (P)	31	94.9	15.4
Sites (S)	2	2217.7	227.2
Rep/Site (R)	2	115.2	3.8
P x S	3	28.8(NS)	3.2(NS)
Error	62	27.7	3.8
mean	93	38.8	8.6
CV		13.5	22.8

Fig.1 MEAN FFB OF PROGENIES AND REGRESSION COEFFICIENT (b)



**Fig.2 MEAN BUNCH NUMBER OF PROGENIES
AND REGRESSION COEFFICIENT (b)**



**Fig.3 MEAN AV.BUNCH WEIGHT OF PROGENIES
AND REGRESSION COEFFICIENT (b)**

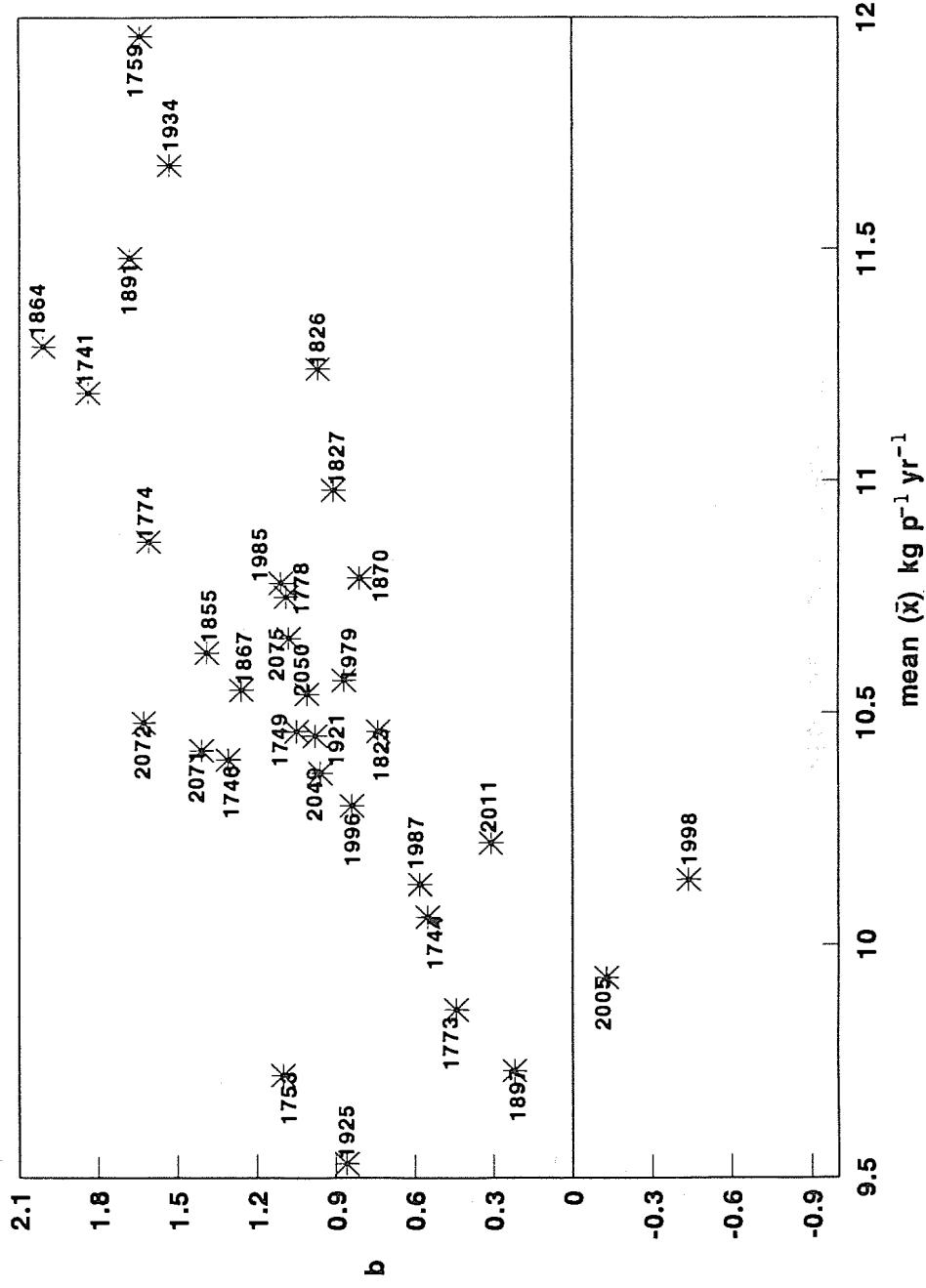


Fig 4 Mean FFB versus CV (DxP Phase II)

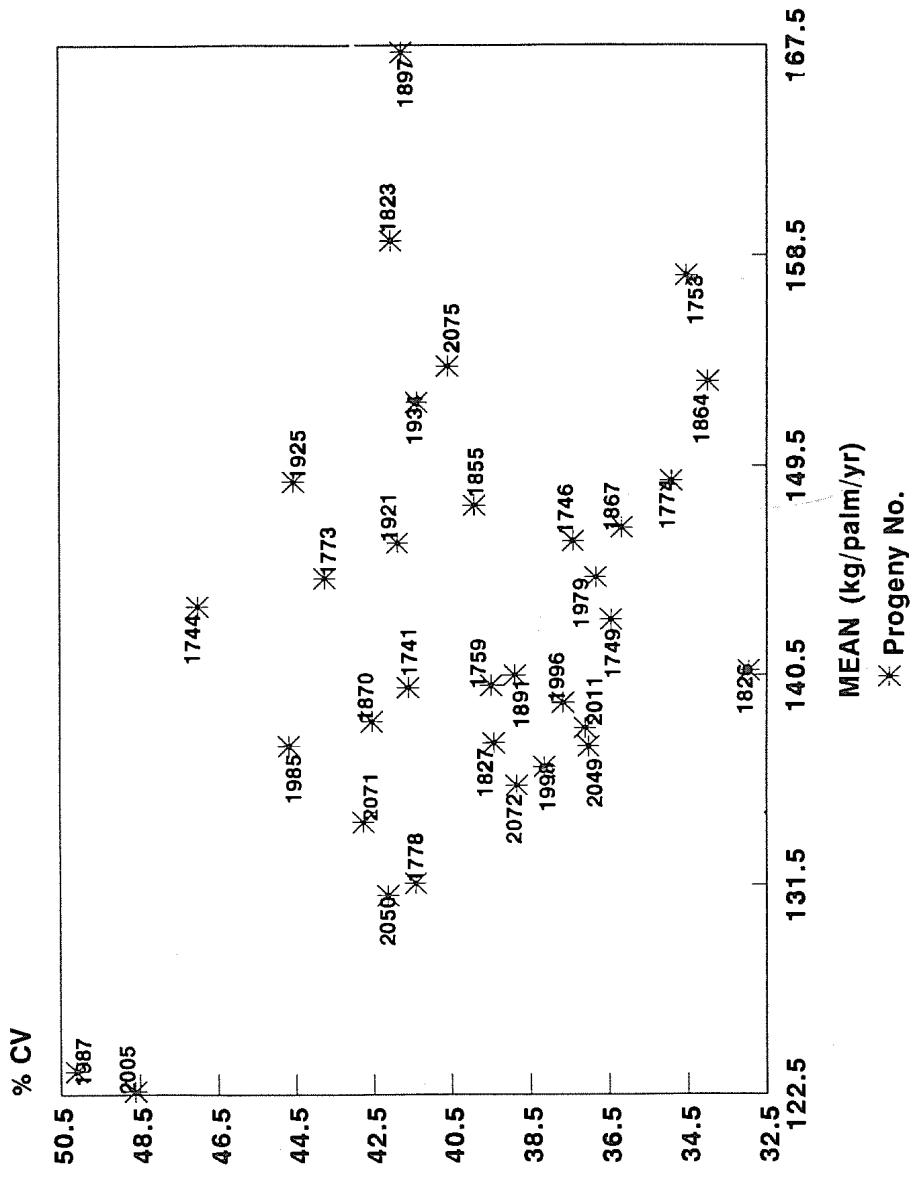


Fig 5 Mean Bunch No. versus CV (DxP Phase II)

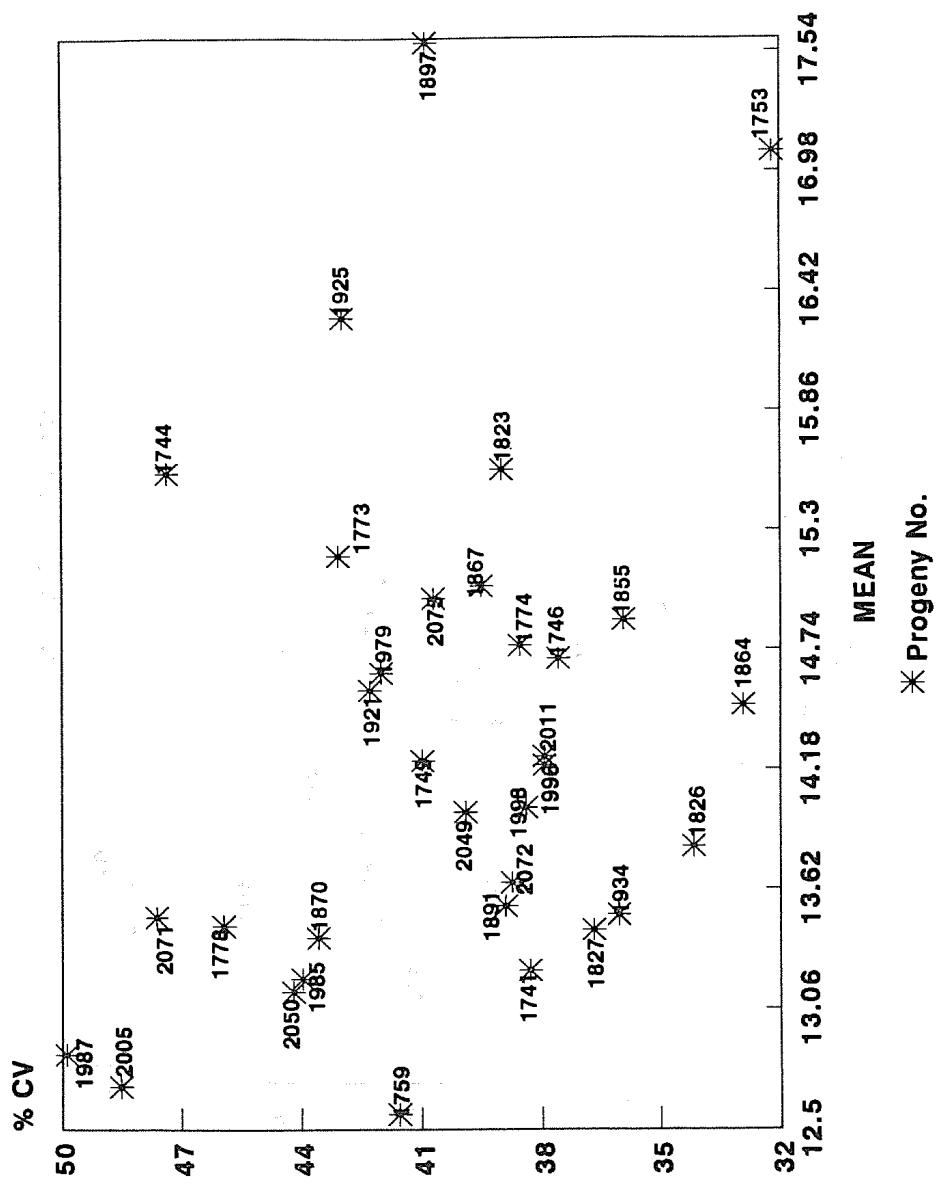


Fig 6 Mean Av. Bunch Wt. versus CV (DxP Phase II)

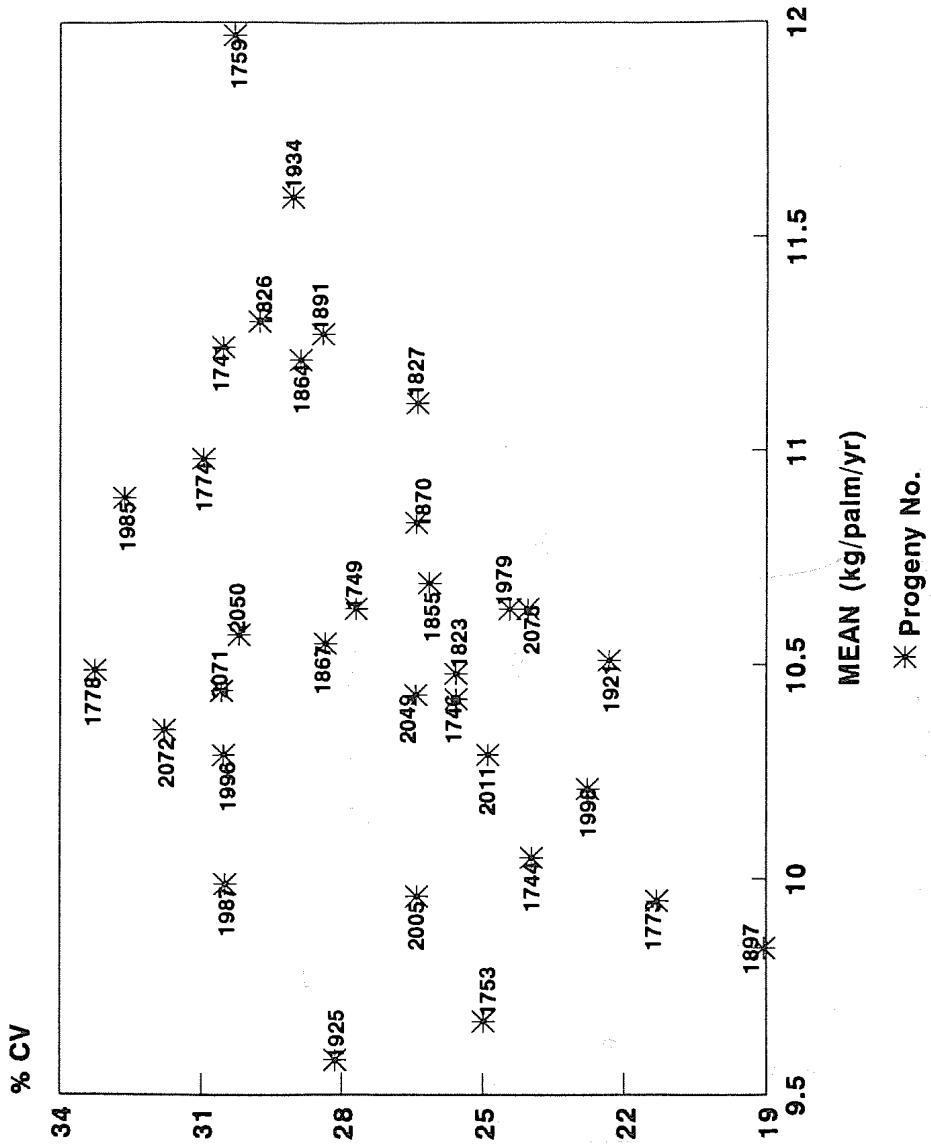


Table 12. GE for bunch analysis at sites 0.822, 0.827 and 0.831

Items	df	F/B ms	M/F ms	O/D ms	O/WM ms
Progeny (P)	37	83.7	65.1	3.6	16.6
Site (S)	2	3259.5	6.5	43.5	76.1
Rep/Site (R)	3	18.4	23.9	58.5	32.0
P x S	74	29.2**	15.6**	3.0(NS)	6.4(NS)
Error	111	17.5	8.1	3.1	6.4
Mean		60.5	78.4	75.5	48.6
CV		6.9	3.6	2.3	5.2

Table 12 (Contd)

Items	df	S/F ms	K/F ms	O/B ms	K/B ms
Progeny (P)	37	48.3	7.0	19.4	3.9
Site (S)	2	22.3	62.8	295.2	23.0
Rep/Site (R)	3	16.2	1.6	20.2	0.6
P x S	74	10.4**	1.5(NS)	5.3(NS)	1.1(NS)
Error	111	5.0	1.3	3.8	0.8
Mean		48.6	9.0	23.8	5.5
CV		5.2	12.6	8.1	15.8

Experiment 2

The overall performance of the unselected, 50 open-pollinated families is given in *Table 13*. The yield was highest in peat soils; 173 kg P⁻¹ as compared to inland soil at Kluang i.e 148 kg P⁻¹ Yr⁻¹. At site 2, coastal alluvial, the palms produced a large number of bunches but the lower bunch weight had affected the overall yield. At site 3, highest yield was realised by having intermediate bunch number and slightly higher bunch weight. However, it was not the case in Experiment 1 where the site with highest bunch number gave the highest yield.

Table 13. Mean Performance - FFB, BNO, ABWT (1982 - 1985)

	FFB	BNO	ABWT
Site 1	148.2	15.6	10.9
Site 2	169.8	19.7	9.0
Site 3	173.2	16.0	12.1
Overall mean	163.8	17.1	10.7

Analysis of variance (ANOVA) was carried out for FFB, BNO and ABWT at each site. Unlike in Experiment 1, there were significant differences for 'Progeny' item and the levels of C.Vs were comparable at all the three sites. The C.V. for FFB varied from 17-13%, being highest for the palms planted in the peat. C.V. for BNO ranged from 21-25% and ABWT 20-29%. The levels of C.V. experienced in this Experiment 2 were lower than those computed in Experiment 1 (*Tables 14-16*).

Table 14. Site 1 (152) Inland Sedentary

Items	df	MS(FFB)	MS(BNO)	MS(ABWT)
Progeny (p)	49	9004.7**	72.9**	78.4**
Replicates (R)	1	159.7	2.5	6.9
P x R	49	1029.7(NS)	20.4(NS)	6.1(NS)
Seedlings	479	1038.6	15.4	6.7
Mean		148.2	15.6	10.9
CV		21.7	25.1	23.8

Table 15. Site 2 (802) Peat

Items	df	(MS(FFB)	MS(BNO)	MS(ABWT)
Progeny (P)	49	10794.6**	62.7**	58.6**
Replicates (R)	1	636.6	14.2	15.7
P x R	49	1983.9(NS)	24.7(NS)	8.4(NS)
Seedlings	463	1535.7	18.6	6.9
Mean		169.8	19.7	9.0
CV		23.1	21.9	29.1

Table 16. Site 3 (803) Coastal alluvial

Items	df	(MS(FFB)	MS(BNO)	MS(ABWT)
Progeny (P)	49	6667.4**	89.5**	62.7**
Replicates (R)	1	11696.9	57.1	5.7
P x R	49	910.2(NS)	17.6(NS)	7.2(NS)
Seedlings	475	898.1	15.9	6.4
Mean		173.2	16.0	12.1
CV		17.3	24.9	20.8

ANOVA of pooled data had shown that there were significant GE for FFB and BNO but not for ABWT (*Table 17*). The overall FFB yield is higher in Experiment 2 (164 kg) than in Experiment 1 (143 kg). The C.V for FFB in Experiment 2 was lower than Experiment 1 but the C.V. levels for BNO and ABWT were comparable.

Table 17. Combined ANOVA

Items	df	(MS(FFB)	MS(BNO)	MS(ABWT)
Progeny (P)	49	22397.6**	173.2**	183.0**
Location (L)	2	102397.3**	2827.7**	1351.3**
Rep in Location (R/L)	3	4166.9(NS)	24.7(NS)	9.5(NS)
P x L	98	2054.7**	25.8*	8.2(NS)
P x R/L	147	1307.9**	20.9**	7.2**
Seedlings	1417	1153.9	16.6	6.7
Mean		163.8	17.1	10.7
CV		20.7	23.8	24.2

The experiment was further analysed for variance components related to genetic components (*Table 18*). The intra-class correlation t (Falconer, 1980) was computed to calculate h^2 estimates. The h^2 estimates were 0.66, 0.40 and 0.86 for FFB, BNO and ABWT respectively. The variation within seedlings (σ_w^2) contributed 55-72% towards the total genetic variation. In the case of Experiment 1, the similar estimate was nearly 90%. In Experiment 2, the Progeny x Site component (σ_{ps}^2) contributed 1-4% of the total genetic variation. The magnitude of the PxS interaction item is similar in both the experiments. However, Experiment 2 planted with germplasm material had a much higher level of genetic variation within the progenies as compared to Experiment 1 which was planted with highly selected material.

Table 18. Estimates of variance components for GE and h^2 for FFB, BNO and ABWT

Items	FFB	BNO	ABWT
$\sigma^2W(\%)$	62	75	55
$\sigma^2fb(\%)$	1	3	1
$\sigma^2fs(\%)$	4	2	1
$\sigma^2f(\%)$	33	20	43
h^2	0.66	0.40	0.86
mean	163.8	17.1	10.7

At site 0.802 (Klang), FFB, BNO and ABWT were recorded over a period of four years (1982-1985). There was significant Progeny x Year (PxY) interaction for ABWT but not for FFB and BNO (*Table 19*).

Table 19. Progeny x Year interaction for FFB, BNO and ABWT in trial 0.802 (1982 - 1985)

Items	df	FFB	BNO	ABWT
		ms	ms	ms
Progeny (P)	49	43582**	251**	235**
Years (Y)	3	423398	2706	2829
Reps/Years (R/Y)	4	1647	64	47
P x Y	147	3505 NS	33 NS	14**
P x R	196	3577**	44**	13**
Seedlings	1865	2844	34	11
mean		169.8	19.7	9.0
CV		31	29.7	37.7

The relationship between the mean performance of progenies and regression coefficient (b) was studied in Experiment 2 (Figures 7-9). Three high yielding progenies, 3811, 605 and 3104 were chosen to study their characteristics. Unlike in Experiment 1, these progenies had intermediate bunch number and bunch weight.

CONCLUSIONS

Experiment 1 was planted with highly selected breeding material and Experiment 2 with unselected semi-wild progenies. The overall FFB yield of semi-wild material is comparable to selected material. The level of genetic variation for family item (σ^2_f) is much higher in Experiment 2 than in Experiment 1 (Table 20). However, the magnitude of GE in both the experiments is quite similar; contributing < 5% towards the total genetic variation. The high yielding progenies in Experiment 2 tend to have intermediate bunch number and bunch weight as compared to Experiment 1 where the high yielding progeny 1897 had high bunch number and low bunch weight. The distribution of family means, 'b's and C.Vs shows that it may be possible to identify stable or responsive progenies for commercial exploitation. GE will be more important in the testing of oil palm clones for specific or general adaptability.

Table 20. Estimates of variance components for GE and h^2 for FFB, BNo and ABWt

	Expt. 1			Expt. 2		
	FFB	BNo	ABWt	FFB	BNo	ABWt
$\sigma^2W(\%)$	91	89	94	62	72	55
$\sigma^2fb(\%)$	5	3	-	1	3	1
$\sigma^2fs(\%)$	2	3	4	4	2	1
$\sigma^2f(\%)$	2	5	2	33	20	43
h^2	0.04	0.10	0.04	0.66	0.40	0.86

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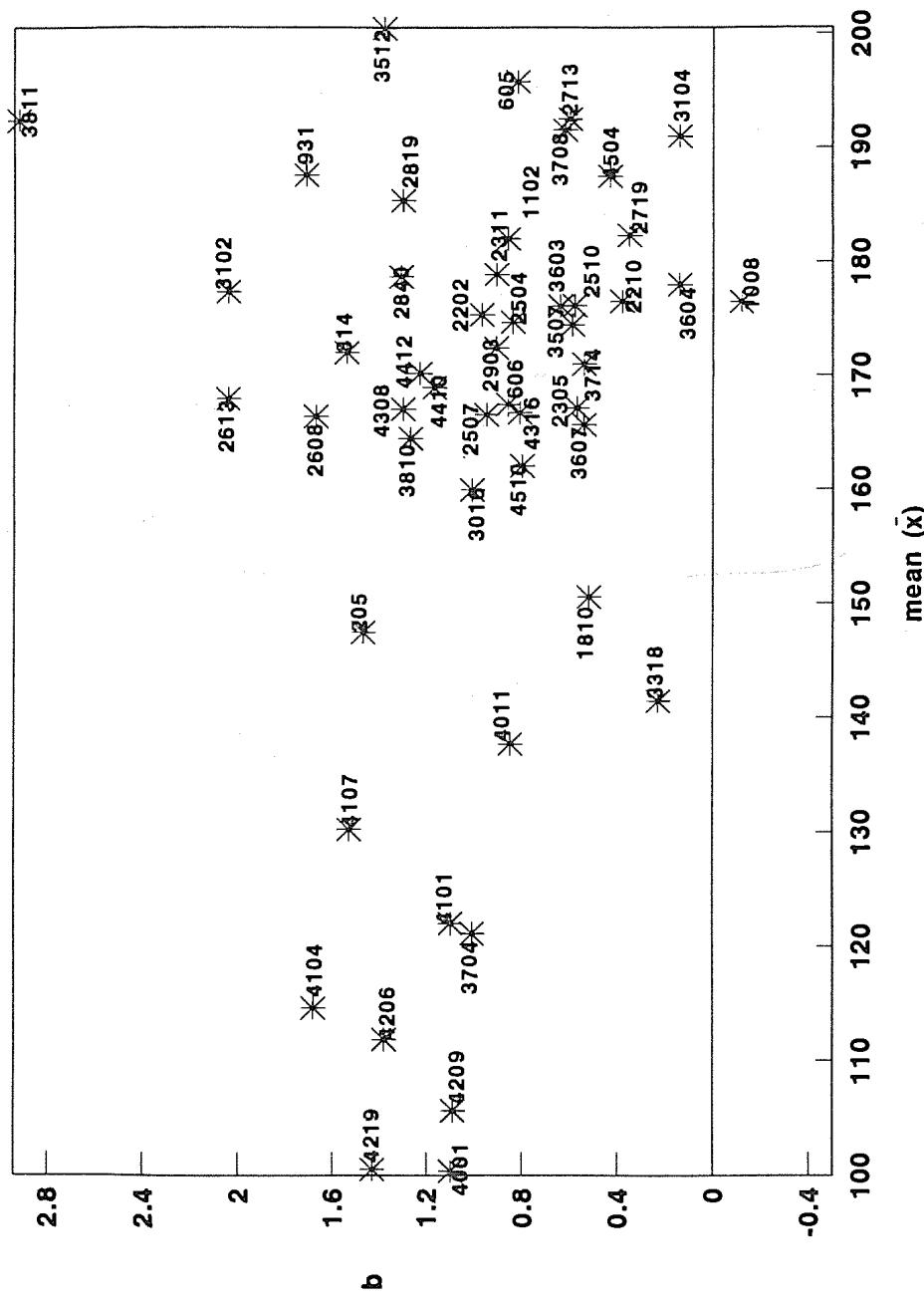
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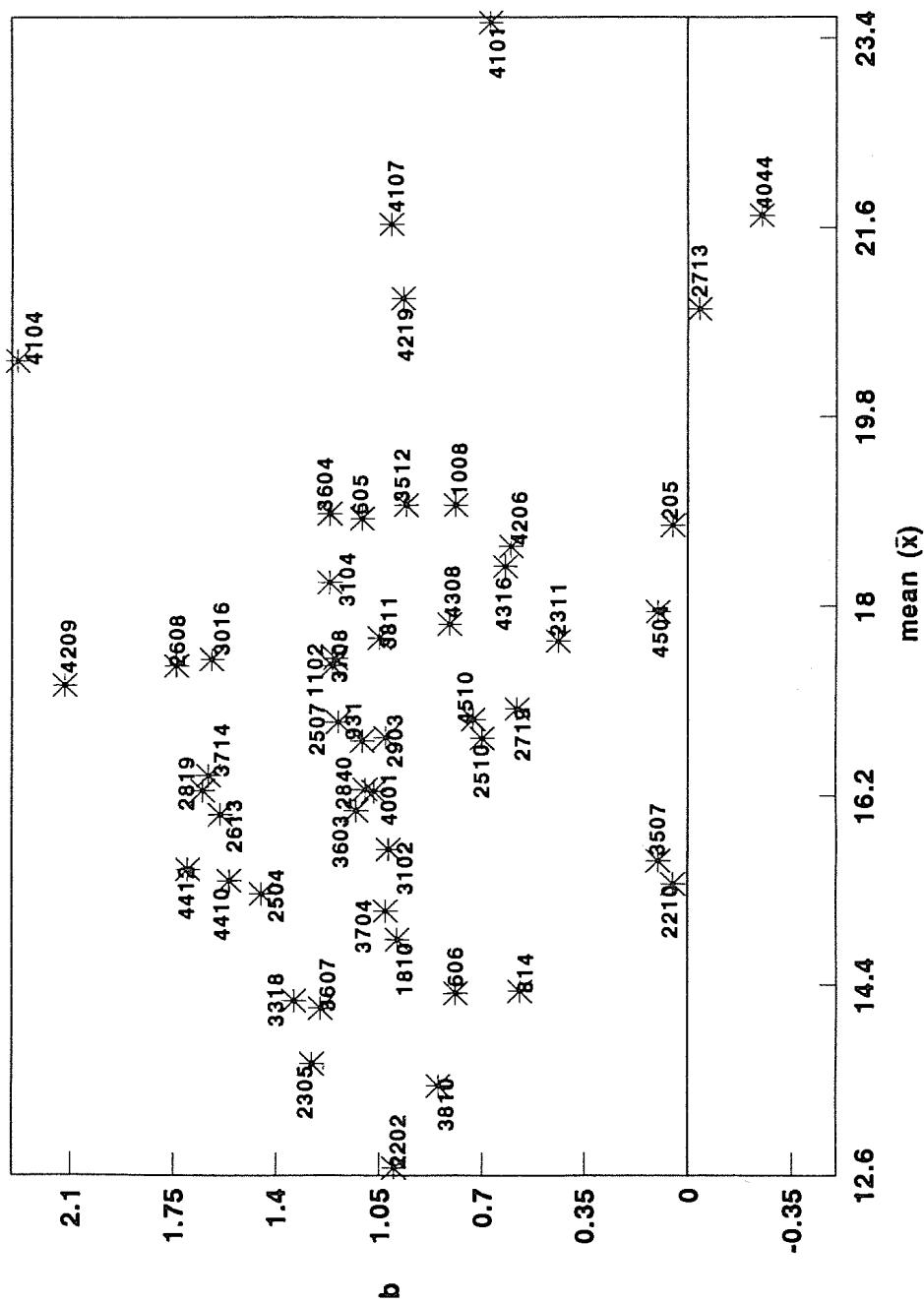
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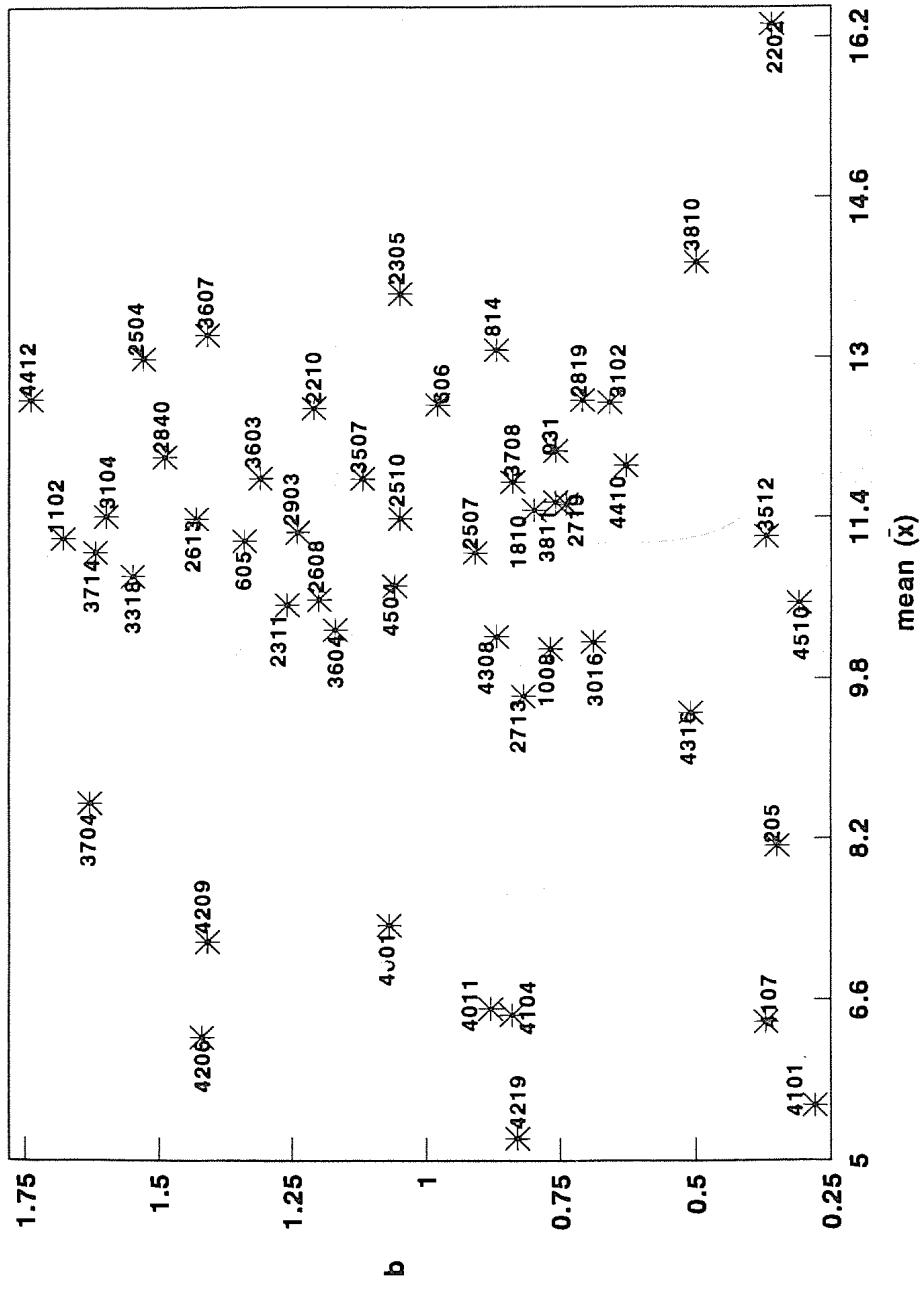
**Fig.7 MEAN FFB OF PROGENIES AND
REGRESSION COEFFICIENT (b)**



**Fig.8 MEAN BUNCH NUMBER OF PROGENIES
AND REGRESSION COEFFICIENT (b)**



**Fig.9 MEAN AV. BUNCH WEIGHT OF PROGENIES
AND REGRESSION COEFFICIENT (b)**



GENOTYPE-ENVIRONMENT INTERACTION IN OIL PALM CLONES

by

Lee Chong Hee¹ and C. R. Donough¹

ABSTRACT

Several oil palm clones from selected and unselected ortets were established in two series of clone trials. In the first series, five clones and three D x P controls were evaluated at three locations for six years. Results indicated no significant genotype-environment interaction for the D x P controls in terms of FFB yield. However, highly significant clone x location, clone x year, clone x year x location interaction effects were obtained for FFB yield and its components. In the second series of trials, six clones were evaluated at two planting densities and three locations for six years. Significant clone x location, clone x year, clone x year x location, clone x density x location interactions were observed for FFB yield and with few exceptions, for its components as well. Clone x density interaction effect was not significant in this study. The combined analyses of variance for some bunch and fruit components were also presented.

Among the seven clones evaluated in both series of trials, clone 54A out yielded D x P controls by an average of 14.1% on both coastal and inland soils. Clone 90A out yielded the D x P controls by 9.7% only on coastal soils but was lower yielding on inland soils. The other clones were generally lower yielding.

Using the genotype-grouping technique, the D x P controls were found to be high yielding and stable over the environments tested. Among the clones evaluated, only clone 54A was high yielding and stable. The other clones were generally found to have high variability in performance over the environments evaluated.

INTRODUCTION

Genotype-environment interaction has in recent years gained importance in oil palm breeding programmes. Plant breeders are interested in developing cultivars which yield consistently well under different environments. As a result, oil palm DxP hybrids are now being evaluated over different locations to study its responses from one environment to another.

There have been a number of studies carried out on genotype-environment interaction in the oil palm. Rosenquist (1982) and Rajanaidu *et al* (1986) reported the absence of genotype-environment

1. OPRS Banting, Golden Hope Plantations Sdn. Bhd.

2. Pamol Plantations Sdn. Bhd.

interaction in the materials they evaluated. Chan *et al* (1986) found no GxE interaction for FFB yield in three sets of trials while in two other sets, GxE interaction was significant for FFB yield and its components. Significant GxE interaction for yield was also reported by Obisesan and Fatunla (1983), Ong *et al* (1986), Lee *et al* (1988), Rajanaidu *et al* (1989 and 1990) and Yong and Chan (1990). Rajanaidu *et al* (1983) in studying vegetative characters, found significant GxE interaction in most of these characters.

The genotype-environment studies reported in the foregoing were carried out on DxP hybrids and other oil palm progenies. Ever since oil palm could be propagated vegetatively by means of tissue culture (Jones, 1974, Rabechault and Martin, 1976), trials had been established to evaluate these clonal palms. The first oil palm clone trial was established in 1977 (Corley *et al* 1981). Initially, the clones evaluated were derived from unselected ortets. It was only from 1981 onwards that clones from selected ortets were planted for field evaluation. Several clones were then planted on several locations and Corley *et al* (1988) had reported on the performance of these clones based on some early results. They found that there was significant clone x year interaction and based on the performance of the clones at different locations they suggested that clone x location interaction may be important.

This paper describes two series of clone trials established in three locations to study the genotype x environment interaction in oil palm clones. The performance of these clones in relation to commercial DxP planting materials are also discussed.

MATERIALS AND METHODS

The trials described in this paper were part of the Bakasawit clone trials programme. Bakasawit was previously a partnership between Unipamol Malaysia Sdn. Bhd. (now Pamol Plantations Sdn. Bhd.) and Harrisons Malaysia Plantations Bhd. (now Golden Hope Plantations Bhd.).

In the first series of trials, five clones and three DxP controls were planted at three locations on Golden Hope estates in October 1981. The clones evaluated were 31A, 90A, 115E (from selected ortets), 926 and 960 (from unselected ortets). These three trials, HCT 2, HCT 3 and HCT 4 were located at West Estate (coastal soils: Carey Series), Diamond Jubilee Estate (inland soils: Rengam Series) and Sungai Samak Estate (coastal soils: Peat). The experimental design used was a randomized complete block design with four replications and a plot size of 8 palms per plot. The planting density at the three locations was 148 palms/hectare. A combined analysis was carried out for the three locations. Years were considered as years following commencement of yield recording/harvesting (April 1984 to March 1990).

In the second series of trials, six clones were planted at three locations, of which two were on Golden Hope estates (HCT 5 and HCT 6) and one on Pamol Plantations estate (PCT 11). The clones evaluated were 31A, 54A, 90A, 115E (from selected ortets), 960 and 997 (from unselected ortets). These three trials HCT 5, HCT 6, and PCT 11 were established in December 1981, November 1981 and May 1981 respectively. They were located at North Estate (coastal soils: Selangor Series), Sepang Estate (inland soils: Serdang/Munchong Series) and Pamol Estate (inland soils: Batu Anam Series) respectively. There were two planting densities for the three trials, one of which was 138 palms/hectare and the other, at a higher density, was 161 palms/hectare for HCT 5/HCT 6 and 173 palms/hectare for PCT 11. The experimental design used was a randomized complete block design with three replications and a plot size of 10 palms per plot for each density. A combined analysis was carried out over the densities and locations. Years were considered as years following commencement of yield recording/harvesting (May 1984 to April 1990 for HCT 5, February 1984 to January 1990 for HCT 6, and March 1983 to February 1989 for PCT 11). The DxP controls were excluded from the analysis as HCT 5/HCT 6 had 3 DxP controls and PCT 11 had only 1 DxP control. Furthermore, the DxP control

from PCT 11 was from a different source.

In the statistical analyses of both series of trials, all effects except replications were considered fixed. FFB yield in the analysis was expressed in tonnes per hectare while bunch number was on per palm basis. The relative stability of the clones and DxP controls was classified for both series of trials using the genotype-grouping technique proposed by Francis and Kannenberg (1978).

RESULTS AND DISCUSSION

Genotype Environment Interaction

In the first series of trials involving HCT 2, HCT 3 and HCT 4, the combined analyses of variance for FFB yield and its components (bunch number and mean bunch weight) are presented in *Table 1*. Results of the analyses indicated that location, genotype (DxP hybrids and clones), genotype x location, year, year x location, genotype x year and genotype x year x location were highly significant for FFB yield and its components.

In order to compare the performance of the DxP controls and the clones separately in these trials, the sum of squares were partitioned into components by the contrast method for genotype, genotype x location (*Table 2*), genotype x year and genotype x year x location (*Table 3*). In the case of FFB yield, the three components of the genotype, that is, between groups (DxP hybrids vs clones), DxP hybrids (DP) and clones were all significant. This indicated that there were significant differences in yield performance among the three DxP controls and the five clones evaluated in these trials. However, it is interesting to note that DP x location, DP x year and DP x year x location were non-significant whereas clone x location, clone x year and clone x year x location were highly significant. This indicated that clones were more sensitive in their relative performance to environmental changes than the DxP hybrids. As clones are basically single genotypes, their interactions with the environment are likely to be greater than with the DxP hybrids which are a mixed group of genotypes (Corley *et al*, 1988). The DP x location was found to be significant for bunch number but not significant for DP x year and DP x year x location. These interactions were however highly significant for mean bunch weight. In the case of clones, all the interactions with year and location and the second order interaction were highly significant for bunch number and mean bunch weight.

The combined analyses of variance for some bunch and fruit components of HCT 2, HCT 3 and HCT 4 are presented in *Table 4*. These analyses were included to provide additional information on the genotype-environment interaction of the materials evaluated. Location effects were highly significant for fruit to bunch (F/B), kernel to fruit (K/F) and oil on wet mesocarp (O/WM), but were not significant for mesocarp to fruit (M/F) and oil to bunch (O/B).

Among the materials evaluated, there were no significant variation among the three DxP controls used for all the characters except F/B. In the case of the clones, highly significant differences were detected among the five clones evaluated for all the bunch and fruit component characters. The genotype x location interaction was significant only for F/B, M/F and K/F but not for O/WM and O/B. In partitioning the genotype x location interaction into components, it was found that its significance was mainly due to the DxP hybrids versus clone x location interaction. The DxP hybrids x location interaction was non-significant for all the characters, and in the case of clone x location interaction, only in F/B it was found to be highly significant. Thus, this indicated that generally for DxP hybrids and clones, there is consistency in their relative performance over the three locations for bunch and fruit components.

Table 1. Analyses of variance for ffb yield and its components (HCT2/HCT3/HCT4)

Source	df	Mean Squares		
		FFB Yield (t/ha)	Bunch No.	Mean Bunch Weight
Location (L)	2	7476.196**	4591.212**	78.036**
Rep/L	9	34.069	7.247	4.649
Genotype (G)	7	474.643**	168.723**	149.877**
G x L	14	103.279**	41.758**	20.993**
G x Rep/L	63	22.800	8.363	2.027
Year (Y)	5	5199.265**	398.948**	1760.167**
Y x L	10	670.201**	240.063**	52.748**
G x Y	35	39.623**	57.393**	12.891**
G x Y x L	70	38.900**	13.945**	4.101**
Error	360	9.158	3.828	0.496

** Significant at 0.01 probability level.

Table 2. Analyses of variance: partitioning genotype and genotype x location into components for ffb yield and its components (HCT 2/HCT 3/HCT 4)

Source	df	Mean Squares		
		FFB Yield (t/ha)	Bunch No.	Mean Bunch Weight
Genotype (G)	7	474.643**	168.723**	149.877**
DP vs C (Betw. Gp)	(1)	1086.406**	179.055**	90.159**
DxP Hybrids (DP)	(2)	111.425*	89.931**	15.238**
Clone (C)	(4)	503.311**	205.535**	232.126**
G x Location	14	103.279**	41.758**	20.993**
Betw. Gp x L	(2)	73.959*	12.738 NS	53.248**
DP x L	(4)	18.120 NS	24.924*	6.028*
C x L	(8)	153.188**	57.431**	20.413*
G x Rep/L	63	22.800	8.363	2.027

*, ** Significant at 0.05 and 0.01 probability levels respectively.

NS Non-significant.

Table 3. Analyses of variance: partitioning genotype x year and Genotype x year x location into components for ffb yield and its components (HCT 2/HCT 3/HCT 4)

Source	df	FFB Yield (t/ha)	Mean Squares		Mean Bunch Weight
			Bunch No.		
Genotype x Year	35	39.623**	57.393**		12.891**
Betw. Gp x Y	(5)	25.399*	63.509**		9.242**
DP x Y	(10)	12.141 NS	6.952 NS		2.205**
C x Y	(20)	56.920**	81.085**		19.147**
G x Y x Location	70	38.900**	13.945**		4.101**
Betw. Gp x Y x L	(10)	40.350**	9.970**		5.108**
DP x Y x L	(20)	10.540 NS	3.902 NS		1.055**
C x Y x L	(40)	52.717**	19.960**		5.372**
Error	360	9.158	3.828		0.496

*, ** Significant at 0.05 and 0.01 probability levels respectively.

NS Non-significant.

Table 4. Analysis of variance for bunch and fruit components (HCT 2/HCT 3/HCT 4)

Source	df	F/B	M/F	Mean Squares		
				K/F	O/WM	O/B
Location (L)	2	231.240**	2.354 NS	4.445**	110.499**	1.595 NS
Rep/L	9	6.427	2.619	0.481	3.679	1.938
Genotype (G)	7	254.459**	194.773**	29.275**	29.741**	20.261**
DP vs C (Betw. Gp)	(1)	96.928**	38.449**	18.701**	47.597**	8.634*
DxP Hybrids (DP)	(2)	26.669**	4.164 NS	1.213 NS	1.620 NS	2.012 NS
Clone (C)	(4)	407.737**	329.158**	45.949**	39.338**	32.293**
G x L	14	17.977**	6.576*	2.133**	4.103NS	2.354 NS
Betw. Gp x L	(2)	32.608**	32.148**	9.520**	2.778NS	0.258 NS
DP x L	(4)	1.286 NS	1.799 NS	1.207 NS	2.803 NS	0.703 NS
C x L	(8)	22.665**	2.572 NS	0.750 NS	5.084 NS	3.703 NS
Error	63	4.843	2.766	0.747	3.164	1.954

*, ** Significant at 0.05 and 0.01 probability levels respectively.

NS Non-significant.

In the second series of trials involving HCT 5, HCT 6 and PCT 11, the combined analyses of variance for FFB yield and its components are presented in Table 5. The environmental factors considered in this study, that is, location, density and year were variable enough to cause significant differ-

ences in FFB yield and its components, except for density effects in the case of mean bunch weight. The six clones evaluated, four of which were from selected ortets and two from unselected ortets showed highly significant differences in these yield characters. The clone x location, clone x year, clone x density x location and clone x year x location interactions were significant for FFB yield and bunch number. This further supports the results obtained in the first series of trials indicating that genotype-environment interaction exists in oil palm clones and affects the relative performance of the different clones from one environment to another. However, in this series of trials, clone x density, clone x year x density, and clone x year x density x location interactions were not significant for FFB yield and bunch number for the six years of recording. In the case of mean bunch weight, clone x location, clone x density, clone x density x location, and clone x year x density x location interactions were non-significant, while the other interactions, clone x year, clone x year x location, and clone x year x density were highly significant.

Table 5. Analyses of variance for ffb yield and its components (HCT 5/HCT 6/PCT 11)

Source	df	Mean Squares		
		FFB Yield (t/ha)	Bunch No.	Mean Bunch Weight
Location (L)	2	625.458**	112.894*	112.596**
Density (D)	1	373.654*	133.026*	1.185 NS
L x D	2	20.298 NS	8.009 NS	4.104 NS
Rep/D/L	12	53.343	18.147	3.282
Clone (C)	5	674.554**	1352.240**	356.582**
C x L	10	78.666**	29.817**	1.717 NS
C x D	5	16.809 NS	7.266 NS	2.297 NS
C x D x L	10	41.263**	8.937*	2.201 NS
C x Rep/D/L	60	14.122	3.950	2.107
Year (Y)	5	7887.823**	716.850**	1665.637**
Y x L	10	1438.198**	575.584**	36.585**
Y x D	5	31.506**	28.982**	1.751*
C x Y	25	46.692**	122.424**	27.149**
Y x D x L	10	29.380**	15.383**	1.515**
C x Y x L	50	92.328**	61.572**	6.384**
C x Y x D	25	6.076 NS	3.398 NS	1.208**
C x Y x D x L	50	7.265 NS	2.848 NS	0.506 NS
Error	360	5.952	2.747	0.645

*, ** Significant at 0.05 and 0.01 probability levels respectively.

