THE MEASUREMENT AND INTERPRETATION OF GENOTYPE-ENVIRONMENT INTERACTIONS

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SUMMARY

The regression analysis developed by Finlay and Wilkinson to investigate genotype-environment interactions and to assess genotypes for their adaptation to a range of environments is reviewed. Their analysis used the mean yield of many genotypes to provide a measure of the environment; it was not measured in physical terms. To reveal aspects of their analysis it was applied to data of the response of genotypes to variation in a single precisely measured environmental factor. The conclusions were extended to consider variation in several environmental factors.

The effects on the regression statistics that occur with different samples of genotypes, sub- and super-optimal environmental conditions, differences in periods of growth, changes in the scale of measurement and the occurrence of several stress factors are outlined.

The study by BREESE (1969) of genotype-environment interaction in *Dactylis glomerata* is considered against a background of these effects.

INTRODUCTION

The objective in many plant breeding programmes is the selection of genotypes that are consistently high yielding over the range of environments that occur in different locations or seasons. This selection is often inefficient due to genotype-environment interactions, the failure of genotypes to have the same relative performance in different environments. Several authors have recently published papers on this subject in which they have considered genotype-environment interactions as linear functions of the environment. The plant breeding aspects of this approach have been brought out by FINLAY and WILKINSON (1963), WRICKE (1965) and EBERHART and RUSSELL (1966) while a genetic development has been due to BUCIO ALANIS (1966), BUCIO ALANIS and HILL (1966) and PERKINS and JINKS (1968a, b). It is the purpose of this note to discuss the basic contention underlying the analysis, namely that genotype-environment interaction may be satisfactorily depicted as linear functions of the environment. An examination will then be made of an analysis undertaken by BREESE (1969) on genotypes of *Dactylis glomerata* L. The genetic developments by BUCIO ALANIS, HILL, PERKINS and JINKS will not be considered.

To exemplify the technique, particular reference will be given to the study of

Finlay and Wilkinson. They examined the ability of barley varieties to yield well over a range of environments by conducting a variety trial in several sites and seasons. The mean yield of the trial at each site in each season was used as a measure of the environment in which the trial had been conducted. The yields of the individual varieties were then plotted against these mean trial yields and regressions were calculated. No attempt was made to measure variation in moisture or nitrogen supply, radiation, temperature, or any other environmental factor; Finlay and Wilkinson depended on the average response of the varieties, at each site, to provide an all-inclusive measure of that environment. A variety with an average response to the different environments in their study had a regression slope of b = 1. A variety with a slope grater than 1, they suggested was adapted to good environments and a variety with a slope less than 1 was adapted to low yielding environments. The other statistics they used to characterize a variety was its average yield over all environments. WRICKE (1965), EBERHART and RUSSELL (1966) and PERKINS and JINKS (1968b) have emphasized the value of the deviation from regression lines as an important attribute when distinguishing between genotypes.

A regression technique, similar to that used by Finlay and Wilkinson had been used previously by YATES and COCHRAN (1938) but Finlay and Wilkinson drew attention to the adaptation aspects of the regression lines, and also suggested that adaptation and mean yield could be distinghuished as separate attributes of a genotype.

