

# A parsimonious statistical design and breeding procedure for evaluating and selecting desirable characteristics over environments\*

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**Abstract.** The concept of stability as described in the literature does not meet all of the desirable criteria required by growers of cultivars. Various types of possible responses are discussed, and these are divided into those desirable from a grower's viewpoint and those not. Measures of stability appearing in the literature are based on variances, linear regression slopes, and/or deviations from regression. The most desirable response type would be denoted as unstable by current concepts of stability. It is shown how to simulate environments that exceed the ranges found in practice. A statistical design is described which is the height of parsimony and has the advantage that the conditions varied are known. The experimental results can then be interpreted in light of the known conditions. The design is optimally cost effective in terms of funds, material, and personnel. A breeding procedure is presented for such characteristics as desired response, stability under current definitions, tolerance (to pests, cold, drought, etc.), protein, quality, fiber, etc.

**Key words:** Desirable response – Response curve – Selection index – Split plot designs – Stability

## Introduction

The stability of crop production, i.e., the relatively constant annual yield of a crop grown by a farmer, is one of

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the most important issues facing world agriculture and food production; in some cases, stability is equally as important as yield itself. Stability is influenced by a cultivar's genetics, the environment in which it is grown, and the cropping system used in the environment. Across a diversity of these three factors, growers, marketers, consumers, and policy makers are confronted with the problem of dependability and predictability of food supply.

In an intensive cropping system such as vegetable production, growers stagger planting dates, knowing that correct (market) timing is more profitable than high yield, and they need cultivars that are predictable across planting dates. For them, instability of yield results in both market and price instability, which adversely affect the farm economy. In intensive cropping systems, commonly practiced in developing countries, stability is of paramount importance if growers are to feed the family and community. In these countries, intercropping is a frequent system of choice because it ensures more production stability and more diversity of food for diet (Francis 1981; Federer 1993).

From the literature, it appears that the concept and definition of stability needs considerably more discussion and precise quantification (Lin et al. 1986; Verma et al. 1978). We shall attempt to make our use of this concept more consistent with the objectives of the grower rather than a statistical criterion. It will be necessary to study and consider various types of possible responses for cultivars grown in environments that range from poor to optimal. The range of environments encountered in practice should be included in the range of environments being considered in experiments studying the concept of stability. It will also be necessary to precisely define what is meant by poor and optimal environments.

One of the objectives of this investigation is to explore and review the concept of stability, environment, and

how they interact and affect a cultivar's response in terms of yield or any other quantitative trait. The second objective is to develop a parsimonious statistical design that allows the estimation of stability, of response parameters, and of a grower's desired response function of yield over changing environments. Our third purpose is to present a framework for the selection of and breeding for a desired response function within the context of parsimonious statistical design. Finally, we discuss a set of breeding investigations where this methodology could be integrated into experimental procedures.

### Environments

It would appear that most experimenters consider an "environment" to be a single trial at a single locality and in a single year. They then attempt to obtain a range of environments by selecting "a random sample" of locations and years. It is not clear how or if this can be accomplished, especially when the population of years or sites is not defined. Others decide to select locations that cover the range of "conditions" to be met in practice. The "conditions" are not defined except to say that these are supposed to be the conditions encountered by farmers who grow these cultivars. If the factors creating the environments or conditions are not defined precisely, how can one cover a range of such "conditions or environments"? We agree with LeRoy Powers, deceased sugar beet and tomato breeder, D. W. (Scotty) Robertson, deceased barley breeder, B.N. Okigbo, IITA, Ibadan, Nigeria, and several others who expounded the idea that the researcher should know precisely what conditions he wishes to use and to create these conditions in an experiment. They contended that cultivar by location (genotype by environment to many researchers) interaction was not of much use unless one knew the elements making environments different. As one forage crop specialist, Jack L. Harlan, put it, "One can make any forage cultivar come out on top simply by changing the dates of cutting." This statement shows the necessity of precisely defining the objectives of the grower of these cultivars.

Now, what are some of the factors causing poor, fair, or optimal growing conditions or environments? Certainly, the amount of water available for a crop at critical times in the growing season is a prime factor. A second one is soil type and fertility. A third would be the number and kind of insects present as well as the type and amount of disease. Another important factor would be the biological, not necessarily calendar, date of planting and harvest. Other factors could be amounts of sunshine, fog, wind, elevation, etc. Regardless of the factors making environments different, it is necessary to precisely define what is meant by poor, fair, and good environments with respect to the characteristic being measured. Once the factors affecting variation in environments and their fre-

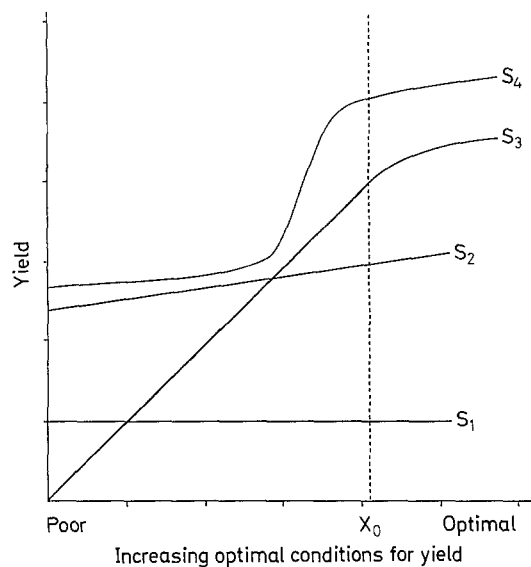


Fig. 1. Cultivar responses to changing environments

quency in the population are determined, experiments can then be conducted that include this range of variation for most of these factors. Breeders do this to some extent when they make their selections under low fertility and high fertility conditions, when they make their bean selections under intercropping with maize, when selections are made under low and high disease or insect infestations, when selections are made under drought and non-drought conditions, etc. Rather than considering changing environments for only one or two factors, selection should be made considering all factors, or at least the major ones, affecting cultivar response grown under various known environmental conditions.