NS Non-significant.

In the combined analyses for bunch and fruit components of HCT 5, HCT 6 and PCT 11, location effects were highly significant for all the characters studied, but not density effects (*Table 6*). The highly significant location effects for O/B were partly due to different oil extraction methods used, with soxhlet extraction being used for HCT 5 (O/B : 25.5%) and HCT 6 (O/B : 26.1%) and cold extraction for PCT 11 (O/B : 23.6%). The cold extraction method would tend to give poorer extraction than the soxhlet method. The clones studied varied significantly in the bunch and fruit characters. The clone x location interaction was also significant for all these characters studied. However, clone x density and the clone x density x location interactions for these characters were not significant.

The variance components for FFB yield, bunch number and mean bunch weight were estimated by equating mean squares to the appropriate expected mean squares. The importance of the various components as sources of variation is indicated by their relative magnitude and the statistical significance. Results (*Table 7*) for HCT 2, HCT 3 and HCT 4 indicated that for FFB yield, the genotype x year x location was the largest of the interaction components and in the case of bunch number, the genotype x year interaction component was the largest. Both interaction components were larger than

the genotypic variance component. In the case of mean bunch weight, the interaction components were smaller than the genotypic component.

Table 6. Analyses of variance for bunch and fruit components (HCT 5/HCT 6/PCT 11)

Source	df	F/B	M/F	Mean Squares		
				K/F	O/WM	O/B
Location (L)	2	79.296**	30.741**	8.307**	210.117**	59.549**
Density (D)	1	7.179 NS	0.274 NS	0.311 NS	0.254 NS	0.719 NS
L x D	2	3.659 NS	1.912*	0.519*	3.647 NS	0.550 NS
Rep/D/L	12	4.730	0.400	0.107	5.178	3.069
Clone (C)	5	500.658**	920.068**	86.292**	101.290**	75.570**
C x L	10	6.975**	4.451**	1.298**	3.287*	3.408*
C x D	5	2.678 NS	0.775 NS	0.299 NS	0.643 NS	0.353 NS
C x D x L	10	1.510 NS	0.677 NS	0.274 NS	1.529 NS	0.533 NS
Error	60	1.672	1.030	0.208	1.576	0.869

* , ** Significant at 0.05 and 0.01 probability levels respectively.

NS Non-significant.

Table 7. Estimates of variance components for ffb yield and its components (HCT 2/HCT 3/HCT 4)

Component	FFB Yield	Bunch No.	Mean Bunch Weight
S^2_G	6.276	2.227	2.053
S^2_{GL}	3.353	1.391	0.790
S^2_{GY}	2.539	4.464	1.033
S^2_{GYL}	7.436	2.529	0.901
σ^2_E	9.158	3.828	0.496

S^2_G = variance component due to genetic difference among genotypes (D x P hybrids and clones)

σ^2_E = error variance

The variance component estimates for the combined analyses of HCT 5, HCT 6 and PCT 11 are presented in *Table 8*. In the case of FFB yield, the clone x year x location was the largest of the interaction component, and was also found to be larger than the clone variance component. For bunch number and mean bunch weight, the clone variance component was found to be more important than the various interaction components. However for bunch number and mean bunch weight, clone x year x location and clone x year were the largest of the interaction components respectively. Both clone x year x location and clone x year contributed the major proportion of the GxE interaction for these yield components. GxE interaction in oil palm clones contributed a large proportion to the total genetic variances for FFB yield and its components as compared to oil palm progenies which had relatively smaller contribution (Rajanaidu *et al*, 1989 and 1990; Yong and Chan, 1990).

The results from the combined analyses of variance and the variance components have indicated the importance of genotype-environment interaction in oil palm clones. It is therefore important to evaluate oil palm clones over different locations and over several years. Corley *et al* (1988) suggested that at least five years' yield records may be needed to give a good indication of a clone's potential. Based on the six years of yield records, clone x density interaction was not significant, and its variance component was rather small and not important in relation to the other interaction components.

Table 8. Estimates of variance components for ffb yield and its components (HCT 5/HCT 6/PCT 11)

Component	FFB Yield	Bunch No.	Mean Bunch Weight
S^2_C	6.115	12.484	3.282
S^2_{CD}	0.050	0.061	0.004
S^2_{CL}	1.793	0.719	0.000
S^2_{CY}	2.263	6.649	1.472
S^2_{DL}	1.508	0.277	0.005
S^2_{CYL}	14.396	9.804	0.957
S^2_{CYD}	0.014	0.072	0.063
S^2_{CYDL}	0.438	0.034	0.000
σ^2_E	5.952	2.747	0.645

S^2_C = variance component due to clones

σ^2_E = error variance

Yield Performance of Oil Palm Clones

The FFB yield performance of the oil palm clones studied was compared with commercial seedling materials or D x P controls in *Table 9*. The D x P yield was an average of 3 D x P controls except PCT 11 which had only one. The low yields recorded in HCT 5 for all the materials tested was due to a pest outbreak in April 1986 which affected FFB yields for over a year.

Results indicated that clone 54A from a selected ortet out yielded the D x P controls on both coastal and inland soils by an average of 14.1%. The results also suggested that clone 54A was rather stable in yield performance as it was high yielding in all the locations evaluated.

Table 9. Mean ffb yield (t/ha/year) of oil palm clones and seedling materials

Trials	31A	54A	90A	115E	926	960	997	D x P
HCT 2	26.1	-	33.8	29.7	24.7	21.6	-	29.8
HCT 4	28.1	-	33.8	26.0	28.3	27.6	-	30.2
HCT 5A	18.5	24.6	23.0	14.7	18.3	18.9	20.9	21.4
HCT 5B	17.2	27.3	25.3	19.7	21.3	21.2	22.9	23.9
Mean % of DxDP(Coastal)	84.8	114.6	109.7	84.2	87.8	85.2	96.8	100
HCT 3	16.3	-	17.3	19.3	13.4	15.6	-	20.4
HCT 6A	16.1	23.4	16.9	17.4	16.8	16.3	21.2	21.6
HCT 6B	20.6	23.8	19.0	18.0	15.5	15.9	19.9	19.6
PCT 11A	16.2	19.4	19.0	15.9	-	15.2	17.1	18.4
PCT 11B	17.6	23.5	18.0	17.8	-	16.0	18.2	19.5
Mean % of DxDP(Inland)	87.6	113.9	91.1	88.9	74.2	79.6	96.5	100
Overall Mean % of DxDP	86.4	114.1	99.4	86.8	82.0	82.1	96.6	100

A : Planting density of 138 palms/ha

B : Higher planting density (HCT 5/HCT 6 at 161 palms/ha and PCT 11 at 173 palms/ha)

Clone 90A, also from a selected ortet out yielded the D x P controls by an average of 9.7% on coastal soils but was found to be lower yielding on inland soils. This demonstrates the importance of multi-lokalional evaluation of oil palm clones in view of the genotype-environment interaction.

The other clones evaluated were lower yielding than the D x P controls. These were clones 31A and 115E from selected ortets and clones 926, 960 and 997 from unselected ortets.

The number of oil palm clones evaluated in these two series of trials was rather limited as these were the initial few clones propagated from selected ortets. With extensive evaluation of a large number of oil palm clones, more high yielding clones could be identified.

Yield Stability

The analysis of variance only provides information on the existence and magnitude of genotype-environment interaction, but no information on the identification of stable genotypes. There are several methods used in the identification of stable genotypes.

The method used in this study is the genotype-grouping technique (Francis and Kannenberg, 1978) which subdivides the genotypes studied into four groups based on their yield and coefficient of variation (CV). These four groups are as follows:-

- High mean yield and low CV - Group I
- High mean yield and high CV - Group II
- Low mean yield and low CV - Group III
- Low mean yield and high CV - Group IV

Those genotypes that falls into group I are considered as stable genotypes since they have high mean yield and consistent performance or low CV.

This technique was used on both series of trials. In Figure 1, involving trials HCT 2, HCT 3 and HCT 4, only the D x P controls were found to be stable, that is, high yielding and low CV. These D x P controls, D x P 1, D x P 2 and D x P 3 were D x P hybrids from Golden Hope Oil Palm Research Station. D x P 1 was mixed commercial D x P planting materials, D x P 2 was mixed D x P hybrids from four identified progenies and D x P 3 was a D x P hybrid family, BM 207/8 x BM 119/16.

Clone 90A was high yielding but had high CV (Group II). The remaining clones were in group IV, that is, low yielding and high CV.

The classification of the genotypes in the first series of trials confirmed the results obtained in the combined analysis of variance whereby the interactions of D x P controls with location, year and year x location were non-significant and clone x environment interactions were highly significant.

In the second series of trials, only HCT 5 and HCT 6 were used for this genotype-grouping technique as both trials have common clones and D x P controls (Figure 2). The D x P controls used were also from Golden Hope Oil Palm Research Station. Results indicated that the D x P controls, D x P 1, D x P 2 and D x P 3 were high yielding and stable (Group I) over the different environments tested (location, density and year). D x P 1 was mixed commercial D x P planting materials, D x P 2 was mixed D x P hybrids from five identified progenies and D x P 3 was a D x P hybrid family, BM 207/8 x BM 119/16.

Clone 54A was the only clone found to have high FFB yield and low CV (Group I). As ob-

served in the first series of trials, clone 90A was also classified in Group II together with clone 997. The other clones, 31A, 115E and 960 were classified under Group IV which was low yielding and high variability in performance.

CONCLUSIONS

Genotype-environment interaction was found to be an important source of variation in oil palm clones as it affected their relative performance from one environment to another. Studies with several oil palm clones indicated the necessity to evaluate clones over different locations and over several years.

Although clones were found to be more sensitive in their relative performance to environmental changes, it was still possible to identify high yielding and stable clones as indicated in this study. Furthermore, clones for specific environment can also be identified. With extensive field testing of a large number of oil palm clones, it is possible to identify more high yielding and stable oil palm clones. Unfortunately, oil palm tissue culture is currently suffering from a temporary setback as a result of the abnormalities in inflorescence and bunch development. It is hoped that these abnormality problems can be resolved as soon as possible paving the way for oil palm clones to be commercial planting materials of the future.

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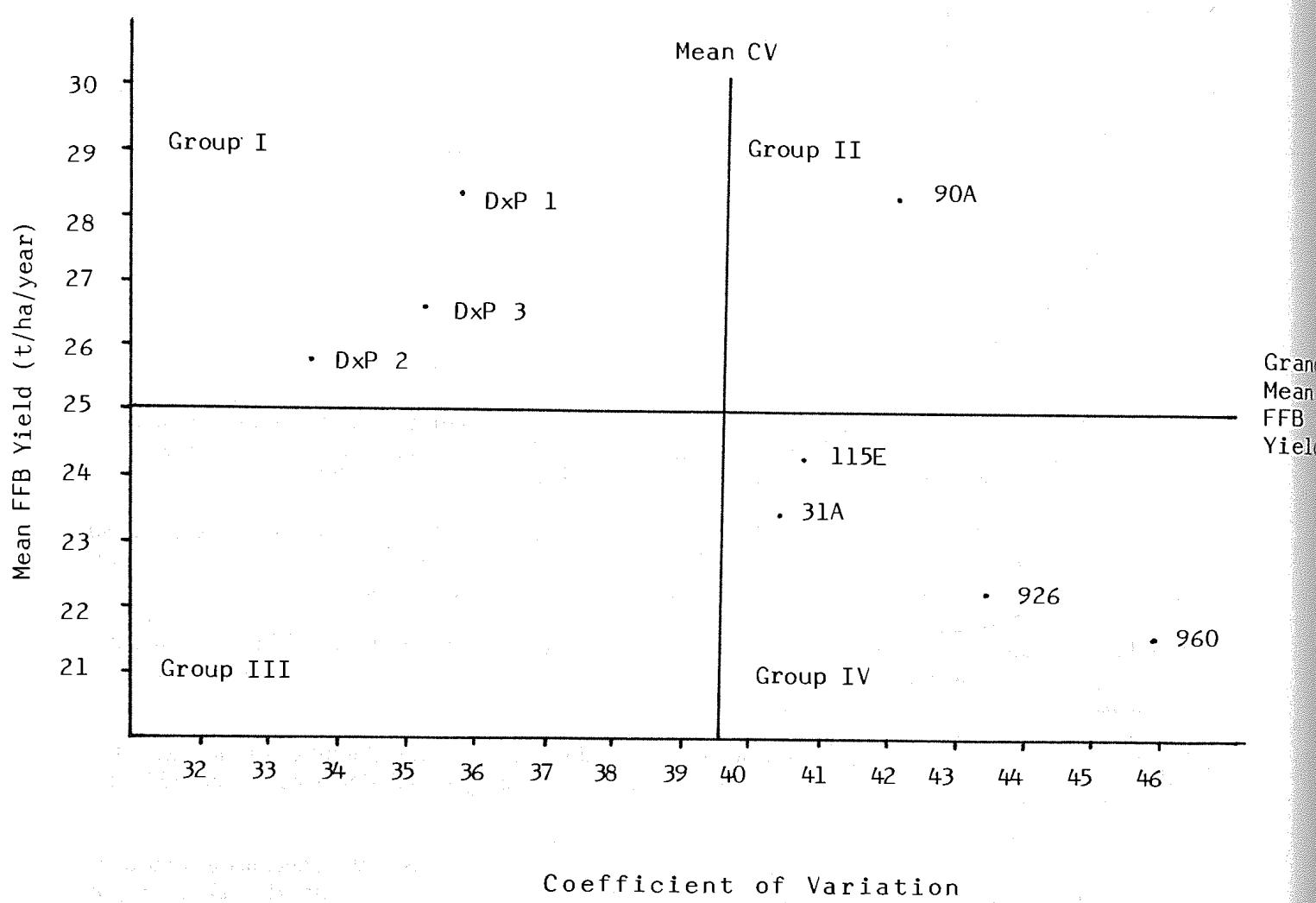


Figure 1. Mean FFB yield of 5 oil palm clones and 3 DxP controls with their CV over 18 environments (HCT 2/HCT 3/HCT 4).

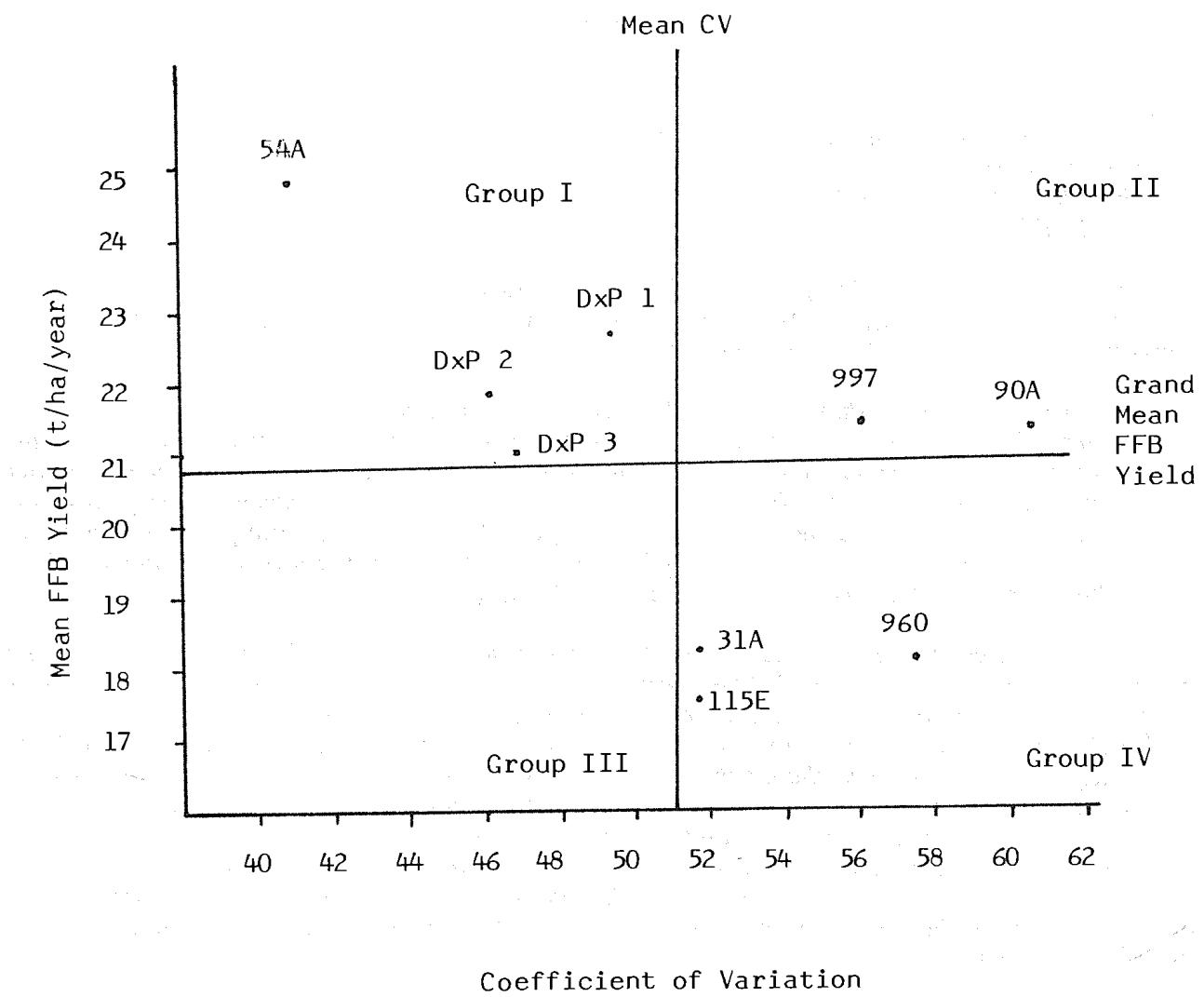


Figure 2. Mean FFB yield of 6 oil palm clones and 3 DxP controls with their CV over 24 environments (HCT 5/HCT 6).

YIELD OF OIL PALM PROGENIES IN ZAIRE, CAMEROUN AND MALAYSIA

by

R.H.V.Corley¹, Tan Y.P.², I.N.Timti³ and W.de Greef⁴¹

ABSTRACT

If genotype \times environment interactions occur, then performance in one environment will not be a reliable predictor of performance in other environments. For a perennial crop, this is a serious problem, as it is not practicable to test each new genotype in more than a very limited range of environments. Therefore, it is important to try to understand why interactions occur, so that performance becomes predictable.

We have studied the yield of DxP oil palm progenies planted at Binga (Zaire), Lobe (Cameroun) and Jenderata (Malaysia), in 1974. Our objective was to use data from Lobe to predict yield, and to identify the best crosses, at the other two sites.

There was little relationship between yield at Binga and at Lobe ($r = 0.28^*$, 54 d.f.), indicating that $G \times E$ effects are important. Losses to vascular wilt, caused by *Fusarium oxysporum*, were heavy in Zaire, and if the most susceptible crosses were excluded, then the correlation between yield at Binga and at Lobe was much improved ($r = 0.73^{***}$, 39 d.f.). There was also a tendency for progenies with above average bunch weight at Lobe to yield relatively poorly at Binga; if those progenies with the heaviest bunches were excluded, then the correlation between Lobe and Binga was further improved, to a level allowing fairly reliable prediction ($r = 0.81^{***}$, 27 d.f.).

The correlation between Lobe and Jenderata was reasonable ($r = 0.54^{***}$, 54 d.f.), but the best progenies at Lobe, which yielded 20% above the mean, averaged only 3% above the mean at Jenderata. The correlation was not improved by excluding wilt susceptible progenies, as expected, since wilt does not occur at either station. In contrast to Lobe and Binga, where the progenies with the heaviest bunches yielded less than the mean, at Jenderata such progenies yielded more than average, while progenies with high bunch numbers yielded relatively poorly. To combine both components, progenies with a weight/number ratio less than 1.0 at Lobe were excluded; this improved the correlation between Lobe and Jenderata ($r = 0.68^{***}$, 32 d.f.). Most of the lowest yielding progenies at Jenderata are shorter than average, and have small leaf area. Exclusion of all short progenies did not improve the correlation, but exclusion of those with below average leaf area gave a higher correlation ($r = 0.76^{***}$, 15 d.f.).

Selection of the best 10% of progenies, based on Lobe data, gave a yield increase at Binga within 10% of that achievable by direct selection in situ, but at Jenderata the best that could be achieved was only 60% of that from direct selection.

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INTRODUCTION

For many years it was thought that genotype x environment interactions were not very important in the oil palm. In several studies, no significant interactions were found (*Table 1, A*), while Rosenquist (1982) found positive correlations between progeny means in Malaysia and PNG for yield and bunch components. Strictly speaking, these studies were of progeny x environment interactions; oil palm progenies are heterogeneous, being composed of many genotypes. In addition, in most studies either the progenies were similar in origin, or the environments compared were actually very similar. The lack of interaction is therefore not entirely surprising. In several studies, though, with more diverse genotypes or environments, significant interactions have been observed (*Table 1, B*). With the development of clonal material, such interactions are likely to become increasingly important; some evidence for clone x environment interactions has already been published (Corley *et al*, 1987). Clone x density interactions are also important (Corley and Donough, 1990).

Table 1. Summary of results of published genotype x environment studies with oil palm

Reference	Locations	Significance of Interactions			
		FFB	B.No.	B.Wt	O/B
A No significant interaction for yield					
Rajanaidu <i>et al</i> 1986a	Malaysia x 3	ns	ns	ns	ns
Rajanaidu <i>et al</i> 1986b	Malaysia x 2	ns	-	-	ns
Chan <i>et al</i> 1986 - Sel 65/1	Malaysia x 2	ns	***	***	-
- Polyallel I	Malaysia x 2	ns	*	*	-
- Diallel	Malaysia x 2	ns	ns	ns	-
B Significant interactions observed					
Obisesan & Fatunla 1983	Nigeria x years	**	**	**	-
Obisesan & Parimoo 1985	Malaysia x ?	*	*	-	-
Chan <i>et al</i> 1986 - Polyallel II	Malaysia x 2	**	***	***	-
Ong <i>et al</i> 1985	Malaysia x 4	***	***	***	***

Genotype x environment studies in other crops appear to have been dominated by statisticians. Elaborate techniques for describing the interactions have been developed, but in most crops these techniques do not seem to have led to much understanding of the reasons for interactions.

One of the major variables the annual crop breeder must contend with is variation in the weather from year to year. This variation is unpredictable, except within broad limits. Breeders have developed the concept of yield stability, or wide adaptability, but this often means accepting a genotype which does reasonably well in all environments, but may not be the best in any environment. Given the weather to contend with, the annual crop breeder may have little alternative to this approach, but perennial crop breeders can, and we suggest should, aim to identify the best progenies or clones for each environment. One cannot test all genotypes in all environments though, so we must look for means of predicting, from results at one location, likely performance at another. Thus, where interactions occur, we must understand why they occur, and which genotypes are likely to be affected.

In this paper we use data from a D x P progeny trial in Cameroun to try to predict yield of the same progenies in Zaire and Malaysia. We show that, by excluding clearly definable groups of progenies, the number to be tested could have been reduced, while still including the best. The correlation between yield in two environments may also be increased, to the point where testing in both environments might not have been necessary.

The first example concerns the effects of *Fusarium* wilt. To most breeders, perhaps, the presence or absence of a disease in a given environment is such an obvious cause of genotype x environment interaction that they hardly consider it as such. However, we see no reason in principle why all genotype x environment interactions should not be explicable in equally simple terms. Other possible causes of interactions include differences in seasonal rainfall distribution, different mean or minimum temperature, and variation in soil composition.

MATERIAL AND METHODS

The 1974 Interorigin Trials

In the early seventies, A.H.Green organised an exchange of commercial D x P crosses between different seed producers. Material from most of these origins was planted in at least 8 different locations.

The original intention was for each producer to supply a series of 30 crosses in an NCM2 design. In practice, there were many delays in transport of the seed, and germination of many crosses was poor. Although most origins were represented at most sites, the individual crosses from each origin varied from site to site, and the number of palms per cross varied both within and between sites. Yields are summarised in *Table 2*.

Table 2. Yields of D x P crosses in Interorigin Trials (tons FFB/ha.yr)
Results summarised from various sources by E.A.Rosenquist

Origin: * Location	A	B	C	D	E	F	G	H	I	Mean
Banting	28.4	28.2	26.1	24.5	-	30.3	32.3	32.6	-	28.9
Jenderata	27.6	28.0	26.7	26.9	27.0	27.8	30.9	31.6	-	28.3
Marihat	25.3	25.2	25.3	25.6	26.9	-	-	-	25.1	26.5
San Alberto	27.0	25.3	24.0	23.1	-	23.0	26.4	27.3	-	25.2
Chemara	20.9	19.6	18.8	18.9	-	18.7	21.5	21.7	-	20.0
Lobe	14.7	14.8	15.1	13.9	-	12.8	15.2	15.3	-	14.5
Binga	12.5	11.8	9.5	12.2	13.4	10.6	11.1	9.3	-	11.3
Yaligimba	10.6	10.2	9.2	11.0	10.3	8.7	10.5	9.7	-	10.0
Mean (excl Marihat)	20.2	19.7	18.5	18.6	-	18.9	21.1	21.1	-	-

* Seed sources:

A: IRHO Deli x La Me
D: Yaligimba
G: Guthrie, Chemara

B: IRHO Deli x Yangambi
E: Binga
H: H & C, Banting

C: Pamol Cameroons
F: United Plantations
I: Marihat, Indonesia

One attempt at an origin x environment analysis has been made, comparing 3 trials in Malaysia (Rajanaidu *et al*, 1986a), but it is not clear whether each origin was represented by the same crosses at all locations. If each origin was actually represented by different progenies, one might expect spurious interactions to appear in the analysis. On the other hand, an interaction between broad origins and environment is less likely than between specific crosses and environment. The Malaysian study did show significant G x E interaction for bunch number and bunch weight, but not for total bunch yield.

Sites

In this paper we have used data from the trials planted at Lobe in Cameroun, Binga in Zaire, and Jenderata in Malaysia. Some details of these environments are given in *Table 3*, together with mean yields for the progenies included in this study. Lobe and Binga both have regular annual dry seasons, but the water deficit at Jenderata is negligible. Binga is at a higher altitude, and has lower temperatures, than the other two sites. It should be noted that the periods of recording were not identical at the three sites; we assume that this did not affect relative yields much.

Table 3. General characteristics of the environments and trials studied

Site:	Lobe	Binga	Jenderata
Soil	Loam	Sandy loam	Clay
Latitude	5° N	2° 30' N	4° N
Altitude (m, approx)	50	400	9
Rainfall (mm/yr)	3478	1789	1775
Water deficit (mm/yr)	204	233	89
Sunshine hours/year	-	2208	2163
Mean max temp (°C)	30.9	27.6	32.2
Mean min temp (°C)	22.4	19.6	23.2
Main diseases	Cercospora	Fusarium	Ganoderma
Years recorded	1977 - 83	1977 - 82	1976 - 80

Planting density was approximately 140 palms/ha at all three sites; fertiliser applications were at levels standard for estates at each site.

Analysis

We have included only the 56 progenies planted at all three locations. Our objective was to use Lobe data to predict performance at Binga and Jenderata. To do this, we calculated simple correlations between progeny means at the sites. We made the assumption that the higher the correlation the more reliable would be the prediction, and we looked for clearly definable groups of progenies whose exclusion increased the correlation. At each step, we checked to see whether any of the 6 best progenies (approx 10% of the total) at the site in question had been excluded. We also selected the best 6 remaining progenies, using data from Lobe, and compared their yield with the trial mean at the site in question, to give an indication of the selection progress achievable at that site.

RESULTS AND DISCUSSION

The correlation between progeny FFB yields at Lobe and Binga was low ($r = 0.28^*$, $df = 54$). There were clearly significant interactions, therefore, and prediction of performance at Binga would not be possible from yields at Lobe. The correlation between Lobe and Jenderata yields was rather better ($r = 0.54^{***}$, $df = 54$), but not good enough for reliable prediction. Can we find reasons for these low correlations?

When the best 6 progenies were selected *in situ*, yield of those selected at Binga was 28% above trial mean, at Jenderata 21% above, and at Lobe 20% above. Selection based on data from another site was much less effective: the 6 progenies giving the best yield at Lobe yielded only 10% above the trial mean at Binga, and 3% above at Jenderata.

Vascular wilt

Lobe - Binga. Vascular wilt, caused by *Fusarium oxysporum* f.sp. *eaeidis*, is a major problem at Binga, and there were large and significant differences in susceptibility, both between origins and between progenies within origins. The worst affected progeny had lost 71% of palms after 10 years, and 5 progenies had lost over 50%, while 11 progenies showed no losses after 10 years. Yield at Binga was calculated per palm planted, rather than per survivor, and there was a highly significant negative correlation between yield and percent wilt losses ($r = -0.63^{***}$, $df = 54$).

The nursery wilt test gives a reasonable indication of resistance in the field (de Franqueville, 1984), and is now usually used to screen progenies before planting at Binga. If the test had been used for this trial, we may assume that the worst affected progenies could have been excluded. Excluding the 5 progenies with more than 50% wilt, the correlation between yields at Lobe and Binga was highly significant (*Table 4*), while excluding progenies with more than 20% wilt increased the correlation still further. Selection progress was also greatly increased: the 6 highest yielding progenies at Lobe, excluding those which were wilt susceptible, yielded 25% above the trial mean at Binga.

Table 4. Yield of progenies at Lobe and Binga

Progenies included	Number of progenies	Yield FFB Lobe	(t/ha.yr) Binga	Correlation Lobe-Binga	Selection progress(%)#
All	56	12.25	9.55	0.28*	110
Wilt losses < 50%	51	12.17	9.97	0.59***	122
Wilt losses < 20%	41	11.91	10.17	0.73***	125
Wilt < 20%, B.wt < 12 kg	29	12.09	10.38	0.81***	124
Direct selection at Binga					128

Selection progress = yield, as % trial mean at Binga, of best six progenies at Lobe, in the groups specified.

Lobe - Jenderata. Excluding wilt susceptible progenies from the Lobe-Jenderata comparison did not improve the correlation ($r = 0.51^{***}$, $df = 39$). As wilt does not occur at either site, this result was expected. Exclusion of susceptible progenies would have eliminated 4 of the 6 highest yielding at Jenderata.

Bunch number and weight

Most authors have found significant genotype x environment interactions for the yield components, bunch number and mean bunch weight (*Table 1*), but the correlations in this study were quite high, suggesting little interaction.

Lobe - Binga. For bunch number, the correlation was 0.61^{***} ($df = 54$), increasing to 0.79^{***} ($df = 39$) if the most wilt susceptible progenies were excluded. For bunch weight, the correlation was 0.64^{***} ($df = 54$), with little improvement from excluding wilt susceptible progenies.

A graph of yield at Binga plotted against that at Lobe revealed some obvious outliers, mostly

from origin F, yielding less at Binga than expected. Origin F is characterised by high bunch weight, relative to the other origins (Rajanaidu *et al*, 1986a). Palms with very high bunch weight may be unsuitable for stressful environments, because abortion of a single bunch makes a larger difference to total yield than for palms with low bunch weight and high bunch number. Yield at Binga is lower than at Lobe (*Table 4*), so we may assume that the environment imposes more stress, probably because of the longer dry season and lower temperature at Binga. This argument is supported by the data in *Table 2*: origin F does less well in the environments with lower average yield. At Banting, F yielded 5% above the trial mean, whereas at Yaligimba it gave 13% below the trial mean.

We therefore assumed that progenies with high bunch weight might be unlikely to do well at Binga, and excluded all progenies with a mean bunch weight at Lobe greater than 12 kg (this was an arbitrary figure; about 25% of progenies were excluded, but mean bunch weight increases with palm age, so the best criterion would be defined in terms of mean and standard deviation). This increased the correlation to 0.81*** (*Table 4*), and did not exclude the best 6 progenies at Binga, but selection progress was not increased.

A correlation of 0.81 is reasonable for predictive purposes, and selection progress equal to 90% of that achievable by direct selection is acceptable. In answer to the original question, as to why there was a poor relationship between yields in the two environments, we can now state, firstly, that wilt susceptible progenies yield poorly at Binga; secondly, the high bunch weight of origin F appears to be a disadvantage at Binga, though some origin F progenies yield well. An unanswered question is why high bunch weight is a disadvantage in some, but not all progenies?

A possible clue comes from comparing the high bunch weight progenies with above average yield at Binga and those with below average yield. At Lobe, the 7 better progenies had a mean bunch weight 7% higher than the 5 worse progenies, but at Binga their bunch weight was 4% lower (*Table 5*). This is not a large difference, but it suggests the possibility that bunch weight may have greater plasticity in some progenies than others.

Table 5. Yield components for progenies with mean bunch weight at Lobe above 12 kg

Yield at Binga	Number of progenies	Yield FFB Lobe (t/ha.yr)	Yield FFB Binga (t/ha.yr)	Bunch weight (kg) Lobe	Bunch weight (kg) Binga	Bunch no./palm.yr Lobe	Bunch no./palm.yr Binga
Above mean	7	12.12	10.82	13.4	9.3	6.3	8.2
Below mean	5	10.63	8.00	12.5	9.7	5.9	5.8

Bunch number of the higher yielding progenies at Binga was nearly 40% above that of the lower yielding progenies (*Table 5*), perhaps partly as a result of the plasticity of bunch weight. Although the relative change in bunch number is much greater than that in bunch weight, it should be remembered that bunch number changes in discrete steps. The rate of abortion of developing inflorescences, and their sex ratio, are affected by current yield (Breure and Corley, 1992; Corley and Breure, 1992). A small reduction in mean bunch weight, and hence in current yield, may be sufficient to prevent abortion of a future inflorescence, and thus increase bunch number by a large percentage (bunch number was only 6 to 8 per year in the high bunch weight progenies at Binga).

Plasticity of bunch weight might be screened for at a single location by studying the effect of severe pruning, which reduces bunch weight. Corley (1976) demonstrated progeny x pruning interactions for FFB yield.

Lobe - Jenderata The correlations for the yield components were high here also: for bunch number, $r = 0.83^{***}$ ($df = 54$), and for bunch weight, $r = 0.82^{***}$ ($df = 54$).

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EVALUATION OF *ELAEIS OLEIFERA X E. GUINEENSIS* INTERSPECIFIC HYBRIDS AT FIVE LOCATIONS FOR GENOTYPE X ENVIRONMENT INTERACTION

by

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ABSTRACT

A cooperative trial evaluating the performance of Elaeis oleifera (E.o) x E. guineensis (E.g) interspecific hybrids at five locations in Peninsular Malaysia and Sabah was conducted by five plantation companies, namely Golden Hope Plantations Bhd, Kumpulan Guthrie Bhd, Industrial Oxygen Incorporated (IOI), Pamol Plantations and Sime Darby Plantations, in the early eighties.

The performances of 52 E.o x E.g hybrids at these five locations of the cooperative trial were studied to determine the effects of locations, considered as environment (E), genotype (G) and GxE interaction on the fresh fruit bunch (FFB) yield and its components, bunch number and average bunch weight.

The combined ANOVA showed that the effects of the environment, genotype and GxE interaction on the FFB yield, bunch number and average bunch weight were all highly significant. High yielding and stable E.o x E.g hybrids could be identified based on the mean and variability of their performances over the five locations.

INTRODUCTION

Genotype x Environment (GxE) studies will indicate the behavior of genotype to changes in the environment. Knowledge of the GxE interaction will help determine the breeding strategies to be employed. A highly significant GxE interaction requires the breeding for stability if the cultivar is to be cultivated in diverse environments or the breeding of high yielding varieties specific to an environment if the cultivar is to be restricted to a particular environment.

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A review of GxE studies in oil palm (Yong and Chan, 1989) indicated that most of the GxE studies have been carried out with *E. guineensis*, the commercially cultivated oil palm and there is a lack of GxE studies in the *E. oleifera x E. guineensis* (*E.o x E.g*) hybrids. The *E.o x E.g* hybridization programme was initiated to incorporate the desirable attributes of the high oil unsaturation of *E. oleifera* into the high yielding *E. guineensis* (Meunier and Hardon, 1976).

The present paper on GxE studies in the *E.o x E.g* interspecific hybrids will not only add to our knowledge of GxE interactions in oil palm but will also help in formulating our breeding and selection strategies. High yielding palms with desirable oil quality and slow vertical growth characteristics arising from this interspecific hybrid programme will provide the oil palm planters with an alternative oil palm planting material.

MATERIALS AND METHODS

The present GxE studies with the *E.o x E.g* hybrids are based on the results of the evaluation of *E.o x E.g* hybrids at five locations which were jointly conducted in the early 1980's by five plantation companies, namely Golden Hope, Guthrie, Industrial Oxygen Incorporated (I.O.I), Pamol and Sime Darby. The experimental details of the co-operative trials are shown in *Table 1*.

Table 1. Evaluation of interspecific *E. oleifera x E. guineensis* (P) hybrids at five locations

	Golden Hope	Guthrie	I.O.I	Pamol	Sime Darby
Location	Carey Estate Selangor	Labu N.S	Bahau N.S	Kimansi (near Sandakan Sabah)	Sg. Buloh Estate Selangor
Soil type	Carey	Rengam	Batu Anair	Lumisir Kayah Inanam	Telok
1981-1990					
Annual Rainfall (mm)	1952	1796	1716	3149	1726
Mean Annual Raindays	116	124	144	165	136
Experimental Design	RBD	10x10 single lattice	10x10 triple lattice	10x10 single lattice	10x10 single lattice
No. of Progenies	95	100	100	100	100
No. Replicates	5	2	2	5	2
Plot size (palms/plot)	5	16	16	5	12
Density (Palms/ha)	99	99	99	99	99
Date planted	Mar '81	Dec '80	Oct '80	Nov '80	Sept '81
Yield records	1984-89	1984-89	1984-89	1984-89	1984-89

The *E. oleifera* female parents were of Colombian, Panamanian and Costa Rican origins while the *pisifera* parents were derived from commercial *pisifera* palms. Only the *E.o x E.g* hybrids which were evaluated at all five locations were considered in the present study. Fifty two hybrids were thus selected.

The fresh fruit bunch (FFB yield), bunch number and average bunch weight were taken from the cumulative production of 1984-1989.

All the five trials were combined in a single ANOVA. FFB yield, bunch number and average bunch weight were computed on per palm basis due to the different plot sizes in the various experiments.

For the combined analysis of the progeny means, the data at each location were transformed to a normal distribution with mean = 0 and variance = 1. A plot of hybrid means against standard deviation was performed to indicate the yielding ability and stability of the hybrids.

RESULTS AND DISCUSSION

The combined ANOVA of the five trials is shown in *Table 2*. Significant effects of location, progeny and progeny x location interaction on the FFB yield, bunch number and average bunch weight were obtained. Location was considered as the environment in the present study. Thus, the significant progeny x location interaction indicated a significant GxE interaction. These results were similar to those obtained by Tan (1987) in his evaluation of 12 Colombian *E.o* x *E.g* hybrids at three locations. Thus, it could be interpreted that the *E.o* x *E.g* hybrids were sensitive to the environment and that they responded in different degrees to the change in environment.

Table 2. A Combined ANOVA of the performance of 52 *Elaeis oleifera* x *Elaeis guineensis* interspecific hybrids at five locations

Source	d.f.	Mean Squares		
		FFB (kg)	B.No. (/palm/year)	Av. Bunch Wt. (kg)
Block	15	102651.66***	1001.86***	27.61***
Location (E)	4	375577.87***	3733.35***	71.20***
Progeny (G)	51	16424.94***	37.63***	13.93***
GxE	204	2524.67***	11.18***	3.11***
Residual	561	1079.16	5.84	1.45

*** : Significant P<0.001

The FFB yield, bunch number and average bunch weight of the 52 *E.o* x *E.g* hybrids at the five locations are shown in *Tables 3, 4, and 5* respectively.

The mean FFB yield of the 52 hybrids at the five locations ranged from 73 kg/palm/year at Bahau estate to 201 kg/palm/year at Carey estate. The FFB yields obtained from Sungai Buloh estate and Kimansi estate were moderately high. The low yield obtained in Bahau probably arose from the low and poor distribution of rainfall. Bahau was known to have distinct rainfall deficit months. However, a high rainfall did not guarantee a high yield as yield in Kimansi was not the highest although it received substantially more rainfall than Carey estate or Sungai Buloh estate.

Among the locations in Peninsular Malaysia, yields obtained in the coastal areas of Carey estate and Sungai Buloh estate were relatively higher than the inland areas of Labu estate and Bahau estate. Tan (1987) had also found higher yields of *E.o* x *E.g* on coastal soils compared to that obtained on inland soils. Location as an environment is the combined effect of the soil type, climate, agronomic inputs and their interactions and more detailed studies would be required to unravel this environmental 'black box'.

Table 3. The 5-year cumulative fresh fruit bunch (FFB) yield (kg/palm/year) of 52 *Elaeis oleifera* x *Elaeis guineensis* hybrids at 5 locations

Progeny No.	Progeny Code	Location (Estates)				
		Labu	Carey	Bahau	S.Buloh	Kimansi
1	SA91	178.8	264.7	146	304.2	276.8
2	SA90	165.8	180.2	121.6	271.1	240.2
3	SA 4	158.2	162.2	126.9	239.6	206.0
4	SA10	149.7	216.2	90.4	236.7	223.5
5	SA11	163.8	173.6	100.9	247.1	222.5
6	SA 7	85.9	199	47.5	137.0	130.9
7	SA 9	130.8	188.3	82.7	208.5	196.7
8	SA 3	151.3	154.1	98.3	210.4	220.4
9	SA 2	144.4	264.9	73.5	236.2	165.0
10	SA72	187.5	237.3	103.4	217.2	281.3
11	SA77	138.5	265.9	57.6	178.0	178.3
12	SA23	142.3	256.6	37.7	199.2	168.9
13	SA73	120.8	218.2	104.8	219.8	192.2
14	SA46	157.1	166.4	89.6	239.1	206.4
15	SA79	143.8	218.3	84.8	214.7	185.7
16	SA17	95.1	145.3	36	78.3	118.4
17	SA18	149.3	114.1	121.4	209.2	232.4
18	SA14	80.1	167.3	54.5	127.1	112.3
19	SA21	84.4	287.1	37.6	124.5	149.9
20	SA16	75.3	149.1	38.8	101.2	115.3
21	SA 1	77.8	209.6	32.9	112.7	107.0
22	SA76	110.6	217.9	104	211.5	188.2
23	MP 4	96.2	199.9	54.7	153.5	183.0
24	MP 5	90.2	122.7	58.3	139.5	163.4
25	MP 6	92.8	142.9	56.2	143.3	118.8
26	MP10	58	161	53	112.2	127.6
27	MP 8	89.9	205.7	57.6	121.9	137.0
28	MP 9	157.3	229.2	73.5	173.4	223.3
29	MP12	117.9	154.8	68	133.8	149.4
30	MP14	93.8	140.3	41.5	139.0	124.3
31	MP15	164.3	234.1	79.5	185.0	216.0
32	MP18	103.6	184.8	46.1	155.6	160.7
33	MP19	118.3	216.5	76.9	168.3	158.7
34	MP20	83.1	179.5	70	159.6	171.5
35	MP23	123.1	268.5	63.3	212.5	189.0
36	MP24	99.2	252	61.4	151.1	197.2
37	MP26	132	193.5	57.4	191.6	155.2
38	MP28	72.4	138.1	54	165.2	106.5
39	MP29	52.8	115.4	41.2	141.8	135.4
40	MP30	94.3	198.1	66.5	160.5	145.4
41	MP33	72.1	167.6	68.4	196.4	169.1
42	MP34	98	158.7	94.9	160.2	150.6
43	MP35	104.1	225.4	74.1	164.5	161.7
44	MP36	104.8	179.3	72.1	178.2	149.9
45	MP37	119.1	267.2	63	191.9	196.2
46	MP39	110.1	182.9	43.5	142.9	133.1
47	MP43	122.1	261.7	118.3	193.3	220.3
48	MP49	115.5	215.2	82.3	183.8	180.8
49	MP42	156.1	253.5	117.8	207.6	192.0
50	MP45	94.9	217.4	59	161.4	187.0
51	MP46	117.4	248	73.6	171.4	192.3
52	MP47	95.6	221.6	67.8	183.3	154.0
Mean		115.99	200.88	73.16	178.19	174.37
						148.52

Table 4. The 5-Year cumulative bunch number per year of 52 *Elaeis oleifera x Elaeis guineensis* hybrids at 5 locations

Progeny No.	Progeny Code	Location (Estates)					Mean
		Labu	Carey	Bahau	S.Buloh	Kimansi	
1	SA91	13.3	26.6	11.4	25.5	19.9	19.35
2	SA90	16	19.9	11.4	24.0	19.7	18.20
3	SA 4	15.1	19.5	10.4	23.2	19.5	17.53
4	SA10	13.4	21.3	8.4	20.5	17.9	16.29
5	SA11	15	17.4	9.7	22.2	19.9	16.83
6	SA 7	12.5	20.2	6.3	16.9	14.4	14.05
7	SA 9	16.6	20.1	8.4	21.4	19.3	17.15
8	SA 3	16	18.6	9.4	20.6	19.5	16.81
9	SA 2	12.4	25.1	6.6	21.5	14.4	15.99
10	SA72	14.9	23.1	8.9	20.5	20.6	17.60
11	SA77	14.6	23.6	6.3	19.0	16.7	16.03
12	SA23	14.8	24.2	5.1	21.9	16.4	16.47
13	SA73	11.6	21.6	8	19.3	16.7	15.45
14	SA46	15.8	18.3	9.4	23.1	19.1	17.15
15	SA79	16.1	23.9	8.7	22.7	19.3	18.14
16	SA17	9.1	16.2	4	7.9	11.2	9.68
17	SA18	13.2	16.4	9	17.0	16.9	14.51
18	SA14	10.6	16.4	6.3	13.8	12.2	11.87
19	SA21	10.2	24.9	5.8	14.3	14.5	13.93
20	SA16	10.6	16.5	5.5	12.7	12.7	11.59
21	SA 1	11	22.8	5.1	14.6	12.6	13.22
22	SA76	11.5	24.4	9.2	18.7	16.1	15.98
23	MP 4	11.5	19.9	5.1	15.5	16.1	13.62
24	MP 5	9.2	13.1	5.1	15.1	14.7	11.43
25	MP 6	9.3	14.4	5.1	15.6	12.3	11.33
26	MP10	7.4	16.9	4.9	12.7	11.5	10.68
27	MP 8	12.5	20.1	5.5	13.0	14.2	13.06
28	MP 9	13.4	21	6.9	17.2	17.5	15.18
29	MP12	12.4	17.3	6.4	15.0	14.3	13.08
30	MP14	9.5	15.1	4.3	14.4	12.1	11.09
31	MP15	15.1	22.4	7.5	18.7	19.4	16.61
32	MP18	10.1	19.2	4.8	15.2	13.8	12.62
33	MP19	11.5	22.1	7	17.4	14.9	14.59
34	MP20	12.1	18.9	6.7	17.4	16.5	14.31
35	MP23	12.3	23.5	5.9	19.7	13.8	15.03
36	MP24	13.3	25.9	6.7	17.6	17.6	16.23
37	MP26	13.1	21.1	6.3	21.1	15.9	15.50
38	MP28	10.6	14.5	5.1	16.7	10.4	11.46
39	MP29	9	13.7	4.6	15.3	13.4	11.19
40	MP30	10.2	19.9	5.7	16.6	12.7	13.02
41	MP33	10.1	18.6	5.9	19.6	14.8	13.79
42	MP34	12.4	16.5	7.1	16.6	13.8	13.27
43	MP35	10.1	19.5	6.9	15.9	13.9	13.25
44	MP36	11.6	19.5	7.4	19.0	14.9	14.48
45	MP37	10.9	24.7	6.4	19.2	15.4	15.32
46	MP39	10.4	19.7	5.7	16.2	12.4	12.88
47	MP43	12.8	20.8	8.9	16.8	17.9	15.44
48	MP49	10.6	20.8	6.8	18.0	15.8	14.40
49	MP42	14.9	22.6	9.3	19.5	18.3	16.92
50	MP45	9.3	20.2	5.8	15.0	15.4	13.12
51	MP46	16	25.9	8	18.6	19.4	17.58
52	MP47	12.8	22.1	6.2	20.0	15.8	15.37
	Mean	12.28	20.21	6.95	17.87	15.73	14.61

Table 5. The 5-Year cumulative average bunch weight (kg) of 52 *Elaeis oleifera* x *Elaeis guineensis* hybrids at 5 locations

Progeny No.	Progeny Code	Location (Estates)					
		Labu	Carey	Bahau	S.Buloh	Kimansi	Mean
1	SA91	13.44	9.95	12.81	11.91	13.91	12.40
2	SA90	10.36	9.06	10.62	11.30	12.20	10.71
3	SA 4	10.48	8.32	12.20	10.34	10.56	10.38
4	SA10	11.17	10.15	10.76	11.57	12.48	11.23
5	SA11	10.92	9.98	10.40	11.15	11.18	10.73
6	SA 7	6.87	9.85	7.54	8.11	9.09	8.29
7	SA 9	7.88	9.37	9.85	9.75	10.22	9.41
8	SA 3	9.46	8.28	10.26	10.24	11.30	9.95
9	SA 2	11.65	10.55	11.14	11.00	11.46	11.16
10	SA72	12.58	10.27	11.62	10.58	13.68	11.75
11	SA77	9.49	11.27	9.14	9.38	10.69	9.99
12	SA23	9.61	10.60	7.39	9.12	10.30	9.41
13	SA73	10.41	10.10	13.10	11.38	11.48	11.30
14	SA46	9.94	9.09	9.53	10.35	10.78	9.94
15	SA79	8.93	9.13	9.75	9.46	9.63	9.38
16	SA17	10.45	8.97	9.00	9.94	10.57	9.79
17	SA18	11.31	9.96	13.49	12.30	13.72	11.55
18	SA14	7.56	10.20	8.65	9.18	9.19	8.96
19	SA21	8.27	11.53	6.48	8.72	10.35	9.07
20	SA16	7.10	9.04	7.05	8.00	9.07	8.05
21	SA 1	7.07	9.19	6.45	7.70	8.51	7.78
22	SA76	9.62	11.14	11.30	11.33	11.66	11.01
23	MP 4	8.37	10.05	10.73	9.89	11.38	10.08
24	MP 5	9.80	9.37	11.43	9.25	11.13	10.20
25	MP 6	9.98	9.92	11.02	9.21	9.67	9.96
26	MP10	7.84	9.53	10.82	8.87	11.06	9.62
27	MP 8	7.19	10.23	10.47	9.36	9.67	9.39
28	MP 9	11.74	10.91	10.65	10.11	12.79	11.24
29	MP12	9.51	8.95	10.63	8.95	10.42	9.69
30	MP14	9.87	9.29	9.65	9.63	10.28	9.75
31	MP15	10.88	10.45	10.60	9.90	11.15	10.60
32	MP18	10.26	9.63	9.60	10.22	11.67	10.28
33	MP19	10.29	9.80	10.99	9.66	10.63	10.27
34	MP20	6.87	9.50	10.45	9.19	10.42	9.28
35	MP23	10.01	11.43	10.73	10.82	13.69	11.33
36	MP24	7.46	9.73	9.16	8.57	11.19	9.22
37	MP26	9.39	9.17	9.11	9.07	9.76	9.30
38	MP28	6.83	9.52	10.59	9.87	10.26	9.41
39	MP29	5.87	8.42	8.96	9.28	10.14	8.53
40	MP30	9.25	9.95	11.67	9.68	11.43	10.40
41	MP33	7.14	9.01	11.59	10.03	11.44	9.84
42	MP34	7.90	9.62	13.37	9.68	10.93	10.30
43	MP35	10.31	11.56	10.74	10.37	11.66	10.63
44	MP36	9.03	9.19	9.74	9.37	10.06	9.48
45	MP37	10.93	10.82	9.84	10.02	12.71	10.86
46	MP39	10.59	9.28	7.63	8.82	10.73	9.41
47	MP43	9.54	12.58	13.29	11.49	12.34	11.85
48	MP49	10.90	10.35	12.10	10.20	11.46	11.00
49	MP42	10.48	11.22	12.6710.63		10.51	11.10
50	MP45	10.20	10.76	10.17	10.80	12.17	10.82
51	MP46	7.34	9.58	9.20	9.22	9.92	9.05
52	MP47	7.47	10.03	10.94	9.17	9.77	9.47
	Mean	9.38	9.86	10.33	9.89	11.01	10.09

The variability in the FFB yield obtained at the various locations was due to the variability in the bunch number rather than the variability in the bunch weight. The bunch number ranged from 7 at Bahau estate to 20 at Carey estate.