Genotype responses to a single environmental factor

In Finlay and Wilkinson's trials it was not known which environmental factor or factors were limiting yields. It is proposed to apply their analysis to situations where the environmental factors are known and thereby to interpret some of its aspects. The simplest possible situation occurs when only one factor of the environment is varied, and where that one factor is precisely controlled. In such studies it has commonly been found that the genotypic response to increased levels of an environmental factor show optima. Citing only a few examples, MITCHELL and LUCANUS (1962) and EAGLES (1967), have documented them for temperature; BRADSHAW et al. (1964) and BARLEY and NAIDU (1964) for nitrogen; ASHER and LONERAGAN (1967) for phosphorus; and LONERAGAN et al. (1968) for calcium. An optimum would probably occur for any factor that was varied over a sufficient range. The example from MITCHELL and LUCANUS' work (1962) will be considered. Optima were obtained when six grass cultivars were grown in a range of temperatures (Fig. 1 upper). Five of the six cultivars were similar in their response to increasing temperature, and were typified by the curve for cocksfoot, while the sixth cultivar, a Paspalum, was different. The means of all six cultivars are given on the graph, since these provide the "environmental means" used to characterize the environment when attempts are made to plot the yields of the genotypes as a linear function of the environment (Fig. 1 lower). They are the values on the abscissa on the new graph. The temperature, at which each of these mean values was derived, is shown as a guide to understanding the effects of the analysis. On this second graph, low yields arising from sub-optimum and super-optimum temperature are juxtaposed and the highest yields are obtained at the optimum temperature. Although it is understandable that sub- and super-optimum tempe-
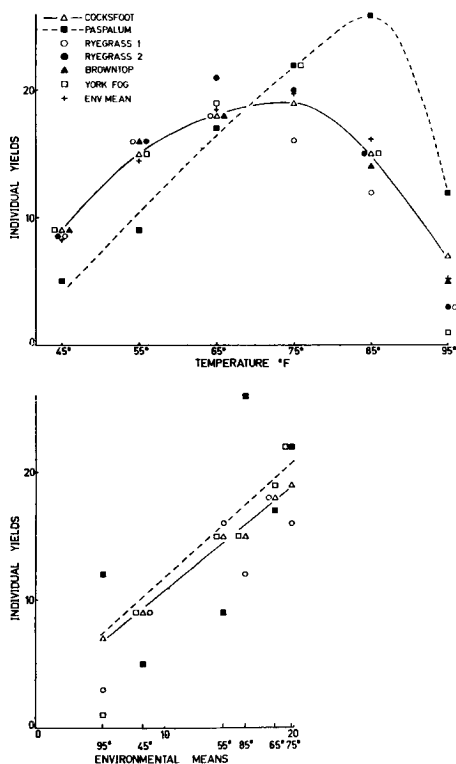
Fig. 1. Upper: Derived from data of MITCHELL and LUCANUS (1962). The response of six cultivars of grass to levels of temperature. Free hand curves have been drawn through the values for cocksfoot and for Paspalum. The mean yields of the six cultivars at each temperature (shown by the symbol +) provide a measure of the environment and are the environmental means in the lower graph.

Lower: The same data plotted with the environmental means on the x-axis. Linear regressions have been plotted for cocksfoot and Paspalum, which have similar b values of 0.83 and 0.92, respectively. Note however the differences in deviation from the fitted regression lines.

ratures result in low mean yields, genotypes usually are not similarly ranked under these extremes of temperature. Therefore to have them juxtaposed on a graph may be misleading. In addition, the change in ranking at low values is not readily detected by regression or deviation from regression, especially if there is a wide range in environmental means.

A second point evident from Fig. 1 is that the five similar cultivars largely determine the values of the environmental means and understandably these cultivars show little deviation from the linear regression; on the other hand the exceptional Paspalum shows a marked deviation from its regression. A genotype that differs from the majority of genotypes under consideration, either below or above their optimum will show a marked deviation around its regression line. This deviation from regression has been termed stability by EBERHARDT and RUSSELL (1966) and BREESE (1969). It is evident that a deviation from regression arising in this way is not a specific property of the Paspalum cultivar; if the experiment had been conducted on five cultivars of Paspalum and one of cocksfoot the Paspalums would have had low deviations and the cocksfoot a high deviation.

The types of response curve present in the upper graph of Fig. 1 have been discussed by ANTONOVICS et al. (1967). These authors were concerned with the response of genotypes to various levels of nutrients in place of temperature. They suggested
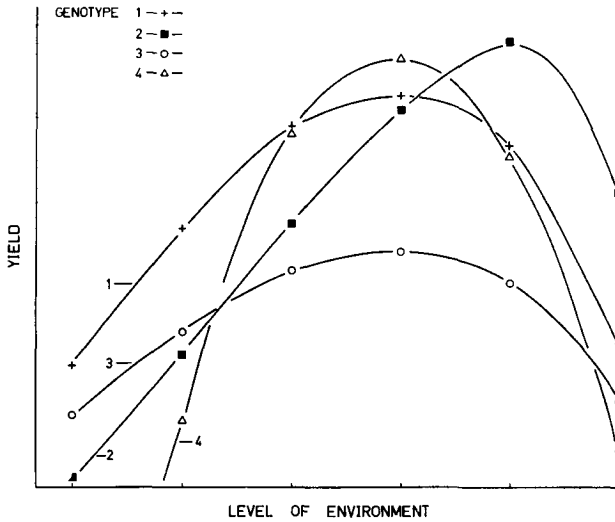
Fig. 2. Typical yield response curves of different genotypes to levels of an environmental factor such as temperature or nutrient supply.

that the curves which they obtained for their genotypes reflected the environment in which the genotypes had evolved. As a result of these adaptations, genotypes may have optima at different levels of the environment (Genotypes 1 and 2 in Fig. 2); they may have similar ranges in response but different overall yields (Genotype 1 and 3); or a restricted adaptation and range in response (Genotype 4). Genotype 4 also illustrates a response to threshold levels in the environment with zero yields at each extreme. There are many variations around these patterns and examples may be found in the literature cited above.