The mean FFB yield of each hybrid in the five locations ranged from 97 kg/palm/year as shown by progeny number 40 to 234 kg/palm/year as shown by progeny number 1. The high FFB yield shown by progeny number 1 was the result of its high bunch number and bunch weight.

The significant GxE interaction for FFB yield and its components indicated that the hybrids responded in different degrees to the change in the environment. Hybrids with high yields and showing minimal response to changes in environment are desirable for selection and further breeding. Such high yielding and stable hybrids could be identified by plotting the mean and standard deviation of FFB yield of the hybrids as shown in *Figure 1*. Hybrids nearer the top left corner (high yield and low standard deviation) are relatively more desirable than the hybrids nearer the bottom right corner (low yield and high standard deviation). Some of the *E.o x E.g* hybrids which might be of further interest were progeny 1, progeny 49, progeny 4 and progeny 47.

CONCLUSION

The evaluation of 52 *E.o x E.g* interspecific hybrids derived from *E.o* female parents of Colombian, Costa Rican and Panamanian origins and *E.g* pisifera male parents at five locations in Peninsular Malaysia and Sabah indicated significant differences among the hybrids and locations for FFB yield, bunch number and average bunch weight. Treating the locations as environments, it was found that the GxE interaction was also significant. It is recommended that in the presence of significant GxE interaction, hybrids for selection should not only be high yielding but also show stability across different environments. Though it might be possible to breed high yielding hybrids for a specific environment, it was not likely to be beneficial as we do not completely understand the factors and their interactions that constitutes the "environment". Furthermore, some of these environmental factors would be beyond the control of the planters.

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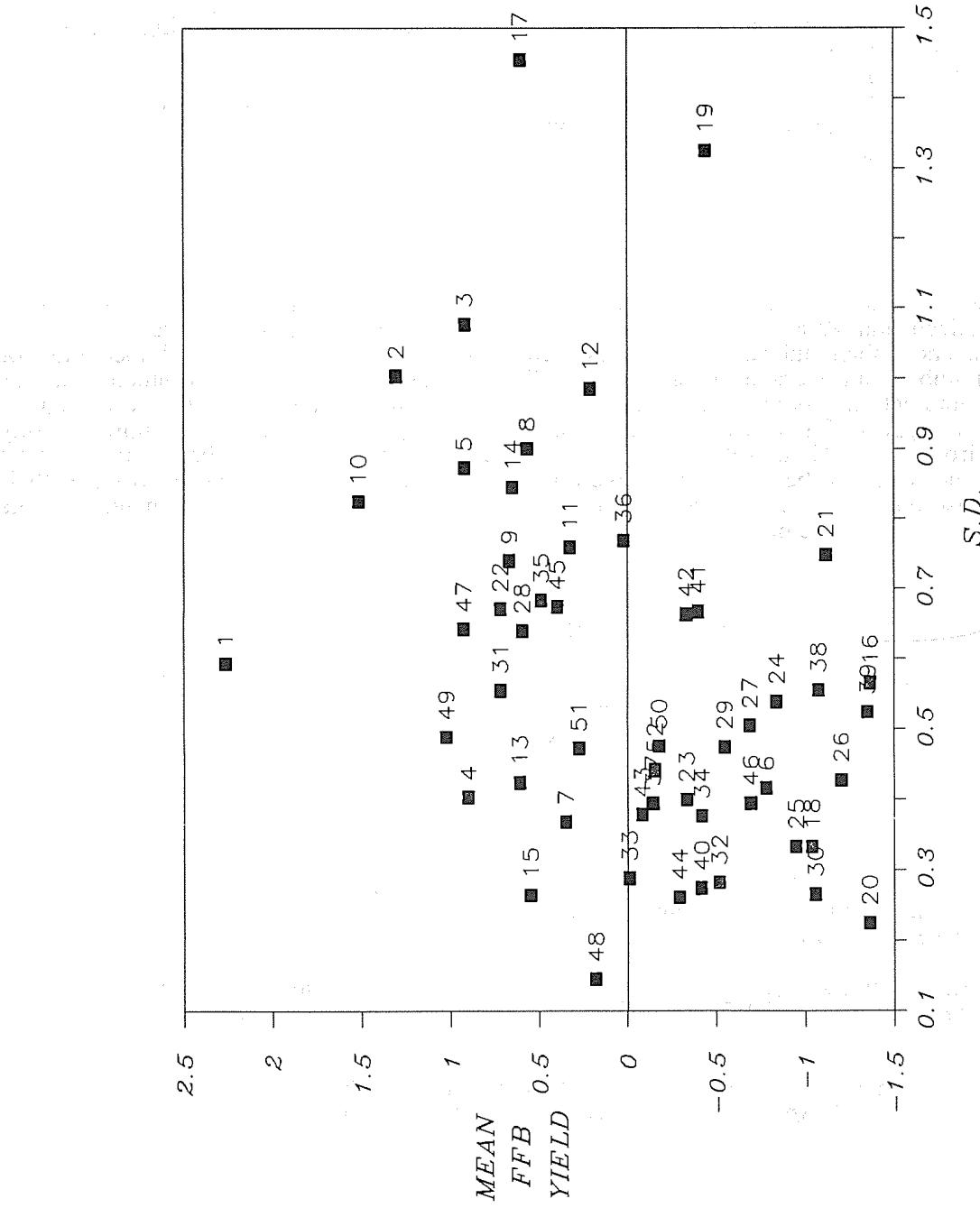


Fig 1 . The mean and standard deviation for the FFB yield of 52 E.O x E.g. hybrids.

SESSION 1 DISCUSSION

Q: Ahmad Alwi - Guthrie Research Chemara, Malaysia.

In Dr. Rajanaidu's paper, the experimental design used is the Completely Randomised Design but the analysis presented is that of a Randomised Block Design. Secondly when combining analysis over experiments the experiments must all have the same plot size as otherwise there will be different variability between experiments which has to be considered in the combined analysis.

A: Dr. N Rajanaidu - PORIM, Malaysia.

In our paper, the Completely Randomised Design has been analysed as a CRD and not a RBD.

Q: Ahmad Alwi - Guthrie Research Chemara, Malaysia.

In Dr Lee's paper when the main effect is considered fixed, can the variance component be calculated?

Secondly in your Genotype Classification you graphed the mean against the CV. I would suggest you use the SD as the CV contains the mean and are correlated parameters.

A: Dr. Lee Chong Hee - Golden Hope, Malaysia

Yes the variance components can be calculated though some or all effects are considered fixed.

Concerning the genotype grouping technique we were in fact following the model by Francis and Kannenberg. Your suggestion on mean versus S.D. is noted.

Q: Dr. R.H.V.Corley - Unilever Plantations PLC, London.

Dr. Lee mentioned a pest attack at one stage in HCT5. Clone 54A did poorly on coastal soils in the early years though it came out best over the whole period of the trial. Could there be differential susceptibility to pest attack in that trial and perhaps 54A was less affected, hence coming out ahead later on?

A: Dr. Lee Chong Hee - Golden Hope, Malaysia.

We had not looked at it specifically during the period of attack but I don't think so as subsequently 54A performed well in both environments.

Q: Dr.Ho Chai Yee - Ebor Research, Sime Darby Plantations, Malaysia.

Is there any reason why 90A was high yielding in the coastal area?

A: Dr. Lee Chong Hee - Golden Hope, Malaysia.

The high yields of 90 A are mainly attributable to high bunch number but we do not know why it does not do well on inland soils.

Q: Mr. Hew Choy Kean - Plantek (M) Sdn. Bhd., Malaysia.

Having made this correlation between three sites viz. Binga, Jendarata and Lobe and having eliminated whatever specific to the environment in terms of diseases, are the materials which are tested fairly stable in these three environments? The top performers, the best 10% or so, are still the best at all three sites, suggesting no GxE.

A: Dr. R.H.V. Corley - Unilever Plantations PLC, London.

Yes, what we looked for is a high correlation between the environments and the ability to predict yield in another environment from yield in the first, so to some extent we have actually looked for stability.

Q: Prof.P.D.S. Caligari - University of Reading, United Kingdom.

I wasn't entirely clear what your aim was. If your aim is to pick out at one site the best one or two genotypes that will do well elsewhere I think it is going to be hard work. But if your aim is to reduce the population, even reducing it by half reduces the work considerably, then I think you have a lot of scope to quite easily achieve that. My question is how intense a selection you were hoping to achieve by your methodology?

A: Dr. R.H.V. Corley - Unilever Plantations PLC, London.

We certainly could have looked at lower selection intensities. We set out with the idea of improving the correlation and I accept Choy Kean's comment that what we were trying to do was to look for yield stability. To make sure that we got the best materials, we looked at two ways of doing it; the first was to see whether we had retained the best progenies at the second site i.e. after excluding some of the progenies at Lobe and in fact very often we hadn't. Rather than drop the selection intensity too low we looked at the selection progress that could be made by prediction i.e. to identify the best at the other site, by the indirect approach.

Q: Mr. Soh Aik Chin - Applied Agricultural Research Sdn Bhd., Malaysia.

I am more interested in the effects of GxE not so much in terms of picking out the best progeny but the best individual plants either for breeding or cloning. Normally it is recommended that yield selection should be postponed to later generations of the breeding cycle as the heritability is low and heavily biased by GxE interactions operating at the individual plant level. My question is, is this GxE similar or a part of the GxE found in multi-locational or multi-seasonal progeny trials? If it is so, perhaps one can estimate the GxE by translating backwards and if not I would think of an experiment reported by IRHO consisting of clones and the recreated crosses from which the clones were obtained. They calculated heritability, in the first instance equating variation within the clones as environmental variation and deducting this from within cross variation, giving the Genotype and GxE variance. They then calculated the parent/offspring regression and since the ortet and parental cross were in different trials this estimate of h^2 would be independent of GxE and likewise with the realised h^2 . If these estimates are compared with the first then we have another estimate of GxE.

A: Prof. P.D.S. Caligari - University of Reading, United Kingdom.

The evidence we have is that those different sorts of GxE interactions are not related. Even if you take different factors in the environment, you find no correlation. So if you are going to breed in a very specific way then I certainly suggest that there is no evidence for it being the same sort of response.

There is a slight mistake in comparing the h^2 in the paper you mentioned because the realised and parent/offspring estimates are h^2 whereas the original is h^2 . Also these indirect methods of subtraction are actually subject to high error variance and I suspect the whole thing will become swamped by that. Theoretically it is a very nice approach that will step hierarchically down the system but I think in practice it will be very difficult to find anything in it.

A: Dr. R.H.V. Corley - Unilever Plantations PLC, London.

Dr. Rajanaidu showed that most of the variance in his analysis was between seedlings within progenies. That of course includes seedlings x environment, which is confounded with the other sources. With clone x environment that interaction is now made visible; it can be separated out in the analysis and to say that DxP cross x Environment interaction is not significant, that is actually a different set of variances from the clone x environment interaction.

Q: Prof. P.D.S. Caligari - University of Reading, United Kingdom.

When you are talking about competition, we must be careful because not having something planted next to something is in fact the same as having a competitor there, only a different type of competition. You said that competition in these situations is likely to be for light. Is there any evidence for this? This is certainly the commonly held view, but our experiments in a number of species shows that this is not actually true. The main competition is below ground. Is there any direct evidence that the competition is for light?

A: Dr. R.H.V. Corley - Unilever Plantations PLC, London.

I don't know of any direct evidence that the competition is purely for light. In these experiments, the correlation between yield and leaf area are stronger in the more favourable environments. In the less favourable environments large leaf area and height don't seem to confer such an advantage. Equally, there is certainly below ground competition, especially in the Malaysian environment but my hypothesis is that it is less important.

Q: Dr. Ian Henson - PORIM, Malaysia.

The general observation was that the clones are much more sensitive and showed much greater GxE than seedling material. Are there any obvious reasons for this ?

A: Dr. Lee Chong Hee - Golden Hope, Malaysia.

In the case of clones it is a single genotype whereas with seedlings it is a mixture of genotypes.

A: Dr. R.H.V. Corley - Unilever Plantations PLC, London.

In a sense it is an artifact of the analysis. With seedlings the individual GxE can't be picked out; as it is lumped with other things but can be identified in clone x environment.

Q: Dr. Ian Henson - PORIM, Malaysia.

I thought that the experimental evidence showed that there is still, even within clones, considerable phenotypic variation. It may be less than that within seedlings but it is still there. The impression I got was that the GxE interaction difference between seedlings and clones was quite large whereas the difference in phenotypic variance within clones and within seedlings does not stand out so much.

A: Dr. R.H.V. Corley - Unilever Plantations PLC, London.

The data from our clone trial show that for almost any character the variation between palms within a clone is less than that between seedlings. How much less varies and is very much in line with what is known about the heritabilities of different characters. For example for yield per palm the variance within a clone is not a great deal less than that for seedlings. For characters of high heritability, such as the fruit characters or vegetative measurements, there is much greater uniformity within clones than between seedlings.

Q: Ho Chai Yee - Ebor Research, Sime Darby Plantations, Malaysia.

Returning to the comment by Dr. Lee Chong Hee, in rubber for example we do get a marked GxE for clones compared to seedlings. Likewise in cocoa, clones are more prone to environmental changes than seedlings. For the Malaysian environment where the climate is not extreme should we be aiming for high bunch number and materials with smaller leaf area ?

A: Dr. R.H.V. Corley - Unilever Plantations PLC, London.

I would refer to Rajanaidu's paper where he found that, at least in one of the trials, the best yields were obtained from progenies with intermediate bunch number and weight. In our selection exercise we deliberately excluded extremes in one direction or the other.

A: Dr. Lee Chong Hee - Golden Hope, Malaysia.

It is encouraging that we found GxE interactions in clones though we worked on only a few clones.

A: Mr. B. Nouy - IRHO, France.

I would like to make some general comments first. As you are aware, the IRHO has considerable experience of many different situations as we have planted our materials in Africa, in Sumatra and in South America. We are specifically experienced with one type of material i.e. Deli x La Me.

When we compare a favourable environment, like Indonesia with a less favourable, but not extreme, like the Ivory Coast there is a very important difference in potential. For example we had systematically planted the same standard cross throughout the world, and in this we observe a twofold difference in oil production between Sumatra and Ivory Coast i.e. in Ivory Coast production is 3 tonnes/ha whereas in Sumatra it is 6 tonnes/ha. This improvement is due mainly to bunch number; the bunch number improving by 80%, bunch weight by 10% and the rest due to the extraction rate. If the other Deli La Me material is compared, we observe generally no interaction e.g. D115D x L₂T in Ivory Coast is 10 - 15% higher yielding than the standard cross and likewise in Sumatra.

When we look at an extreme situation like Pobe which is very dry, some material can die or is very drought susceptible and we can consider this to be genetic x environment interaction. Similarly in South America, where radiation can be very low we observe an interaction. Some materials are very susceptible to low radiation and the ranking is not the same. But there is no interaction between two good environments such as Ivory Coast and Indonesia.

Comment: M.J. Redshaw - PTTP London Sumatra, Indonesia.

There is no point in doing this sort of (GxE) analysis unless we draw conclusions. It is useful to know that there are differences but it would be more useful to understand the differences and be able to utilize them. In the trials which Dr. Lee reported there is a clear result where one clone has done well at all three sites and another one has done well at one site but is poor at the other two sites. We need to know why. We also need to be sure that the results are clear results and not artifacts of, perhaps, the experimental design.

Comment: Dr. N. Rajanaidu - PORIM, Malaysia.

In my data, at four of the six sites which were also far from my station and hence less under my control, the CVs were high. It may be necessary to remove sites showing very high CVs and use only sites with more reliable data for reporting if there are sufficient sites.

ISSUES IN GENOTYPE-BY-ENVIRONMENT INTERACTION

by

Manjit S. Kang¹

Genotype-by-environment (GxE) interaction has been a challenging issue for breeders, geneticists, and agronomists engaged in research on agronomic as well as tree crops. GxE interaction is noticeable when varieties rank differently in performance in different environments or locations. This could mean that no single variety would be outstanding in all environments or locations. GxE interaction is one of the most important factors that impedes a breeder's progress. A significant GxE interaction necessitates evaluation of varieties in several different environments. Selection and recommendation of varieties may become more difficult because of a large GxE interaction when testing is done in diverse environments (Kang *et al.*, 1991). The number and choice of test environments can influence the cost of a breeding program and the rate of advance of populations towards the intended goal (Busey, 1983). Multiple locations protect against inappropriate product development and against bad recommendations to growers (Busey, 1983). The dilemma created by GxE interaction can be overcome by use of a stability statistic derived from performance data. However, in practical situations, most researchers tend to ignore GxE interaction by simply selecting varieties on the basis of mean performance across environments. Some workers may try to avoid GxE interaction by grouping genotypes and/or environments via clustering procedures. However, I am of the opinion the instead of ignoring or avoiding GxE interaction, we can utilize it to make selection process more precise and refined.

STABILITY STATISTICS:

GxE interaction may preclude the use of genotype means across environments for selection purposes. The question then is what to do about GxE interaction or how to select superior genotypes across environments? This introduces the concept of stability of performance. Some stability measure must be used. Which statistic should be used and how to use it are important issues. Investigations have been carried out but there is no consensus among researchers on which method is most suitable or how to use it in performance trials. It is also important to determine the environmental factor(s) that may be responsible for stability or instability of a genotype across test environments.

Two stability statistics, Shukla's (1972) σ_i^2 and Wricke's (1962) W_i or ecovalence, that partition GxE interaction into components assignable to each genotype may be useful to plant breeders and geneticists for selecting stable and consistently performing genotypes. The σ_i^2 and W_i efficiently determine contributions of each genotype to GxE interaction and have similar meanings (Kang *et al.*, 1987). The σ_i^2 is a coded value for W_i .

The formula for calculating σ_i^2 is as follows:

$$\sigma_i^2 = [1/(s-1)(t-2)] \times [t(t-1)\sum_j (u_{ij} - \bar{u}_{i\cdot})^2 - \sum_i \bar{\Sigma}_j (u_{ij} - \bar{u}_{i\cdot})^2],$$

where $u_{ij} = X_{ij} - X_{i\cdot}$, $\bar{u}_{i\cdot} = \sum_j u_{ij}/s$, s = number of environments, t = number of genotypes, X_{ij} = trait value of i th genotype in j th environment, and $X_{i\cdot}$ = mean of all genotypes in j th environment.

INTEGRATION OF STABILITY AND PERFORMANCE:

In the past, much emphasis had been placed on calculating a stability statistic for a particular trait only to assess whether or not performance of a genotype(s) was stable across test environments. Several stability statistics have been examined to study stability of genotypes with respect to an individual trait (Kang

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and Miller, 1984; Lin *et al.*, 1986; Kang and Gorman, 1989; Pham and Kang, 1988). Integration of stability of performance with yield is necessary for selecting high-yielding, stable genotypes. Both yield and a stability statistic should be considered simultaneously to reduce the effect of GxE interaction (Kang and Pham, 1991). Only a few reports (Hühn, 1979; Kang, 1988a; Eskridge, 1990; Hühn, 1990; Kang and Pham, 1991; Kang *et al.*, 1991) have stressed the importance of joint use of a stability statistic and yield performance in making selection decisions. In a recent study, Kang and Pham (1991) compared Kang's (1988a) rank-sum method, Hühn's (1979) S_i^3 and S_i^6 statistics, and Lin and Binns (1988) superiority measure, P_i (defined as the distance mean square between a cultivar's response and the maximum response averaged over all locations), and concluded that P_i favoured selection for yield only and that Kang's rank-sum method and Hühn's S_i^3 and S_i^6 would be useful for simultaneously selecting for yield and yield stability. Kang's rank-sum method employs Shukla's (1972) stability-variance statistic (σ_i^2); its usefulness and application to CIMMYT's international maize (*Zea mays* L.) yield trials was demonstrated by Kang *et al.* (1991). The rank-sum method was recently incorporated into **VARTEST (1991)**, a computer program package for variety field trials, developed at Dep. of Agronomy, Purdue University, West Lafayette, Indiana.

The rank-sum method (Kang, 1988a) assigned equal weights to yield and stability-variance statistic, wherein rank were assigned for mean yield, with the genotype with the highest yield receiving the rank of 1; similarly, ranks were assigned for σ_i^2 , with the lowest estimated value receiving the rank of 1. The two ranks for each genotype were summed and the lowest rank-sum was regarded as most desirable. This method, however, did not take into account significance levels of σ_i^2 's. The σ_i^2 's can be tested for significance using an approximate F test. A proposed modification of the rank-sum method is to assign a stability rating of 0 for non-significant σ_i^2 , 4 for σ_i^2 significant at the 5% probability level, and 8 for σ_i^2 significant at the 1% probability level (Kang, 1991). This rating is added to the yield rank of a genotype, and selection is based on the sum. Genotypes with the lowest sums are selected. Stability ratings of 0, 1, and 2, respectively, for non-significant, 5%, and 1% levels of probability were considered, but these ratings did not cause substantial changes in genotype rankings based on yield alone. Stability ratings of 0, 3, and 6 also were found to be inadequate. Implementation of stability ratings of 0, 4, and 8 changed the original yield rankings of genotypes. In this system, genotypes that are judged to be unstable are penalized in accordance with the significance level of σ_i^2 , and genotypes judged to be stable maintain their original, numerical yield-rank values. The modified rank-sum method was found to be more yield-oriented than the original rank-sum method (Kang *et al.*, 1990). The new method is illustrated below with maize yield data from Kang and Gorman (1989) *Table I*:

Table 1. Mean yield (t/ha), yield rank (Y), ca. 50% selections based on yield, σ_i^2 s, stability rating(Z), and ca. 50% selections based on yield rank and stability rating (Y+Z)

Genotype	Mean yield t/ha	Rank (Y) (S)	Selected genotypes	σ_i^2 (Z)	Stability rating	Rank sum (Y + Z) (S)	Selected genotypes
Coker 21	7.38	5	S	2.47	0	5	S
G4522	5.93	17	-	1.6	0	17	-
G4673A	7.25	7	S	0.57	0	7	S
G4733	6.78	13	-	2.61	0	13	-
G4765	7.07	9	S	1.86*	0	9	S
McCurdy 8150	6.92	10	-	3.58*	4	14	-
McCurdy 8172	7.81	2	S	3.58	4	6	S
PB 3147	7.91	1	S	2.72**	0	1	S
PB 3165	7.28	6	S	4.25	8	14	S
PB 3320	7.08	8	S	2.27	0	8	S
PB 3358	6.43	14.5	S	2.56	0	14.5	-
PB 3389	6.89	11	-	1.56*	0	11	S
Sunbelt 1802	6.79	12	-	3.48**	4	16	S
Sunbelt 1827	7.49	4	S	5.16	8	12	S
Sunbelt 1860	7.66	3	S	2.38*	0	3	S
8951	6.43	14.5	-	3.45*	4	18.5	-
8990	6.16	16	-	3.53	4	20	-

* , ** Significant at the 5% and 1% probability level, respectively.

In the above example, an assumption is that the top nine (ca. 50%) genotypes out of a total of 17 are to be selected (marked "S"). When selection is based on both yield rank and stability rating ($Y + Z$), PB 3165, which was selected on the basis of yield rank, is not selected. On the contrary, PB 3389, which was not selected on the basis of yield rank, is selected on the basis of the rank sum. These results revealed that if a broader adaptation were the goal, PB 3389 would be a better choice than PB 3165. Of course, one can examine the mean performance in individual environments and determine which locations were not conducive to high performance for PB 3165.

The modified rank-sum method identified nine genotypes with a mean yield of 7.39 t/ha, which is slightly less than the mean yield (7.44t/ha) of the nine genotypes identified on the basis of yield alone. The original rank-sum method would have identified nine genotypes with a mean yield of 7.07 t/ha, eight of which would be the same as those identified by the modified rank-sum method. Therefore, the modified rank-sum method may be preferable as it selects higher yielding, more stable genotypes than the original rank-sum method.

REMOVAL OF HETEROGENEITY FROM GxE INTERACTION:

Shukla's s_i^2 statistic, which is calculated following removal of heterogeneity due to a covariate from genotype-by-environment interaction, can be useful for obtaining additional information on stability of genotypes when heterogeneity (nonadditivity) is found to be significant. Equations [15] and [16] of Shukla (1972) are used to remove the linear effect of a covariate from total GxE interaction and to partition the remainder of the GxE interaction into variance components (s_i^2) assignable to each genotype. Shukla's Eq. [15] is as follows:

$$b_i = \sum_j [u_{ij} - u_{i.}] Z_j / \sum_j Z_j^2,$$

where b_i is a regression coefficient of the i th genotype, and Z_j is a covariate for the j th environment. [Note: Shukla's $b_i(b_i - Sh)$ is equivalent to Eberhart and Russel's (1966) $b_i(b_i - ER)$ when environmental index is used as a covariate.]

Shukla's Eq [16] is given below:

$$s_i^2 = [t(t-2)(s-2)] [S_i - \sum_i S_i / t(t-1)],$$

$$\text{where } S_i = \sum_j (u_{ij} - u_{i.} - b_i Z_j)^2$$

COMPUTER PROGRAMS:

A Statistical Analysis System (SAS) program, written in the Matrix programming language of SAS (two versions: **PROC MATRIX** and **PROC IML** are available) (Kang 1989) and an interactive BASIC program (Kang, 1988b) have been developed to calculate the σ_i^2 , b_i , and s_i^2 statistics. The two SAS versions are available free of charge, but there is a nominal charge for the BASIC program. The use of these programs is increasing in plant breeding programs throughout the world.

UNDERSTANDING GxE INTERACTION VIA COVARIATES:

It is extremely useful to understand the mechanism underlying observed nonadditivity or heterogeneity (Freeman, 1973). Freeman and Perkins (1971) stressed the use of physical measurements of environments in explaining GxE interactions. Shukla (1972) showed how to use a covariate (e.g., environmental index to remove heterogeneity due to a covariate) from GxE interaction and how to partition the remainder of GxE interaction into s_i^2 components assignable to each genotype. A significant s_i^2 indicates that a genotype was unstable following removal of heterogeneity (the effect of a covariate) from GxE interaction. A comparison of σ_i^2 and s_i^2 for a genotype reveals whether that genotype was

stable or unstable due to the linear effect of the covariate used. The covariate can be any measured characteristic of the environment, e.g., temperature, rainfall, relative humidity, environmental index, disease/insect damage rating, fertility level, etc. By using weather variables as covariates, their relative contribution was examined for maize (Kang and Gorman, 1989), and sorghum (Gorman *et al.*, 198). In these studies, weather variable means were used as covariates and there was only one yield measurement, i.e., at final harvest. Studies need to be done by taking yield measurements at several dates prior to final harvest date and determining contributions of weather variables to GxE interaction during the various intervals. Such studies should allow us to determine magnitudes of GxE interaction at different harvest dates during the grain filling period. Baker (1990) and Gravos *et al.*, (1990) did not use Shukla's s_i^2 statistic but identified differential disease ratings from different environments as a contributing factor to GxE interaction. Further research needs to be conducted by using different combinations of these factors as a single covariate to study their contributions to GxE interaction.

GxE INTERACTION AND GENE LOSS:

Because of GxE interaction, there is a danger of discarding a genotype(s), especially in early stages of a breeding program, evaluated at only one location. The discarded genotypes could have the potential to do well at another location or in another environment. Eliminating genotypes on the basis of a limited testing could result in a serious gene loss. Strategies to minimize gene loss need to be developed. Gene loss is an important issue but it has rarely been addressed in GxE interaction studies. LeClerg (1966) suggested that in the early stages of a testing program, it would be better to have only one replication per location, with as many locations as possible. This could be easily done with hybrid crops such as maize or clonally propagated crops such as sugarcane. However, when segregating progeny from a cross are evaluated, which may not be clonally propagated, a particular genotype can be evaluated at only one location. In such cases, a strategy should be not to plant all seed of a segregating genetic material in one year or at one location, rather a small aliquot of seed from each cross should be planted in several environments. This may, on an average, ensure preservation of virtually all genes present among genotypes. This strategy may not allow breeders to identify individual genotypes that would be stable in performance across environments, but it should allow them to compare performance stability of different crosses. A breeding program should be designed to identify genotypes with superior, stable performance across environments at as early a stage as possible (Kang and Martin, 1987). Unadapted and unacceptable genotypes should be eliminated as quickly as possible to minimize expenditure of resources such as time, labor, space, and money. To achieve this goal, research would be needed to determine the minimal plot size that would be large enough to provide an accurate estimate of yield potential.

REPEATABILITY OF STABILITY STATISTICS:

A trait or parameter to be used effectively in selecting superior crop cultivars, must be repeatable across different sets of environments (Eagles and Frey, 1977). Using data from international maize yield trials conducted by CIMMYT, Pham and Kang (1988) studied repeatability of several stability statistics. They found that repeatability of σ_i^2 , s_i^2 , S_i^2 (Lin *et al.*, 1986), and CV_i or coefficient of variability (Francis and Kannenberg, 1978) between high-yielding and low-yielding environments was negligible, indicating that stability of genotypes estimated from low-yielding environments would not be useful in predicting the stability of those genotypes when they are grown in high-yielding environments, and vice versa. Repeatability was also negligible between statistics estimated from each of two randomly chosen subsets of environments. Repeatability of mean yield between the two random subsets varied from a non-significant correlation coefficient (r) of 0.38 to 0.96** for five yield trials. When four random subsets of environments were used, repeatability of all the stability statistics examined between pairs of subsets was low, but repeatability of mean yield was significant in 12 out of 30 cases (Pham and Kang, 1988). Because of poor repeatability of these stability statistics between different subsets of environments, they provide useful information to breeders for a particular set of environments. Little or no information is available on heritability of these stability statistics. If a stability statistic with a reasonably high heritability were available, it could be an excellent selection criterion.

SITE SELECTION:

The σ_i^2 statistic can help identify locations or environments that differentiate genotypes similarly. The use of this statistic helped identify similar locations in a sugarcane variety performance evaluation program (Glaz *et al.*, 1985). After σ_i^2 identified similar location pairs, single degree of freedom interactions were calculated to determine which of the location pairs identified by σ_i^2 contained the two most similar locations. Use of the above procedure can assist in making optimum location assignments in a breeding program (Glaz *et al.*, 1985).

GxE INTERACTION AND PLANT BREEDING SYMPOSIUM-1990:

Symposia and conferences are useful avenues for sharing and advancing scientific knowledge. A number of participants at the **GENOTYPE-ENVIRONMENT INTERACTION AND PLANT BREEDING** symposium held in February 1990 at Louisiana State University made very useful and thought-provoking comments and suggestions. For example, Dr. Bill Beavis of Pioneer Hi-Bred International wrote, "There are regions of the genome that provide consistent (stable?) responses across environments. Also, there are regions of the genome that affect the expression of a trait only in certain environments." Certainly, molecular aspects of GxE interaction need to be explored. Dr. Tony Ramey of Asgrow Seed Company commented, "Need to push more for practical application and move away from regression approach. Need to try to explicitly tie in genotypic and environmental information to explanation of GxE interaction". The second sentence in Dr. Ramey's statement reaffirms our efforts to determine contributions of weather variables or other physical factors to GxE interaction.

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GENOTYPE x ENVIRONMENT (GxE) STUDIES IN RUBBER (*HEVEA*) CLONES

by

Tan H.¹

ABSTRACT

The paper reviews previous reports on GxE studies for rubber clones by various researchers. In particular it emphasises the major findings pertaining to GxE study carried out at the Rubber Research Institute of Malaysia. At the RRIM, some statistical techniques such as conventional ANOVA and regression approaches, were used to study the GxE effects on yield and girth data of rubber clone trials over different environments. In these studies, significant GxE interaction effects were detected and clones with varying degrees of stability were identified. The potential usefulness of the findings for Hevea breeding and selection will be discussed.

INTRODUCTION

One of the main tasks in *Hevea* breeding is the comparative evaluation of a series of clones, either bred locally or imported from other countries, over a wide range of environments in rubber planting areas. The testing of these planting materials in different environments is necessary because of the environmental influence on the yield and girth performance of rubber trees. In addition, it has also been observed that a particular clone which performs well in one environment may not perform as well in another environment relative to a given set of clones. This phenomenon of clone (genotype) - environment (GxE) interaction effect can therefore make conclusive assessment of the value of individual clones for final clonal recommendation to the planting industry difficult.

In the past RRIM recommended the same set of planting materials to different rubber planting areas. After recognising the existence of GxE effects, an improved approach known as regional planting recommendation was instituted, in which certain recommended clones with known secondary defects are advised not to be planted in certain part of the country which shows specific environmental constraints, such as severe wind damage and incidence of major diseases (Ho *et al.*, 1969; Rubber Research Institute of Malaya, 1973). In 1974, difficulties were encountered when demarcating boundaries of environmental constraints, and this led to the new concept of "Enviromax Planting Recommendation" (Ho *et al.*, 1974). The principle underlying this planting recommendation is to maximise the yield potential in a particular locality, subject to the inhibitory influence of the environmental factors (including soil type, terrain, drought etc), through the choice of appropriate planting materials.

Although the importance of GxE effects have been recognised and made use of in the late sixties, GxE interaction studies began only in the early seventies in the Rubber Research Institute of Malaysia (Tan, 1974; Rubber Research Institute of Malaysia, 1979). In Sri Lanka, GxE studies in 1975 and

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subsequent work were reported by Jayasekera *et al.*, (1977), Jayasekera (1983), Jayasekera and Karunasekera (1984) and Jayasekera (1984). Reports of findings of GxE studies from Indonesia (Aidi-Daslin *et al.*, 1986), Nigeria (Onokpise *et al.*, 1986) and India (Rajeswari Meenattoor, 1991) are more recent.

The aim of this paper is to review previous reports on GxE studies with special emphasis on the work carried out in the Rubber Research Institute of Malaysia. The following four questions pertaining to these studies will be examined and highlighted:

- Extent of GxE interaction.
- Nature of GxE interaction.
- Stability estimates of clones.
- Major factors causing GxE interaction.

Data Source

Two sets of trials, namely, RRIM 700 Series (first selection) and 1954 Foreign Exchange Clone Trials were used for this study. The former (referred to as Trial A) consists of sixteen locally bred clones, while the later (referred to as Trial B) consists of ninety one clones of diverse genetic and geographic origins, which were bred and selected by local and foreign institutions. These two sets of trials were sited in co-operating estates in different parts of Peninsular Malaysia representing certain environmental constraints such as leaf disease, wind severity and soil type in rubber growing areas. Lattice designs, which are resolvable into randomised block design, were used in these trials (Tan, 1989). Experimental details of the trials have been described before (Paardekooper, 1959, 1961, 1962, 1964 a, b; 1965). Some basic information for the trials is given in *Table 1*.

Two important economic characters, namely yield and girth, were emphasized in this study. For yield performance, yield per tree (g per tree per year), which reflects largely the yield potential of an individual tree for a given clone, and yield per ha (kg per ha per year), which included the number of tapped stand and tapping intensity in yield estimation in a given area for a given clone, over a three and / or seven-year periods, were considered. For girth performance, fourth year girth data were used.

Table 1. Some information on the trials in this study

	Trial A	Trial B
No. of clones	16	91
Locations	6	5
Trial sites	Selangor (2) N. Sembilan (1) Malacca (1) Kedah (1) Johore (1)	Selangor (2) N. Sembilan (1) Malacca (2)
Design	4 x 4 Balanced Lattice	Simple Lattice
Replication	5	2

Bracketed figures refer to number of trials.

Extent of GxE interaction

Conventional techniques of analyses of variance and variance components were used to detect the presence of GxE interaction and its contribution to the total variation. Yield and girth data from Trials A and B were examined and were shown to have significant GxE interaction effects, in addition to the large and significant main effects (clone or genetic and environmental). The respective variance components and their contributions over the total variance components are presented in *Table 2*.

Table 2. Variance components for yield and girth performance and their relative contributions in trials A and B

Variance Component	Yield per tree	Yield per ha	Girth
Trial A			
Genetic (G)	22.86 (59.6)	48 836 (55.2)	8.48 (42.5)
Environmental (E)	9.36 (24.4)	18 777 (21.2)	8.53 (42.7)
G x E	4.70 (12.3)	17 095 (19.3)	2.52 (12.6)
Remainder	1.45 (3.8)	3 787 (4.3)	0.44 (2.2)
Trial B			
Genetic (G)	29.77 (45.5)	-	6.50 (28.6)
Environmental (E)	23.79 (36.4)	-	11.94 (52.6)
G x E	7.45 (11.4)	-	2.85 (12.6)
Remainder	4.40 (6.7)	-	1.40 (6.2)

Bracketed figures refer to percent contribution in relation to the total variance component.

Contributions of genetic variance component in relation to the total variance components for yield performance in both the trials are the highest (45.5% to 59.6%), followed by environmental variance component (21.1% to 36.4%). The GxE variance component for yield, on the other hand, accounted for an average of 14.3% (range: 11.4% - 19.3%) of the total variance components. It is shown that GxE variance component for yield per ha was higher than that for yield per tree. This is expected as yield per ha took into account factors arising from major environmental effects, for example, tree loss due to wind and diseases resulting in a lower tapping stand. For girth performance, both the genetic and environmental variance components jointly contributed 81.2% to 85.2% of the total variance components, with environmental variance component being larger in Trial B. The GxE variance component accounted for 12.6 % of the total variance components for the two trials.

Taking the two trials together, major variations of yield and girth performance over a set of environments are contributed mainly by the individual genetic and environmental effects. The contribution of GxE effects, though significant, was small; making up an average of 13.6% (range: 11.4% - 19.3%) of the total variance components.

Studies on GxE contribution over the total variation for some *Hevea* characters have been made by researchers in other countries. Jayasekera *et al.* (1977), who studied ten clones over eight locations, reported 16.8%, 7.5% and 37.9% of the total variance components to be accounted for by the GxE variance component with reference to 1st height, 2nd height and survival rate respectively. Aidi-Daslin *et al.* (1986), in a study of twenty-three clones in two locations, reported 8.5%, 38.9%, 11.1%, 12.0%, 6.8% and 11.6% of the total variance components accounted for by GxE variance component for yield, girth, bark thickness, dry rubber content, plugging index and number of latex vessel respectively.

In general, the contributions of GxE variance components over the total variance components for the various *Hevea* characters studied so far are small with an average of 15.7% (range: 7.5% for 2nd height to 38.9% for girth).

Nature of GxE interaction

The nature of GxE interaction has been studied using joint regression analyses (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966). In this approach, GxE interaction can be further regressed on to a measure of the environmental effect (usually environmental mean). The GxE interactions are partitioned into two terms, namely, the heterogeneity of regressions and deviations from regression. Each of these terms can be compared with the residual experimental error, and the heterogeneity of regression further compared with the deviations in order to see if it accounts for a significantly large part of the observed interaction. Although some limitations of this regression approach have been mentioned (Freeman and Perkins, 1971), this method has been used fairly widely in GxE studies in practice.

Table 3 presents results of the joint regression analyses for yield and girth performance of clones in Trials A and B. It is noted that mean squares of heterogeneity of linear regression are not significant for yield performance in either of the trials. On the other hand, significant mean squares for deviations from regression are detected for the same characters. For girth performance, a slightly different picture is obtained. A border-line significance ($P < 0.10$) for Trial A and high significance ($P < 0.01$) for Trial B for mean squares due to heterogeneity of linear regressions are detected. The mean squares for the deviation from regressions are also large and highly significant for girth in both the trials.

The above results suggest that the nature of GxE interaction of yield and girth performance could be largely non-linear although linear GxE interaction is detected for girth performance to some extent.

Jayasekera (1984) reported similar studies using the joint regression analysis of Perkins and Jinks (1968). The author suggested non-linear GxE interaction for survival rate and two height measurements and mainly linear GxE interactions for second year test-tapping yield and sixth year girth.

The finding of non-linear GxE interactions for clonal performance with reference to the characters studied suggests the involvement of more than one major environmental factor in causing GxE interaction and the differential clonal responses towards these environments.

Stability estimates of clones

Several statistical techniques are available to describe clonal response over a range of environments. Some of these require *a priori* assumption of linearity in response while others do not need this assumption. The subject of these stability estimates has been reviewed by a number of researchers (Lin *et al.*, 1986; Becker and Loon, 1988). Some of the techniques used and the results obtained in this study are described below.

Regression and deviation

Regression estimates of individual genotypes are usually estimated in conjunction with the regression method of studying GxE interaction, like those described by Finlay and Wilkinson (1963) and Eberhart and Russell (1966). While there may be a difference in the definition of stability, the meaning of regression in describing clonal response over environments is basically similar. Genotypes with regression coefficients not significantly different from one are those performing almost similarly with the average performance of all clones in the environments tested. Genotypes with regression coefficients significantly higher than one are those which can adapt very well to good environments but perform poorly in unfavourable environments. Genotypes with regression coefficients significantly below one are those which are less sensitive to environmental changes, with relatively small fluctuation in performance in poor as well as in good environments.

TABLE 3

MEAN SQUARES OF JOINT REGRESSION ANALYSES FOR YIELD
AND GIRTH IN TRIAL A AND B

CHARACTER	CLONE (G)	ENVIRONMENT (E)	LINEAR REGRESSION			DEVIATIONS FROM REGRESSION			REMAINDER
			G x E						
YIELD PER TREE									
TRIAL A	120.45 *** (15)	155.86 *** (4)	6.15 *** (60)	3.75 NS (15)		6.95 *** (45)		1.45 (300)	
TRIAL B	160.68 *** (90)	2176.51 *** (4)	11.85 *** (360)	12.91 NS (90)		11.49 *** (270)		4.40 (483)	
YIELD PER HA									
TRIAL A	265059.6 *** (15)	321309.7 *** (4)	20881.8 *** (60)	16593.7 NS (15)		22311.2 *** (45)		3787.0 (300)	
GIRTH									
TRIAL A	53.81 *** (15)	139.47 *** (5)		2.96 *** (75)		4.24 + (15)		2.64 *** (60)	0.44 (360)
TRIAL B	36.76 *** (90)	1090.75 *** (4)		4.23 *** (360)		6.45 ** (90)		3.49 *** (270)	1.40 (483)

Bracketed figures refer to degrees of freedom.

NS : Not significant at $P < 0.05$.

+, *, **, *** : Significant at $P < 0.10$, 0.05 , 0.01 and 0.001 respectively.

Eberhart and Russell (1966) regarded the first group ($b=1$) as genotypes with average adaptability/stability, the second group ($b > 1$) as below average adaptability and the third group ($b < 1$) as above average adaptability. Another statistic, i.e. deviation from regression, was incorporated as a second stability parameter to describe clonal stability (Eberhart and Russell, 1966). A small deviation associated with the regression was considered more stable. These stability estimates are always considered together with average clonal performance to serve as a basis for clonal selection.

The three parameters (mean, regression coefficient and deviation from regression) were estimated for the clones involved in Trials A and B with regard to yield and girth performance. Clones with various degrees of adaptability/stability were identified and this information became useful as a supplementary guide for *Hevea* clonal selection (Tan, 1974; Rubber Research Institute of Malaysia, 1979).

The nature of regression estimates obtained from Trial A and B were examined in relation to its distribution into different classes. The results are summarised in *Table 4*.

Table 4. Distributions of regression coefficient (b) into groups in trials A and B

Character	$b = 0$		$b = 1$		$b = 0$		$b = 1$		Total
	NS	NS	NS	S	S	NS	S	S	
Yield per tree									
Trial A	0		0		4		0		4 (25.0) ^a
Trial B	0		0		40		2		42 (46.2)
Yield per ha									
Trial A	0		0		3		0		3 (18.8)
Girth									
Trial A	0		0		13		1		14 (87.5)
Trial B	0		0		54		7		61 (67.0)
Combined	0		0		114		10		124 (53.9)

a : % over total no. of regressions in trial A ($N = 16$) and trial B ($N = 91$).

NS : Not Significant at $P < 0.05$.

S : Significant at $P < 0.05$.

In Trial A, out of sixteen clones, only three to four clones had significant regression and all were shown not significantly different from one with reference to yield performance. For girth performance, fourteen out of sixteen clones showed significant regression and not significantly different from one, except for one case which showed significant difference from one.

In Trial B, forty-two out of ninety-one clones tested had significant regression coefficients for yield performance. Forty regression coefficients were not significant from one while two were significantly different from one. An increased number of significant regression coefficients were noted for girth character; fifty-seven cases were not significantly different from one while seven were significantly different from one.

Combining all the regression estimates (230 cases) for yield and girth characters of both trials, 53.9% (124 cases) of the regression coefficients were shown to be significant; 92% (114 cases) of the

significant regression coefficients were not significantly different from one; 8% (10 cases) of the significant regression coefficients were significantly higher or below one. This result implies that only a portion of clonal performance can be described by linear regression. Majority of the clones which can be described by linear regressions exhibited a characteristic similar or close to average adaptability / stability. Only a few clones can be classified as above or below average adaptability. The result also agrees with earlier suggestions that GxE interaction cannot be easily expressible by linear regression alone.

Table 5 shows the stability parameters of some selected clones. Most of these clones have been recommended as Class I and/or Class II clones at one time or another in the RRIM planting recommendation since 1952. They are generally characterized as having above average yield, regression coefficients around one or below one and small deviation from regressions. A few clones such as RRIM 526 ($b=1.39$), RRIM 605 ($b=1.39$), and PB 5/63 ($b=1.51$), had higher regression coefficients (though not significantly different from one) and large deviations from regression. Clone PR 255 ($b=0.72$) and PR 261 ($b=0.66$) which still remain as Class I clones in the RRIM Planting Recommendation (Rubber Research Institute of Malaysia, 1989) had the highest yield, relatively low regression and large deviations from regression. Clone RRIM 519 ($b=0.38$) with below to average yield had the smallest regression coefficient and low deviation from regression. It should be pointed out that the regression estimates of these three clones are not significantly different from zero, thus not providing reliable interpretation of linear response across the environmental sites tested.

In other studies, Jayasekera *et al* (1977) estimated the regression coefficients for 1st height, 2nd height and survival rate of ten clones at eight sites. Suhendi (1989) obtained regression estimates of sixteen clones tested in three locations. These authors illustrated the use of the information as a guide in clonal planting recommendation.

While useful information can be obtained from the above stability estimates, it deserves some comment in its use and interpretation. Firstly, rubber clone trials are usually conducted in a few sites or locations which at times fall into a narrow environmental range. This would result in poor estimation of regression coefficients associated with individual clones, thereby not providing meaningful and reliable interpretation. Secondly, the linear component of GxE interaction accounts for only a limited portion of the interaction. It is therefore prudent to caution on the use of linear regression coefficient as a basis for GxE interpretation and stability studies.

CV and Variance

In view of the limitations mentioned above, *Hevea* breeders attempted other methods which do not require assumptions of linear regression response. This approach makes use of conventional coefficient of variability as a measure as suggested by Francis and Kanenberg (1978). The CV and mean performance of individual clones over a number of environments tested were used for constructing a scatter diagram with mean and CV along the two (x,y) axis. The average CV and grand mean performance of all clones were drawn on their corresponding axis to form four quarters. Thus, four groups of clones are identified :-

Group 1 : High mean, small CV

Group 3 : Low mean, small CV

Group 2 : High mean, large CV

Group 4 : Low mean, large CV.

Depending on the characters in question, some clones belonging to specific groups would be favoured in terms of clonal selection. In the context of clonal selection for yield, Group 1 and 2 clones are considered candidates for selection as both groups have high average yield. Group 1 is considered more stable with less fluctuation in performance over different sites while group 2 clones are more sensitive to environmental changes and may be better adapted to specific or certain environments. The method described above was used to assess clonal performance over different sites in Trials A and B.

TABLE 5

**STABILITY PARAMETERS OF YIELD PERFORMANCE OF SOME
SELECTED CLONES IN TRIAL B
(EBERHART AND RUSSELL'S METHOD)**

CLONE	MEAN YIELD (g/t/t)	REGRESSION COEFFICIENTS	DEVIATIONS FROM REGRESSION
RRIM 501	36.7	1.20	5.13
RRIM 513	28.7	0.62	1.03
RRIM 519	27.7	0.38 *	-1.08
RRIM 526	25.6	1.39	6.80
RRIM 605	32.6	1.39	10.17
RRIM 607	29.4	0.65	0.50
RRIM 623	33.9	1.07	-1.89
PB 86	22.0	1.12	15.96
PB 5/51	31.3	0.79	1.04
PB 5/63	37.0	1.51	11.79
RRIC 6	30.5	0.89	0.07
LCB 1320	28.3	0.54 +	-0.87
GT 1	29.9	0.93	-0.80
PR 107	25.7	0.53	1.18
PR 251	34.6	1.02	8.54
PR 255	39.9	0.72	8.05
PR 261	40.7	0.66	22.32
Trial Mean	28.7	1.00	
Range	16.5-41.0	0.24-2.15	

+, *, : Significant from unity at P < 0.10 and 0.05.
respectively.

Table 6 gave results for some selected clones with reference to yield performance in Trial B. Most of the clones fall into groups 1 and 2 as expected since they were recommended material before. For instance, the present class I clone PR 255 and PR 261 fall into Group 1 and Group 2 respectively.

A parallel approach as described by Jinks and Mather (1955) has also been used (Jayasekera, 1983). Instead of CV, variance of a clone across environment was used as a measure of stability. A similar method of characterizing various stability properties of clones for early height measurement and survival rates was demonstrated.

Ecovalence and other stability variance

Other stability parameters such as Wricke's ecovalence (Wricke, 1962), Baker's variance (Baker, 1969) and Shukla's stability variance (Shukla, 1972) were attempted in *Hevea*. Using these stability parameters for the ninety one clones with reference to yield performance, different degrees of stability were obtained (Rubber Research Institute of Malaysia, 1979). A sample of these stability estimates for some selected clones is illustrated in *Table 7*. The information obtained from these three estimates were shown to be almost similar. When a clone had large Shukla's stability variance, it also had a large Wricke's ecovalence and a large Baker's variance. Both the highest yielding Class I clones PR 255 and PR 261 had relatively high stability variances.

Rajeswari Meenattoor *et al* (1991) used a very unconventional set of girth increment data during "summer" and "winter" seasons (as environments) over eight years in one trial testing five rubber clones to carry out stability studies. The authors estimated ecovalence and Shukla's stability variance for the clones which showed various degrees of stability (adaptability).

Possible Factors Causing GxE Interaction

Systematic studies on the factors underlying GxE interaction have not been carried out so far for rubber tree performance. This is understandable because of the complexity of environmental factors influencing yield performance and difficulties in isolating specific factors for the study. However, from a number of observations and evaluations in field trials, two major factors have emerged as likely candidates in causing GxE interaction. One factor is disease while the other factor is wind damage. These two factors can cause drastic differences in yield and girth performance in rubber clones. For example, RRIC 103 which is very susceptible to *Corynespora* could perform reasonably well in Kedah area where *Corynespora* leaf disease is not conducive or prominent. However, this clone can hardly grow to full maturity (up to tapping) and became the worst performer in the same set of trials in other states (e.g. Johore) where there is serious *Corynespora* leaf disease problem. RRIM 703, a wind susceptible clone, can yield well (in kg per ha) in non-wind prone areas but performs poorly in wind prone areas, resulting in a reverse of ranking in a given set of clones tested in the same trials.

Although other factors such as soil type and terrain, climate, agronomic inputs, tapping system and intensity etc, are known to influence rubber performance, their roles as major factors in GxE interaction have not been demonstrated. Yew (1989), who carried out a preliminary pot experiment involving different soil types and several clones, reported no evidence of soil x clone interaction in his early growth study. Chan and Pushparajah (1972), on the other hand, reported certain soil-type may cause different types of wind damage. Perhaps, soil-type may exert its interaction effect through wind damage incidence of certain clones.

CONCLUSIONS

From the foregoing studies the following conclusions can be drawn :

- GxE interaction exists in *Hevea*. It accounts for about 14% (range: 11% - 19%) of total variation in yield and girth performance in the present study. An estimate of 16% (range: 8% - 39%) was obtained when combined with other studies.

- Differences of linear regressions accounted for only a small proportion of the total GxE interaction effects, suggesting GxE interaction is probably non-linear for most of the characters (yield, early height and survival rate) studied. Linear GxE interaction however was detected for girth and test-tapping yield, but this linearity alone cannot account for the total GxE interaction.
- Relatively large and significant mean square deviation from regressions accounted for a major part of GxE interaction effects, reinforcing the suggestion of non-linear GxE interaction for most of the characters studied.
- Regression approach can be useful in the study of clonal performance over a set of environments. However, due to poor estimation of regression coefficient, partly due to small degrees of freedom in few tested sites in clone trials, its interpretation in GxE interaction on the basis of linearity needs to be cautious.
- Statistical parameters such as CV or variance and mean of genotypes over different trial sites can serve as practical and useful guides in clonal selection. Other parameters such as Wricke's ecovalence, Shukla's stability variance and Baker's variance can also provide information on clonal sensitivity over different environments.
- Disease and wind damage are likely major factors in causing GxE interaction.
- For more effective evaluation of clones, choice of trial sites including various environmental constraints and an increased number of trial sites are important in providing suitable data for GxE studies and to improve efficiency of selection. This would, therefore, further refine rubber clonal recommendations.

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TABLE 6

STABILITY PARAMETERS OF YIELD PERFORMANCE OF
SOME SELECTED CLONES IN TRIAL B
(FRANCIS AND KANNENBERG'S METHOD)

CLONE	MEAN YIELD (g/t/t)	CV (%)	GROUP
RRIM 501	36.7	17.6	1
RRIM 513	28.7	12.6	1
RRIM 519	27.7	8.8	3
RRIM 526	25.6	28.8	4
RRIM 605	32.6	23.3	2
RRIM 607	29.4	12.6	1
RRIM 623	33.9	16.0	1
PB 86	22.0	30.6	4
PB 5/51	31.3	14.0	1
PB 5/63	37.0	22.1	2
RRIC 6	30.5	15.4	1
LCB 1320	28.3	11.0	3
GT 1	29.9	16.2	1
PR 107	25.7	12.9	3
PR 251	34.6	17.0	1
PR 255	39.9	23.9	2
PR 261	40.7	13.6	1
Trial Mean	28.7	20.7	
Range	16.5-41.0	8.9-37.4	

TABLE 7 WRICKE'S, SHUKLA'S AND BAKER'S STABILITY VARIANCE
FOR YIELD PERFORMANCE OF
SELECTED CLONES IN TRIAL B

CLONE	WRICKE'S ECOVALENCE	SHUKLA'S STABILITY VARIANCE	BAKER'S VARIANCE
RRIM 501	32.4	8.2	8.1
RRIM 513	30.4	7.6	7.6
RRIM 519	46.5	11.8 *	11.6
RRIM 526	48.0	12.1 *	12.0
RRIM 603	28.2	7.1	7.1
RRIM 605	58.6	14.8 *	14.6
RRIM 607	26.4	6.6	6.6
RRIM 623	8.0	1.9	2.0
PB 86	62.6	15.9 **	15.6
PB 5/51	20.4	5.1	5.1
PB 5/63	73.4	18.6 **	18.4
RRIC 6	14.6	3.6	3.7
LCB 1320	30.9	7.8	7.7
GT 1	11.3	2.8	2.8
PR 107	37.4	9.4	9.4
PR 251	38.9	9.8	9.7
PR 255	44.7	11.3 *	11.2
PR 261	91.1	23.2 *	22.8

* , ** : Significant at $P < 0.05$ and 0.01 respectively.

ANALYSES OF GENOTYPE X ENVIRONMENT INTERACTIONS - AN ILLUSTRATIVE EXAMPLE IN CASSAVA

by

S.L. Tan¹ and C. Mak²¹

ABSTRACT

Studies to detect genotype x environment interactions have practical value in the selection of stable genotypes. However, the breeder has still to decide on whether a genotype may be recommended for general planting because of wide adaptability, or only for specific environments. Combined analyses of variance provide the means of determining if genotype x environment effects exist in the expression of a particular trait.

The joint regression analysis is often used to study genotype x environment interactions in individual genotypes. Variations in the use of parameters arising from the joint regression analyses give rise to different definitions of a stable genotype. Data from Cercospora disease scores at six and 12 months in 15 cassava clones tested in six locations over two seasons per location were used to show these differences, and implications on the final selection of clones which are less susceptible to Cercospora brown leaf spot.

INTRODUCTION

It is generally observed that genotypes differ in their response to environmental variation. Statistically, this difference is considered as an interaction between genotypes and environments. Therefore, in plant breeding experiments, much efforts are made to carry out multi-environmental trials in order to determine the relative importance of genotype, environment and the genotype x environment ($g \times e$) interaction so that an appropriate breeding strategy may be planned. At the same time, practical use of $g \times e$ studies lies in the selection of stable genotypes. A stable genotype is one which displays little or no change in its performance compared with other genotypes over a range of environmental variation. Many of the environmental factors encountered in $g \times e$ studies vary simultaneously, uncontrollably and in unknown proportions. Thus, no study could include all environmental variables of the many physical and biological factors and in all the combinations that a genotype might encounter in actual situations. For this reason, the effects of these environments are often grouped according to location and season. One concept of stability is in keeping with the concept of homeostasis postulated by Lerner (1954), i.e. the ability of a genotype to show constant response in a character over a range of environmental conditions. However, this concept of stability is not what is desirable from an agronomic

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mist's point of view. A genotype which is able to respond positively with improved environmental conditions (either climatic, edaphic or agronomic) is much to be preferred - in other words, genotypes showing no genotype x environment interactions of the cross-over type. This type of g x e interaction has been defined as agronomic stability (Becker, 1981).

Methods of studying genotype x environmental interaction

Genotype x environment interactions may often be detected by a combined analysis of variance of a set of genotypes tested over a number of environments (either locations, seasons, a combination of location and season, or even varying levels of an agronomic practice).

The basic statistics for the study of g x e interactions are simply the mean performance of a genotype in respect of any trait averaged over all environments, and the variation in performance over these environments. *Table 1* illustrates the combined analysis of variance for n random sample of genotypes tested in r number of replicates per experiment at each of several locations (l) in each of several seasons (s).

In this model, the variation among environmental effects is expressed in terms of averages of each location (l) and for each season (s), as well as a residual called $l \times s$ interaction. Similarly, the genotype x environment interaction (g x e) component can also be subdivided into three components, namely, $g \times l$, $g \times s$ and a residual called $g \times l \times s$. The expectations of mean squares assume all factors are random. The various effects can be tested by calculating the appropriate F-ratios (*Table 1*.)

Table 1. Combined analysis of variance for n genotypes evaluated in trials with r replications at l locations over s seasons

Source of variation	df	Expected mean squares		F-ratio
Locations (L)	l-1	$\sigma^2 + n\sigma^2_r + r\sigma^2_{gls} + rs\sigma^2_{gl} + nr\sigma^2_{ls} + nrs\sigma^2_l$	(M ₁)	(M ₁ +M ₈)/(M ₃ +M ₆)
Seasons (S)	s-1	$\sigma^2 + n\sigma^2_r + r\sigma^2_{gls} + rl\sigma^2_{gs} + nr\sigma^2_{ls} + nrl\sigma^2_s$	(M ₂)	(M ₂ +M ₈)/(M ₃ +M ₇)
L x S	(l-1)(s-1)	$\sigma^2 + n\sigma^2_r + r\sigma^2_{gls} + nr\sigma^2_{ls}$	(M ₃)	(M ₃ +M ₉)/(M ₄ +M ₈)
Replicate within (LxS)	sl(r-1)	$\sigma^2 + n\sigma^2_r$	(M ₄)	M ₄ /M ₉
Genotypes (G)	n-1	$\sigma^2 + r\sigma^2_{gls} + rs\sigma^2_{gl} + rl\sigma^2_{gs} + rsl\sigma^2_g$	(M ₅)	(M ₅ +M ₈)/(M ₆ +M ₇)
G x L	(n-1)(l-1)	$\sigma^2 + r\sigma^2_{gls} + rs\sigma^2_{gl}$	(M ₆)	M ₆ /M ₈
G x S	(n-1)(s-1)	$\sigma^2 + r\sigma^2_{gls} + rl\sigma^2_{gs}$	(M ₇)	M ₇ /M ₈
G x L x S	(n-1)(l-1)(s-1)	$\sigma^2 + r\sigma^2_{gls}$	(M ₈)	M ₈ /M ₉
Pooled error	sl(n-1)(r-1)	σ^2	(M ₉)	

Approximate degrees of freedom for the composite numerator and denominator in the F-ratio may be obtained by using Satterthwaite's approximation (1946) [quoted by Cochran and Cox, (1957)]:

Suppose the F-ratio has a general form :

$$(M_1 + M_2)/(M_3 + M_4), \text{ then}$$

df for the numerator =

$$\frac{(M_1 + M_2)^2}{(M_1^2/df_{m1} + M_2^2/df_{m2})}$$

and df for the denominator =

$$\frac{(M_3 + M_4)^2}{(M_3^2/df_{m3} + M_4^2/df_{m4})}$$

The components of variance can be estimated as linear functions of the mean squares:

$$\begin{aligned}\sigma^2 &= M_9 \\ \sigma^2_g &= (M_5 + M_8 - M_6 - M_7)/rsl \\ \sigma^2_l &= (M_1 + M_8 - M_3 - M_6)/nrs \\ \sigma^2_s &= (M_2 + M_8 - M_3 - M_6)/nrl \\ \sigma^2_{ls} &= (M_3 + M_9 - M_4 - M_8)/nr \\ \sigma^2_{gl} &= (M_6 - M_8)/rs \\ \sigma^2_{gs} &= (M_7 - M_8)/rl \\ \sigma^2_{gls} &= (M_8 - M_9)/r\end{aligned}$$

Thus, the phenotypic variance, $\sigma^2_p =$

$$\sigma^2_g + \sigma^2_{gl}/l + \sigma^2_{gs}/s + \sigma^2_{gls}/ls + \sigma^2/rls$$

By contrast, the joint regression or stability analysis - with its several variations (*e.g.* Finlay & Wilkinson, 1963; Perkins and Jinks, 1968; Eberhart & Russell, 1966) - allows for a degree of interpretation of the type of genotype x environment interactions (whether linear) for each of the tested genotypes. Using the method after Perkins and Jinks, the model takes the form given in *Table 2*.

The sum of squares for genotypes, environments and G x E are derived from a combined analysis of variance on macro-environments using genotype means over replicates. Here, the macro-environment refers to a combination of location and season, *i.e.* location and season effects are not partitioned separately. The sum of squares for the pooled error is extracted from the combined analysis of variance over macroenvironments. The sum of squares for heterogeneity between regressions is derived by totalling the regression sum of squares of individual genotypes on environments. The remainder sum of squares is then the balance from subtracting the heterogeneity between regressions sum of squares from the G x E sum of squares. The heterogeneity between regressions and remainder mean squares are tested against the pooled error. Heterogeneity between regressions is also compared against the remainder or deviation term to determine if it accounts for a significantly large part of the observed g x e interaction.

**Table 2. Joint regression analysis for n genotypes evaluated over t environments
(after Perkins and Jinks, 1968)**

Source of variation	df	Sum of squares
Genotypes (G)	(n-1)	$t \sum_i (d_i)^2$
Environments (E)	(t-1)	$g \sum_j (E_j)^2$
G x E	(n-1)(t-1)	
Heterogeneity between regressions	(n-1)	$\sum_i (\beta_i)^2 - \sum_j (E_j)^2$
Remainder	(n-1)(t-2)	$\sum_{ij} \delta_{ij}^2$
Pooled error	$t(n-1)(t-1)$	

where

n	=	number of genotypes
t	=	number of environments
r	=	number of replicates
δ_{ij}^2	=	deviation of the i^{th} genotype from regression in the j^{th} environment
β_i	=	regression coefficient for the i^{th} genotype
d_i	=	genetic component
E_j	=	additive environmental component of the j^{th} environment

Often enough, a genotype x environmental reaction in a particular genotype manifests itself in either of two ways: a difference in magnitude of response in relation to the population mean, or cross-over effects where a genotype may perform better in poorer environments but worse in better environments (or *vice versa*). These differences have been pointed out by various workers (Haldane, 1946; Gail and Simon, 1985; Gregorius and Namkoong, 1986; Baker, 1988). Noncross-over effects are of practical value because genotypes which exhibit such effects are generally adapted (or non-adapted) to a range of environmental conditions for a specific trait. Cross-over effects make it difficult to predict the reaction of a particular genotype to contrasting environments. Such genotypes have to be recommended for specific adaptation to certain designated environments.

The joint regression analysis by itself gives no clear indication of which type of genotype x environment interaction is in play. The parameter $b_i - 1$ (Finlay & Wilkinson, 1963) or β_i (Perkins & Jinks, 1968) has been used to define stability, a stable genotype with no genotype x environment interaction being one with $\beta_i = 0$. High relative mean performance is also an important consideration to avoid selection of stable genotypes which are below-average over environments.

Eberhart & Russell (1966) used an additional parameter δ_i^2 , which measures deviations from the regression on the environmental index). A stable variety would be one with as small as possible a value of δ_i^2 while having $b_i = 1$. Again, high mean values should also be considered to ensure above-average performance over all environments.

The method of Eberhart and Russell permits the graphical representation of genotypes for conclusions to be drawn on their stability characteristic. However, it is the simple plot of the regression line of a genotype against the environmental means and in comparison with the population mean which enables cross-over effects to be clearly seen.

An illustrative example using *Cercospora* disease scores in cassava

Cassava (*Manihot esculenta* Crantz) is the most important root crop in Malaysia in terms of area of cultivation as well as raw material for industries, particularly the starch extraction industry. One of the most commonly occurring diseases in cassava, generally in the tropics and specifically in this country, is *Cercospora* brown leaf spot, caused by *Cercospora henningsii* Allescher. It has been reported that this disease, if uncontrolled, can cause up to 23% losses in yield in susceptible cassava clones (Teri, 1978).

Experimental

The data were extracted from a genotype x environmental study involving fifteen cassava clones, chosen for their variability in morphological characteristics and agronomic performance. These clones were tested at six locations in Peninsular Malaysia representing each of the three major agro-ecological zones (AEZ). These AEZ are defined by their rainfall pattern (Nieuwolt *et al.*, n.d. [1982]); briefly, AEZ 1 has a distinct dry season of 2-4 months, AEZ 2 a distinct dry season of 1-2 months, and AEZ 3 with no distinct dry season throughout the year. Three of the locations were sited on mineral soils, and the remaining three on drained peat. The trials were also repeated over two cropping seasons per location.

A randomized complete block design was adopted with three replications. Plot sample size was 5 x 5 plants, spaced 0.9 m apart in a square planting arrangement. Border rows were included around each plot. Normal agronomic practices recommended for cassava cultivation on mineral soils and on drained peat (Chan *et al.*, 1983) were used.

Disease infection was rated using an area diagram key based on the percentage of leaf area covered by the disease lesions (Tan and Geh, 1984) as shown in *Figure 1*. Scoring was on the most severely infected leaf in the lower quarter of the plant canopy. A mean value was computed from five plants per plot. Scoring was carried out at two growth stages, *viz.* at six months after planting, and at 12 months when the crop was due for harvest.

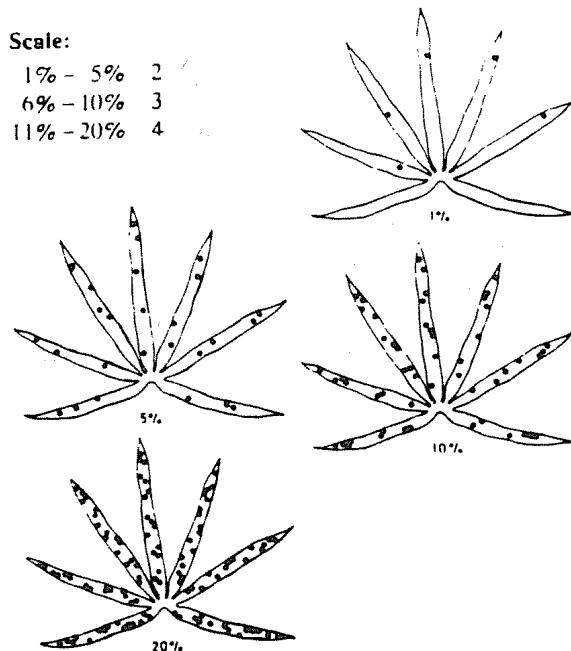


Figure 1. Key based on percentage diseased leaf area and scale used in the assessment of brown leaf spot.

Analyzing for genotype x environmental effects

Combined analyses of variance

Assuming a random effects model, data from the 12 trials (six locations and two seasons per location) were used in a combined analysis of variance (ANOVA) on the two sets of *Cercospora* disease scores. As may be seen from *Table 3*, there were significant effects due to genotypes and environments, and significant genotype x environment interactions were detected. When a combined ANOVA was carried out with environments separated out into locations and seasons (further partitioning in *Table 3*), significant genotype x location x season effects were detected for both sets of disease scores, while the genotype x location interaction was only significant for the disease score at 12 months and the genotype x season interaction only for disease score at six months.

Table 3. Combined analysis of variance over six locations and two seasons per location for *Cercospora* disease scores at six and 12 months

Source of variation	df	MS of <i>Cercospora</i> disease scores	
		6 months	12 months
Replicates within Environment	24	0.3863**	0.2336
Genotypes (G)	14	4.4163**	6.0663**
Environments (E)	11	9.1947**	19.1089**
Locations (L)	5	13.4556	33.7123
Seasons (S)	1	11.8815	3.6507
L x S	5	4.3964**	7.5971**
G x E	154	0.2813**	0.4056**
G x L	70	0.2570	0.5802*
G x S	14	0.6223**	0.2296
G x L x S	70	0.2374**	0.2663**
Pooled error	336	0.0895	0.1688

Variance components

Variance components are given in *Table 4* for genotype, environment (or location and season) and g x e (or g x l, g x s, g x l x s). The order magnitude of the g x e interaction term is smaller than the genotype and environment variance components, especially when compared with the latter for disease score at 12 months. When the g x e interaction term was partitioned into g x l, g x s, g x l x s, again the individual variance components were much smaller in magnitude than the genotype as well as the location variance components. However, compared to the season variance component, the g x s and g x l x s interaction components for disease score at six months as well as the g x l and g x l x s

components for disease score at 12 months were larger.

Table 4. Selected variance components from combined analyses of variance on *Cercospora* disease scores at 6 and 12 months over macro-environments and over locations and seasons

Variance component	<i>Cercospora</i> disease scores at	
	6-month	12-month
<i>By macro-environments</i>		
σ^2_g	0.1149	0.1572
σ^2_e	0.1915	0.4142
σ^2_{ge}	0.0639	0.0790
σ^2	0.0895	0.1688
<i>By location and season</i>		
σ^2_g	0.1048	0.1534
σ^2_l	0.1004	0.2867
σ^2_s	0.0263	-0.0145
σ^2_{gl}	0.0033	0.0523
σ^2_{gs}	0.0214	-0.0020
σ^2_{gls}	0.0493	0.0325
σ^2	0.0895	0.1688

Thus, it may be concluded that the location component within an environment effect is far more important than the season component as a source of variation. The implication would be that it would be far better to test for tolerance or resistance to *Cercospora* brown leaf spot over more locations rather than over a number of seasons in a few locations. Also, since genotype was by comparison an important variance component, screening clones to select for resistance to *Cercospora* leaf spot disease is practical.

From the variance components, heritability estimates for *Cercospora* disease scores may be computed, using the relationship:

$$h^2 = \sigma^2_g / \sigma^2_p$$

The estimates obtained are as follows:

<i>Cercospora</i> disease score	<i>h</i> ² estimates from ANOVA by	
	Macroenvironments	Locations and seasons
6 months	0.828	0.854
12 months	0.835	0.910

It would appear that by either method, heritability of disease score was high, but especially so when the variance components estimated from a combined ANOVA with partitioning of the environments into locations and seasons were used in calculating the genotypic and phenotypic variances for disease score at 12 months.

Joint regression analyses

Joint regression analyses after the manner of Perkins and Jinks (1968) detected significant effects due to heterogeneity between regressions for *Cercospora* disease score at 12 months but not at 6 months. Deviation effects, on the other hand, were significant (at 5% level of probability) for disease score at 6 months but not significant for the score at 12 months (*Table 5*). Also, the heterogeneity between regressions effects tested significant against the deviation effects for the 12-month disease score. The implication is that genotype x environment interactions do exist for *Cercospora* disease scores; these interactions follow a linear relationship with the environmental values at the later plant growth stage (when it formed a significant portion of the observed interaction), and a nonlinear one at mid-season of the crop.

Table 5. Analyses of variance for regression on macro-environments for *Cercospora* disease score at six and 12 months

Source of variation	df	MS of <i>Cercospora</i> disease scores	
		6 months	12 months
Genotypes (G)	14	1.4729**	2.0238**
Environments (E)	11	3.0709**	6.3741**
G x E	154	0.0939	0.1353
Het. Regress. Deviations	14 140	0.0535 0.0979*	0.5117***++ 0.0976
Pooled error	336	0.0895	0.1688

++ : Heterogeneity of regressions MS significant at 1% level of probability when tested against deviations MS

The means, regression coefficients and the standard deviations of the individual clones are given in *Table 6*.

Using Eberhart and Russells's graphical presentation, it may be seen that for disease score at six months, CM 621-22, CM 845-13, CM 982-2 and CM 982-7 were clones which were stable with below average infection (*Figure 2*). At 12 months, CM 621-22, CM 845-13 and CM 982-7 still showed stability for below average disease score. Additionally, CM 621-7 also qualified for this group, but CM 982-2 did not (*Figure 3*).

Cross-over effects

Regression coefficients (β_i) were computed for each of the 15 cassava clones. For each set of disease scores, the clonal mean (averaged over three replicates) were plotted against the environmental mean (after the fashion of Finlay and Wilkinson [1963]). The theoretical regression line for $\beta_i = 1.0$ was also plotted in the same graph (*Figures 4 and 5*). For the first set of disease scores recorded at six

months, although all the clones showed significant regression coefficients, none showed any cross-over effects. Black Twig, Red Twig, C 5, CM 305-8, CM 378-17, M Mex 1-20, 17/A and CM 462-6 all showed above-average stability for disease susceptibility in all locations in both seasons, *i.e.* scores were higher than average. CM 621-7, CM 621-22, CM 621-42, CM 845-13, CM 942-28, CM 982-2 and CM 982-7, by contrast, all showed below-average stability for susceptibility to *Cercospora* brown leaf spot at six months. In other words, these seven latter clones were stable for low disease infection over all the 12 macroenvironments.

Table 6. Means, regression coefficients and standard deviations for *Cercospora* disease scores at 6 and 12 months for individual clones

Clone	Score at 6 months			Score at 12 months		
	Mean	β	s[dev]	Mean	β	s[dev]
Black Twig	1.07	0.310	0.01	1.90	0.396	0.02
Red Twig	1.18	-0.178	0.05	1.69	-0.415	0.00
C 5	1.33	0.029	0.13	2.16	-0.674	0.06
CM 305-8	1.19	0.036	0.15	1.91	0.022	0.13
CM 378-17	1.14	-0.123	0.04	1.71	-0.115	0.08
CM 621-7	0.43	-0.245	0.07	0.91	-0.037	-0.01
CM 621-22	0.37	0.133	0.05	1.00	-0.112	0.01
CM 621-42	0.55	0.034	0.05	1.39	0.481	0.08
CM 845-13	0.37	-0.090	0.11	0.92	-0.096	0.09
CM 942-28	0.56	-0.050	0.02	1.09	-0.257	-0.01
CM 982-2	0.41	-0.104	0.05	1.09	0.262	0.02
CM 982-7	0.47	-0.123	0.03	1.01	0.052	0.00
M Mex 1-20	0.89	0.032	0.01	1.60	0.270	0.01
17/A	0.98	0.318	0.00	1.69	0.471	0.02
CM 462-6	0.93	0.021	0.15	1.50	-0.248	0.02

For disease scores at 12 months, the β values for all the clones were significant except for clone C 5. This implies no genotype x environmental interaction operated in C 5 and that the clone showed homeostasis. At this later stage of growth, disease reaction showed cross-over effects in Red Twig, CM 621-42, M Mex 1-20, 17/A and CM 462-6. Except for CM 621-42, the cross-over effects were such that disease scores were higher than average in those environments generally low for disease incidence but lower than average in those environments which tended to have greater disease incidence. In the case of CM 621-42, the reverse was true, *i.e.* the disease scores were lower than average in those environments generally less favourable for disease development but higher than average in the more favourable environments. In other words, CM 621-42 is specifically adapted to environments which have a lower incidence to *Cercospora* brown leaf spot at the later stages of cassava crop growth. Conversely, Red Twig, M Mex 1-20, 17/A and CM 462-6 are better adapted to those environments which are more favourable to disease development.

Thus, it may be seen that there are distinct differences in interpretation of results, depending on the method of analysis used. By using Eberhart and Russells' graphs and plots of regression lines, it was possible to pick up genotypes which by both definitions were stable with below average disease infections, namely, CM 621-22, CM 845-13, CM 982-2 and CM 982-7 for low scores at six months, and CM 621-7, CM 621-22, CM 845-13 and CM 982-7 for low scores at 12 months.

Eberhart and Russell's method was not able to pick out cross-over effects for disease score at 12 months, which makes the plots of regression lines still the most practical tool for selecting clones for specific adaptability.

Other implications

Disease scores tended to be higher at the peat sites (Jalan Kebun, Pontian and Teluk Intan) than on mineral soil sites. That *Cercospora* brown leaf spot is more prevalent in cassava grown on peat has been reported by Geh (1981), and has been attributed to the more humid below-canopy conditions which favour disease development (Tan and Geh, 1984).

CM 982-7 is a clone which has been reported to give high yields over the six locations in relation to Black Twig, the current commercially grown variety (Tan, 1989). Since the present results also singles CM 982-7 out as one of those genotypes with stability for low disease infection, and exhibiting no cross-over effects, this clone may be recommended for general planting. It will probably be ideal especially for peat areas where there is generally a higher incidence of *Cercospora* brown leaf spot in cassava.

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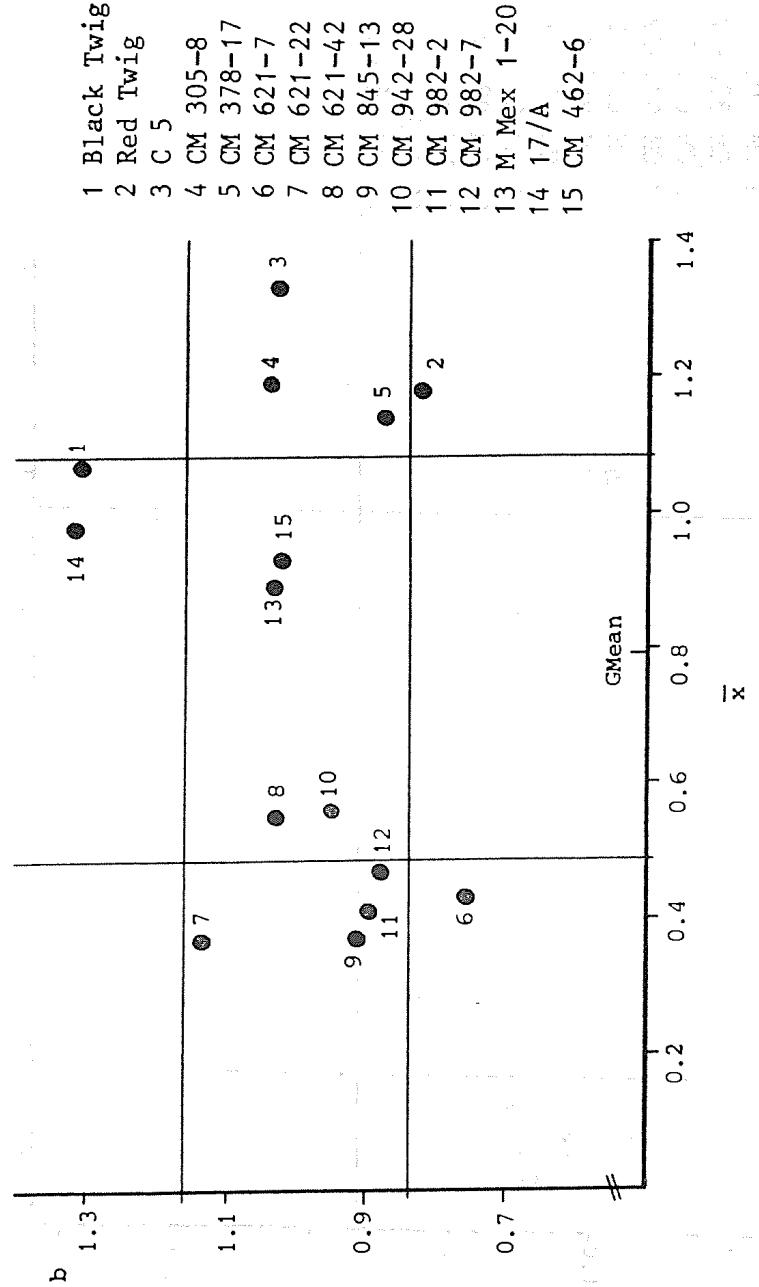


Figure 2. Plots of genotype means (\bar{x}) against their respective regression coefficients (b) for Cercospora disease score at six months
 [vertical lines: Grand mean ± 1 SD; horizontal lines: $(b=1) \pm 1$ SD]

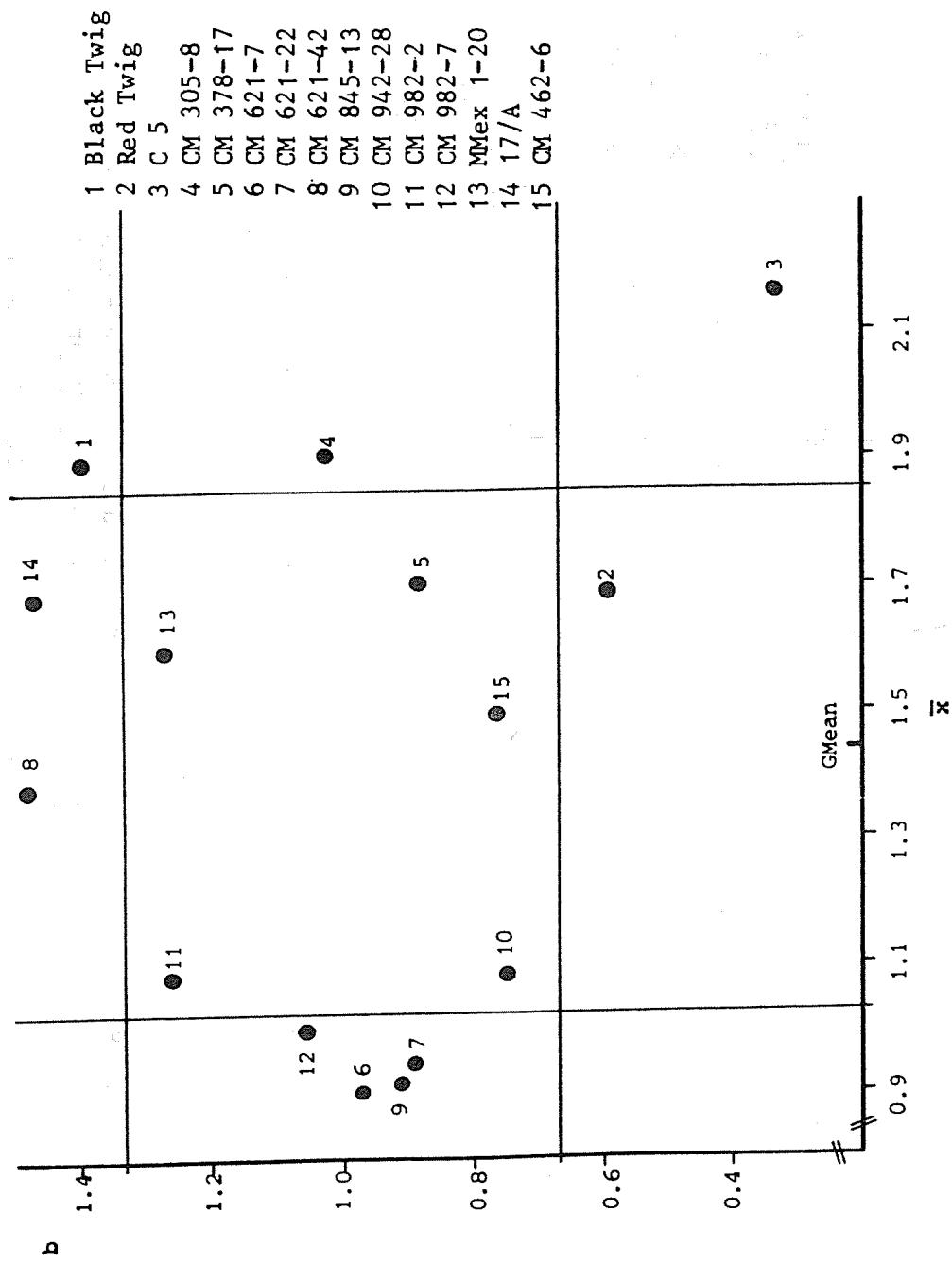
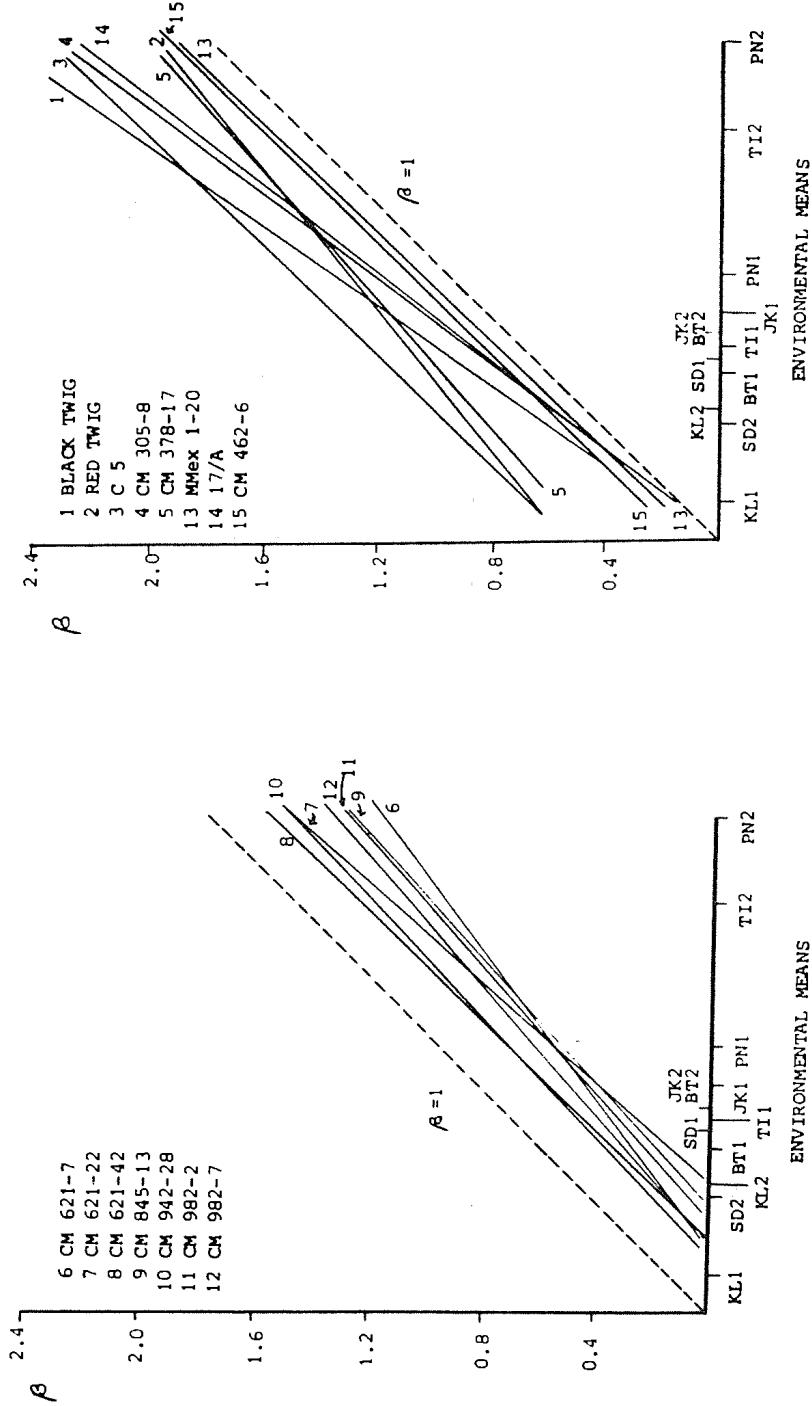
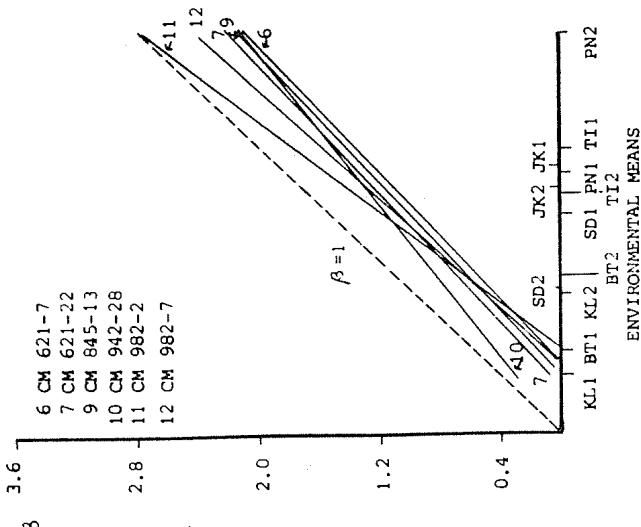


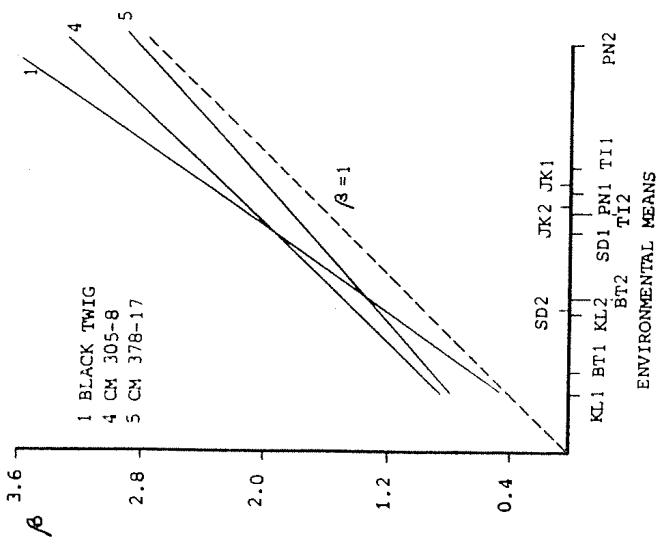
Figure 3. Plots of genotype means (\bar{x}) against their respective regression coefficients (b) for *Cercospora* disease score at 12 months [vertical lines: Grand mean ± 1 SD; horizontal lines: ($b=1$) ± 1 SD]





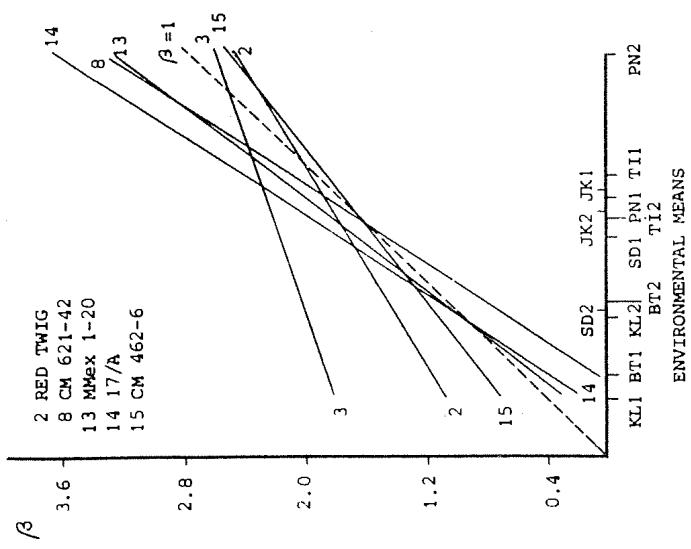
A. Genotype with lower scores

Figure 5. Plots of regression coefficients (β) of genotypes and population mean ($\beta=1$) against environmental means for Cercospora disease score at 12 months
 [KL: Kluang, BT: Bukit Tangga, SD: Serdang, JK: Jalan Kebun, PN: Pontian, TI: Teluk Intan;
 1: 1st season, 2: 2nd season]



B. Genotype with higher scores

Figure 5. Plots of regression coefficients (β) of genotypes and population mean ($\beta=1$) against environmental means for Cercospora disease score at 12 months
 [KL: Kluang, BT: Bukit Tangga, SD: Serdang, JK: Jalan Kebun, PN: Pontian, TI: Teluk Intan;
 1: 1st season, 2: 2nd season]



C. Genotype showing cross-over effects

Figure 5. Plots of regression coefficients (β) of genotypes and population mean ($\beta=1$) against environmental means for Cercospora disease score at 12 months
 [KL: Kluang, BT: Bukit Tangga, SD: Serdang, JK: Jalan Kebun, PN: Pontian, TI: Teluk Intan;
 1: 1st season, 2: 2nd season]

CLONE x ENVIRONMENT INTERACTIONS IN TEA

by

J.K. arap Rono¹, J. Kenduyiwa¹ and R.H.V. Corley²

ABSTRACT

Two trials with tea clones were planted at two different altitudes at Kericho, in Kenya. Shoot growth rate, and hence yield of tea is known to be sensitive to temperature. The difference in altitude between sites leads to a difference in temperature, and as expected, mean yields were greater at the lower and warmer site. There were highly significant clone x site interactions, with some clones showing a greater decrease in yield with altitude than others.