If these four genotypes were a sample of a large number of genotypes in an experiment then the "environmental means" could be calculated for each level of the environmental factor. These means would be points on an average curve of response. The average curve would give a perfect linear regression on the Finly-Wilkinson graph since it is plotted against itself; this is still true if the curve is asymmetric about its optimum. Its line would have a slope of 1 and go through the origin. Of greatest interest then are the atypical genotypes; those that have a regression slope significantly different from 1, whose lines do not go through the origin, or those that have a significant deviation around their regression. All these atypical responses can be readily interpreted with reference to Fig. 2.

As a basis for comparison the response curve of genotype 1 will be taken as the average response of the large number of genotypes and it will have the average linear regression outlined above. The other genotypes are then atypical. Genotype 2 would have an average yield, a slope $b \approx 1$, but a large deviation; genotype 3 below average yield, a slope $b < 1$ and a small deviation; genotype 4 a below average yield, a slope $b > 1$ and a small deviation.

In Finlay and Wilkinson's terminology genotypes with high b values have low

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stability and are specifically adapted to high yielding environments and conversely low b values indicate a high stability and adaptation to low yielding environments. As indicated above, Eberhardt and Russell and Breese have referred to deviation from regression as stability. In view of the interpretation of the b values from the response curves it appears that Finlay and Wilkinson's terminology is preferable as being indicative of a low fluctuation in yield with changing environment.

In field situations super-optimum conditions may not always be encountered and the response is confined to the sub-optimal parts of the curve. Deviation from regression is then not likely to be large except as a result of experimental error. Upward extrapolation of the regression line may have some meaning, but if the results have been obtained covering superoptimal environmental conditions then extrapolation of the regression line is nonsensical, as it would imply yields higher than those obtained at the optimum.

The values in a response curve result from the growth of organisms and are increased by time, thus a longer period of growth may lead to the same proportional increase of each value in the curve. To combine results for different periods of growth can be misleading. On the Finlay and Wilkinson graph optimum yields obtained from a short period will be juxtaposed with sub- and superoptimum yields from a longer period and genotypic ranking cannot be expected to be the same. The situation is made worse if growth is not proportional but is logistic, or subject to growth phases and plants under one environmental level have completed a phase while those at another level are still in the initial stages. This point is relevant to the growth of grasses where the initiation of the reproductive phase is usually determined by the environment, where large genotypic differences in initiation occur and where yields from plants in the reproductive or vegetative phase are very different (KNIGHT, 1965).

In their original analysis Finlay and Wilkinson used a logarithmic scale which induced a reasonable homogeneity in experimental error and also a high degree of linearity in the regressions. The effect of logarithmic transformation is to minimize the genotypic differences at the high values, that is at the optimum, and maximize differences at the low sub- and super-optimum values. A plant breeder discriminating between genotypes on the basis of regression values calculated on a logarithmic scale may be laying stress on differences at low yields for his discrimination. The transformation may induce linearity if differences between genotypes at the optima are greater than those below them.

If the reverse situation occurs as in Fig. 1 the transformation induces curvature. Another difference, attributable to the scale used, arises from the fact that exceptionally high yield values have a greater influence on the mean yield and the regression coefficient when calculated on a arithmetic scale, than when calculated on a logarithmic scale. As a result the mean yield and regression coefficient for a genotype are often positively correlated when on an artithmetic scale, when there is no correlation on a logarithmic scale. This lack of correlation was exhibited in Finlay and Wilkinson's study as a triangular distribution of coordinates when mean yield was plotted against regression coefficient.

A final point relevant to the scale used in the regression analysis is that the underlying mathematical model relating yield of a genotype to the environment is different if the scale is arithmetic or logarithmic and different biological conclusions will be drawn.