INTRODUCTION

Tea (*Camellia sinensis*(L.) O.Kuntze) has been propagated vegetatively, using single node cuttings, since the thirties and commercial planting material is almost exclusively clonal. Large numbers of clones have been developed in India, Sri Lanka and East Africa, but there has been relatively little exchange between countries, mainly because of disease risks. Although a great deal is known about individual clones, in terms of yield, quality and disease resistance, little has been published on clone x environment interactions. The subject of clone x environment interactions was not mentioned by Visser (1969) in his review of tea breeding.

In this paper, we describe results of two clone trials in Kenya, in which significant clone x site interactions were observed.

MATERIAL AND METHODS

Clones were propagated by standard procedures (TRFK, 1986). Most clones were new selections, but two standard clones were included in each trial.

Both trials were planted at three sites, at three altitudes, in the Kericho district of Western Kenya but the trials at the intermediate site were severely damaged by hail early in 1990, and results are excluded from the analyses. The two sites studied were Jamji estate, at an altitude of 1780 m, and Cheymen estate at 2015 m. Planting density was 10,764 bushes/ha. Soils at the two sites were similar Nitisols.

Trial 1 was planted in 1987, and included 29 clones. Yields were recorded from the start of production in 1988 until the first pruning, at the end of March, 1991. At the time of pruning, the dry weight of prunings per bush was recorded, together with the mean bush surface area. A "harvest index" was calculated from the ratio of yield to yield plus prunings. The later underestimates total dry matter production, as all dry matter below the pruning height is excluded; thus true harvest index is

1. Brooke Bond Kenya Ltd.
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lower than the figures given here.

Trial 2 included 59 clones, planted in 1988. Yield data from 1989 to the first quarter of 1991 are analysed here.

RESULTS

Table 1 shows the analysis of variance for yield of both trials, with a significant clone x site interaction in each trial.

Table 1. Analysis of variance for yield of tea clone trials

Source of variance	Degrees of freedom	mean square
Trial 1		
Clones	28	740.1***
Sites	1	15471.5***
Clones x sites	28	63.4***
Blocks	2	-
Pooled error	56	19.6
Trial 2		
Clones	58	106.2***
Sites	1	25874.4***
Clones x sites	58	24.7***
Blocks	2	-
Pooled error	116	8.9

Yields of the best five - eight new clones and the standard clones at each site are given in *Tables 2 and 3*. There are important differences in ranking between sites. Clone 1-1 was the best in trial at Jamji, but ranked only ninth at Cheymen, while clone 1-3 moved from fourth at Cheymen to first at Jamji. Clone 1-3 outyielded the standard clone 31/8 at Cheymen, but none of the new clones were better than 31/8 at Jamji.

Table 2. Yield of best 5 new clones at each site in trial 1 (tons made tea/ha, 3.25 years)

Clone	Site 1 - Jamji		Rank at site	Site 2 - Cheymen		Rank at site
	Yield as % mean			Yield as % mean		
New clones						
1-1	13.20	153	1	5.96	117	9
1-2	12.40	144	3	7.85	154	3
1-3	12.06	140	4	8.89	174	1
1-4	11.85	138	5	7.57	148	4
1-5	11.36	132	6	7.26	142	5
Standards						
31/8	13.17	153	2	8.01	157	2
BBK35	8.15	95	15	4.58	90	16
Trial mean	8.60			5.10		

Table 3. Yield of best 8 new clones at each site in trial 2 (tons made tea/ha, 2.25 years)

Clone	Site 1 - Jamji		Rank at site	Site 2 - Cheymen		Rank at site
	Yield mean	as %		Yield mean	as %	
New clones						
2-1	8.36	172	1	3.06	181	2
2-2	6.82	140	3	2.05	121	11
2-3	6.63	136	4	2.04	121	13
2-4	6.33	130	5	2.03	120	14
2-5	6.06	125	6	2.32	137	6
2-6	5.51	113	11	2.46	146	3
2-7	4.92	101	26	2.39	141	4
2-8	4.89	101	25	2.42	143	5
Standards						
S15/10	7.78	160	2	3.52	208	1
BBK 35	5.74	118	8	1.97	117	19
Trial mean	4.86			1.69		

In trial 2 the differences in ranking are even more striking. Two clones, 2-7 and 2-8, which gave a yield equal to the trial mean at Jamji, yielded more than 40% above the mean at Cheymen. Clone 2-1 outyielded the standard 15/10 at Jamji, but none of the new clones were better than 15/10 at Cheymen.

Dry matter production data from two clones in trial 1 are shown in *Table 4*. At Jamji, both clones had above average dry matter production and harvest index. The relatively lower yield of clone 1-1 at Cheymen appears to be due mainly to low total dry matter production, with only a small change in harvest index.

Table 4. Dry matter production of two clones in trial 1

Component	Site 1 - Jamji			Site 2 Cheymen		
	Clone 1-1	Clone 1-3	Trial mean	Clone 1-1	Clone 1-3	Trial mean
Yield of tea (kg/bush)	1.20	1.09	0.78	0.54	0.81	0.46
Weight of prunings (kg/bush)	4.13	3.95	3.11	2.12	2.62	1.99
Total dry matter (kg/bush)	5.33	5.04	3.89	2.66	3.43	2.45
Harvest index	0.23	0.22	0.20	0.20	0.24	0.19
Bush surface area (cm ²)	0.82	0.84	0.80	0.93	0.93	0.81
Dry matter (kg)/m ² bush surface	6.50	6.00	4.87	2.86	3.69	3.03

DISCUSSION

Yield of the best of the new selections was quite good. Several clones in trial 1 yielded over 5 tons made tea per hectare in 1990 and the best exceeded 6 tons. Harvest index was overestimated by the method adopted here, but was still low compared to many other crops, as noted by Magambo and Cannell (1981). There is obvious scope for future yield increases by improving harvest index of tea.

The difference in altitude between the sites is the most likely cause of the observed interactions. Mwakha (1985) showed a correlation between shoot growth rate and altitude in Western Kenya. Temperature decreases with increasing altitude, and tea shoot growth is known to be highly sensitive to temperature (Squire, 1979; 1980; Tanton, 1982). These workers demonstrated that tea shoot growth stops at temperatures below about 12.5°C. Above that temperature, the amount of shoot growth is directly proportional to cumulative degree-days.

There is some evidence that clones may vary in their response to temperature (Obaga *et al*, 1988; 1989; Obaga and Ngetich, 1989; Stephens and Carr, 1990). There may be differences both in base temperature and in the slope of the response to thermal time above the base temperature, either of which could cause interactions with altitude.

The difference in altitude between the two sites caused a difference of about 2°C in mean temperature (mean at Cheymen 17.3°C, Jamji 19.2°C). Assuming a base temperature for tea shoot growth of 12.5°C, the expected reduction in shoot growth rate at the upper site relative to the lower can be estimated at about 28%. If this were the sole effect of altitude, then the reduction in yield should be similar, but in trial 1, the more mature of the two trials, the reduction is about 40%. (In the younger trial the difference is greater, but differences are probably exaggerated in the period before all clones have established complete ground cover). This suggests that the lower temperatures have other effects beside reducing shoot growth rate. A reduced shoot growth rate will mean that shoots take longer to reach pluckable size. As shoot number increases with time, because one plucked shoot is often replaced by two new shoots from axillary buds, a lower growth rate is likely to result in a slower build up of shoot numbers. Obaga and N'getich (1989) found a reduction in the number of shoots per bush with increasing altitude for one clone, but not for another.

Comparing clones 1-1 and 1-3 the weight of pruned branches is much more reduced by altitude in clone 1-1 than in 1-3, or than the trial mean. A reduction in shoot growth rate and numbers might be expected to have little effect on the rate of accumulation of dry matter in the branches. If yield is sink-limited (Tanton, 1982) then a reduction in shoot growth might actually increase the amount of dry matter diverted to the branches, as Squire (1977) showed that photosynthesis continued at temperatures well below the threshold for shoot growth. It is possible, therefore, that the rate of photosynthesis is reduced with altitude in clone 1-1.

It is important to be able to predict performance of new clones at sites where they have not been tested, and an understanding of clonal responses to temperature may help in this. Clones 1-1 and 1-3 were selected for further study of shoot growth and photosynthesis in relation to temperature, but no data are available yet. In future clone trials, yield components will be recorded in more detail, so that effects on shoot number and weight can be distinguished.

ACKNOWLEDGEMENTS

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GENOTYPE X ENVIRONMENT STUDIES ON PAPAYA AND PINEAPPLE

by

Chan, Y.K.¹

ABSTRACT

Genotype x environment (GxE) trials of papaya and pineapple were carried out at MARDI following the breeding and selection of two new varieties, the Eksotika papaya and the Johor pineapple. These were tested with contemporary popular varieties over several localities to evaluate their performance and stability using linear regressions.

Unlike most GxE trials where yield stability is of prime consideration, the characters evaluated for fruits were different, with emphasis given to fruit quality and other traits. For the Eksotika papaya and Johor pineapple, the characters given priority were also different because the former was bred for dessert fruit while the latter was bred for canning. Yield stability was evaluated for both crops, percent total soluble solids reflecting the sugar content was emphasized for the papaya while vegetative growth which determined earliness was given priority in the pineapple.

Although stability estimates gave useful information with regards to the genotypic responses to environmental changes, high means for yield and fruit qualities also have to be considered before final selection. This is perhaps true for many fruit crops where cosmetic appearance, storage life, and eating qualities may override stabilities for yield alone.

In the choice of locations for evaluation, diverse environments encompassing infertile, low yielding sites would be inappropriate for fruit trials. This is because they do not reflect the true situation in which fruit crops are usually given the best environment and management to obtain high production of premium quality produce.

The choice of varieties for the two trials were constrained by the inavailability of bona-fide cultivars. This problem would also be expected in GxE trials of other lesser known tropical fruit species where breeding and selection has not been extensively carried out.

INTRODUCTION

The occurrence of genotype-environment (GxE) interactions masks the superiority of genotypes and puts doubts to their selection because it does not permit the breeder to generalize their overall superiority when grown over diverse environments. This complicates selection and recommendation because the worth of the genotype can only be related to the specific environment in which it is grown. GxE studies to understand this complexity have been widely carried out, particularly for cereal and forage crops, but considerably less so for horticultural crops and rarer still for tropical fruit crops.

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Several reasons underlie this observation. The first is that breeding of tropical fruits, for example, pineapple and papaya, has not been widely carried out, and until now, has resulted in the development of only a few *bona fide* varieties. Indeed, for these two fruits, the commercial varieties that account for the world's production are restricted to only a handful. The second reason is that for these semi-perennials with a crop cycle period of two to three years, a considerable amount of time, space and resources are required to carry out such trials over locations and seasons. Finally, it seems that stability estimates for yield, which is the most common parameter for GxE studies for cereals, forages and other crops, may have to take a backseat for a high valued crop such as fruits where quality, cosmetics and consumer preference may override the requirements of high yields.

Notwithstanding these reasons, MARDI has carried out two GxE trials, one for papaya and another for pineapple. The trials coincided with the development of new varieties for these two fruit types, and GxE testing appeared justified to test their performance and adaptability over diverse environments. These two fruit types are also good examples to consider, because the variety of papaya was bred for a dessert fruit while the pineapple variety was developed for the canning industry. As can be seen later, the emphasis in selection and the variables considered for stability studies were rather different in the two trials.

Genotype x Environment Study of Papaya

In 1987, MARDI released a new papaya variety called the Eksotika. It was developed from a backcross breeding programme involving the Sunshine Solo variety as the recurrent parent and Subang 6 variety as the non-recurrent parent. Before its release, the Eksotika (then known as the Backcross Solo) was put in a GxE study together with three other varieties, Subang 6 and Sitiawan which were popular local varieties and Maradol, an established variety from Cuba (Chan, 1985). Only four varieties were used for the study because of the restricted availability of *bona fide* gynodioecious varieties in the world.

Four locations were chosen for the trial. All were situated on the west coast of Peninsular Malaysia, in areas identified as agro-ecologically suitable for papaya cultivation. There were some differences in soil type, however, with three situated on mineral soils i.e Serdang, Pontian and Batu Pahat stations and the other i.e Jalan Kebun, on peat soil.

Two important characters i.e yield and percent total soluble solids (T.S.S) were found to have significant GxE interactions. Stability analysis was done on these two characters using the structural relationship method proposed by Tai (1971).

The results are shown in Figure 1 and Figure 2. With regards to yield, Maradol was found to be perfectly stable ($a < 0, n = 1$) while Eksotika ($a = 0, n = 1$) had average stability. Both Sitiawan and Subang 6 were unstable for different reasons. Subang 6 ($a = 0, n > 1$) appeared to be a non-conformist to the general linear trend and showed large deviations from linearity while Sitiawan ($a > 0, n = 1$) was a more predictable performer with deviations from the linear trend but was more sensitive to changes to the environment index. For T.S.S. which reflects the sweetness of the papaya, all four varieties had average stability ($a = 0, n = 1$).

Although the stability statistics gave responses or behaviour of varieties to changing indices, they cannot be used solely for selection of genotypes, especially in the case of papaya.. The choice of varieties invariably will also have to depend on high mean yield and good quality (high T.S.S) especially if the selection is for dessert varieties. Sitiawan had the highest mean yield (28.7 kg/tree) over all locations (Table 1), but its large fruit size (1.49kg) and low T.S.S will not make it suitable for a dessert variety especially for export. As a matter of fact, none of the varieties other than Eksotika (11.6-13.2%) had high enough sweetness to be considered a good quality dessert fruit. Unlike most crops, where high mean yield and stability are important, for fruits therefore, the quality specifications may usually dictate the choice of a variety. In this trial, it was fortunate that the Eksotika showed medium to high yields, high T.S.S and average stability for both characters.

theoretical distributions of the stability statistics for the four papaya varieties under different conditions of π and p . The theoretical distributions are plotted in Figure 1. The vertical axis (α) ranges from -1.0 to 1.0, and the horizontal axis (π) ranges from 0 to 6. The curves represent the distribution of α for different values of p (0.80, 0.90, 0.95) when $\pi_0 = 1$. The four papaya varieties are plotted as points on the graph: Sitiawan (top left), Subang 6 (middle right), Maradol (bottom left), and Backcross Solo (bottom right). The curves for $p = 0.95$ are the uppermost, followed by $p = 0.90$, and then $p = 0.80$.

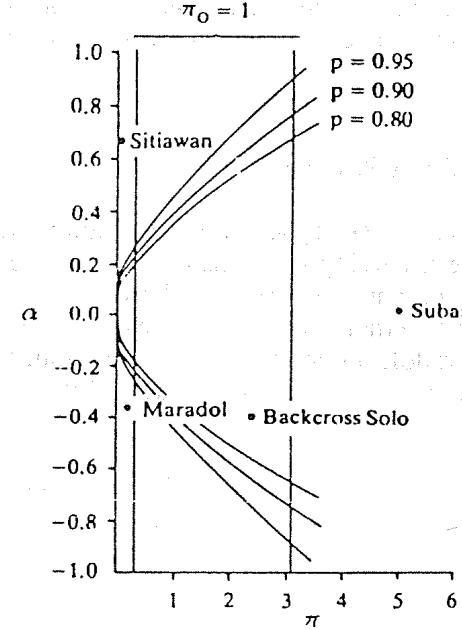


Figure 1. Distribution of stability statistics of four papaya varieties for yield.

the four papaya varieties were Backcross Solo, Maradol, Sitiawan and Subang 6. The distribution of stability statistics of these four papaya varieties for total soluble solids % is shown in Figure 2. The vertical axis (α) ranges from -1.0 to 1.0, and the horizontal axis (π) ranges from 0 to 6. Three curves are plotted for $\pi_0 = 1$ and $p = 0.95, 0.90, 0.80$. The curve for $p = 0.95$ is the uppermost, followed by $p = 0.90$, and the lowermost is for $p = 0.80$. The point "Backcross Solo" is located on the upper curve for $p = 0.95$ at $\pi \approx 4.2$ and $\alpha \approx 0.35$. The points "Maradol", "Sitiawan", and "Subang 6" are located on the lower curves for $p = 0.80$ at $\pi \approx 0.5$ and $\alpha \approx -0.15$, $\pi \approx 0.5$ and $\alpha \approx -0.25$, and $\pi \approx 0.5$ and $\alpha \approx -0.35$ respectively.

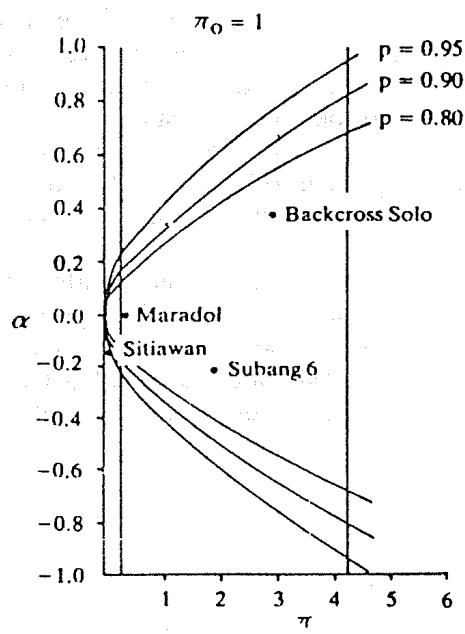


Figure 2. Distribution of stability statistics of four papaya varieties for total soluble solids %.

Table 1. Means of various characters over four locations for the papaya GxE trial

Genotype	Fruit wt (kg)	TSS %	Yield (kg/tree)
Eksotika	0.62c	12.2a	23.6ab
Sitiawan	1.49a	10.1b	28.7a
Maradol	1.35a	10.6b	16.9c
Subang 6	1.02b	10.1b	22.2ab

Values followed by the same alphabet are not significantly different at $p=0.1$ according to Duncan's Multiple Range Test.

The restricted availability of true breeding, gynodioecious varieties had forced the comparison of the new variety with only three other varieties which were rather diverse in form and morphology. It would have been more meaningful had the trial been conducted with varieties that have very similar fruit qualities and appearance so that selection may be based on stability parameters alone. However, this was not possible because varieties similar to Eksotika were not available. As was found in this trial, even high yielding (and stable) varieties may have to be overlooked because their fruit forms and quality did not suit the specifications of a dessert variety with export potential.

With regards the locations chosen, all showed acceptable yields ranging from 12kg/tree in Serdang for Marado variety to 38.3kg/tree for Sitiawan in Jalan Kebun (Chan, 1985). The highest yield worked out to be about 80 tonnes/ha which was close to the highest papaya yields reported in the world. Poor areas or poorly managed plots were deliberately avoided because these will not present real circumstances in papaya cultivation. Being a high value crop, the fruits are grown with special care for obtaining premium quality and price.

Genotype x Environment Study of Pineapple

The GxE study, for pineapple was initiated in 1983 following the development of a new hybrid called Nanas Johor (formerly known as the Hybrid 1) (Chan and Lee, 1985). It was selected from a F1 population generated from a cross between Singapore Spanish and Smooth Cayenne. The new hybrid, like the Eksotika papaya, was tested with several popular local cultivars e.g Gandul, Sarawak, Moris and Masmerah. These four cultivars probably constitute 99% of all pineapples grown in Malaysia. The small number of varieties for the trials, like the GxE study on papaya, was due to limitation in availability of cultivars.

Seven locations were chosen for the trial, four on peat soils and others on mineral soils. Peat is the predominant soil type for cultivation of pineapples in Malaysia and the sites chosen were Pontian, Simpang Rengam and Jalan Kebun (two sites). At Jalan Kebun, virgin peat (previously uncultivated) and cultivated peat were tested. The sites on mineral soils were Serdang, with two different forms of management (with or without irrigation) and at Bukit Ridan.

Two important characters i.e fruit size and D leaf were considered. Fruit size is synonymous with yield because the varieties have a standard planting density and with effective flowering hormones, each plant should bear a fruit. The D leaf or the tallest leaf in the plant, is the most recently matured leaf, and was used as a measure of vegetative vigour of the plant. Vegetative vigour in pineapple is an import consideration because it affects the time of flower hormone treatment in pineapple. The more vigorous it is, the earlier the hormone treatment can commence, and the more productive in terms of yield per unit time.

The results of the trial showed that in so far as sites were concerned, there was a definite preference of pineapple for peat areas, reflecting the fact that many of these varieties were developed for peat soils. As indicated in Figure 3, The D leaf weights were very poor on mineral soils i.e Bukit

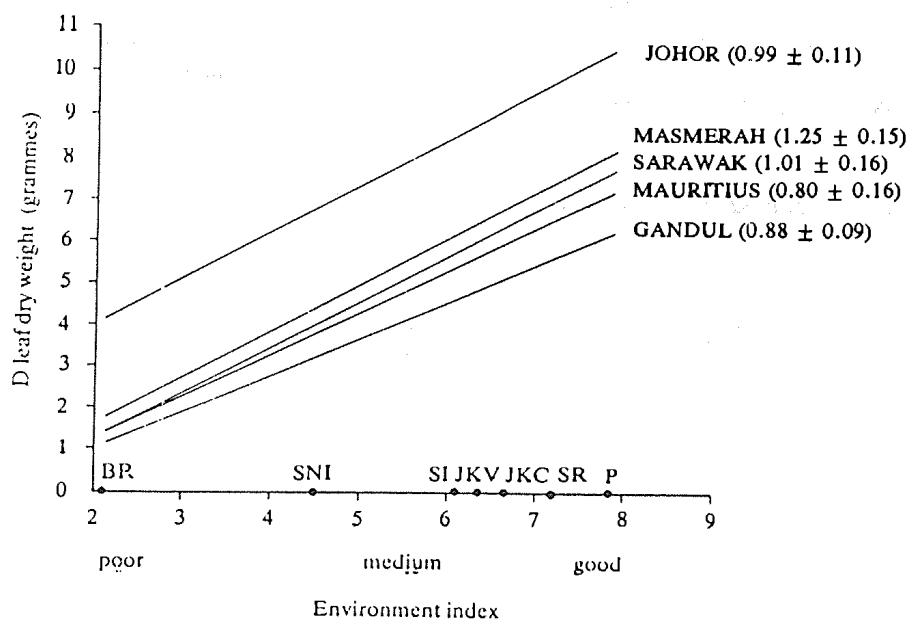


Figure 3. Comparative vegetative growth ($D_{leaf\ dry\ wt.}$) of five pineapple cultivars grown on seven locations

Ridan, non-irrigated Serdang and irrigated Serdang. This was also true for fruit production where the three mineral soil sites also showed small fruit size. As a matter of fact, the site at Bukit Ridan was so poor that many varieties were unfruitful and consequently, the mean of the site could not be computed.

The analysis of stability followed the model proposed by Eberhart and Russell (1966). Nanas Johor, the new hybrid, was clearly the most outstanding both in vigour as well as fruit yields. It has average to very good stability ($b = 0.99$ and 0.66) for D leaf and fresh fruit weight respectively (Figure 3 and Figure 4) and the most important was that it outperformed all the varieties by at least twice as much as in poor environments and 25% more in good environments. There was a change-in-rate type of interaction with yield gaps closing gradually between the new hybrid and the rest as the environment improved. There was a theoretical chance that the other three varieties might bear larger fruits when the regression lines were extrapolated to super fertile environments (Figure 4) but this was unlikely to come true because they would probably juxtapose when Masmerah and Moris can produce 3-6 kg fruits which was biologically not possible with these two small-fruited varieties.

It appeared that the selection of Nanas Johor would be a good choice, based on the vigour and yield stabilities, and was thought to have the potential to replace standard canning varieties like Gandul and Masmerah. But this was not so because in later canning trials it was found to be susceptible to marbling, a disease which blemishes the flesh of the fruit and reduced recovery during canning.

GENERAL CONSIDERATIONS FOR GxE STUDIES ON FRUITS

Characters

All the methodologies for analysis of GxE effects, whether using linear regression, cluster analysis, principal component analysis and others, have the single objective of describing the behaviour of the genotype or groups of genotypes in response to the changing environment. Many of the examples used in GxE studies have been based on yield stability, a parameter of paramount importance for crops such as cereals, forages and tuber crops. However, for many horticultural crops, particularly for ornamentals and fruits, this parameter may not be as important as the aesthetic values and quality considerations of the variety. From the two examples cited for papaya and pineapple it is clear that other criteria for judgement of performance may also be appropriate. Total soluble solids was given emphasis as a quality criterion for the desert papaya, but this was largely ignored for selection of canning pineapple because sugars can be added during processing. On the other hand, vigour was an important consideration in breeding pineapple for early cropping while for papaya, vigour *per se* was perhaps less important than an optimum harvest index or its balance of fruit load and vegetative growth. There are perhaps many more specific criteria for fruits such as keeping quality, vitamin content, cannery recovery etc. which may be higher priorities for selection than yield. GxE trials for fruits therefore, seemed more complicated with these additional considerations.

Sites

In view of sites for fruit GxE trials, it may not be necessary to include infertile or poorly managed environments because these would not reflect the actual environments in which the crop will be finally grown. In the cultivation of these high valued crops, it is sometimes even necessary to modify the environments (eg. greenhouses, rainshelters, hydroponics, soil amendments etc) to meet requirements for high production and good quality rather than to fit adaptable cultivars to poor environments to obtain subsistent and often poor quality fruits which would not be marketable anyway.

Sometimes, however, it may seem justified to test the varieties on soil types in which it had not been previously grown before. Such was the case in the papaya trial in which the varieties were tested on peat soil. The results were promising and indicated that, with some agronomic adjustments, peat may be a potential soil for production of papaya in Malaysia.

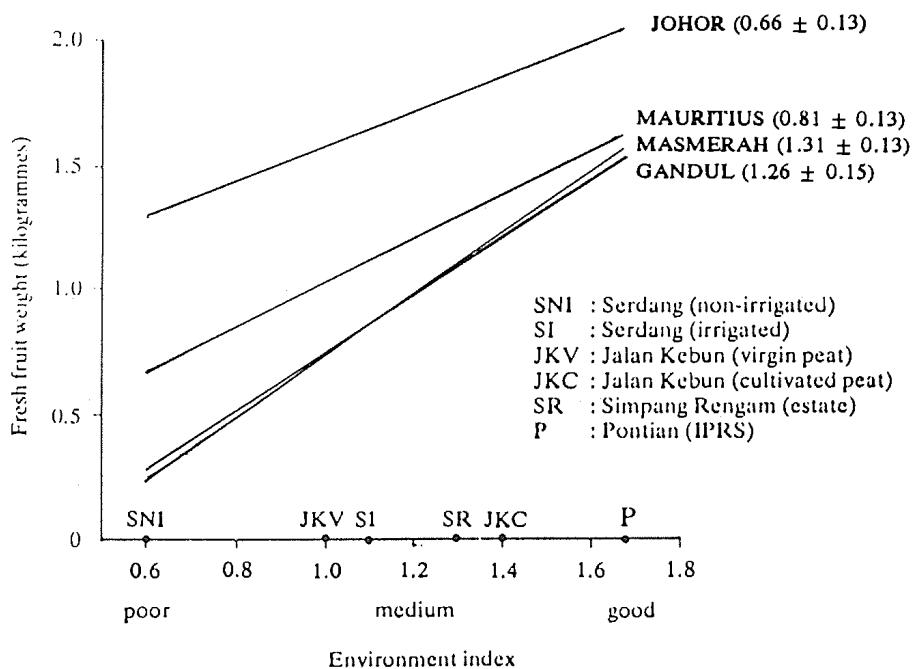


Figure 4 .Comparative fruit size of four pineapple cultivars grown on six locations

Varieties

An important point to consider in the choice of varieties for testing is that it makes sense to use, where possible, a group of varieties that have homogeneous characteristics and developed for the same requirements of the industry. This would first reduce the spurious occurrence of 'unstable' outliers arising from non-conformity but more importantly, it would also allow selection efforts to be focussed on stability *per se*. In the case of papaya, stability estimates did not play an important role in selection of genotype because those that qualified in this criterion, failed to meet other specifications such as fruit size and fruit quality. As mentioned earlier, the choice of a small number of diverse genotypes in the papaya trial and to some extent, in the pineapple trial, arose because of the limited availability of bona fide varieties. It can be expected that this difficulty would be experienced in many other GxE trials for tropical fruit species in which little breeding work has been carried out.

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SESSION 2 DISCUSSION

Q: Ho Chai Yee - Ebor Research, Sime Darby Plantations, Malaysia.

In your trials I suppose the environments are fairly similar so you don't get the GxE effect. When looking at yields, the ranking for PBC 130 and PBC 140 in trials are different, PBC 130 gives average yields of about 3 tonnes in commercial areas compared to PBC 140 which only yields about 2.5 whereas in your trials it is the reverse. Is there any explanation for this? From our own experience one should not generalise for Peninsular Malaysia, for example in Johor PBC 130 is very susceptible to VSD and the yields are very low.

A: Chong Choon Fong - Golden Hope, Malaysia.

You are right. PBC 130 is a very sensitive clone. Its performance is influenced even by soil conditions, for example its yields are low in sandy soils. Whereas PBC 140 is more consistent. But both clones are very high yielding; the ranking sometimes changing. Another pertinent factor for the differences in yield is the management, they are not both under the same management.

Q: Mr. Hew Choy Kean - Plantek (M) Sdn. Bhd., Malaysia.

I would like to be clear about another difference cited above. It was said that the yield difference was due to management. So do we include management as an environmental condition or is it separate. So where is the genotype x environment interaction?

Furthermore, in the last slide the mixture of clones yielded about 1296 kg whereas for seedlings it is about 970 kg with a 35 % difference. In another slide you show the clones themselves exceeding 2 800 kg. So a few clones give double that of a mixture of seven clones. Can this be explained?

(A) Chong Chon Fong - Golden Hope Plantations, Malaysia.

In Polyclonal planting not all clones are high yielding i.e. not all the top ranking clones only are planted together as some clones are included for other reasons such as PBC 159 for flavour and high fat yield, though not among the highest yielding.

Management is an important aspect of the environment.

Q: Dr. Soh Aik Chin - Applied Agricultural Research Sdn. Bhd.

In perennial crops we are not certain whether to include years as environments in our GxE studies because in our perennial crops there are seasonal cycles such as a biennial or triennial cycle. In some of the presentations years has been used as an environmental effect. Is this right as the yield of one year affects that of subsequent years and individual years are no more random. Is it valid then to look at genotype x single year effects ?

A: Prof. Manjit Kang - Louisiana State University, USA.

Allard has cautioned plant breeders about breeding for stability with respect to years as years are so unpredictable. Either one has to have so many years data before arriving at a reliable estimate of an average effect or one is faced with something that is not very heritable. Locations are more predictable and can be manipulated by management practices but years are probably beyond one's control unless there is a built in crop effect, as one is working with same plant. Taking sugar cane as an example where there is ratooning or stubbling and something is known about the stubbling effect so we know that next year certain things would be expected. In such a situation I think we could use years as year and crop is confounded. And if that is the case I think you could develop varieties that have stability to years otherwise it is questionable.

Comment: Prof. Mak Chai - Universiti Malaya, Malaysia.

With perennial crops the age of the plant will also be another confounding effect.

Q: Yong Yit Yuan - Guthrie Research Chemara, Malaysia.

Prof. Kang mentioned that the computations of the stability parameters have been programmed in SAS and BASICA. Is the BASICA program marketed or distributed free?

A: Prof. Manjit Kang - Louisiana State University, USA.

Both the SAS run programs are free while for the BASICA we have been charging US\$10 per copy.

Comment: Dr. N. Rajanaidu - PORIM, Malaysia.

In Dr. Tan Hong's paper most of the GxE interaction mean squares are non linear i.e. deviations from regression. I found a similar trend in oil palm progenies where the linear regression is non-significant and the interaction is mainly non-linear. Obviously this will make it more difficult for breeders in terms of selecting varieties whose response over many environments can be predicted.

Q: Prof. P.D.S. Caligari - University of Reading, United Kingdom.

A lot of the speakers use the linear regression approach and talk of a plant breeding situation. I would be intrigued to know really where they see the advantage of the linear approach rather than simply taking the variance or the square root of the variance over the environment as a selection criterion?

A: Dr. Tan Hong - RRI, Malaysia.

Actually in the selection of rubber, we are still empirical in our approach and mainly concerned with the most important characters i.e. productivity or rubber yield and coupled with it will be other considerations about secondary characters of the plant. We characterise the plants and identify environmental constraints and try to match to obtain maximum productivity in a specific environment. We have done linear regressions as they were popular then but we are still very comfortable with our empirical approach.

Q: Dr. V. Rao - EPA Management Sdn. Bhd., Malaysia.

While sympathetic to breeders who have to select for characters such as "cosmetics" of fruits I wonder if there is any inherent difficulty. For example the character "oily" in oil palm has been broken down into oil/dry mesocarp, moisture content, etc. Can't characters such as "cosmetics" be similarly handled?

A: Mr. Chan Ying Kok - MARDI, Malaysia.

As the breeding programme progresses and gets more advanced, and as the industry gets more advanced, then certain other requirements will need looking into; for example 10 years ago when we went into papaya breeding we did not think of cosmetics but as the industry grows and as we got some varieties into the market and as consumers taste these fruits their expectations increase.

A: Dr. R.H.V. Corley - Unilever Plantations PLC, London.

Quality is a very crucial factor in tea. It has to taste nice, but it is a very subjective criterion. Unfortunately we don't have anything like total solids or sugar content to assess quality. Our approach in the breeding and clone selection program is to select for high yield and to do a screening at the end on the basis of quality as tested by tea tasters. Until we have an objective assessment of quality, which we don't have, we have to do it that way, though quite frustrating. But it is very important to take account of what the market wants.

Q: Mr. Tan Tack Nee - Gula Perlis Sdn. Bhd., Malaysia.

Dr. Corley's slide showed differences in tea yield between site 1 and site 2 which were at high and low altitudes. But what about in money terms?

(A) Dr. R.H.V. Corley - Unilever PLC, London.

There was also a highly significant difference in money terms but not as big as the difference in yield as quality tends to improve with altitude. It seems that the slower the tea grows the better the quality so at the high altitude the quality on average is better and hence the crop is slightly more valuable, but otherwise yield translates directly into dollars and cents.

Q: Dr. Ho Chai Yee - Ebor Research, Sime Darby, Malaysia.

Dr. Tan Hong mentioned that in the case of rubber, the linear relationship is very low because of the very large number of factors involved. Oil palm yield seems to be very dependent on just a few factors and hence the oil palm situation may be simpler than rubber. What are your comments?

A: Tan Hong - RRI, Malaysia.

Firstly, the regression was only an attempt at applying to rubber. We only had 5 - 6 sites some of which clustered suggesting that their environments do not vary very much. Hence because of the limited d.f. the analysis itself may not be satisfactory. Perhaps it may be useful to include more sites that are more variable. Whether it is simpler or more complex than oil palm I am not certain.

A: Dr. R.H.V. Corley - Unilever Plantation PLC, London.

An oil palm produces a certain amount of crop in a year. It decides how much to produce, partly dependent on where it is planted and what inputs are given but generally the tree decides what to produce. Rubber, I guess, and in tea certainly the yield is much more 'flexible' and under management control. In tea one can get whatever yield wanted by playing off against quality. So in comparing different sites, unless the management is identical, there will be interactions between genotypes and harvesting systems as well as between sites and the environment 'black box' becomes very complicated. The same may be true for rubber and tapping systems; the optimum system differing between environment and between clones, hence complicating the analysis and interpretation.

Q: Dr. V. Rao - EPA Management Sdn. Bhd., Malaysia.

In one of the methods of GxE analysis you showed, you combine the yield and stability parameters and use the combined figure for selection purposes. In using the stability parameter, you give points on whether it is significant or otherwise, for example four points for 5% significance and eight points for 1%. Is this not rather arbitrary?

A: Prof. Manjit Kang - Louisiana State University, USA.

The figure is arbitrary to some extent and has been arrived at by hit and trial and there were other values that were given for significance at 5% and 1% but they did not cause any change in the original yield rankings so they weren't any different and this was the first value or reading that did cause a change. It can be modified; all of these things are arbitrary and subject to question and evaluation.

PERFORMANCE OF COCOA CLONES AT DIFFERENT SITES

by

Chong Choon Fong¹

INTRODUCTION

Cocoa is a very sensitive crop. Its growth and yields are greatly influenced by environmental factors. Many progeny and clone trials have been undertaken since late 1960s by Golden Hope Plantations Bhd., with an aim to improve cocoa planting materials. Equal emphasis has been placed on the production of both hybrid seedlings and clonal materials, as the improvement of one will always be followed by the improvement of the other. Nevertheless, in view of considerable advancement made in the development of clonal materials by research establishments in this country in recent years, clones have now featured prominently in new planting or replanting programmes.

Briefly, Golden Hope's approach on clone evaluation is as follows:-

Clones are evaluated in two stages, i.e preliminary proof and further proof stages. Preliminary Proof (PP) clone trials are designed to permit the screening of very large numbers of new clones derived from ortet selection in plots of adequate size for evaluation of their merits.

The most promising preliminary proof clones are tested in Further Proof (FP) trials in environments representative of major cocoa-growing areas. A randomised complete block design has been adopted in all trials, each clone being planted in at least three replicates of 50-80 tree plots. Under normal circumstances, only 10% of the clones in the PP trials will be selected for evaluation in the FP trials.

To study the effects of environment on genotypes, results of some Preliminary Proof and Further Proof trials are considered.

GENOTYPE/ENVIRONMENT INTERACTION

Further Proof trials No. 1 and 2 were established in 1975 in two different locations. Trial particulars are given in *Table 1*.

FP 1 was terminated after only four years of harvesting as the site was replanted with other cultivars. Yield data of the first four years of the seven clones common in both trials are presented in *Table 2*.

Yields of clones in the FP Trial No. 2 were very much lower than those of the FP 1 trial mainly because of unfavourable coastal clay soil environment where water-table was high and drainage was a problem. From the results it is obvious the yield differences within clones in these two locations were very significant. However, the ranking on yield of individual clones is quite similar.

Significant differences in pod values and bean sizes of clones in the inland and coastal situations were also apparent (*Table 3*). The pod value is the number of cocoa pods required to provide one kilogram of dry beans. Ideally, the pod value of a clone should not exceed 25. The desirable average bean weight of cocoa should be 1 g or slightly above. Both pod value and bean weight are yield

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components of cocoa and they are interrelated i.e, the reduction of bean weight of a clone due to adverse environment condition will increase the pod value.

Table 1. Particulars of Further Proof Trials Nos. 1 & 2

Particulars	FP No. 1	FP No. 2
Location	Prang Besar	Flemington
No. Clones	14	14
Area (Ha)	2	2.5
Source of Clones	P.P. 1	P.P. 1
Planting System	Mono-cocoa	Cocoa-coconut
Soil Type	Inland (Munchong)	Coastal Marine clay (Bernam)
Year Budded	1975	1975
Design	RCBD	RCBD
Plot size	50	50
Stand/ha.	1075	900
Replication	3	3
Permanent Shade	Parkia, Durian	Tall Coconuts

Table 2. Yield (Kg/Ha) in FP 1 and FP 2

PBC Clones	Trial	1ST Yr	2ND Yr	3RD Yr	4TH Yr	Av.	Ranking
102	FP 1	189	1541	1541	1737	1252	4
	FP 2	302	557	630	1092	645	4
105	FP 1	197	1213	1488	1344	1061	5
	FP 2	179	332	558	765	459	6
106	FP 1	154	1211	1521	1270	1039	6
	FP 2	159	320	481	502	366	7
109	FP 1	188	1195	1455	1284	1031	7
	FP 2	228	374	686	662	488	5
110	FP 1	213	1439	1990	1567	1302	3
	FP 2	366	544	916	932	690	2
112	FP 1	353	1536	2201	2124	1554	2
	FP 2	307	494	982	871	664	3
113	FP 1	314	1657	2245	2016	1558	1
	FP 2	302	722	829	1028	720	1
Av.	FP 1	230	1399	1777	1620		
	FP 2	263	478	726	836		

Table 3. Pod value and bean size of clones in FP 1 & FP 2

PBC Clones	Pod Value		Bean Size (g)	
	FP 1	FP 2	FP 1	FP 2
102	27.1	31.0	1.04	0.87
105	22.3	26.6	1.32	1.12
106	26.2	34.6	1.16	0.88
109	31.6	37.5	0.89	0.77
110	26.9	33.9	0.98	0.83
112	23.8	30.8	1.05	0.86
113	20.9	25.3	1.19	0.96
Av.	25.5	31.4	1.09	0.90

Although bean weight is genetically determined, it can be influenced significantly by environmental circumstances. Further Proof Clone Trial No. 2 provided clear evidence of the extent to which unfavourable soil environment can depress bean weights. In that trial, the average bean weights of the seven clones were about 20% lower than those recorded in Further Proof Trial No. 1 which was located on a more favourable inland soil. Accordingly, emphasis must be placed on the selection of clones with above-average bean size; i.e more than 1 g, for planting in environments where soil and environment conditions are sub-optimal.

Although more detailed analyses are desirable, preliminary results of the FP 1, FP 2 and other clone trials, however, indicated limited genotype and environment interactions, i.e the ranking of individual clones were very similar over a range of circumstances, except in areas where diseases, particularly vascular streak dieback (VSD), were troublesome and disease tolerance conferred an advantage.

In Malaysia, VSD caused by the fungus *Oncobasidium theobromae* has become the most troublesome disease particularly in the main cocoa growing areas in Sabah. Experience and observations to date have indicated that in high rainfall and VSD-prone areas, cocoa planting may not be viable unless VSD tolerant planting materials are used. Performances of some clones in high VSD environment are illustrated in *Table 4*.

Table 4. Effects of VSD on performances of cocoa (Giram Estate)

Planting Material	Yield kg/ha			VSD		
	SH*	1st Yr	2nd Yr	Pod Value	Bean Size (g)	Tolerance Rating
PBC 123	970	3104	3863	24.3	1.19	4
PBC 130	267	291	1381	19.3	1.43	1
UIT 1 x Na 33	144	379	615	28.6	1.06	1

*SH - scout harvesting

VSD tolerance - 5 very tolerant
- 1 least tolerant

Clone PBC 130, which was very high yielding in Peninsular Malaysia, did not perform well in trials at Giram Estate, Sabah mainly because it readily succumbed to the very high VSD inoculum pressure there. On the other hand, PBC 123 which was fairly tolerant to the disease had performed very well in the high VSD inoculum pressure but favourable volcanic environment.

As susceptibility to VSD is genetically determined, clone trials conducted in the high disease inoculum region may present a rapid means of selecting disease-tolerant cultivars for planting.

YIELD STABILITY

Yields of some recommended clones for planting have been very stable and consistent in trials and commercial plots in Peninsular Malaysia. Although they may fluctuate to some extent from one year to the next as the result of differing climatic patterns, consistently high yields of recommended clones PBC 123, PBC 130 and PBC 140 as indicated in *Tables 5 and 6*, have been maintained over a long period in environments where VSD was not troublesome.

Table 5. Yields (kg/ha/year) of recommended clones in PP trial No. 9

	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	1-9th
PBC 123	197	719	1255	1598	1468	1688	1453	2064	2358	1421
PBC 130	161	1067	1774	1980	2192	2297	1995	2379	2388	1803
PBC 140	265	1474	2184	2885	2393	2915	2276	2582	3321	2255

Table 6. Yields of recommended clones (kg/ha/year) in commercial plots

	83/84	84/85	85/86	86/87	87/88	88/89	89/90	90/91	Av. 8 yrs
PBC 123	2027	2063	1960	1942	1938	1807	2193	1914	1981
PBC 130	3135	3145	3155	3485	3599	3163	2831	2416	3116
PBC 140	3130	2629	2638	2820	2960	2669	3022	2844	2839

Based on their consistent performances in trials and small scale polyclone plantings, 12 clones have been recommended since 1982 for polyclone planting on Golden Hope Estates and cocoa growing areas in Peninsular Malaysia. Results to date from commercial plantings have been very encouraging. The first generation of clones have consistently out-yielded mixed hybrid seedlings by 30-50% in large scale plantings in early 1980s.

Besides their high yields, the clones also possessed desirable secondary characteristics, such as reasonably large and uniform beans, some VSD tolerance and above-average fat content etc.

Based on latest results, the list of recommended clones has been revised recently. The new list of clones is as follows:

Vigorous : PBC 113, 130, 207, 221, 236 and 247

Less vigorous : PBC 123, 140, 159, 179, 208, 211, 223, and 230

It is expected that these clones should provide 50-80% higher yield than the currently recommended seedling materials.

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EVALUATION OF KKM COCOA CLONES AND THEIR RESPONSES TO DIFFERENT ENVIRONMENTS

by

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ABSTRACT

Evaluation of KKM clones for their responses to environment was carried out in multi-location clonal trials. Trials were established in new cocoa growing areas, in traditional growing areas and in usually non-growing areas (Env. A, Env. B and Env. C). This paper reports on the performance and the relative stability of KKM clones to these three environments. The clones used were recently released KKM clones (KKM 1, 2, 3, 4, 5, 6 and 7) and a control ICS 95. The traits evaluated were the pod production capacity, average bean number per pod and the mean dry bean weight. These traits are the most important yield parameters in cocoa. It was observed that there was highly significant variation due to environment, clones and clone x environment (GxE) interaction for the traits studied. KKM 4 is superior in all the three locations but it generally favours good environments. KKM 1 is quite a stable clone with average pod yield and performs well in a less favourable environment. ICS 95 produced the least pod yield and is an unstable clone.

INTRODUCTION

The performance of cocoa progenies has been observed to vary in different environments (Ooi and Chew, 1985). For the evaluation of the performance of KKM cocoa clones, multi-location clonal trials were carried out. Variations in performance occur when yield differences among the clones are not of the same magnitude in different environments. This clone x environment interaction (GxE) has made the selection of clones and testing strategies more complicated. It is even more complicated when one has to make selection for commercial clones and recommendations for a particular environment.

This paper is an attempt to obtain information as to whether cocoa clones respond differently when grown under different environmental conditions.

MATERIALS AND METHODS

Eight cocoa clones were used in this trial; seven selected commercial KKM clones and 1 control clone. The clones used were KKM 1, KKM 2, KKM 3, KKM 4, KKM 5, KKM 6, KKM 7 and ICS 95. Three sites were selected for the analyses of GxE interactions. The sites were in Pahang with an inland soil type which represent a new cocoa growing area, Perak on coastal clay soils typical of cocoa growing areas and in Perlis on a very marginal soil type not usually a cocoa growing area (Env.

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A, Env. B and Env. C respectively). The experimental design was a Randomised Complete Block Design with three replications. Each plot consisted of 20 plants. The plants were spaced at 3.0 m triangular pattern planted in a monoculture system with *Gliricidia* as the shade tree. Standard agronomic practices were followed for all the sites.

Data analysis were on total pods produced per year (1988-1990) and pod analyses (bean number and average bean weight) during the peak seasons of the three years. Combined analysis of variance and Eberhart and Russell's Model (1966) were used in the analysis of data.

RESULTS AND DISCUSSION

Analysis of variance

Clones, environments and their interactions contributed to highly significant variation for each of the yield parameter (*Table 1*).

Table 1. Mean squares for the combined analyses of variance across three environments in 1988-1990 for total pods produced per year

Source	df	Pod yield ms	Bean number ms	Mean dry bean ms
Rep(Env.)	6	201212.0	5.0	0.004
Environment	2	4644110.0	83.1	0.346**
Clones	7	1951510.0**	216.6**	0.253**
Env. x Clones	14	2040544.0**	18.3*	0.177**
Error	42	779859.0	9.7	0.012
CV, %		22	8	9

Relative influences of clones (genotype), environment, and their interactions on pod yield, average bean and mean dry bean weight are shown in *Table 2*. Environment had a notably larger influence on variation in pod yield and mean dry bean weight compared to average bean number. Genotypic variance was larger than the environmental effect on the number of beans. Bean number is a highly heritable trait in cocoa.

Table 2. Mean squares for clones, environments and their interactions for yield parameters

Source	df	Pod Yield ms	Bean number ms	Mean dry bean ms
Clones	7	278787.2**	216.6**	0.253**
Environment	2	2322055.0**	83.1**	0.346**
Rep/Env	6	33535.3ns	5.0ns	0.004ns
Clone/Env	14	145752.6**	18.8ns	0.117**
Error	42	18568.2	9.71	0.012

The analysis of variance for each clone for the differences in stability and performance is shown in *Table 3*. Bean number was significantly controlled by the clone (genotype). KKM 6 varied in its performance in the three environments.

Table 3. Analysis of variance for estimated stability parameters of clones

Source	df	Pod yield ms	Bean number ms	Bean wt. ms
Clone	7	92929.1ns	72.2**	0.084ns
Env + (c1 x Env)	16	139263.6	8.9	0.048
Env (Linear)	1	1548038.0**	55.5**	0.231**
C1 x Env(Linear)	7	55111.5ns	10.8**	0.059*
Pooled deviation	8	36799.8	1.4	0.016
KKM 1	1	9546.9ns	4.3ns	0.012ns
KKM 2	1	48929.2*	0.009ns	0.001ns
KKM 3	1	13157.9ns	1.3ns	0.022*
KKM 4	1	1129.0ns	2.5ns	0.001ns
KKM 5	1	121023.4**	2.2ns	0.016*
KKM 6	1	52012.7**	0.6ns	0.044**
KKM 7	1	7834.0ns	0.2ns	0.006ns
ICS 95	1	40765.3*	0.3ns	0.027*
Pooled error	48	6813.0	3.0	0.003

Stability for yield

The average performance of each clone for the three yield components are given in *Table 4*,

Table 5 and *Table 6*.

Table 4. Mean pod yield (kg per year), regression coefficient, variance of mean, deviation from regression and stability parameter of each clone

Clone	Mean pod	Regression coef. (b)	Variance mean	Deviation fr. reg.	Stability parameter
KKM 1	450.4de	0.90	168501	9546.9	3357.5
KKM 2	590.3cd	1.42	440459	48929.2	42739.7
KKM 3	437.6de	0.30	30918	12157.9	6968.5
KKM 4	841.4a	1.20	280168	1129.0	-5060.4
KKM 5	672.0abc	1.86	793190	121023.4	114834.0
KKM 6	591.7bcd	0.36	78363	52012.7	45823.3
KKM 7	820.3ab	1.22	298681	7834.0	1644.6
ICS 95	363.2e	0.70	137935	40765.3	34575.8

In terms of pod production, the performance of KKM 4 was superior in all the three locations but generally it favoured the more favorable environment ($b = 1.20$). So did KKM 7 which will perform well in a good environment ($b = 1.22$). KKM 1 is a stable clone but is average for pod production and its performance was relatively better in a less favourable environment ($b = 0.90$). ICS 95 is quite an unstable clone ($b = 0.70$) and it produced the lowest pod yield. KKM 3 and KKM 6 produced higher pod yields than ICS 95 but they are considered the most unstable clones ($b = 0.30$ and $b = 0.36$ respectively).

Table 5. Mean bean number per pod, regression coefficient, variance of mean, deviation from regression and stability parameter of each clone

Clone	Mean bean	Regression coef. (b)	Variance mean	Deviation fr. reg.	Stability parameter
KKM 1	49.6a	-0.97	10.9	4.360	1.12
KKM 2	33.4d	1.01	7.0	0.009	-3.22
KKM 3	40.8b	2.25	36.6	1.365	-1.87
KKM 4	38.3bc	0.87	7.9	2.587	-0.65
KKM 5	39.7bc	0.38	3.2	2.285	-0.95
KKM 6	36.4bcd	-0.06	0.6	0.656	-2.58
KKM 7	35.3cd	2.89	58.2	0.231	-3.00
ICS 95	39.3bc	1.62	18.5	0.315	-2.92

KKM 1 and KKM 2 are the most stable clones ($b = -0.97$ and $b = 1.01$ respectively). In terms of average bean number per pod KKM 1 performed well even in a less favourable environment and KKM 2 was an average performer. The number of beans developed depends on the pollination efficiency and microenvironment of the area. If the microenvironment is conducive for pollinators to breed and to pollinating activities, all potential beans (ovules) will be formed.

KKM 3 was the most stable clone for average bean size ($b = 0.98$) and its performance was quite consistent even in an unfavourable environment. Of all the clones tested, KKM 6 was the most unstable clone ($b = 3.92$) and required a very good environment to perform well. KKM 4 had quite an unstable average bean size but it maintained the commercially accepted bean size even in an unfavourable environment.

Table 6. Mean dry bean weight, regression coefficient, variance of mean, deviation from regression and stability parameter of each clone

Clone	Mean wt.(g)	Regression coef. (b)	Variance mean	Deviation fr. reg.	Stability parameter
KKM 1	1.47a	0.78	0.029	0.012	0.007
KKM 2	1.18bc	0.57	0.011	0.001	-0.002
KKM 3	1.03cde	0.98	0.050	0.022	0.018
KKM 4	1.17bcd	0.10	0.006	0.001	-0.003
KKM 5	1.21b	-0.75	0.032	0.016	0.012
KKM 6	1.08b	3.92	0.490	0.044	0.040
KKM 7	0.97e	2.11	0.135	0.006	0.002
ICS 95	0.98e	0.26	0.029	0.027	0.023

CONCLUSIONS

It has been observed in this study that there was highly significant variation due to environment, clone and clone x environment (GxE) interactions for all the traits tested. Environment had a large influence on the variation in pod yield and average bean size. Strong genotypic influence was observed only on the number of beans per pod. Highly significant GxE interaction was also observed on pod yield and mean dry bean weight.

For pod yield KKM 4 performed well in all the three locations but it generally favoured good environments. KKM 1 was a stable clone with average pod yield and performed well in a less favourable environment. ICS 95 produced the lowest pod yield and was quite an unstable clone.

KKM 1 and KKM 2 were stable for average bean number per pod and they performed well in a slightly unfavourable environment. KKM 3 was the most stable clone for average bean size. It can produce commercially acceptable bean size in all the three environments. KKM 4 varied in average bean size with environments but could still maintain acceptable average bean size even in an unfavourable environment.

From the above information, it is concluded that KKM 4 and KKM 1 are stable clones in the three diverse environments and they can perform well in both favourable and unfavourable environments.

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INTERACTION: ITS ANALYSIS AND INTERPRETATIONS

by

Yukio Yamada¹

INTRODUCTION

It is well known that the expression of many traits varies over a wide range of environments, so that genotypes which are superior in one environment may not be correspondingly superior elsewhere. Different developmental mechanisms in manifesting the trait may underlie this variation. The phenomenon is called GE interaction. The mechanism of the GE interaction may be phenotypic plasticity within a genotype, difference in phenotypic plasticity between genotypes, or different genes being switched on and off.

Classical analysis of GE interaction is performed by use of two-way analysis of variance. In this approach the genetic part of the trait expressed in different environments is assumed to be the same, in addition to the homogeneous error variance within environments. The interaction part is the deviation of the phenotype from the expected values of genotypic value and error effect. Haldane (1946) showed that six possible relations may exist, four of which lead to interactions. Interactions may be caused by different scales in each environments. This type of interaction can be removed by suitable transformation of data. The second form of GE interaction is caused by changing ranks on different environments. The third case is the combination of above two cases.

Falconer (1962) introduced the concept of genetic correlation, in which the measurements of a trait in different environments are assumed different traits. The theoretical basis for Falconer's concept had to wait until Robertson (1959) provided it. He showed clearly that the interaction variance is composed of two parts, one for differential genetic variances under two environments and another for the deviation of genetic correlation of the trait among genetic groups under two environments from unity. The former is referred to as the scaling effect and the latter as rankings of genotypes under two environments. Yamada (1962) showed later the above relationship shown by Robertson (1959) hold true irrespective of statistical models (Random or Mixed), whereas the formulae for estimating the genetic correlation must change according to the model used. Replacement of GE interaction into genetic correlation makes it easier to predict the genetic gain of the trait under different environments. However, this concept has not been fully utilized in plant breeding.

In the area of plant breeding, people are more concerned with other characteristics of the interactive behaviour of genotypes or cultivars, such as the stability of genotypes over a range of locations. Much of the works in plant breeding were with crop plants. The regression approach was proposed by Yates and Cochran (1938). It was rediscovered for plant breeding by Finlay and Wilkinson (1963). Eberhart and Russell (1966) extended the approach and Mather and his school use a somewhat different model (Freeman & Perkins, 1971; Perkins and Jinks, 1968; Moav et al. 1975).

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The purpose of the present paper is to explain statistical methods for detecting these GE interactions and discuss the merit of each method in conjunction with oil palm breeding.

STATISTICAL METHODS

1. Analysis of variance

The standard method of 2-way analysis of variance is given in Table 1, with appropriate mean squares, based on the model, $Y_{ijk} = u + E_i + G_j + e_{ijk}$.

Table 1. Analysis of variance for k environments

Sources	d.f.	MS	EMS*
Environments (E)	k-1	not relevant	
Genotypes (G)	g-1	MS (G)	$\sigma_e^2 + (1-k)/k \sigma_I^2 + nk \sigma_G^2$
G x E (i)	(k-1)(g-1)	MS (I)	$\sigma_e^2 + n\sigma_I^2$
Error (e)	gk(n-1)	MS (e)	σ_e^2

* $k = K$ if the model is Random; $k/K = 1$ if Mixed model.

Table 2. Analysis of variance and covariance in one-way model

Source	d.f.	EMS	EMP
Genotypes	g-1	$\sigma_{ei}^2 + n\sigma_{Gi}^2$	$n\sigma_{Gij}$
Error	g(n-1)	σ_{ei}^2	-

Yamada (1962) attempted to explain the variances in two-way model in terms of variance and covariance in one-way model and obtained the following:

$$\sigma_I^2 = (\sigma_{Gi} - \sigma_{Gj})^2 + \sigma_{Gi}\sigma_{Gj}(1 - r_{Gij})$$

or more generally, $\sigma_I^2 = V(\sigma_{Gi}) + \overline{\sigma_{Gi}\sigma_{Gj}}(1 - \bar{r}_{Gij})$, where $V(\sigma_{Gi})$ is the variance of σ_{Gi} for $i = 1, 2, \dots, k$, and $\overline{\sigma_{Gi}\sigma_{Gj}}$ average of two genetic standard deviations of all combinations of two environments, and \bar{r}_{Gij} is the average of the genetic correlations for all i, j combinations.

For Random model in which both genetic groups and environments are assumed to be random, $k/K = 0$ in Table 1, and thus,

$$r_G = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_I^2 - (\sigma_{Gi} - \sigma_{Gj})^2/2} \quad \text{or} \quad \frac{\sigma_G^2}{\sigma_G^2 + \sigma_I^2 - V(\sigma_{Gi})}$$

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INTERACTION: ITS ANALYSIS AND INTERPRETATIONS

by

Yukio Yamada¹

INTRODUCTION

It is well known that the expression of many traits varies over a wide range of environments, so that genotypes which are superior in one environment may not be correspondingly superior elsewhere. Different developmental mechanisms in manifesting the trait may underlie this variation. The phenomenon is called GE interaction. The mechanism of the GE interaction may be phenotypic plasticity within a genotype, difference in phenotypic plasticity between genotypes, or different genes being switched on and off.

Classical analysis of GE interaction is performed by use of two-way analysis of variance. In this approach the genetic part of the trait expressed in different environments is assumed to be the same, in addition to the homogeneous error variance within environments. The interaction part is the deviation of the phenotype from the expected values of genotypic value and error effect. Haldane (1946) showed that six possible relations may exist, four of which lead to interactions. Interactions may be caused by different scales in each environments. This type of interaction can be removed by suitable transformation of data. The second form of GE interaction is caused by changing ranks on different environments. The third case is the combination of above two cases.

Falconer (1962) introduced the concept of genetic correlation, in which the measurements of a trait in different environments are assumed different traits. The theoretical basis for Falconer's concept had to wait until Robertson (1959) provided it. He showed clearly that the interaction variance is composed of two parts, one for differential genetic variances under two environments and another for the deviation of genetic correlation of the trait among genetic groups under two environments from unity. The former is referred to as the scaling effect and the latter as rankings of genotypes under two environments. Yamada (1962) showed later the above relationship shown by Robertson (1959) hold true irrespective of statistical models (Random or Mixed), whereas the formulae for estimating the genetic correlation must change according to the model used. Replacement of GE interaction into genetic correlation makes it easier to predict the genetic gain of the trait under different environments. However, this concept has not been fully utilized in plant breeding.

In the area of plant breeding, people are more concerned with other characteristics of the interactive behaviour of genotypes or cultivars, such as the stability of genotypes over a range of locations. Much of the works in plant breeding were with crop plants. The regression approach was proposed by Yates and Cochran (1938). It was rediscovered for plant breeding by Finlay and Wilkinson (1963). Eberhart and Russell (1966) extended the approach and Mather and his school use a somewhat different model (Freeman & Perkins, 1971; Perkins and Jinks, 1968; Moav et al. 1975).

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Thus, each genotype-environment interaction sum of squares can be partitioned into that due to heterogeneous variances, $SS(HV)_i$, and that due to imperfect correlations, $SS(IC)_i$; as shown in *Table 3*.

Table 3. Sum of squares for two-way partitioning of the genotype by environment interaction for fixed genotypes based on Method 1.

Genotype	Type of interaction		Total
	$SS(HV)_i$	$SS(IC)_i$	
1	$n \sum_{i \neq 1} (S_1 - S_i)^2 / 2g$	$n \sum (1 - r_{1i}) S_1 S_i / g$	$SS(GxE)_1$
2	$n \sum_{i \neq 2} (S_2 - S_i)^2 / 2g$	$n \sum (1 - r_{2i}) S_2 S_i / g$	$SS(GxE)_2$
g	$n \sum_{i \neq g} (S_g - S_i)^2 / 2g$	$n \sum (1 - r_{gi}) S_g S_i / g$	$SS(GxE)_g$
Total	$SS(HV)$	$SS(IC)$	$SS(GxE)$

$$S_i^2 = \sum (\bar{Y}_{ij} - \bar{Y}_{i..})^2 \text{ and } r_{ii'} = \sum (\bar{Y}_{ij} - \bar{Y}_{i..})(\bar{Y}_{i'j} - \bar{Y}_{i'..}) / S_i S_{i'}$$

The equivalent partitioning for Method 2 would separate the interaction into that due to each environment, but it is generally not useful.

By adopting these two methods, Muir et al. (1991) have shown that the interpretation of GE interaction in statistical modes becomes more meaningful. Those are summarized as follows:

(1) Genotypes fixed, environment random

If genotypes are fixed and environments are random, the problem is either (1) to identify that genotype which is most stable, or (2) choose that genotype which gives optimal performance averaged over the sampling space of environments.

If the interaction is significant, the first term of Method 1 indicates the size of the interaction which is due to differential environment sensitivity. Neither portion of Method 2 related to this question. Therefore, partitioning by Method 1 is more appropriate for this situation.

(2) Genotypes random and environments fixed

If genotypes are random and environments are fixed, the problem is to determine if there is genetic variability for adaptation to specific environments. In this case, the first part of Method 1 indicates the presence of differential genetic variability for environmental sensitivity, while the second portion gives little useful information. In contrast with Method 2, if the majority of the interaction is due to the first portion, the interaction is generally considered to be of unimportant nature since the ranks of the genotypes remain constant across environments. But, if the interaction is mainly due to the second portion, a specific breeding recommendation can be made. Specialized genotypes or lines should be developed for each environment since re-ranking of genotypes in alternative environments is occurring. Thus, partitioning by Method 2 is more appropriate for this case (Mixed model).

(3) Genotypes random and environment random

This is called Random model. In this situation, only a general breed or single cultivar can be developed since a fix environment cannot be provided. A general breed could be developed by measuring individuals in a random sample of environments from the inference space of environments. If an interaction is due to heterogeneous variances, or scale effects, the best genotype will remain the best in all environments since re-ranking of genotypes are generally not occurring in alternative environments and one only needs to measure performance in one environment. Partitioning by Method 2 provides a breakdown based on these criteria whereas Method 1 does not.

(4) Genotypes fixed and environments fixed

If both factors fixed, the solution is simple: choose that genotype which gives optimum performance in each specific environment. Further analysis is not necessary. Partitioning by Method 1 is more appropriate for addressing questions posed with fixed genotypes, while Method 2 is more appropriate for random genotypes.

(5) Numerical example

Comparison of analysis and interpretation based on each method will be made on two hypothetical sets of data. Computations for analysis are greatly simplified by first calculating the total sum of squares for the interaction and the sum of squares for the first partition. The sum of squares for the second partition is then found by subtraction.

Hypothetical data, for which $n=1$, are presented in Table 4 for two cases: 1) Ranks of genotypes remain the same, but the magnitude of differences between genotypes differs among environments. 2) Ranks and magnitude of difference between genotypes change among environments. Analysis for each case and method is presented in Table 5. Each method gives greatly different results. Note particularly the reverse in sum of squares between methods for Case 1. The interpretation is also entirely different for each method. For Case 1, both genotypes show equal response to the environment but in opposite directions. Thus, partitions based on Method 1 indicate equal responsiveness, with all of the interaction due to imperfect correlations. Despite the fact that all of the sum of squares was due to imperfect correlations, the ranks of the genotypes remained the same. However, Method 1 also gave the same result for Case 2 because the genotypes still show exactly the same responsiveness to environments. In contrast, Method 2 gave different results for the two cases. In the first case, all of the interaction was shown to be due to heterogeneous variances and one would correctly conclude that no re-ranking occurred. In the second case, Method 2 gave a mixed signal with the majority (72%) of the interaction being attributed to imperfect correlation. These examples clearly illustrate that it is imperative that the correct partitioning and interpretation be used depending on the purpose of the research.

Table 4. Hypothetical data for two types of genotype-environment interactions.

Case	Genotype	Environment				
		1	2	3	4	5
1	A	10	11	12	13	14
	B	10	9	8	7	6
2	A	8	9	10	11	12
	B	12	11	10	9	8

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The assessments of height, diameter and girth at breast height (Dbh) of 25 trees in the inner part of each plot were carried out 4 years after planting.

Means of each treatment plot were subjected to analysis of variance. If differences were significant the data were further analysed using Duncan's multiple range test.

Table 1. Location of the different provenances of *Acacia mangium* used in the trial

Provenance	Seedlot Number	Latitude (South)	Longitude (East)	Altitude (meter)
1. Rex Range NR. Mossman, Qld	12992	16° 30'	145° 32'	306
2. Broken Pole Creek, Qld	13241	18° 21'	146° 03'	50
3. Cassowary Range, Qld	13534	16° 32'	145° 25'	60
4. Piru, Ceram Ind.	13621	3° 04'	128° 12'	150
5. Sidei, Ind.	13622	0° 46'	133° 34'	30

RESULTS AND DISCUSSIONS

At site 1, Provenance 4 outperformed the rest in height growth but the ranking was reversed for girth and diameter at breast height in which provenance 5 ranked the best. At site 2, provenance 3 was the best provenance for height growth but the ranking also reversed for girth and diameter at breast height with provenance 2 at the top. At sites 3 and 4, provenance 2 came out as the best provenance for all traits and at site 5 provenance 5 was the best for all traits (Appendix 2, 3 and 4).

Individual site analysis for all traits indicate significant differences between provenances at all sites except for diameter at breast height and girth at site 5 (Appendix 1). This may be due to the higher fertility of this site, where better genotypes are able to fully express their potential (Appendix 2).

Information on variability within each provenance is lacking as the analysis was carried out using mean values. The above results nevertheless showed considerable variation between provenances. Such variation could warrant good response to selection.

Interaction between provenances and sites was found to be highly significant for all the traits studied (Table 2). Furthermore, examination of Figures 1, 2 and 3 suggests that the interaction is mainly due to large differences between provenances rather than changes in provenance ranking across the sites. It shows that the performance of some of the provenances across the sites is not consistent. This would suggest that testing over many potential planting areas is of some value in determining relative performance of provenances at all sites. Highly significant interactions for all traits also suggest that any results from a single site are inadequate for making provenance recommendations for other sites. Similar observations were reported in *Pinus caribaea* (Gibson, 1982; Nikles, 1977; Binet, 1963; King, 1975; Falkenhagen, 1977).

Ignorance of this provenance and site interaction may result in growth and mortality loss. Such loss in *Pinus caribaea* has been reported by Binet (1963), King (1975) and many others.

Provenance 2 and 5 were the best two among all provenances in all of the traits analysed, i.e height (Appendix 2), diameter (Appendix 3) and girth (Appendix 4). This is further supported by the relatively high mean and low coefficient of variation for these provenances (Figures 1, 2 and 3). Except for site 1, which was the poorest site, height growth of provenance 2 was consistent at all the other sites (Appendix 2).

Table 2. Mean squares for traits

Source of Variation	d.f.	Mean Square		
		Ht	Dbh	Girth
Site	4	228.6 ***	136.2 ***	1344.0 ***
Block (Si)	20	2.9 ns	2.5 ns	24.6 ns
Prov	4	20.1 *	52.8 ***	521.2 ***
Prov x Si	16	7.5 ***	6.8 ***	67.3 ***
Error	80	2.2	2.2	21.4

ns not significant, * significant at 5% level, *** significant at 1% level.

CONCLUSION AND RECOMMENDATION

Base on these data, provenance 2 and 5 are the best provenances; grow best at all sites and exhibit a high mean with low coefficient of variation for all traits under study.

The presence of very strong provenance and environment interaction in these traits implies that special attention is required in planting various provenances at present as well as new sites.

Besides height, diameter and girth, data on other traits such as stem form, forking habit, branching habits, wood quality, and general health are required. These are also important and have to be given some weight in determining the best provenance or the average provenance at all sites.

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Figure 1: Provenances versus sites
1. Height

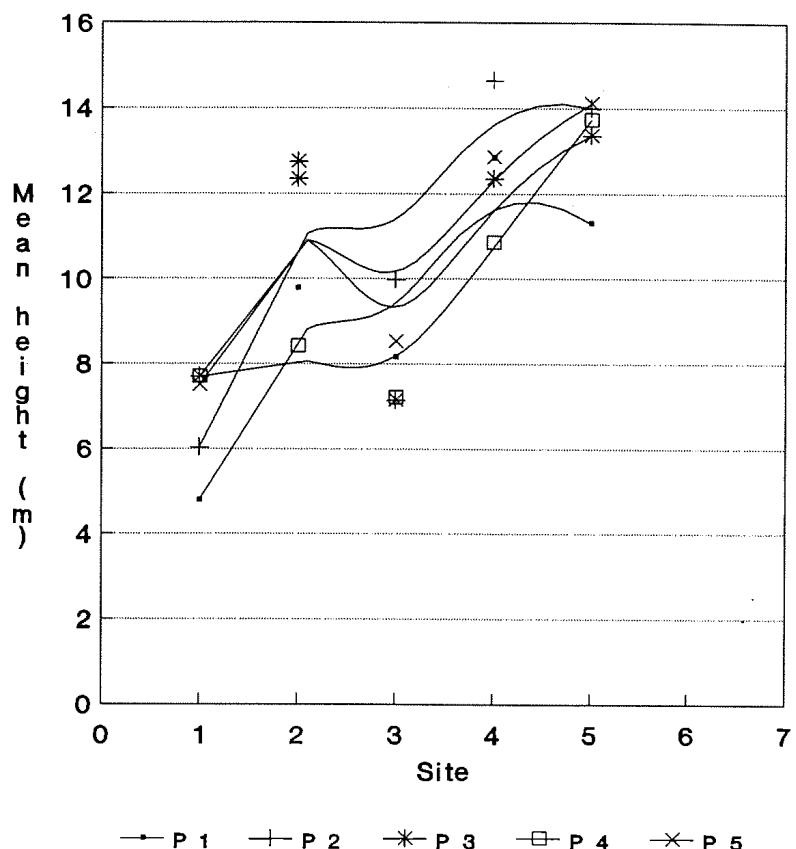
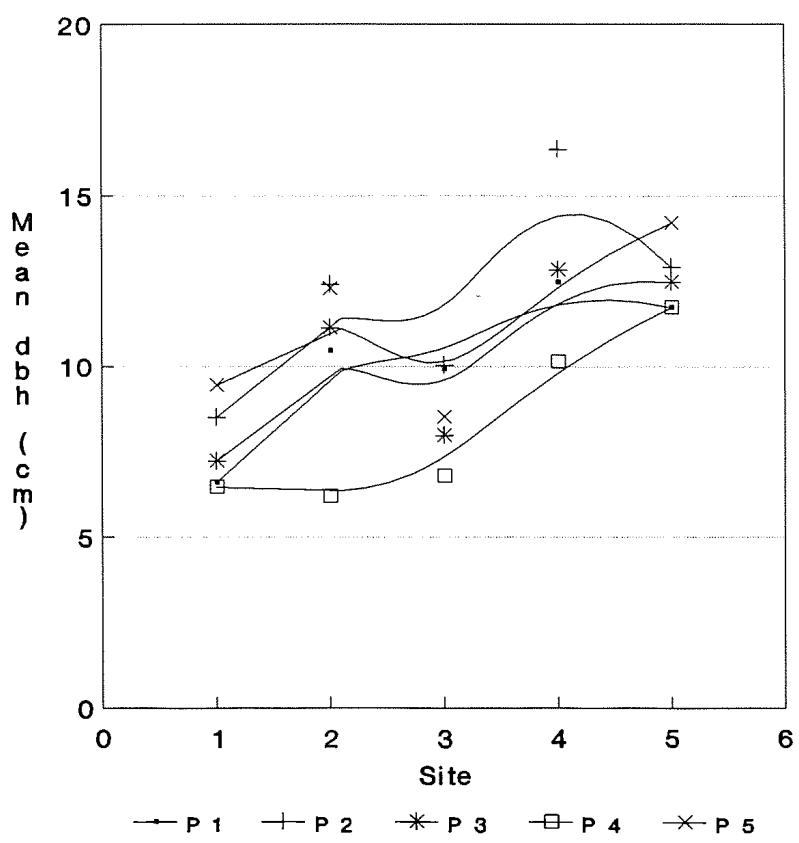


Figure 2: Provenances versus sites
2. Diameter



**Figure 3: Provenances versus sites
3. Girth**

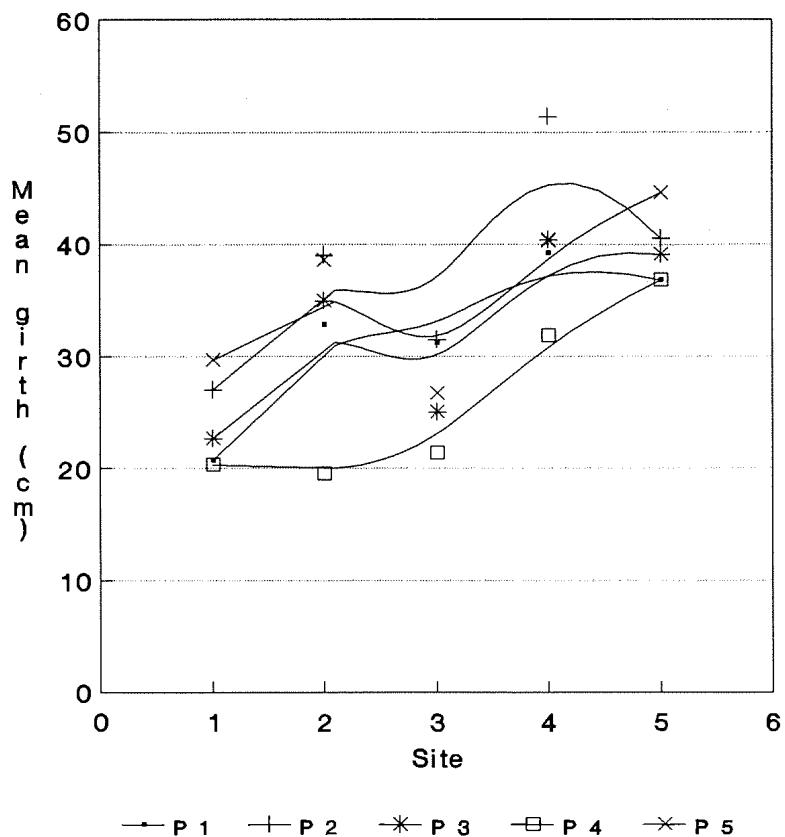


Figure 4: Provenance mean versus coefficient of variation for height

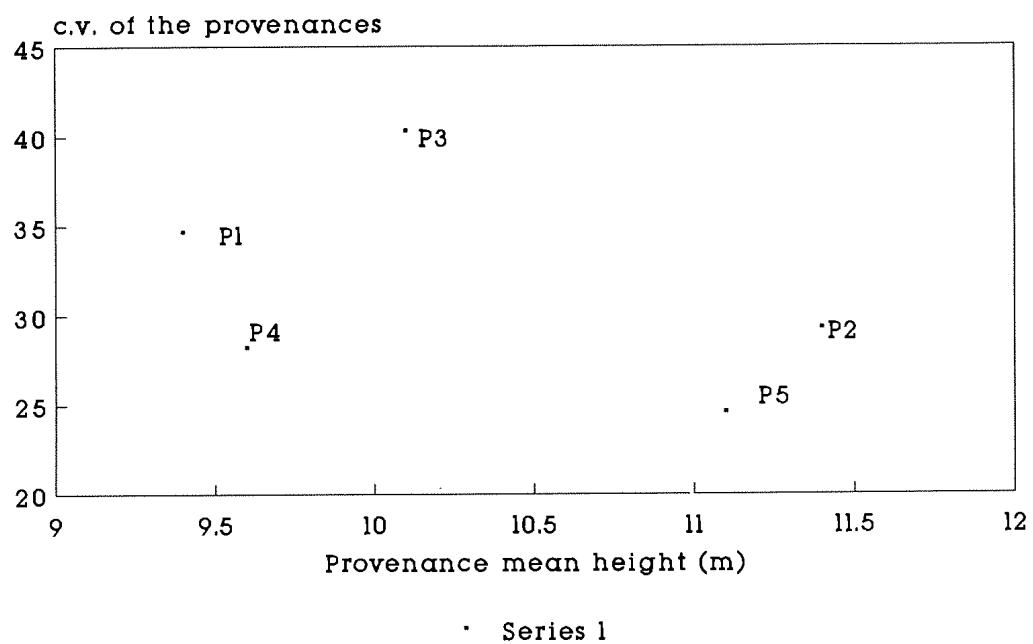


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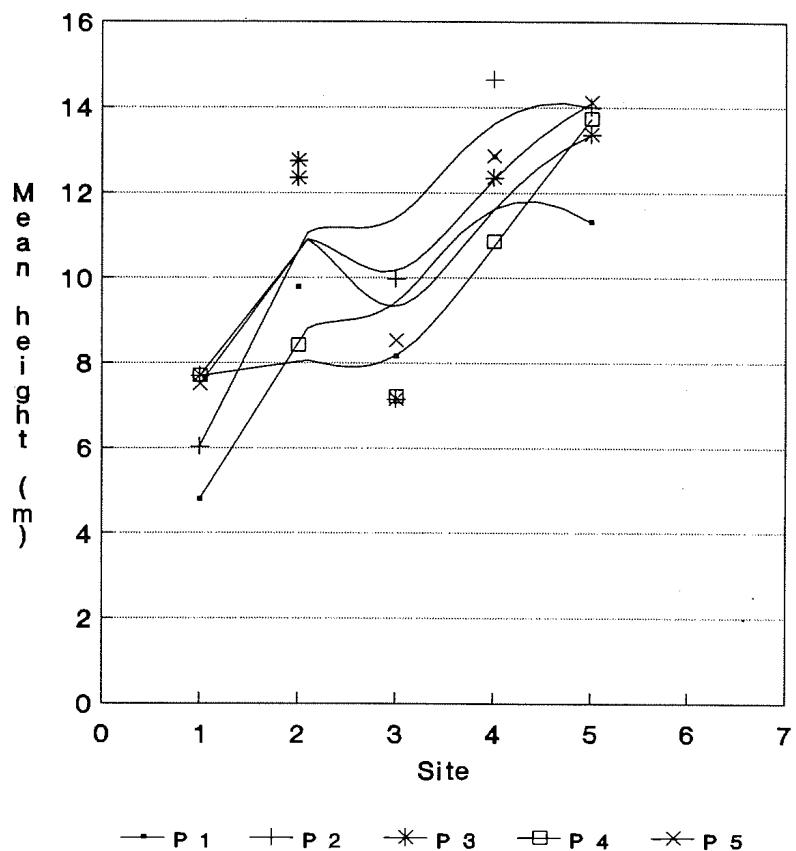
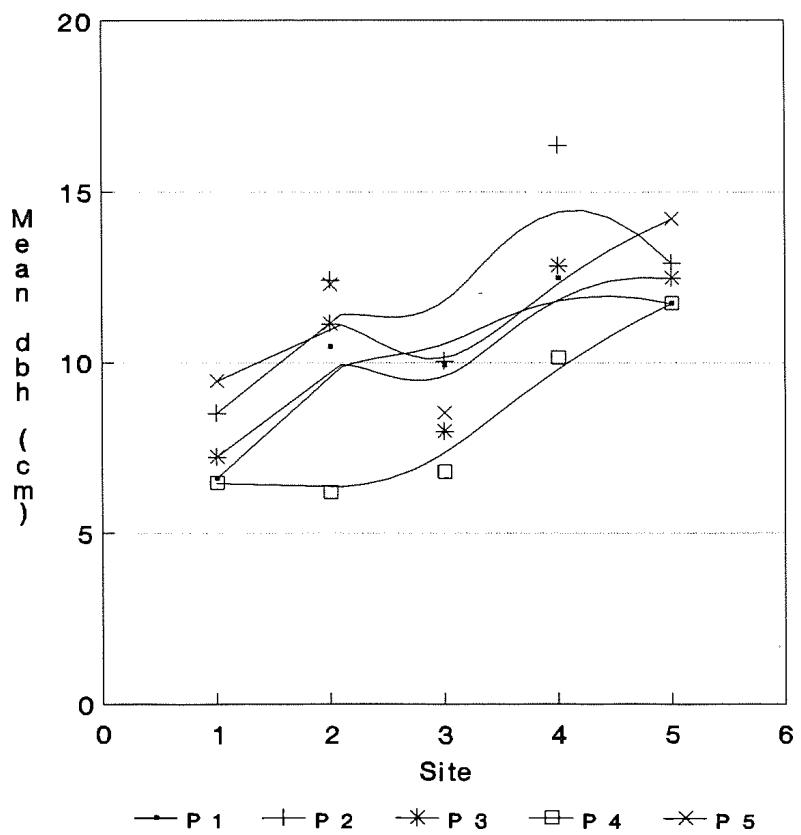


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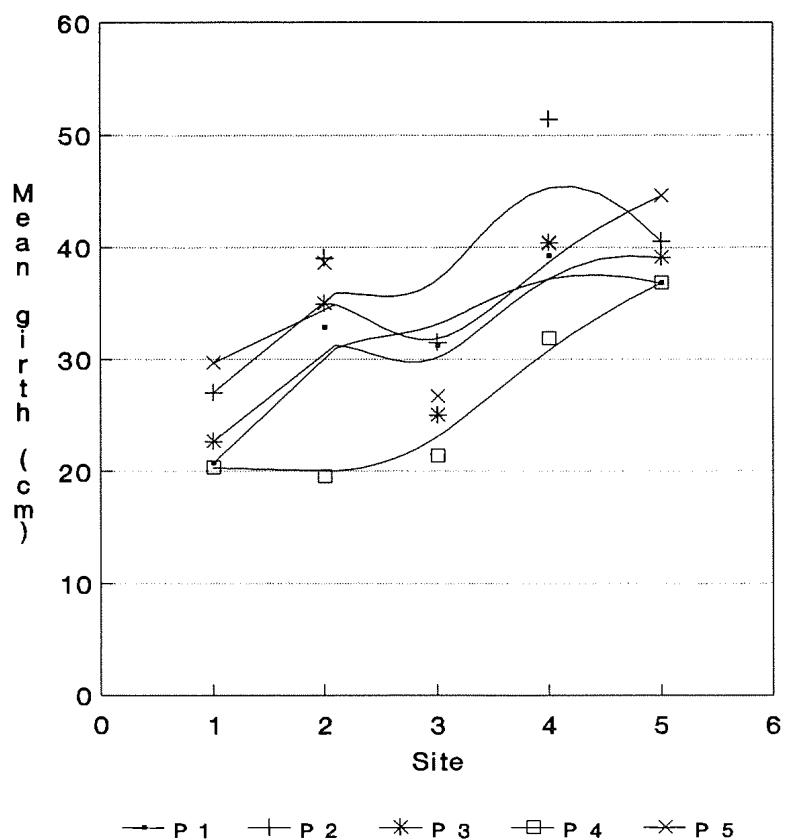


Figure 4: Provenance mean versus coefficient of variation for height

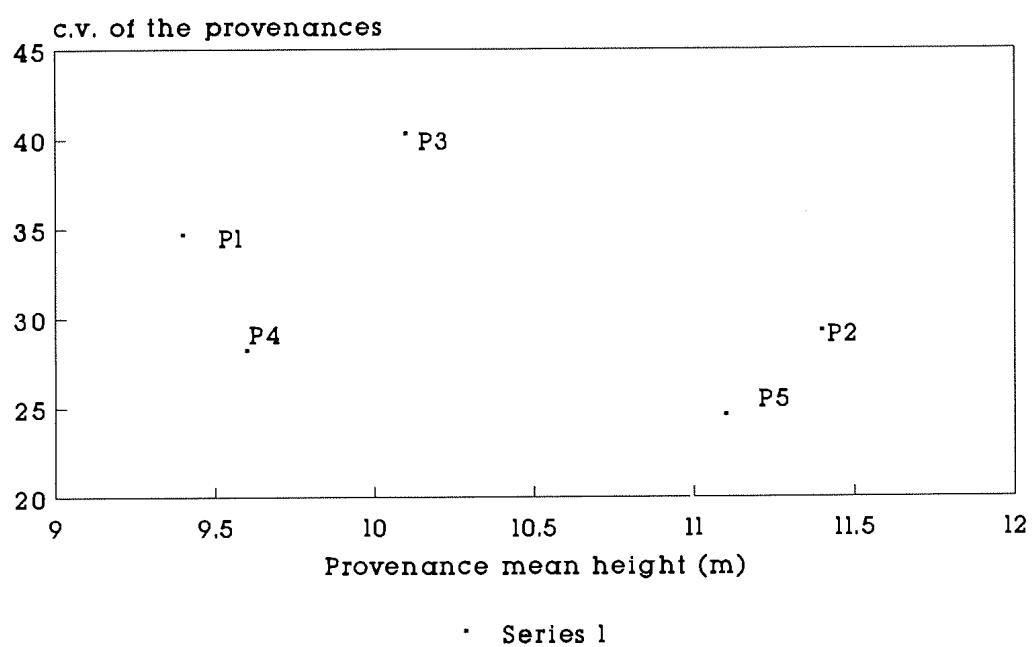


Figure 5: Provenance mean versus coefficient of variation for dbh

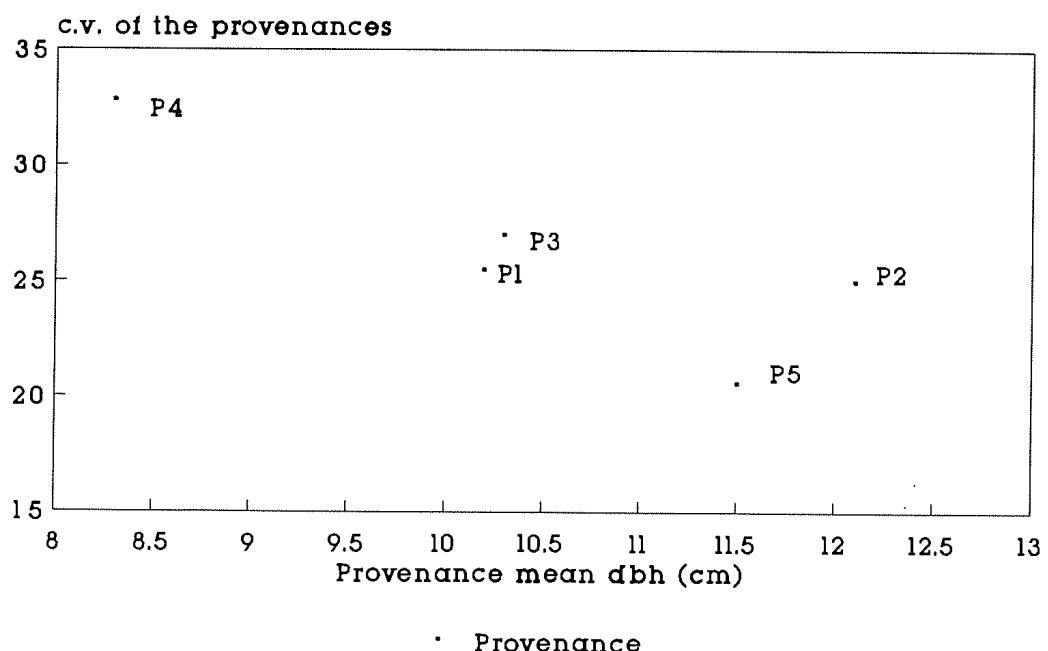
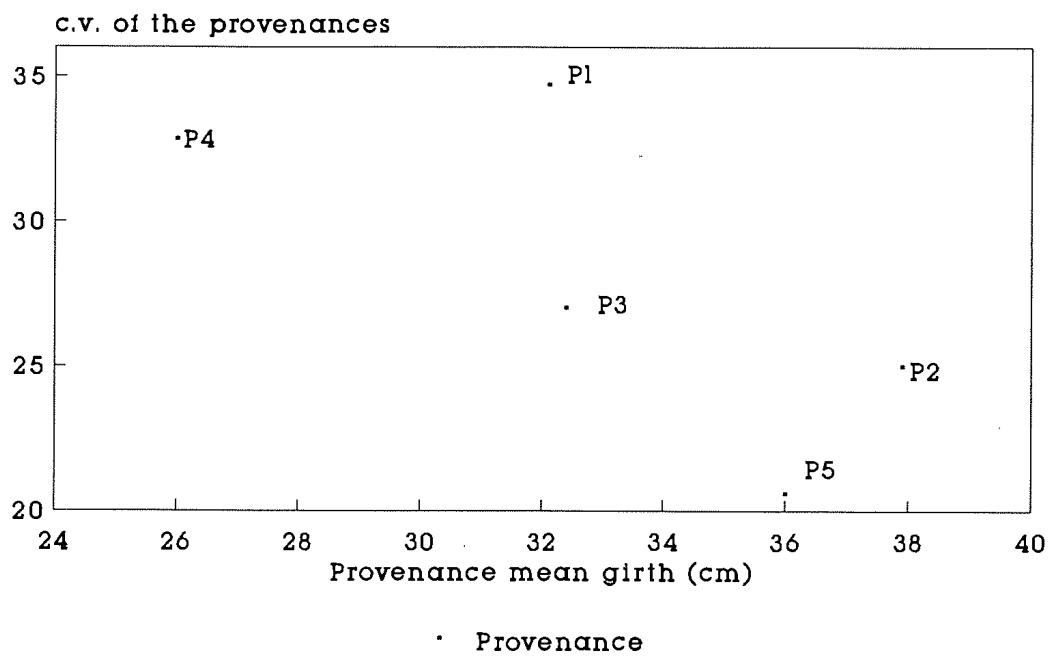


Figure 6: Provenance mean versus coefficient of variation for girth



GENOTYPE - ENVIRONMENT INTERACTIONS AND YIELD STABILITY STUDIES IN HYBRID COCONUT CULTIVARS

by

Mukesh Sharma and Tan Yap Pau¹

INTRODUCTION

Like most crops under cultivation, hybrid coconut cultivars are known to perform variably at different localities. Their growth and subsequent performance is dependent on genetic, environmental, and agronomic factors and their interactions.

Ibrahim *et al* (1988) advocated the evaluation of a number of hybrid coconut cultivars over a range of different environments as a means to determine their adaptability.

The ANOVA, Regression and Genotype Stability analysis are useful methods for determining the relative adaptive values of hybrid coconut cultivars.

As very little work has been published in this regard for the coconut palm, this paper attempts to present some data on the early growth and performance of four types of hybrid coconut cultivars.

MATERIALS AND METHODS

This trial details were as follows :-

- Date Planted : April 1982
- Planting Density : 76.7 palms/ha.
- Plots Size : 20 palms
- Layout : 4x4 Latin square
- Location : Hilir Perak District, Perak, Peninsular Malaysia
- Soil Type : Bernam over Selangor series (Coastal clay)
- Hybrid Cultivars :
 - 1) MAWA (PB121) - (Malaysia Red Dwarf x West African Tall)
 - 2) WATREN - West African Tall x Rennel Tall

¹ United Plantations Berhad, Teluk Intan, Perak, Malaysia

- 3) WATMAT - West African Tall x Malayan Tall
 4) MATMAT - Malayan Tall x Malayan Tall

The period of recording for the various parameters is shown in *Table 1* below.

Table 1. Period of Recording for the Parameters Studied

Parameters Measured	No. of Years Recorded
1. Yield Components :	
- No. of Nuts/Ha.	4
- No. of Empty Bunches/Ha.	4
- No. of Bunches/Ha.	4
2. Vegetative Characters :	
- Frond Production	4
- Rachis Length (m)	4
- Height of Stem (m)	3

In the analysis of the results, three methods were used; i.e ANOVA, Linear Regression and plotting the coefficient of variation values against the mean.