GENOTYPIC RESPONSES TO SEVERAL ENVIRONMENTAL FACTORS

For simplicity the foregoing discussion has been restricted to variation in a single factor. When several are involved, the results will change, as the optimum level of an environmental factor for a genotype is not a constant but varies with levels of other environmental factors. This has long been recognized; LANG in 1920 stated "An increase in yield can be obtained not only by improvement in the one factor present at a relative minimum but by improvement in all factors which are removed from the optimum to a greater or less extent." What is required to interpret genotype-environment interactions is therefore, the response of the genotypes to various combinations of levels of several factors. Such comprehensive data can be obtained only from very large experiments. The data can be depicted and analyzed as response surfaces if two factors are varied but with more factors the data would have to be analyzed as multiple regressions.

In field situations many environmental factors influence growth and yield. Of these, some such as temperature, radiation and moisture cannot be controlled; they fluctuate rapidly and their levels are relatively difficult to record. It was for this reason that Finlay and Wilkinson used the average response of genotypes to measure the environment. Their approach is valuable where an assessment is being made of many varieties but ultimately it will be necessary to determine the major limiting factors influencing yields. A biological interpretation of their analysis will remain difficult when juxtaposed low yields have arisen indistinguishably from suboptimal or super-optimal responses to one environmental factor or as a response to suboptimal levels of different factors. Just as it could not be expected that the ranking of genotypes would be the same under sub- and superoptimal levels of one factor, so it will not be the same when low yields have been caused by low levels of different factors such as moisture and temperature. As before when one factor was being considered, this change in ranking at low values does not greatly influence the regression line or deviation from regression when the range in environmental means is large, and one might again conclude that the genotype-environment interaction could be satisfactorily depicted as a linear function of the environment.

To study the response to several environmental factors of 277 genotypes, the number in Finlay and Wilkinson's original analysis, would be a Herculean task; this should be possible, however, if the breeder is studying a small number of genotypes. The chances of making a reasonable guess at the important limiting factor is greater if yield is obtained in a short period of growth, e.g. from frequent cutting of pasture grasses or in situations where the final variation in yield of a cereal is determined largely in the interval between heading and grain maturation.

GENOTYPE-ENVIRONMENT INTERACTION IN DACTYLIS GLOMERATA L.

Detailed reference will now be made to the study by BREESE (1969) of five populations of *Dactylis glomerata*. The yields of regrowth herbage from plants cut 5 times during a growing season or cut only 2 times (hay and aftermath) were combined in this analysis. The trial was conducted for two seasons at two sites in Great Britain, Gogerddan and Acton Piggot, but no data were given about these environments
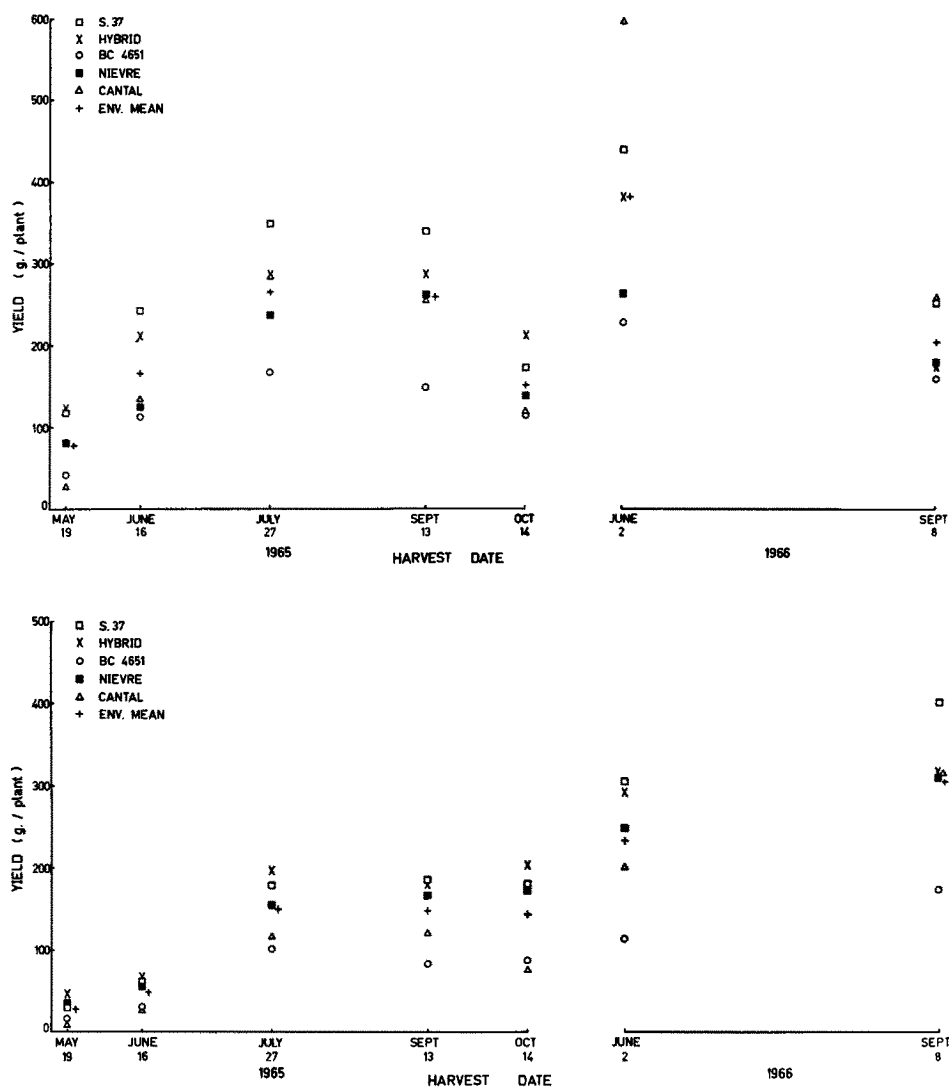
Fig. 3. The yields of five populations of cocksfoot when cut frequently (1965) or when cut as "hay and aftermath" (1966) at Gogerddan (above) Acton Piggott (below). The environmental means are the mean yields of the populations.

except the fact that they were different. The yields at each date of harvest under the two frequencies of cutting are given in Fig. 3. Similar growth patterns are commonly obtained in *Dactylis glomerata* when ecotypes from different environments are compared (KNIGHT, 1966, 1968). Ecotypes from the Mediterranean region are adapted to mild winters and summer droughts and are winter-growing and summer-dormant, whereas those from continental cool temperate regions are adapted to freezing winters

Table 1.

Population	Environment of origin	
S. 37	Maritime cool temperate.	Bred in U.K.
BC 4651	Maritime Mediterranean.	Atlantic seaboard of Portugal.
Nievre	Continental cool temperate.	Low altitude in France.
Cantal	Continental cool temperate.	High altitude in Massif Centrale of France.

and mild summers and are winter-dormant summer-growers. Ecotypes subject to a maritime influence do not have marked summer or winter dormancy as the maritime effect tempers the environment. BREESE's 4 populations, which together with one hybrid were considered in the study, may be placed in the categories given in Table 1. In view of their origin it is probable that the main adaptation of these ecotypes is to temperature.

The hybrid was the cross S. 37 × BC 4651. The growth patterns in Fig. 3 reflect the origins of the populations, particularly if the summers of 1965 and 1966 at Gogerddan were warmer than at Acton Piggot. For example Cantal had relatively low yields in cold conditions and high yields in warmer conditions. Breese considered that each period of regrowth occurred in a different unspecified macro-environment which could be evaluated quantitatively from the mean yield of the five populations. For each population he drew a linear regression of its individual yields against the 14 environmental means. The results for three of his populations are reproduced in Fig. 4.
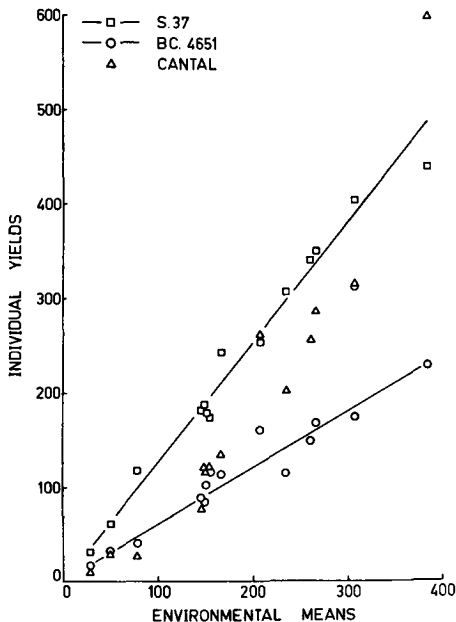

Fig. 4. The yields of S. 37, BC 4651 and Cantal when plotted against the environmental means. The estimated regression lines have been drawn only for S 37 and BC 4651.