For the statistical analysis using ANOVA, the years (Y) were considered as different environments (E) and the hybrid cultivars or varieties (V) were taken to be genotypes (G) and so it follows that V x Y is synonymous (in this context) with G x E or genotype x environment interaction.

RESULTS

1. Environmental Variations

1.1 Rainfall and its Distribution

Of the climatic factors, rainfall is considered to be one of the most important factors affecting the yields of the coconut palm (Murray, 1977).

The total annual rainfall and its distribution is shown in *Table 2(a)* for the period 1985-1990. The range of 1,484 mm to 2,071 mm obtained is well within the 1,300 mm to 2,300 mm range which was quoted to be optimal for coconuts (Murray, 1977). The coefficient of variation (%) at 15.4% is considered to be low indicating a fairly uniform rainfall over the six years under evaluation. The distribution of the rain-days was also fairly uniform as indicated by the low C.V. (%) value of 12.5% whilst the mean number of rain-days/year for the 1985/1990 period was fair at 121 days/year.

The mean monthly rainfall and its distribution is shown in *Table 2(b)* for the 1985-1990 period. The weighted mean of 144 mm of rain/month and 10 rain-days/month again showed good uniformity. However, the C.V. (%) of the weighted data over the six year period showed a considerable degree of variation at 55.9% for rainfall per month and 43.9% for number of rain-days/month. The C.Vs. (%) for the monthly rainfall and number of rain-days/month for each of the six years of recording are

shown in *Table 2(c)*. The results show that there was a considerable degree of variation in the amount of rainfall and number of rain-days per month over the six years.

Table 2(a). Total annual rainfall and number of rain-days of the trial for 1985-1990

Period	Total Rainfall mm	No. of Rain-Days
1985	1,484	108
1986	1,714	103
1987	1,528	111
1988	2,043	137
1989	2,071	137
1990	1,531	127
Mean	1,729	121
C.V. (%)	15.4	12.5

Table 2(b). The mean monthly rainfall and number of rain-days/month of the trial for 1985-1990

Period	Amount (mm)	No. of Rain-Days
1985	124	9.0
1986	143	8.6
1987	127	9.3
1988	170	11.4
1989	173	11.4
1990	128	10.6
Overall Mean*	144	10.0
Overall C.V. (%) *	55.9	43.9

* Refers to weighted data.

Table 2(c). Coefficient of variation (%) of the monthly rainfall and number of rain-days during the period of 1985 - 1990

Period	Coefficient of Variation (%)	
	Monthly Rainfall	No. of Rain Days
1985	68.4	49.0
1986	44.8	49.5
1987	66.7	48.6
1988	51.7	28.6
1989	45.9	45.0
1990	64.0	44.0
Overall C.V. (%)*	55.9	43.9

* = Weighted value.

1.2. The Minimum and Maximum Temperature and its Variations

From the results in *Table 3*, there appeared to be little variation for the minimum and maximum temperature between years for the period of 1985-1989 as shown by the very low C.V. (%) values obtained.

Table 3. The mean monthly minimum and maximum temperatures for the trial

Period	Mean Monthly Temperature (°C)	
	Min. (°C)	Max. (°C)
1985	23.2	32.0
1986	23.3	32.2
1987	23.5	32.4
1988	23.5	32.2
1989	23.1	32.2
1990	Not Available	
Mean*	23.3	32.2
C.V. (%)*	2.2	1.8

* Refers to weighted data (1985-1989).

2. The Analysis of Variance (ANOVA)

2.1 For yield components

The combined analysis of variance (ANOVA) for the yield components; i.e. nut production, bunch production and empty bunch production, is shown in *Table 4*.

Table 4. ANOVA for the yield components

Source	d.f.	Mean Squares		
		No. of nuts per ha.	No. of bunches per ha.	No of empty bunches per ha.
Rep./Year	12	1,320,829.00*	7,701.08ns	2,574.15*
Years (Y)	3	99,127,810.00**	973,613.30**	40,778.36**
Variety (V)	3	90,309,120.00**	441,960.00**	24,991.67**
V x Y	9	2,547,485.00**	74,884.45**	833.06ns
Error	36	620,657.80	5,674.53	1,063.48

* = Significant at $P = 0.05$

** = Significant at $P = 0.01$

ns = Not significant.

The above table shows that year (Y), variety (V) and V x Y are highly significant for both nut production (nuts/ha.) and total number of bunches produced/ha. This indicates that both variety and environment (year) influenced both these traits whilst for empty bunch production (negative traits in selection); the differences observed were largely varietal in nature.

2.2 For Vegetative Components

Table 5 shows the combined ANOVA for the vegetative components; i.e. frond length (m), frond production and total stem height (m).

Table 5. ANOVA for the vegetative components

Source	d.f.	Frond	Frond	d.f.	Height of
		Production	Length		Stem
		Mean Square	Mean Square	d.f.	Mean Square
Rep./year	12	0.801**	0.209ns	9	0.074*
Years (Y)	3	3.618**	0.298ns	2	25.941**
Variety (V)	3	1.704**	0.723**	3	0.252**
V x Y	9	0.147ns	0.115ns	6	0.146**
Error	36	0.117	0.155	27	0.034

* = Significant at $P = 0.05$

** = Significant at $P = 0.01$

ns = Not significant

Varietal differences were highly significant for all the three vegetative components analysed whilst significant differences for environment (years) were obtained for frond production and stem height. The latter also showed highly significant V x Y interaction indicating a strong genotype x environment interaction for stem height in the trial.

3. Analysis for Nut Production Per Hectare against the Environment index using the Linear Regression Method

The relationship between the number of nuts produced per hectare against the environment index for the four coconut hybrid cultivars under evaluation is shown in Figure 1.

From the early yields, it can be seen that although the ranking of the cultivars remained unchanged, there was a differential rate of response. The MAWA hybrid showed consistently higher yields and better stability compared with the other three hybrid cultivars under evaluation.

The MATMAT was the poorest yielding hybrid and showed the highest rate of response as shown by the regression coefficient (b) in *Table 6*. The range for the b-values observed for the hybrid coconut cultivars evaluated was 0.7248 - 1.2309. WATMAT and MATMAT hybrids showed b-values of above one, indicating that they were very sensitive or responsive to the changes in the environment.

Table 6. Regression coefficients (b) for the four coconut hybrid cultivars

Hybrid	Regression Coefficient (b)
MAWA	0.7248
WATREN	0.8438
WATMAT	1.2005
MATMAT	1.2309

4. Genotype Stability of the Various Coconut Hybrid Cultivars for Yield Components

The coefficient of variation (C.V. in %) was plotted against the mean for all four hybrid cultivars with respect to nut production, bunch production and empty bunch production on a per hectare basis to compare the relative stability or uniformity between the different types of hybrids.

4.1 Number of Nuts/Ha.

From Figure 2(a), it is clear that the MAWA hybrid was both the highest yielding and most uniform of the hybrid cultivars whilst the MATMAT hybrid was the both the lowest yielding and most variable for nut production.

FIG. 1. THE RELATIONSHIP BETWEEN YIELD OF NUTS/HA. WITH
THE ENVIRONMENT INDEX USING LINEAR REGRESSION

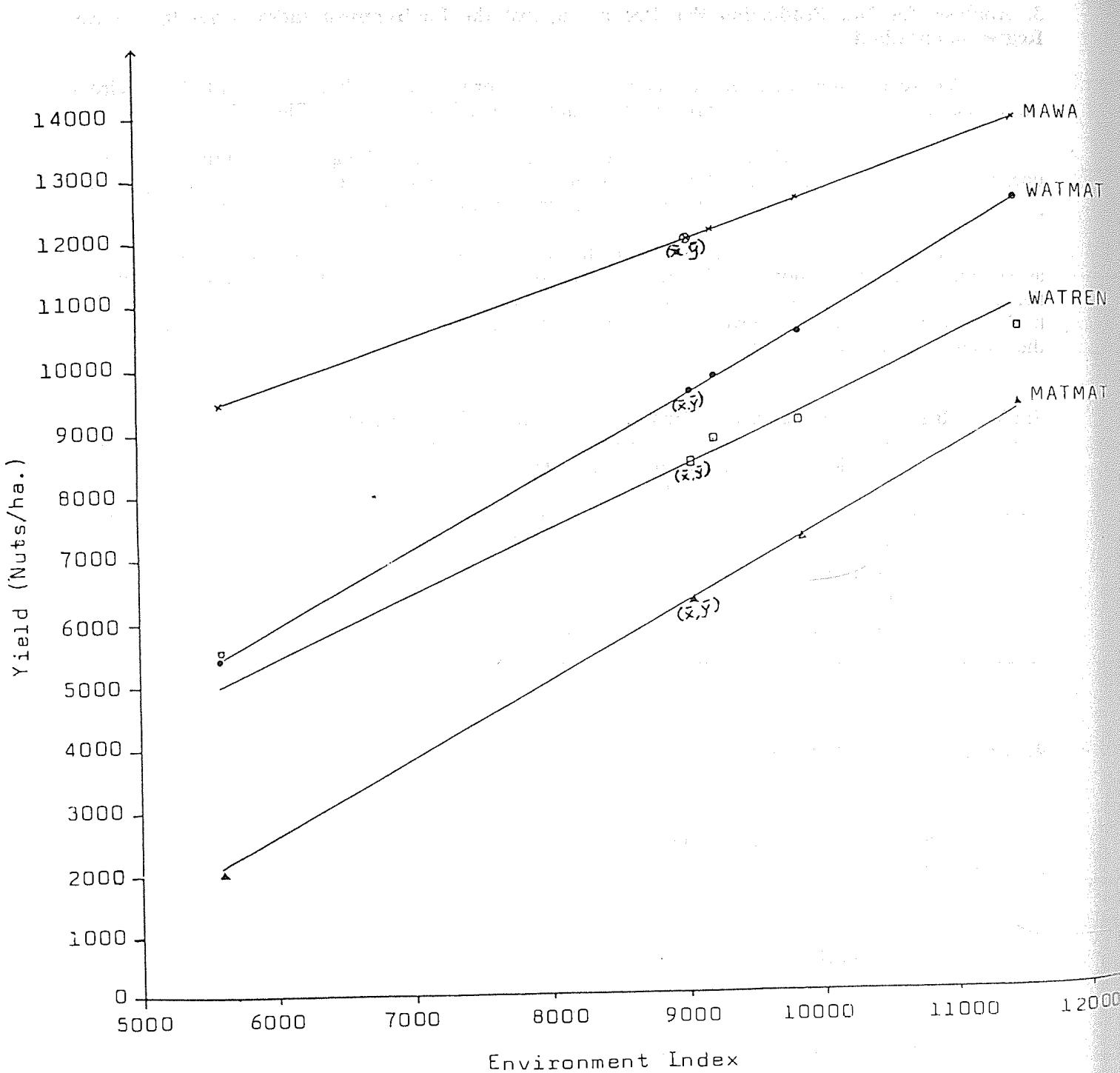


Fig. 2(a). Number of Nuts/Ha.

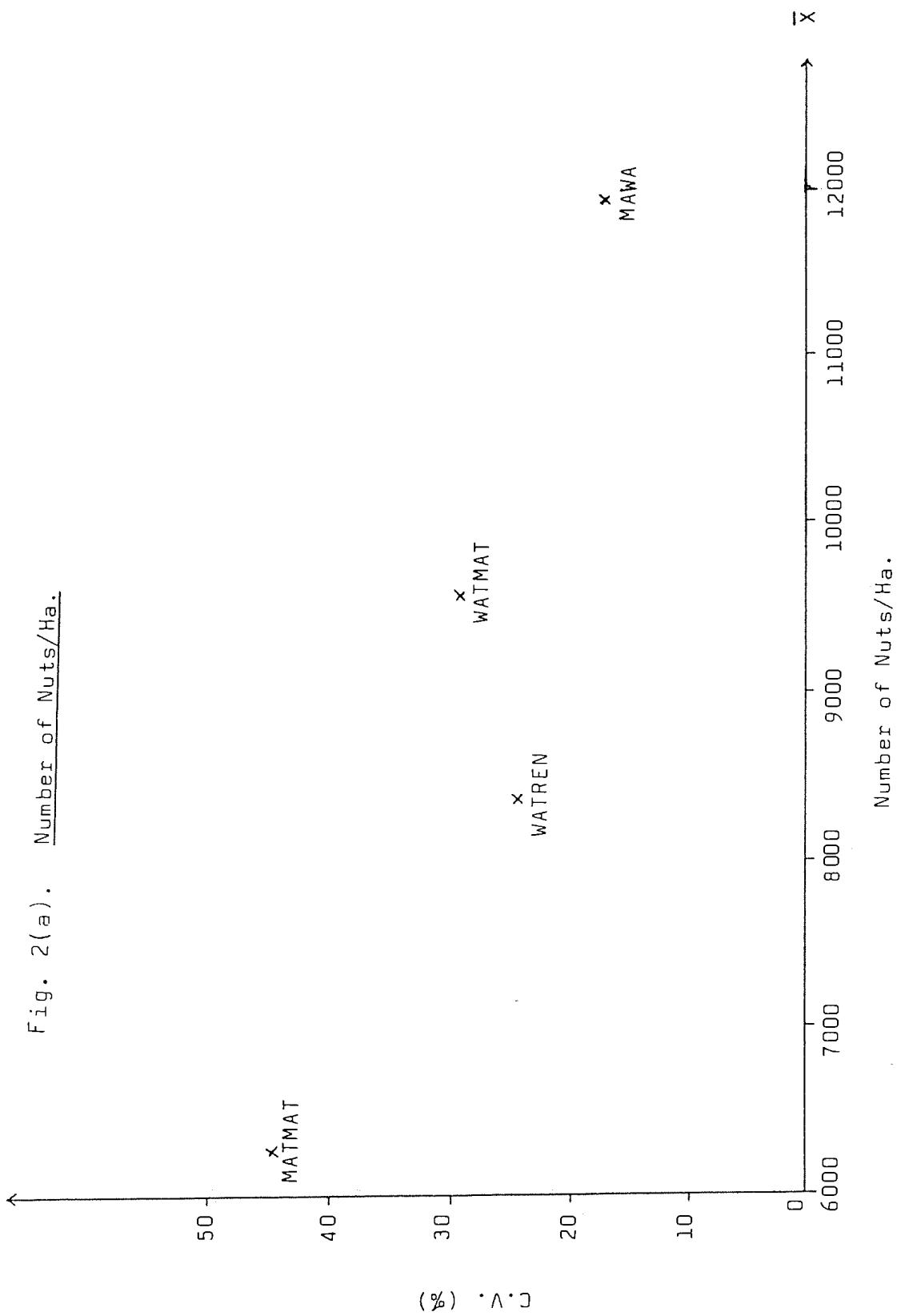


Fig. 2(b). Number of Bunches/Ha.

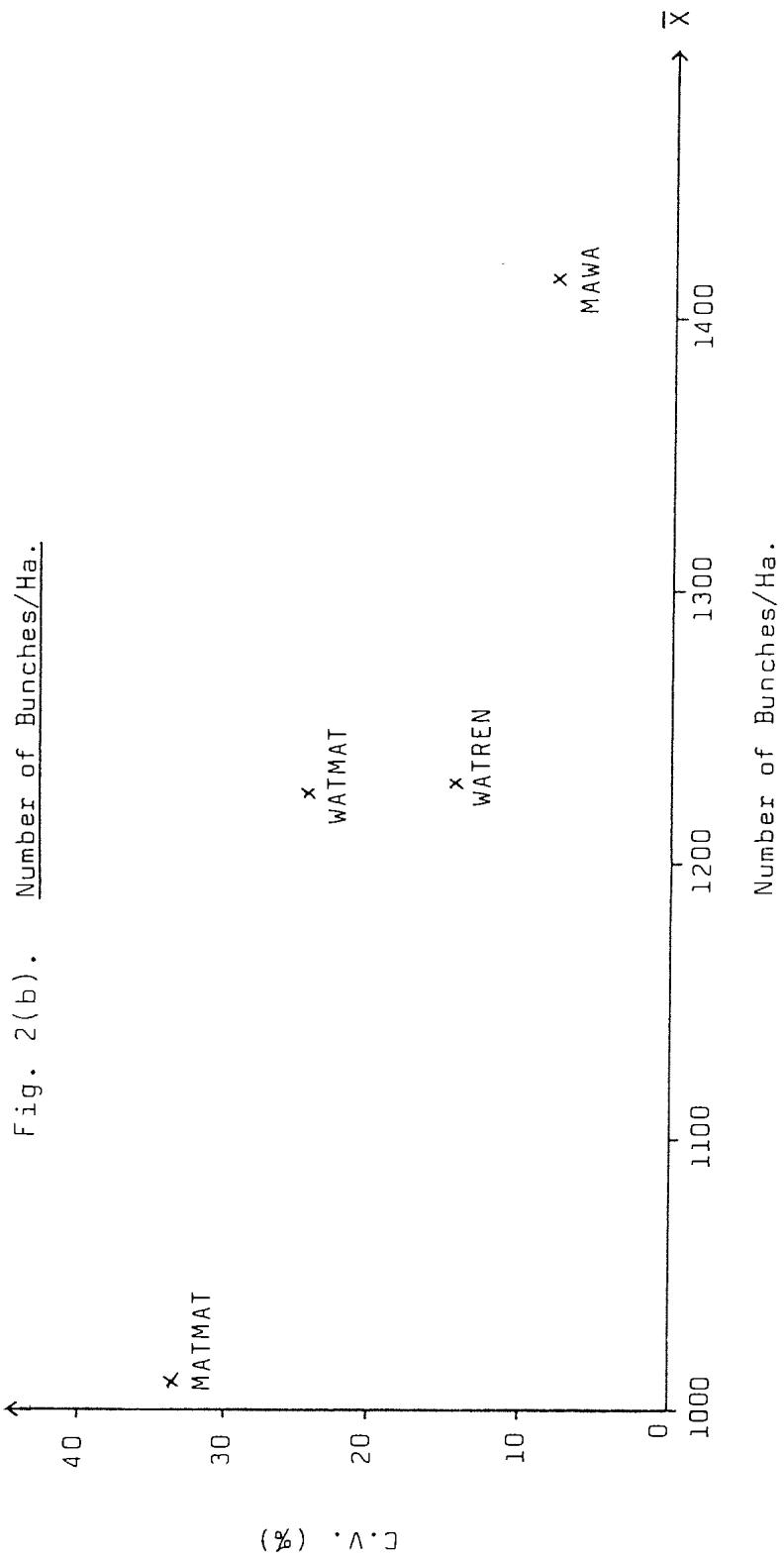
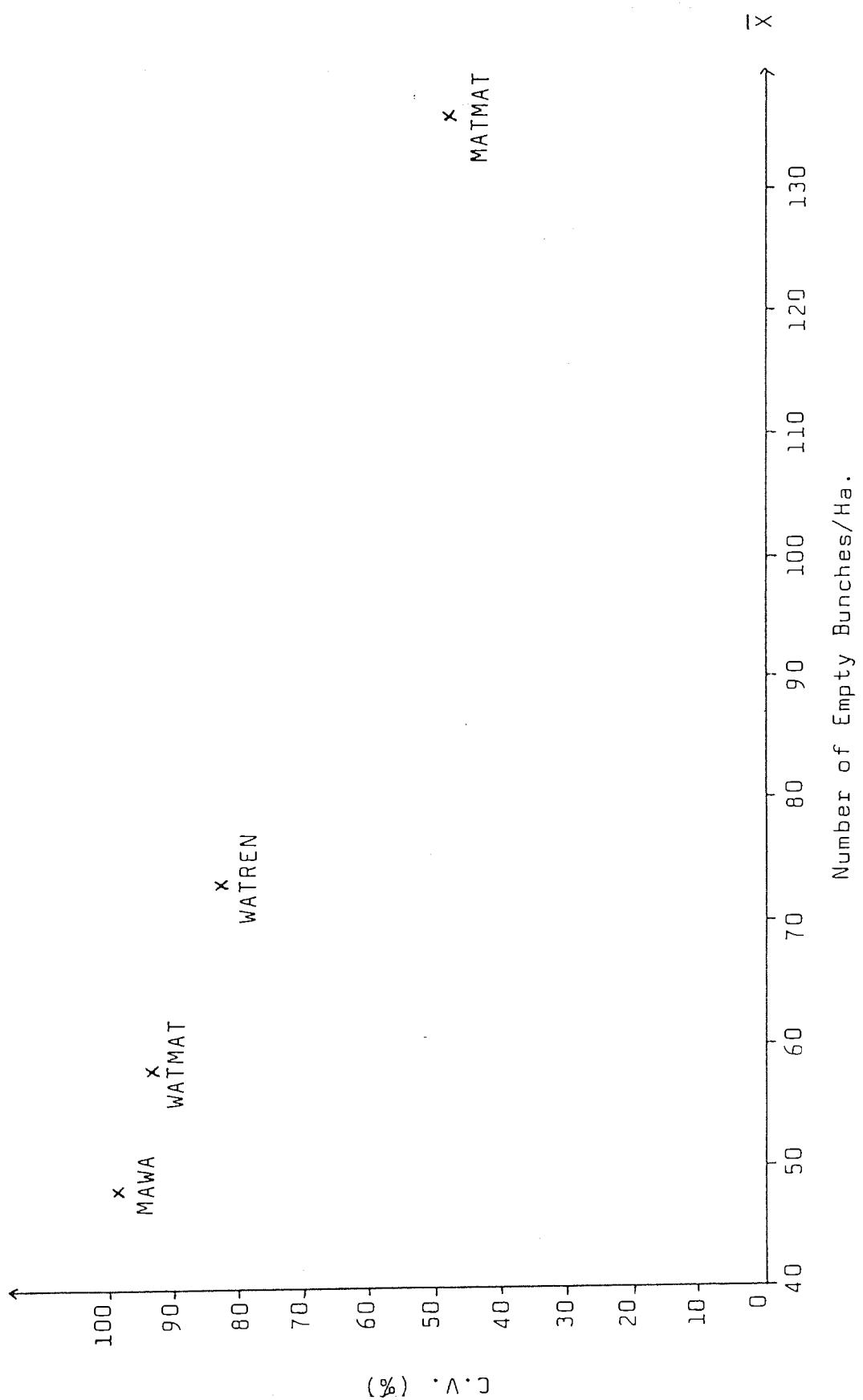


Fig. 2(c). Number of Empty Bunches/Ha.



4.2 Number of Bunches/Ha

Bunch production followed the same trend as nut production, with the MAWA being the most uniform hybrid and showing the highest bunch production amongst the hybrid cultivars tested (Figure 2b).

4.3 Number of Empty Bunches/Ha.

This is an undesirable trait and from the results (Figure 2c), the incidence was highest in the MATMAT hybrid, its low C.V. (%) indicates a high incidence of palms producing empty bunches. The MAWA hybrid, on the other hand, had very low empty bunch production.

5. Genetic Stability of the Various Coconut Hybrid Cultivars for Vegetative Components

5.1 The Length of Frond Number 14

From the results, the MAWA was the most uniform for this trait whilst the MATMAT and WATMAT hybrids were the most variable (Figure 3a).

5.2 The Number of Fronds Produced/Year

The MAWA hybrid recorded the highest mean frond production besides showing the lowest C.V. (%) whilst the MATMAT was the most variable for this trait as shown in Figure 3b .

5.3 Height of Stem at Frond Number 25

Figure 3c shows that the MAWA was the most uniform whilst the MatMat showed the highest variability for this trait amongst the hybrids tested.

DISCUSSION AND CONCLUSIONS

It is acknowledged that the results are confounded to some degree by the age of the palms. Nevertheless, it is felt that these results are still useful in providing some indication about the general trend in the relative performance of the different types of hybrid cultivars tested.

The climate and growing conditions at Hilar Perak district are generally considered to be close to optimum for coconuts. Although variation for total annual rainfall between years and for mean minimum and maximum monthly temperatures is low, the high C.V. values for monthly rainfall and number of rain-days/month during the 1985-1990 period, suggests that this distribution could have affected the growth and subsequent performance of the palms. This is supported by the results obtained from the ANOVA and Regression analysis.

The regression analysis, which has been increasingly used since the mid-1960s to measure yield stability over a range of environments (Sneep *et al*, 1979), indicated that in Hilir Perak agro-ecological conditions, the MAWA hybrid has the greatest stability for yield.

The MAWA is also found to be the most uniform of the hybrid coconut cultivars tested. This is contrary to the experience in Kuala Terengganu (along the East Coast of Peninsular Malaysia), where Jamadon *et al* (1988) reported that it was more sensitive to the extreme environmental conditions of the sandy bris soils. They reported that the MAWA gave greater C.V. values for all the vegetative components when compared to the MATMAT, in 280 hectares of selected smallholdings studied, and suggested that nutrient, moisture availability as well as agro-management practices were the major limiting factors accounting for the poor early growth of the MAWA.

The greater uniformity of the MAWA over the other hybrids could be largely due to the fact that its Malayan Dwarf parents are highly inbred and its West African Tall parents are comparatively more homogeneous than the other Talls used in the hybrid crossings.

It would be of interest to observe the trend in later years, when the growth and yields of the palms have presumably stabilised.

ACKNOWLEDGEMENTS

The authors wish to thank United Plantations Berhad for permission to present this paper.

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Fig. 3(a). Length of Frond No. 14

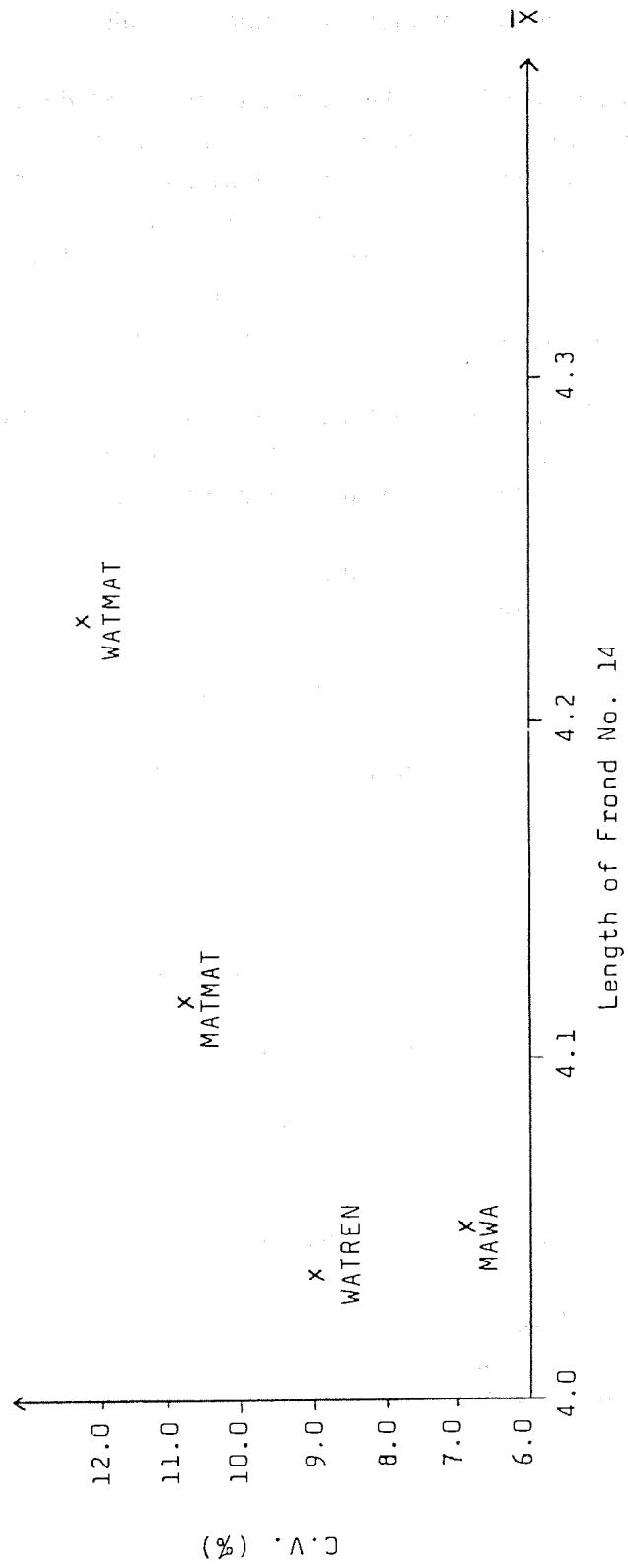


Fig. 3(b). Number of Fronds Produced/Year

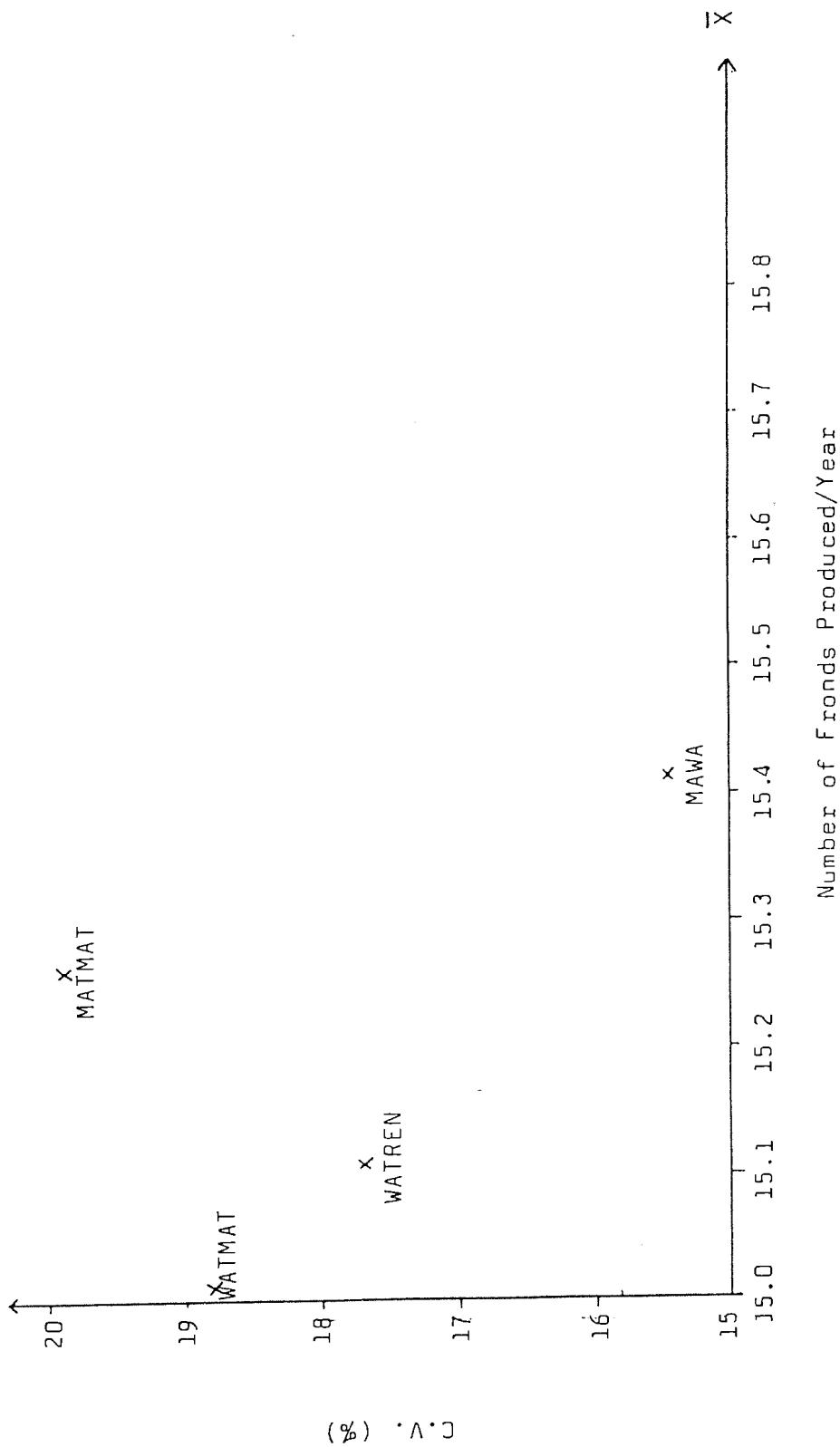
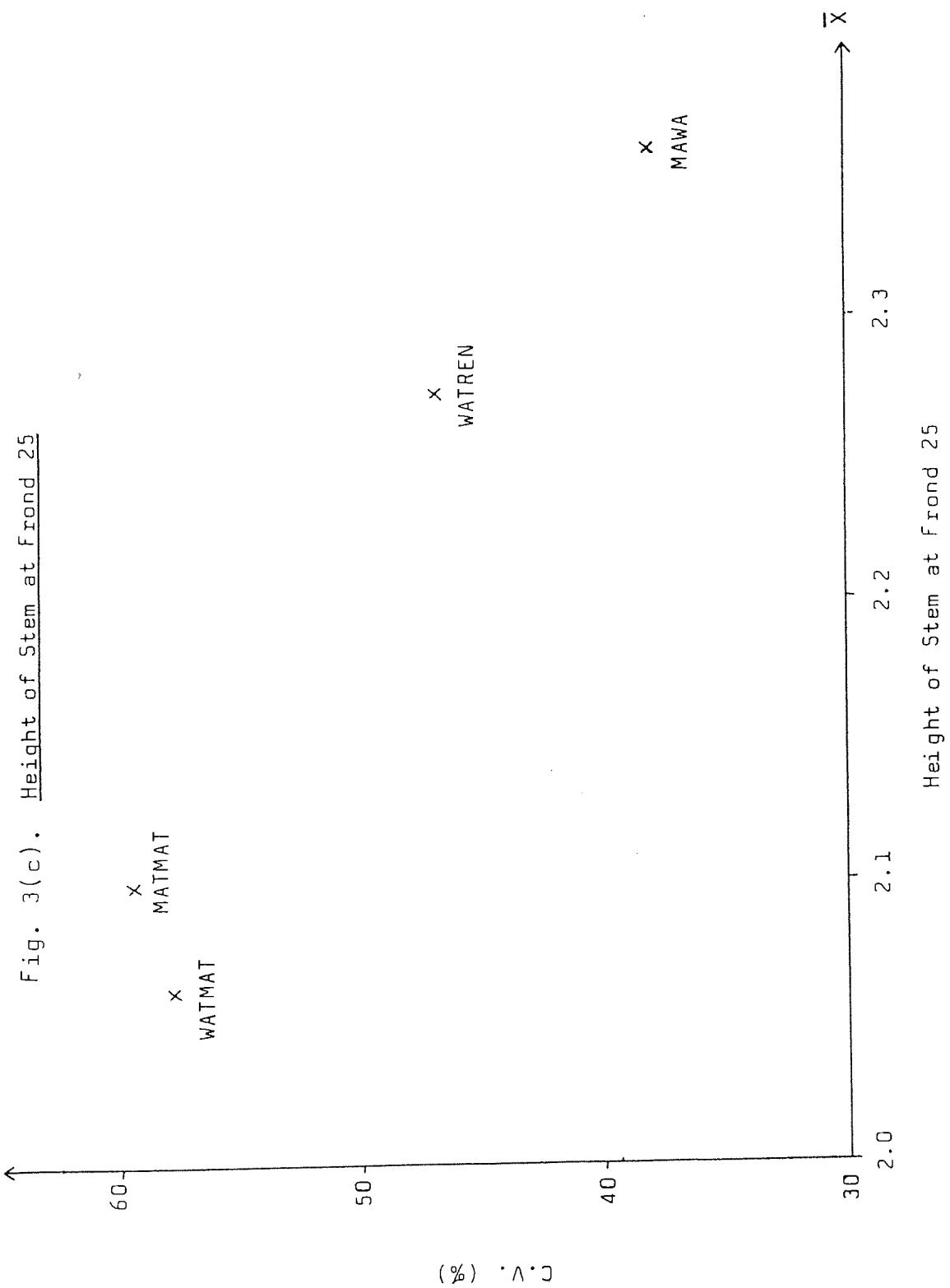


Fig. 3(c). Height of Stem at Frond 25



SESSION 3 DISCUSSION

Q: Mr. Mohamad Lokmal Ngah - FRIM, Malaysia.

With forestry data I often find the R^2 value from ANOV is very low, sometimes about 0.2 - 0.3 and the CVs are very high at 40 - 50%. Transformations do not improve the picture very much. What would you advice.

A: Prof. Manjit Kang - Louisiana State University, USA.

If you have high CVs, which could be due to non-reliable data, my first advice would be to repeat the experiment or measurement and secondly try some transformations but I am not a statistician.

Q: Dr. Soh Aik Chin - Applied Agricultural Research Sdn. Bhd., Malaysia.

Mr. Lokmal, when you mention provenance material, do the seeds come from bulked seed or from a few selected trees in a location ?

A: Mr. Mohamad Lokmal Ngah - FRIM, Malaysia.

Bulked seed, normally from at least 40 - 50 trees.

Q: Dr. Soh Aik Chin - Applied Agricultural Research Sdn. Bhd., Malaysia.

Is it possible that some of the GxE you see is a consequence of the fact that some of the hybrids are not as homogeneous as MAWA?

A: Mr. Mukesh Sharma - United Plantations, Malaysia.

Yes, it is possible. For example in the Malayan Tall x Malayan Tall crosses, we just use palms from the commercial fields, not breeding lines.

Q: Dr. V. Rao - EPA Management Sdn. Bhd., Malaysia.

I would like the statistician's view on what is loosely termed GxY. Two important features of some perennial tree crops are the genotypes own unique endogenous yield cycles over years and the occasional year whose effects (low rainfall for example) affect all genotypes to a greater or lesser extent.

A: Mr. Chow Chee Sing - PORIM, Malaysia.

Combination over years may be carried out but it is recommended that years be taken as fixed effects. If this is done mean yield over 2 - 3 years should be preferred to avoid the yield cycle.

Q: Mr. Chow Chee Sing - PORIM, Malaysia.

In the ANOVA model especially that of G, E and GxE, the effects of a factor e.g. the G are usually taken as fixed or random, since the general statistical model allows sampling from a finite population; is there any experience in having such a case where $(1-k/k)$ is something between 0 and 1?

A: Prof. Yamada - University Pertanian Malaysia.

I don't know any paper dealing with the value between 0 and 1. This is a matter of statistical concept rather than reality.

Q: Dr. Soh Aik Chin - Applied Agricultural Research Sdn. Bhd., Malaysia.

Prof. Yamada you said that the GE variance can be partitioned into the heterogeneity of variance for the genotypes between the environments, the other component being a function of the genetic correlation between genotypes in one environment and another. You gave the impression that if the GxE is contributed mainly by heterogeneity of variance than one needs only to transform and proceed with the analysis. Wouldn't an examination of the heterogeneity of variance allow one to pick out the environment which discriminates genotypes much better. Furthermore when the heterogeneity component is high, meaning a high genetic correlation of genotypes between one environment and another then such information will be useful, i.e. to find the environment that allows us to discriminate between genotypes.

A: Prof. Yamada - Universiti Pertanian Malaysia.

I call such a environment which gives high heterogeneity of variance as best breeding environment, because we can discriminate genetic differences more clearly. But unfortunately, the best environment for one trait is not the same for another trait. Another way to categorize the environments is to use genetic correlations. But I do not know which is the best way to identify the environment that discriminates the genotypes best.

Q: Mr. Hew Choy Kean - Plantek (M) Shd. Bhd., Malaysia.

Management practices have been emphasized as important in cocoa yield. Can you include management as environment and how is this considered under GxE interaction?

A: Mr. Chong Choon Fong - Golden Hope, Malaysia.

Management practices should obviously be included as an environmental factor. How they are to be included in the GxE interaction analysis depends on whether they can be quantified.

Q: Dr. Mak Chai - University Malaya, Malaysia.

Is it practical to measure yield and environmental variables at different stages of plant growth?

A: Prof. Manjit S. Kang - Louisiana State University, USA

In annual such as maize : yes; but it maybe impractical in tree crops. However you have a large number of fruits on a tree, you may try to harvest a small sample at different intervals - then of course it would be practical.

Q: Chan Kook Weng - Guthrie Research Chemara, Malaysia.

How much emphasis should be place on avoidance and exploitation of GxE interaction?

A: Prof. Manjit S. Kang - Louisiana State University, USA

I am in favour of exploiting GE interactions rather than avoiding it. I think we need to get a better understanding of GE interaction. DNA based techniques such as RFLP genetic analysis may be useful in obtaining profiles of highly stable and highly unstable genotypes. This type of information will be useful for breeding purposes.

SUMMING UP OF G X E SYMPOSIUM

by

**Prof. Dr. Jalani Sukaimi
Director, Biology Division
PORIM**

Ladies and Gentlemen

It is my turn now to do another summing up, the second in one week. It is a daunting task for many reasons. As the host of PORIM Conference, there are many chores to attend to. It would be wonderful if I could sit and listen to all papers, or if all papers are in the secretariat so that I could read and digest them. I will then be able to do a better summing up and, hence, make my own life easier. But neither is, unfortunately, possible. To make it worst and more burdensome, the abstracts are 'too abstract' and many of them will have the ending.....will be discussed!

In any case, I will attempt to make a summary of this one and a half-day GxE Symposium.

Ladies and Gentlemen

It would be fair to say that essentially there were three keynote addresses, the main one lead by Prof. Peter Caligari, then complemented by Prof. Manjit Kang and Prof. Yukio Yamada.

Components to be considered in GxE interaction are: Assessment, Biology, Genetics and Exploitation. Attention must be given to statistical and analytical concepts of GxE interaction. Components of the physical environment must be appropriately examined to determine their interactions with the genotype.

The response to each component of the environment is vital in assessing the degree of stability or instability of a particular genotype. This information would be useful in a breeding programme to help in the selection or elimination of genotypes.

The history of GxE analyses was also highlighted and with time later findings became more specific and sophisticated over previous ones. Techniques and methods of partitioning also vary depending on the hypotheses or theories. While the presence and implications of GE interactions have been known in many crops, there is a need now to more effectively harness it in improvement. The environment axis of the GxE equation must be more critically and dissectingly examined. Physical measurements of the growing plants' environment may help to better explain the GxE presence. This will in turn help more efficient use of resources spent on multi-location and multi-season testing of varieties.

As far as the genotype axis is concerned, the breeder, faced with a significant GE interaction, must consider incorporating stability and environment sensitivity parameters in his selection methodologies. We have seen the genetic implications of rapidly eliminating genotypes too early in a breeding programme but breeding perennial crops is expensive and it befalls on the breeder to do the balancing act using his knowledge of the crop to stand on and clever strategies, to help him balance.

It was enlightening to hear the divergent approaches taken in the interpretation of GxE interactions by plant and animal breeding. The former's heavily influenced by the search for varieties of general or specific adaptation, as the need may be, while GxE theory in animal breeding has, on the other hand, been developed by looking at genetic correlations between different environments. This not only allows prediction of correlated responses across different environments but also suggests optimal designs for testing. Not surprisingly the explanations are converging in recent work and a more complete framework for both general and specific utility will, I am sure, emerge.

Ladies and Gentlemen

The applications of GxE in perennial tree crops is clearly dependent on species, materials and traits. In oil palm, GxE interactions seem to be small for progenies, but substantial and certainly significant for clones and *oleifera x guineensis* hybrids. Where oil palm progenies are to be planted at very variable sites and if the objective is to narrow down from a large number to a smaller number, a simple approach would be to correlate yields taking into account known factors causing low correlations.

The situation in rubber is of course different from oil palms in that clones are the commercial planting materials. Clones exhibit very clear GxE interactions and this has influenced breeding and cultural practices leading to concepts such as Enviromax.

The detailed analysis of GxE using the joint regression method was well illustrated in *Cassava* where the influence of the environment, the genotype and their interaction was shown to affect incidence of *Cercospora* leaf spot.

In tea the most important environmental factor is temperature and we were shown that clones can significantly interact with it. It will be interesting to examine this interaction further when more data, from growth chamber experiments for example, are available.

Unlike the other crops it would appear that tropical fruit breeders perhaps hope not to have to entangle with GxE. While it is true that commercial fruit cultivation generally tries to achieve an optimum environment, it is nevertheless important I believe to examine for GxE effects produced by the components of that environment.

While the rubber breeder has learned to live with GxE interactions I am afraid the life of the oil palm breeder contemplating clones and now the cocoa breeder as well is going to be more complicated. Certainly for pod production and mean bean weight we may have to worry about which clone is to be planted where.

Ladies and Gentlemen

In dealing with perennial tree crops I am afraid our problems are not only multi-location but multi-season. The latter was well illustrated in coconuts where differences between coconut varieties varied between years.

Finally, I am afraid a piece of bad news for you ladies and gentlemen. As we try to leave behind our complications and worries in breeding, GxE and what have you, and head for the quiet forest, I am sorry to say that should you meet *Acacia mangium* and perhaps other forest species even more perennial you may meet GxE again. Maybe it is an old familiar friend after all.

Thank you.

Figure 5: Provenance mean versus coefficient of variation for dbh

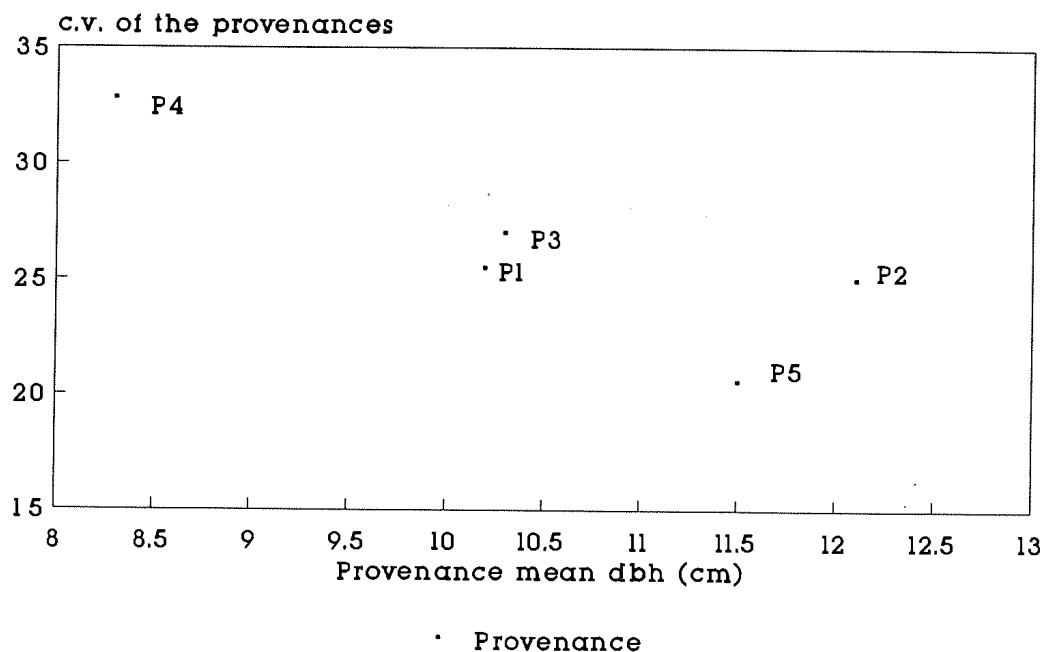
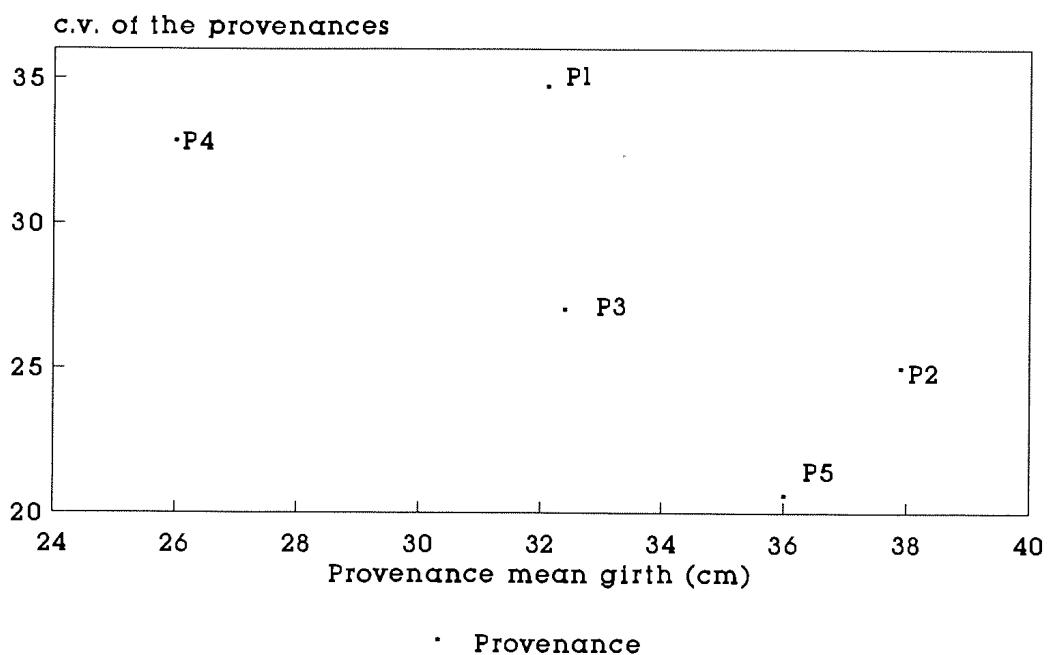


Figure 6: Provenance mean versus coefficient of variation for girth



GENOTYPE - ENVIRONMENT INTERACTIONS AND YIELD STABILITY STUDIES IN HYBRID COCONUT CULTIVARS

CIVIL ENGINEERING

by

Mukesh Sharma and Tan Yap Pau¹

INTRODUCTION

Like most crops under cultivation, hybrid coconut cultivars are known to perform variably at different localities. Their growth and subsequent performance is dependent on genetic, environmental, and agronomic factors and their interactions.

Ibrahim *et al* (1988) advocated the evaluation of a number of hybrid coconut cultivars over a range of different environments as a means to determine their adaptability.

The ANOVA, Regression and Genotype Stability analysis are useful methods for determining the relative adaptive values of hybrid coconut cultivars.

As very little work has been published in this regard for the coconut palm, this paper attempts to present some data on the early growth and performance of four types of hybrid coconut cultivars.

MATERIALS AND METHODS

This trial details were as follows :-

- Date Planted : April 1982
- Planting Density : 76.7 palms/ha.
- Plots Size : 20 palms
- Layout : 4x4 Latin square
- Location : Hilir Perak District, Perak, Peninsular Malaysia
- Soil Type : Bernam over Selangor series (Coastal clay)
- Hybrid Cultivars :
 - 1) MAWA (PB121) - (Malaysia Red Dwarf x West African Tall)
 - 2) WATREN - West African Tall x Rennel Tall

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- 3) WATMAT - West African Tall x Malayan Tall
 4) MATMAT - Malayan Tall x Malayan Tall

The period of recording for the various parameters is shown in *Table 1* below.

Table 1. Period of Recording for the Parameters Studied

Parameters Measured	No. of Years Recorded
1. Yield Components :	
- No. of Nuts/Ha.	4
- No. of Empty Bunches/Ha.	4
- No. of Bunches/Ha.	4
2. Vegetative Characters :	
- Frond Production	4
- Rachis Length (m)	4
- Height of Stem (m)	3

In the analysis of the results, three methods were used; i.e ANOVA, Linear Regression and plotting the coefficient of variation values against the mean.

For the statistical analysis using ANOVA, the years (**Y**) were considered as different environments (**E**) and the hybrid cultivars or varieties (**V**) were taken to be genotypes (**G**) and so it follows that **V x Y** is synonymous (in this context) with **G x E** or genotype x environment interaction.

RESULTS

1. Environmental Variations

1.1 Rainfall and its Distribution

Of the climatic factors, rainfall is considered to be one of the most important factors affecting the yields of the coconut palm (Murray, 1977).

The total annual rainfall and its distribution is shown in *Table 2(a)* for the period 1985-1990. The range of 1,484 mm to 2,071 mm obtained is well within the 1,300 mm to 2,300 mm range which was quoted to be optimal for coconuts (Murray, 1977). The coefficient of variation (%) at 15.4% is considered to be low indicating a fairly uniform rainfall over the six years under evaluation. The distribution of the rain-days was also fairly uniform as indicated by the low C.V. (%) value of 12.5% whilst the mean number of rain-days/year for the 1985/1990 period was fair at 121 days/year.

The mean monthly rainfall and its distribution is shown in *Table 2(b)* for the 1985-1990 period. The weighted mean of 144 mm of rain/month and 10 rain-days/month again showed good uniformity. However, the C.V. (%) of the weighted data over the six year period showed a considerable degree of variation at 55.9% for rainfall per month and 43.9% for number of rain-days/month. The C.Vs. (%) for the monthly rainfall and number of rain-days/month for each of the six years of recording are

shown in *Table 2(c)*. The results show that there was a considerable degree of variation in the amount of rainfall and number of rain-days per month over the six years.

Table 2(a). Total annual rainfall and number of rain-days of the trial for 1985-1990

Period	Total	Annual Rainfall
	mm	No. of Rain-Days
1985	1,484	108
1986	1,714	103
1987	1,528	111
1988	2,043	137
1989	2,071	137
1990	1,531	127
Mean	1,729	121
C.V. (%)	15.4	12.5

Table 2(b). The mean monthly rainfall and number of rain-days/month of the trial for 1985-1990

Period	Mean Monthly Rainfall	
	Amount (mm)	No. of Rain-Days
1985	124	9.0
1986	143	8.6
1987	127	9.3
1988	170	11.4
1989	173	11.4
1990	128	10.6
Overall Mean*	144	10.0
Overall C.V. (%) *	55.9	43.9

* Refers to weighted data.

Table 2(c). Coefficient of variation (%) of the monthly rainfall and number of rain-days during the period of 1985 - 1990

Period	Coefficient of Variation (%)	
	Monthly Rainfall	No. of Rain Days
1985	68.4	49.0
1986	44.8	49.5
1987	66.7	48.6
1988	51.7	28.6
1989	45.9	45.0
1990	64.0	44.0
Overall C.V. (%)*	55.9	43.9

* = Weighted value.

1.2. The Minimum and Maximum Temperature and its Variations

From the results in *Table 3*, there appeared to be little variation for the minimum and maximum temperature between years for the period of 1985-1989 as shown by the very low C.V. (%) values obtained.

Table 3. The mean monthly minimum and maximum temperatures for the trial

Period	Mean Monthly Temperature (°C)	
	Min. (°C)	Max. (°C)
1985	23.2	32.0
1986	23.3	32.2
1987	23.5	32.4
1988	23.5	32.2
1989	23.1	32.2
1990	Not Available	
Mean*	23.3	32.2
C.V. (%)*	2.2	1.8

* Refers to weighted data (1985-1989).

2. The Analysis of Variance (ANOVA)

2.1 For yield components

The combined analysis of variance (ANOVA) for the yield components; i.e. nut production, bunch production and empty bunch production, is shown in *Table 4*.

Table 4. ANOVA for the yield components

Source	d.f.	Mean Squares		
		No. of nuts per ha.	No. of bunches per ha.	No of empty bunches per ha.
Rep./Year	12	1,320,829.00*	7,701.08ns	2,574.15*
Years (Y)	3	99,127,810.00**	973,613.30**	40,778.36**
Variety (V)	3	90,309,120.00**	441,960.00**	24,991.67**
V x Y	9	2,547,485.00**	74,884.45**	833.06ns
Error	36	620,657.80	5,674.53	1,063.48

* = Significant at $P = 0.05$

** = Significant at $P = 0.01$

ns = Not significant.

The above table shows that year (Y), variety (V) and V x Y are highly significant for both nut production (nuts/ha.) and total number of bunches produced/ha. This indicates that both variety and environment (year) influenced both these traits whilst for empty bunch production (negative traits in selection); the differences observed were largely varietal in nature.

2.2 For Vegetative Components

Table 5 shows the combined ANOVA for the vegetative components; i.e. frond length (m), frond production and total stem height (m).

Table 5. ANOVA for the vegetative components

Source	d.f.	Frond	Frond	d.f.	Height of
		Production	Length		Stem
		Mean Square	Mean Square	d.f.	Mean Square
Rep./year	12	0.801**	0.209ns	9	0.074*
Years (Y)	3	3.618**	0.298ns	2	25.941**
Variety (V)	3	1.704**	0.723**	3	0.252**
V x Y	9	0.147ns	0.115ns	6	0.146**
Error	36	0.117	0.155	27	0.034

* = Significant at $P = 0.05$

** = Significant at $P = 0.01$

ns = Not significant

Varietal differences were highly significant for all the three vegetative components analysed whilst significant differences for environment (years) were obtained for frond production and stem height. The latter also showed highly significant V x Y interaction indicating a strong genotype x environment interaction for stem height in the trial.

3. Analysis for Nut Production Per Hectare against the Environment index using the Linear Regression Method

The relationship between the number of nuts produced per hectare against the environment index for the four coconut hybrid cultivars under evaluation is shown in Figure 1.

From the early yields, it can be seen that although the ranking of the cultivars remained unchanged, there was a differential rate of response. The MAWA hybrid showed consistently higher yields and better stability compared with the other three hybrid cultivars under evaluation.

The MATMAT was the poorest yielding hybrid and showed the highest rate of response as shown by the regression coefficient (b) in *Table 6*. The range for the b-values observed for the hybrid coconut cultivars evaluated was 0.7248 - 1.2309. WATMAT and MATMAT hybrids showed b-values of above one, indicating that they were very sensitive or responsive to the changes in the environment.

Table 6. Regression coefficients (b) for the four coconut hybrid cultivars

Hybrid	Regression Coefficient (b)
MAWA	0.7248
WATREN	0.8438
WATMAT	1.2005
MATMAT	1.2309

4. Genotype Stability of the Various Coconut Hybrid Cultivars for Yield Components

The coefficient of variation (C.V. in %) was plotted against the mean for all four hybrid cultivars with respect to nut production, bunch production and empty bunch production on a per hectare basis to compare the relative stability or uniformity between the different types of hybrids.

4.1 Number of Nuts/Ha.

From Figure 2(a), it is clear that the MAWA hybrid was both the highest yielding and most uniform of the hybrid cultivars whilst the MATMAT hybrid was the both the lowest yielding and most variable for nut production.

FIG. 1. THE RELATIONSHIP BETWEEN YIELD OF NUTS/HA. WITH
THE ENVIRONMENT INDEX USING LINEAR REGRESSION

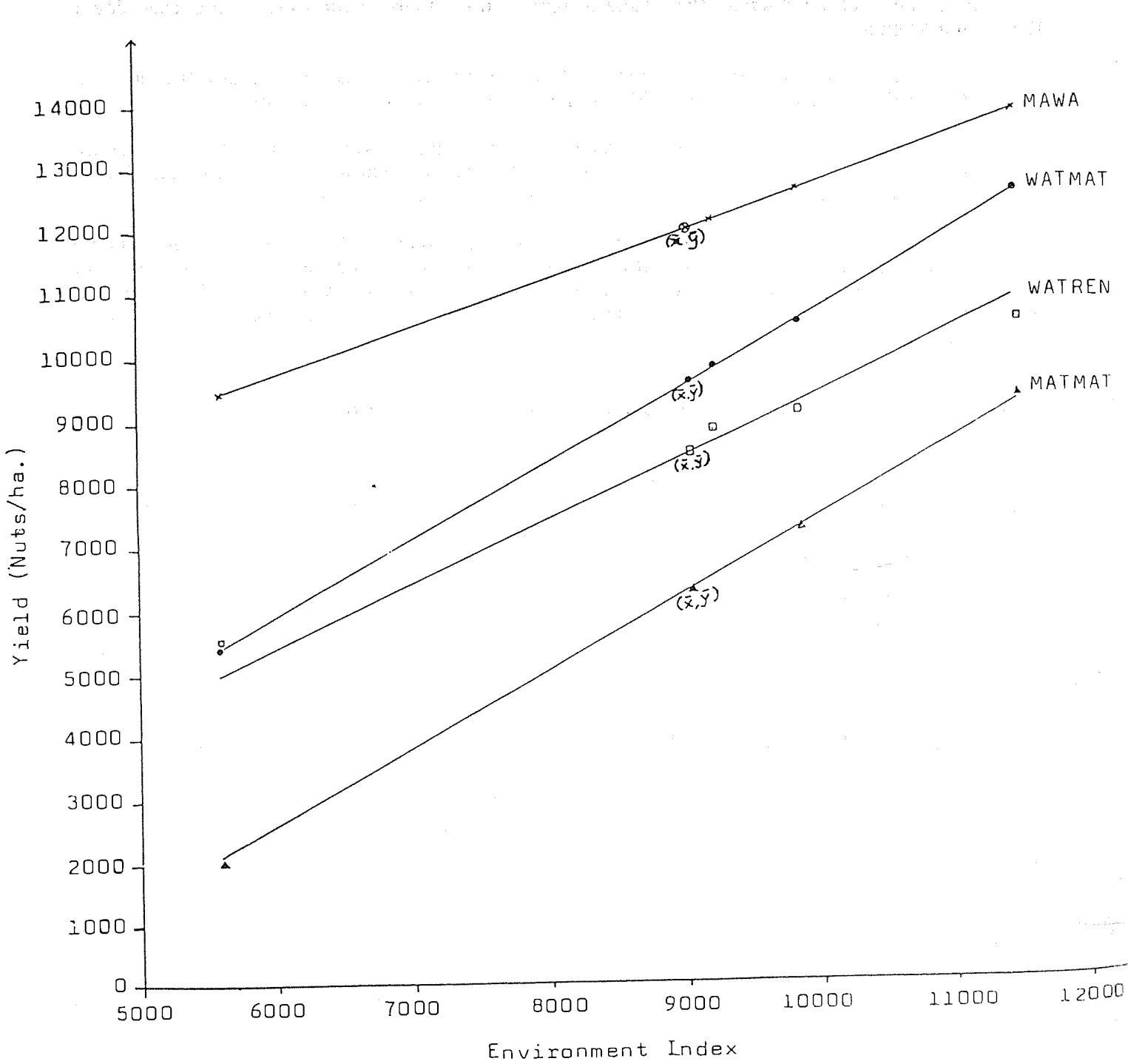


Fig. 2(a). Number of Nuts/Ha.

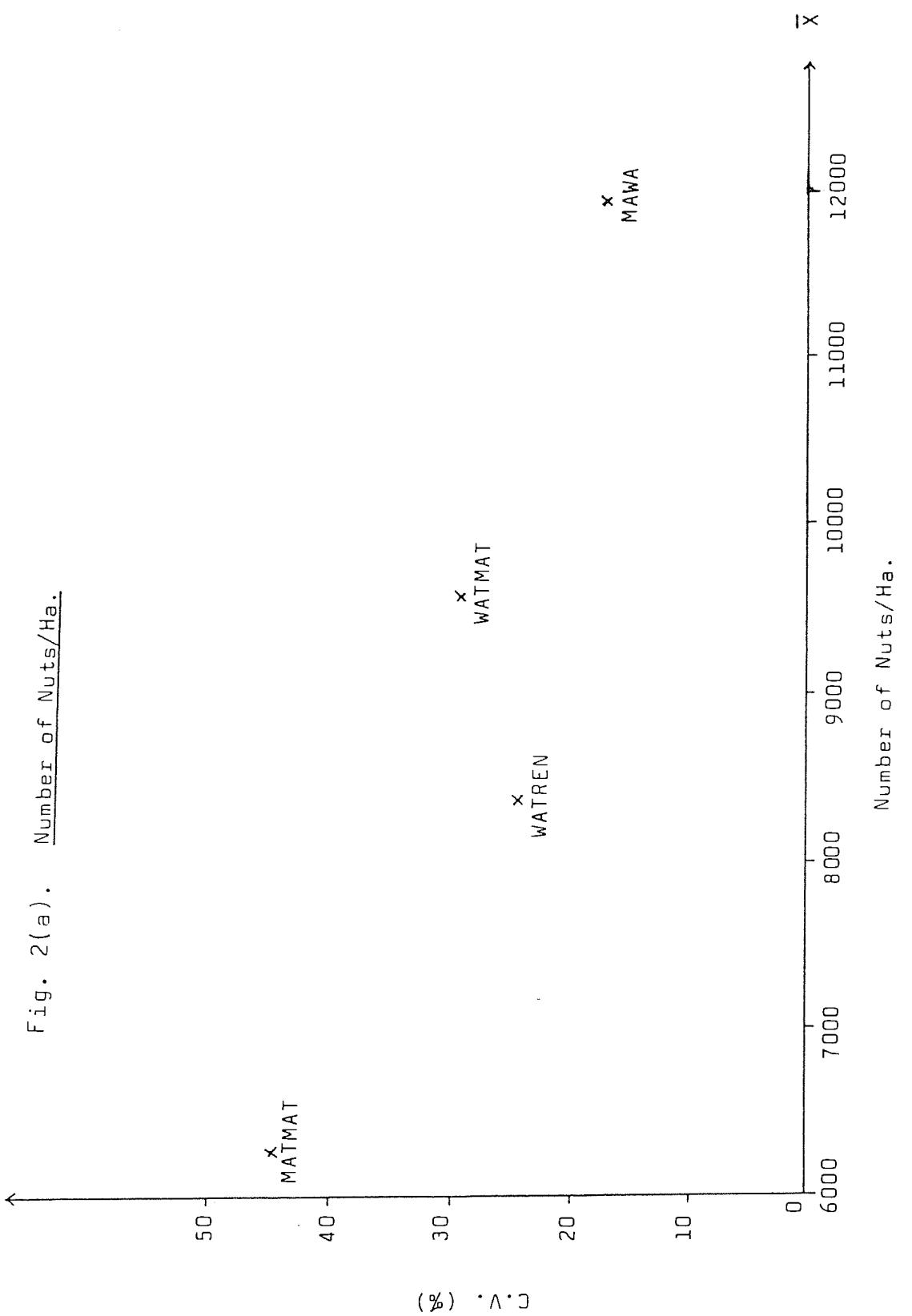


Fig. 2(b). Number of Bunches/Ha.

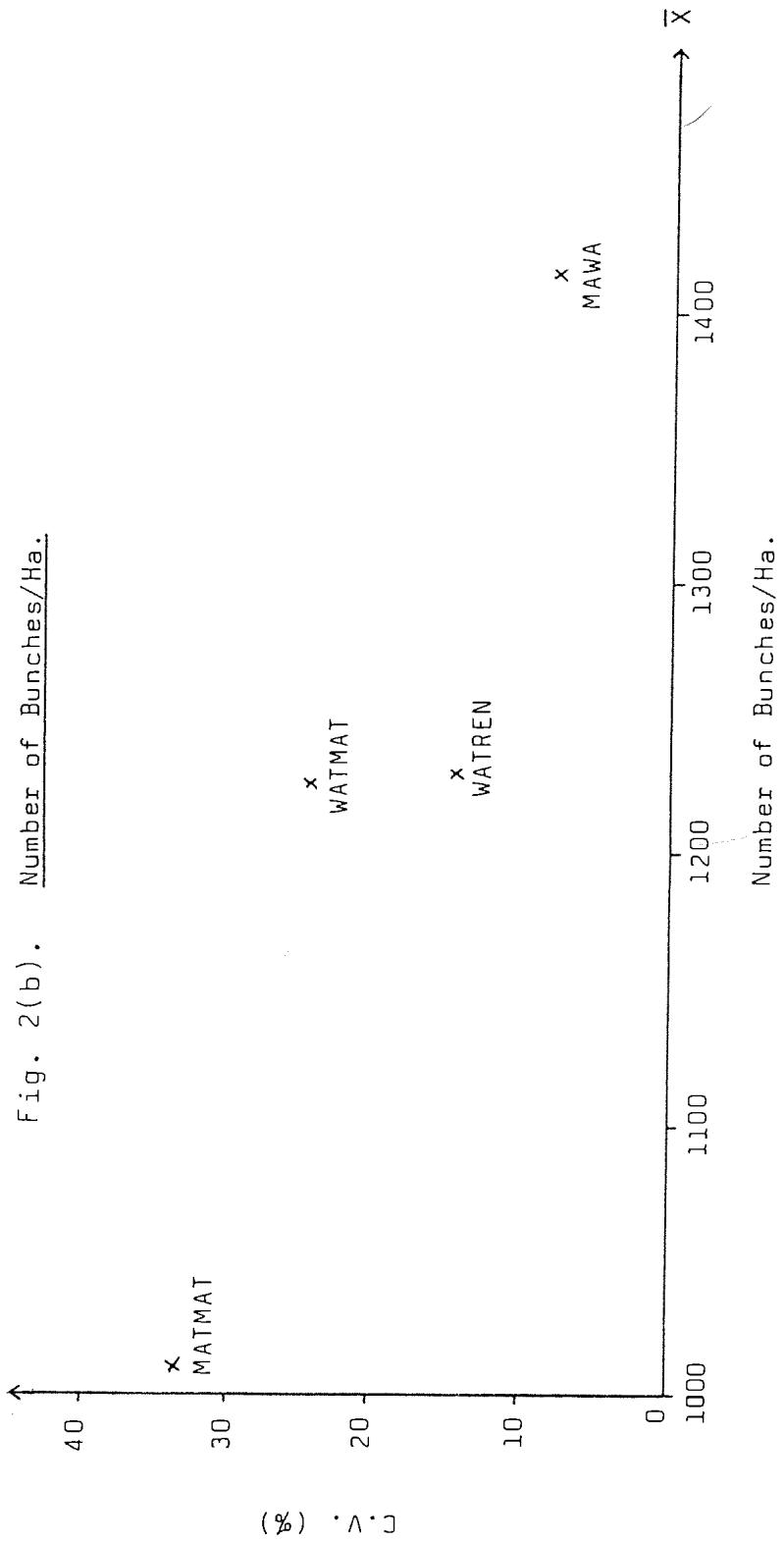
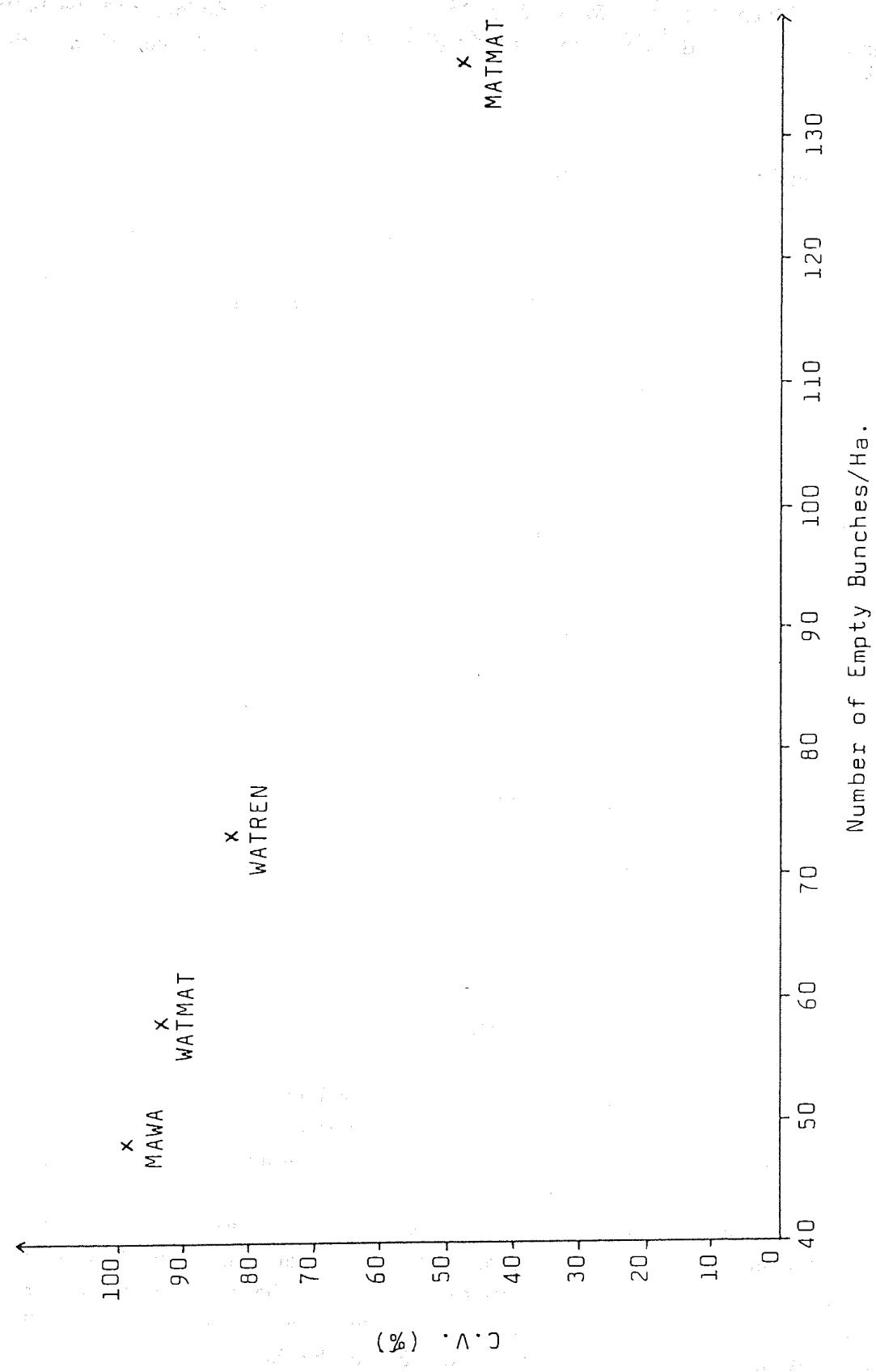


Fig. 2(c). Number of Empty Bunches/Ha.



4.2 Number of Bunches/Ha

Bunch production followed the same trend as nut production, with the MAWA being the most uniform hybrid and showing the highest bunch production amongst the hybrid cultivars tested (Figure 2b).

4.3 Number of Empty Bunches/Ha.

This is an undesirable trait and from the results (Figure 2c), the incidence was highest in the MATMAT hybrid, its low C.V. (%) indicates a high incidence of palms producing empty bunches. The MAWA hybrid, on the other hand, had very low empty bunch production.

5. Genetic Stability of the Various Coconut Hybrid Cultivars for Vegetative Components

5.1 The Length of Frond Number 14

From the results, the MAWA was the most uniform for this trait whilst the MATMAT and WATMAT hybrids were the most variable (Figure 3a).

5.2 The Number of Fronds Produced/Year

The MAWA hybrid recorded the highest mean frond production besides showing the lowest C.V. (%) whilst the MATMAT was the most variable for this trait as shown in Figure 3b .

5.3 Height of Stem at Frond Number 25

Figure 3c shows that the MAWA was the most uniform whilst the MatMat showed the highest variability for this trait amongst the hybrids tested.

DISCUSSION AND CONCLUSIONS

It is acknowledged that the results are confounded to some degree by the age of the palms. Nevertheless, it is felt that these results are still useful in providing some indication about the general trend in the relative performance of the different types of hybrid cultivars tested.

The climate and growing conditions at Hilir Perak district are generally considered to be close to optimum for coconuts. Although variation for total annual rainfall between years and for mean minimum and maximum monthly temperatures is low, the high C.V. values for monthly rainfall and number of rain-days/month during the 1985-1990 period, suggests that this distribution could have affected the growth and subsequent performance of the palms. This is supported by the results obtained from the ANOVA and Regression analysis.

The regression analysis, which has been increasingly used since the mid-1960s to measure yield stability over a range of environments (Sneep *et al*, 1979), indicated that in Hilir Perak agro-ecological conditions, the MAWA hybrid has the greatest stability for yield.

The MAWA is also found to be the most uniform of the hybrid coconut cultivars tested. This is contrary to the experience in Kuala Terengganu (along the East Coast of Peninsular Malaysia), where Jamadon *et al* (1988) reported that it was more sensitive to the extreme environmental conditions of the sandy bris soils. They reported that the MAWA gave greater C.V. values for all the vegetative components when compared to the MATMAT, in 280 hectares of selected smallholdings studied, and suggested that nutrient, moisture availability as well as agro-management practices were the major limiting factors accounting for the poor early growth of the MAWA.

The greater uniformity of the MAWA over the other hybrids could be largely due to the fact that its Malayan Dwarf parents are highly inbred and its West African Tall parents are comparatively more homogeneous than the other Talls used in the hybrid crossings.

It would be of interest to observe the trend in later years, when the growth and yields of the palms have presumably stabilised.

ACKNOWLEDGEMENTS

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Fig. 3(a). Length of Frond No. 14

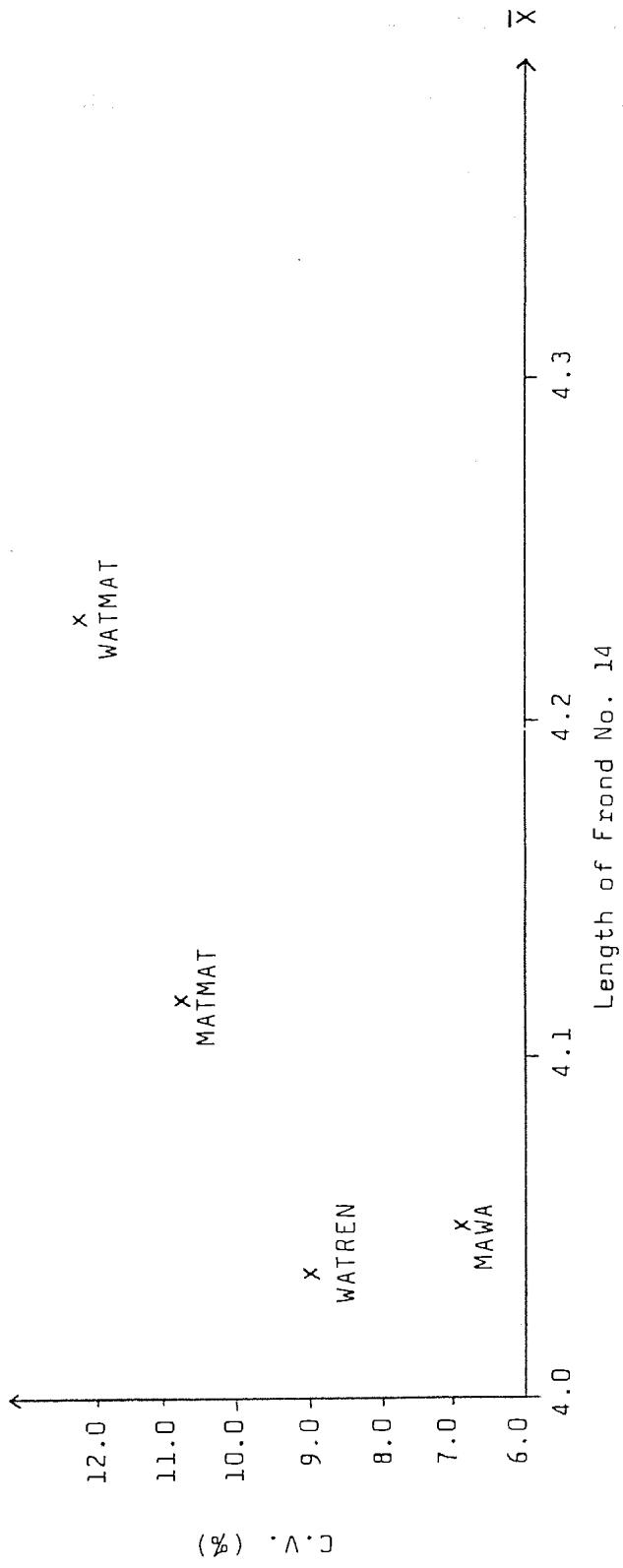


Fig. 3(b). Number of Fronds Produced/Year

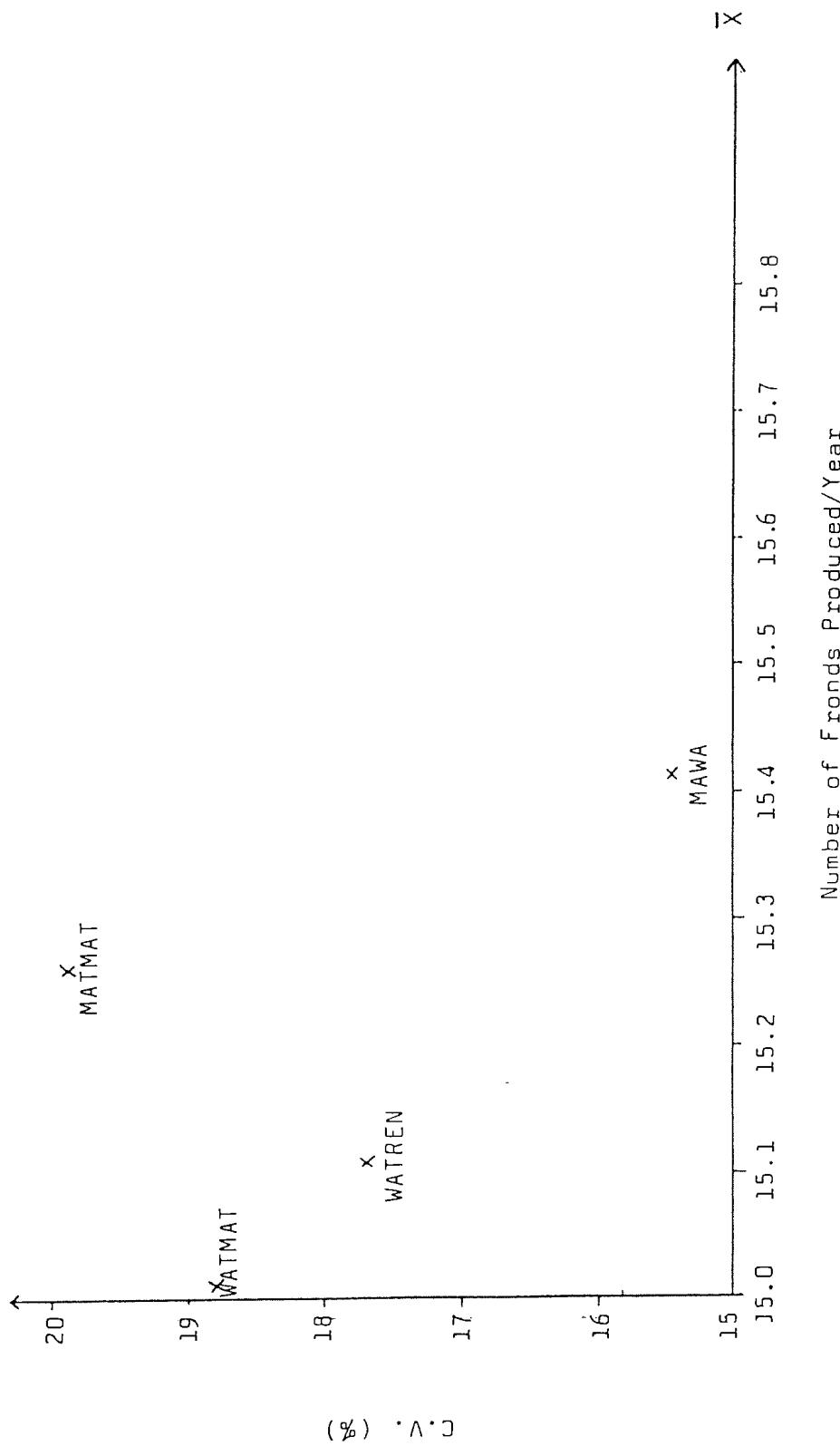
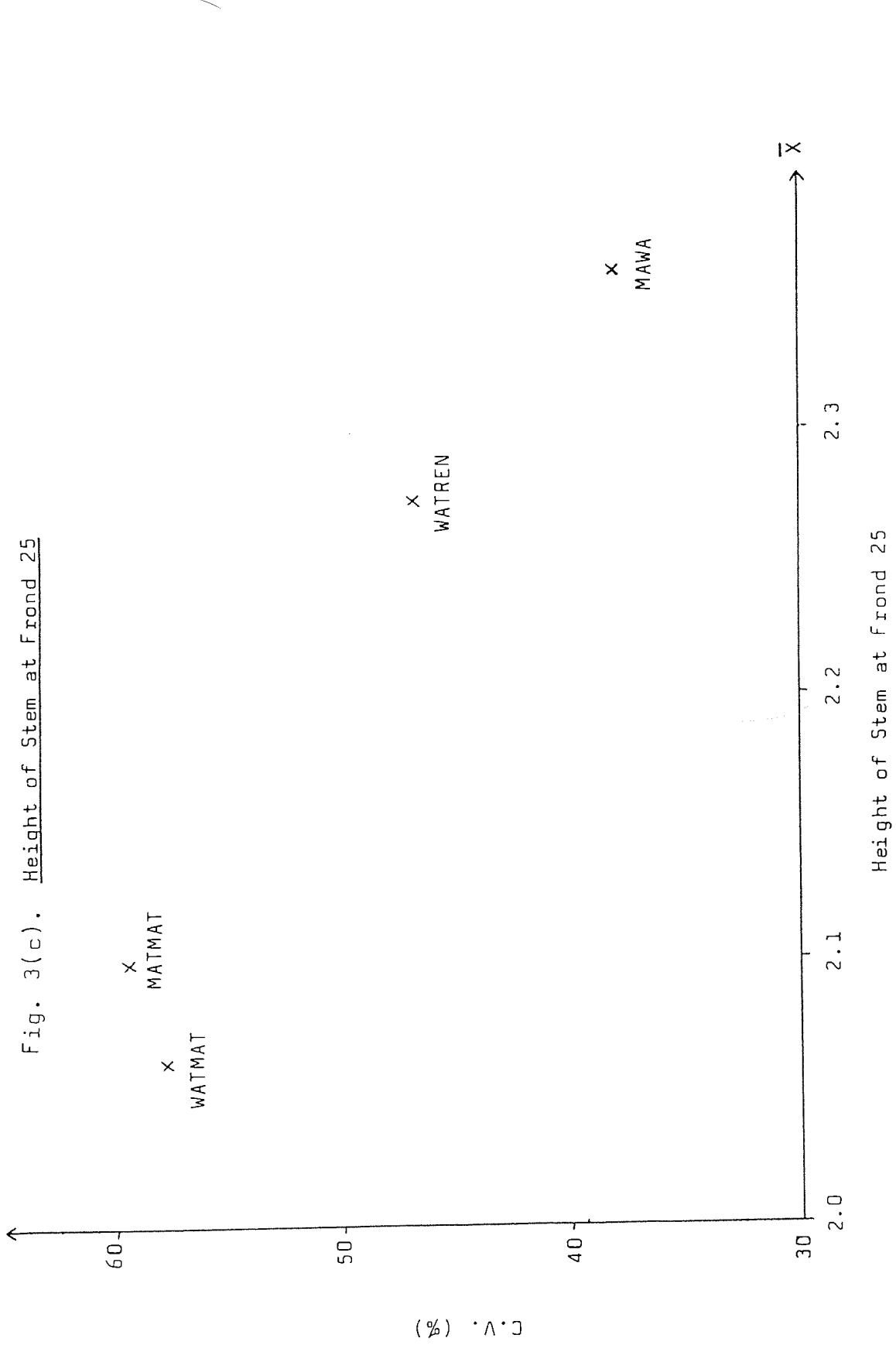


Fig. 3(c). Height of Stem at Frond 25



SESSION 3 DISCUSSION

Q: Mr. Mohamad Lokmal Ngah - FRIM, Malaysia.

With forestry data I often find the R^2 value from ANOV is very low, sometimes about 0.2 - 0.3 and the CVs are very high at 40 - 50%. Transformations do not improve the picture very much. What would you advice.

A: Prof. Manjit Kang - Louisiana State University, USA.

If you have high CVs, which could be due to non-reliable data, my first advice would be to repeat the experiment or measurement and secondly try some transformations but I am not a statistician.

Q: Dr. Soh Aik Chin - Applied Agricultural Research Sdn. Bhd., Malaysia.

Mr. Lokmal, when you mention provenance material, do the seeds come from bulked seed or from a few selected trees in a location?

A: Mr. Mohamad Lokmal Ngah - FRIM, Malaysia.

Bulked seed, normally from at least 40 - 50 trees.

Q: Dr. Soh Aik Chin - Applied Agricultural Research Sdn. Bhd., Malaysia.

Is it possible that some of the GxE you see is a consequence of the fact that some of the hybrids are not as homogeneous as MAWA?

A: Mr. Mukesh Sharma - United Plantations, Malaysia.

Yes, it is possible. For example in the Malayan Tall x Malayan Tall crosses, we just use palms from the commercial fields, not breeding lines.

Q: Dr. V. Rao - EPA Management Sdn. Bhd., Malaysia.

I would like the statistician's view on what is loosely termed GxY. Two important features of some perennial tree crops are the genotypes own unique endogenous yield cycles over years and the occasional year whose effects (low rainfall for example) affect all genotypes to a greater or lesser extent.

A: Mr. Chow Chee Sing - PORIM, Malaysia.

Combination over years may be carried out but it is recommended that years be taken as fixed effects. If this is done mean yield over 2 - 3 years should be preferred to avoid the yield cycle.

Q: Mr. Chow Chee Sing - PORIM, Malaysia.

In the ANOVA model especially that of G, E and GxE, the effects of a factor e.g. the G are usually taken as fixed or random, since the general statistical model allows sampling from a finite population; is there any experience in having such a case where $(1-k/k)$ is something between 0 and 1?

A: Prof. Yamada - University Pertanian Malaysia.

I don't know any paper dealing with the value between 0 and 1. This is a matter of statistical concept rather than reality.

Q: Dr. Soh Aik Chin - Applied Agricultural Research Sdn. Bhd., Malaysia.

Prof. Yamada you said that the GE variance can be partitioned into the heterogeneity of variance for the genotypes between the environments, the other component being a function of the genetic correlation between genotypes in one environment and another. You gave the impression that if the GxE is contributed mainly by heterogeneity of variance than one needs only to transform and proceed with the analysis. Wouldn't an examination of the heterogeneity of variance allow one to pick out the environment which discriminates genotypes much better. Furthermore when the heterogeneity component is high, meaning a high genetic correlation of genotypes between one environment and another then such information will be useful, i.e. to find the environment that allows us to discriminate between genotypes.

A: Prof. Yamada - Universiti Pertanian Malaysia.

I call such a environment which gives high heterogeneity of variance as best breeding environment, because we can discriminate genetic differences more clearly. But unfortunately, the best environment for one trait is not the same for another trait. Another way to categorize the environments is to use genetic correlations. But I do not know which is the best way to identify the environment that discriminates the genotypes best.

Q: Mr. Hew Choy Kean - Plantek (M) Shd. Bhd., Malaysia.

Management practices have been emphasized as important in cocoa yield. Can you include management as environment and how is this considered under GxE interaction?

A: Mr. Chong Choon Fong - Golden Hope, Malaysia.

Management practices should obviously be included as an environmental factor. How they are to be included in the GxE interaction analysis depends on whether they can be quantified.

Q: Dr. Mak Chai - University Malaya, Malaysia.

Is it practical to measure yield and environmental variables at different stages of plant growth?

A: Prof. Manjit S. Kang - Louisiana State University, USA

In annual such as maize : yes; but it maybe impractical in tree crops. However you have a large number of fruits on a tree, you may try to harvest a small sample at different intervals - then of course it would be practical.

Q: Chan Kook Weng - Guthrie Research Chemara, Malaysia.

How much emphasis should be place on avoidance and exploitation of GxE interaction?

A: Prof. Manjit S. Kang - Louisiana State University, USA

I am in favour of exploiting GE interactions rather than avoiding it. I think we need to get a better understanding of GE interaction. DNA based techniques such as RFLP genetic analysis may be useful in obtaining profiles of highly stable and highly unstable genotypes. This type of information will be useful for breeding purposes.

SUMMING UP OF G X E SYMPOSIUM

by

**Prof. Dr. Jalani Sukaimi
Director, Biology Division
PORIM**

Ladies and Gentlemen

It is my turn now to do another summing up, the second in one week. It is a daunting task for many reasons. As the host of PORIM Conference, there are many chores to attend to. It would be wonderful if I could sit and listen to all papers, or if all papers are in the secretariat so that I could read and digest them. I will then be able to do a better summing up and, hence, make my own life easier. But neither is, unfortunately, possible. To make it worst and more burdensome, the abstracts are 'too abstract' and many of them will have the ending.....will be discussed!

In any case, I will attempt to make a summary of this one and a half-day GxE Symposium.

Ladies and Gentlemen

It would be fair to say that essentially there were three keynote addresses, the main one lead by Prof. Peter Caligari, then complemented by Prof. Manjit Kang and Prof. Yukio Yamada.

Components to be considered in GxE interaction are: Assessment, Biology, Genetics and Exploitation. Attention must be given to statistical and analytical concepts of GxE interaction. Components of the physical environment must be appropriately examined to determine their interactions with the genotype.

The response to each component of the environment is vital in assessing the degree of stability or instability of a particular genotype. This information would be useful in a breeding programme to help in the selection or elimination of genotypes.

The history of GxE analyses was also highlighted and with time later findings became more specific and sophisticated over previous ones. Techniques and methods of partitioning also vary depending on the hypotheses or theories. While the presence and implications of GE interactions have been known in many crops, there is a need now to more effectively harness it in improvement. The environment axis of the GxE equation must be more critically and dissectingly examined. Physical measurements of the growing plants' environment may help to better explain the GxE presence. This will in turn help more efficient use of resources spent on multi-location and multi-season testing of varieties.

As far as the genotype axis is concerned, the breeder, faced with a significant GE interaction, must consider incorporating stability and environment sensitivity parameters in his selection methodologies. We have seen the genetic implications of rapidly eliminating genotypes too early in a breeding programme but breeding perennial crops is expensive and it befalls on the breeder to do the balancing act using his knowledge of the crop to stand on and clever strategies, to help him balance.

It was enlightening to hear the divergent approaches taken in the interpretation of GxE interactions by plant and animal breeding. The former's heavily influenced by the search for varieties of general or specific adaptation, as the need may be, while GxE theory in animal breeding has, on the other hand, been developed by looking at genetic correlations between different environments. This not only allows prediction of correlated responses across different environments but also suggests optimal designs for testing. Not surprisingly the explanations are converging in recent work and a more complete framework for both general and specific utility will, I am sure, emerge.

Ladies and Gentlemen

The applications of GxE in perennial tree crops is clearly dependent on species, materials and traits. In oil palm, GxE interactions seem to be small for progenies, but substantial and certainly significant for clones and *oleifera x guineensis* hybrids. Where oil palm progenies are to be planted at very variable sites and if the objective is to narrow down from a large number to a smaller number, a simple approach would be to correlate yields taking into account known factors causing low correlations.

The situation in rubber is of course different from oil palms in that clones are the commercial planting materials. Clones exhibit very clear GxE interactions and this has influenced breeding and cultural practices leading to concepts such as Enviromax.

The detailed analysis of GxE using the joint regression method was well illustrated in *Cassava* where the influence of the environment, the genotype and their interaction was shown to affect incidence of *Cercospora* leaf spot.

In tea the most important environmental factor is temperature and we were shown that clones can significantly interact with it. It will be interesting to examine this interaction further when more data, from growth chamber experiments for example, are available.

Unlike the other crops it would appear that tropical fruit breeders perhaps hope not to have to entangle with GxE. While it is true that commercial fruit cultivation generally tries to achieve an optimum environment, it is nevertheless important I believe to examine for GxE effects produced by the components of that environment.

While the rubber breeder has learned to live with GxE interactions I am afraid the life of the oil palm breeder contemplating clones and now the cocoa breeder as well is going to be more complicated. Certainly for pod production and mean bean weight we may have to worry about which clone is to be planted where.

Ladies and Gentlemen

In dealing with perennial tree crops I am afraid our problems are not only multi-location but multi-season. The latter was well illustrated in coconuts where differences between coconut varieties varied between years.

Finally, I am afraid a piece of bad news for you ladies and gentlemen. As we try to leave behind our complications and worries in breeding, GxE and what have you, and head for the quiet forest, I am sorry to say that should you meet *Acacia mangium* and perhaps other forest species even more perennial you may meet GxE again. Maybe it is an old familiar friend after all.

Thank you.