In this graph the low yields of early spring and late autumn are juxtaposed, as are the higher yields under frequent cutting with the lower yields of the hay and aftermath treatments.

The cultivars S. 37 and BC 4651 may be likened to genotypes 1 and 3 in Fig. 2. These cultivars largely determined the environmental means in BREESE's study for three reasons: they gave the extremes of yield at most harvests, their yields tended to constant proportionately and they made up, with their hybrid, 3 of the 5 cultivars contributing to the environmental means. The proportionality was evident both in short periods of regrowth (5 cuts) or long periods (hay and aftermath). Because these cultivars largely determined the environmental means, they showed little deviation from their regressions (Fig. 4). The cultivar Cantal, coming from a cold continental climate may be similar to genotype 4 in Fig. 2, in being adapted to grow in a limited environmental range. It would be dormant in the winter. Magnification of its response curve by a long growing period (hay and aftermath) could lead to yields greather than those of other cultivars if conditions were near optimum but lower yields if conditions were suboptimum. This cultivar is showing a different growth response, it displays a high deviation from regression to the point where it is probably misleadling to plot a single regression line through all its coordinates. This is illustrated in Fig. 5 where Cantal is depicted alone, but where sites and cutting frequencies are distinguished. In this graph any attempt at extrapolation from one macro-environment to another, by extrapolating the regression lines would lead to serious errors of interpretation.

It is possible that a great deal of the variation and genotype–environment inter-action found in Breese's study could be accounted for by considering temperature and
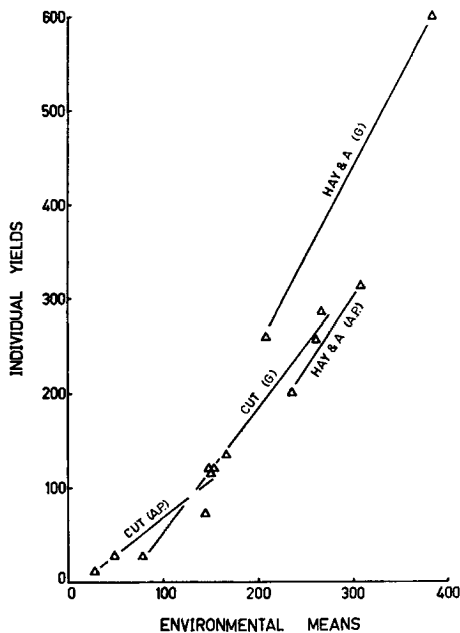

Fig. 5. The same data for the cultivar Cantal as depicted in Fig. 4 but with the individual treatments and sites demarcated.

using an accumulated day degree function to accommodate daily fluctuations of temperature in the field. Nevertheless, any attempt at relating the growth of ecotypes to temperature would have to recognize differences in time available for regrowth under the two frequencies of cutting.

CONCLUSION

The study of genotype environment interaction in the field will remain intractable until we have some knowledge of the response of genotypes to combinations of environmental factors. The present alternative of plotting the yield of a genotype as a linear function of the environment, where the environment is measured as the mean yield of several genotypes is a valuable technique for the plant breeder when making a broad study of a collection of varieties. It is, however, essential to realize that the technique uses a transformation to make linear an average genotypic response. When making biological interpretations, recognition should be taken of the following:

1. That if the environmental variation in one factor ranges both below and above the optimum, then sub- and superoptimum mean yields of equal value are juxtaposed.

2. That different limiting factors (e.g. frost or drought) result in equally low mean yields. Genotypes are unlikely to be similarly ranked under these factors but this difference in ranking is not readily detected by the existing regression technique.

3. That there may be no yield from some of the genotypes if a threshold level is surpassed.

4. That combining in the one analysis data from different lengths of growing period, or different growth phases, can be very misleading.

5. That the interpretation will be greatly affected by the scale in the analysis. It is possible that no one scale will be appropriate for all genotypes in a trial. If these possibilities are recognized the procedure of plotting the yields of a variety as a regression on the mean yields of many varieties will continue to aid the plant breeder in his task of selecting genotypes with various responses to the environment.

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