### Cultivar responses

Responses of cultivars to varying environments can be completely different. There is no set pattern or form of response as this depends upon the genotype. Some possible responses of cultivars to changing environments is depicted in Fig. 1. A type  $S_1$  response would be for a low-yielding cultivar that did not make use of the better environmental conditions. Note that the extreme case of a type  $S_1$  response is where a cultivar has zero yield under any environmental condition.

The type  $S_2$  response is for a cultivar that performs well (compared to  $S_1$ ) in poor environments and takes some advantage of improved environments in a linear manner. This cultivar would have a small slope when its yield  $Y$  is plotted against the environmental index  $X$  (often taken to be the yield of a large number of cultivars at a specified site and year). Likewise, its variance in yield over all environments is small.  $S_1$ , however, has zero slope and zero variance, which under several proposed stability measures (see Lin et al. 1986) would be optimal.

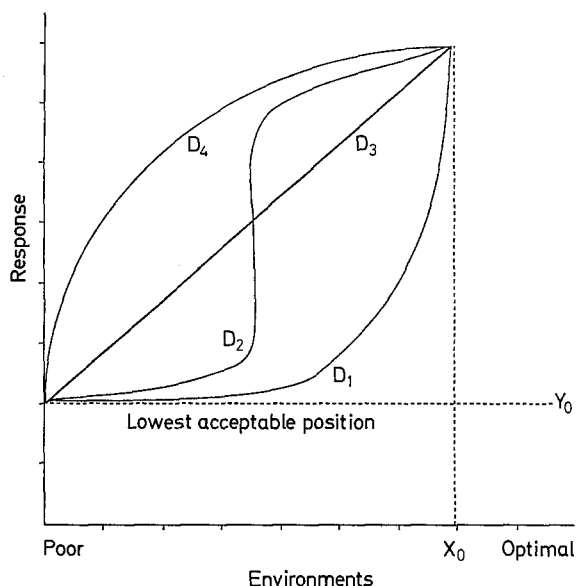


Fig. 2. Types of desirable responses for cultivars

$S_2$  would also rate high in stability under these measures. However,  $S_2$  would be much preferred to  $S_1$  from a grower's viewpoint and needs.

$S_3$  is a cultivar that responds poorly to poor environments but responds in a linear fashion to increasing environmental indices up to some point  $X_0$ . After  $X_0$ , the  $S_3$  response tends to change with  $X$  in curvilinear manner and reaches some asymptotic level. The high slope and high variance of  $S_3$  would make it an "unstable" cultivar under current definitions found in the literature. In good environments,  $S_3$  would be superior to  $S_2$  from a grower's point of view and if only good environments were to be considered,  $S_3$  would be the selected cultivar. Likewise, if poor environments were encountered infrequently,  $S_3$  might still be selected over the "stable" cultivar  $S_2$ . This would depend upon whether or not the grower could afford to have the low yields of  $S_3$  in poor environments on an infrequent basis.

The  $S_4$  type of response would be the desirable one for most growers.  $S_4$  gives relatively high yields in poor environments and is able to take advantage of increasingly optimal environments. Although this cultivar response would have a relatively high slope and variance and would be classified as unstable, it would be the desired response that many growers would want. This is in agreement with Verma et al. (1978) and Pooni and Jinks (1980), who suggest a segmented regression approach rather than the sigmoid response curve given in Fig. 1.

There are various types of responses of the form given by  $S_4$ . Some of these are given in Fig. 2. It is assumed that to have a desirable form of response there is some minimum level of response at poor conditions that can be tolerated, i.e.,  $Y_0$ . This level for subsistence farmers would be the minimum yield required for the family's

survival. All acceptable cultivars must be above this level in all environments to be encountered. Response type  $D_1$  would be for a cultivar that only responds well to quite good environments. Response  $D_2$  is similar to  $S_3$  in Fig. 1. Cultivars with response  $D_3$  respond in a linear manner to increasing environmental indices up to some point  $X_0$ . Cultivars which respond to increasingly optimal conditions very quickly and then level off are of type  $D_4$ . This type of response would certainly be desired over all the other types of responses if the goal were to maximize yields over all environments. Cultivars having the  $D_2$  response would be those having a type of threshold value of the environment before they could take advantage of a more favorable environment. For each cross, a breeder could evaluate the various kinds of responses to determine which of the responses,  $D_1$  to  $D_4$ , are encountered, how frequently, and from what type of parents.

#### *A parsimonious statistical design*

The present situation for evaluating stability, genotype by environment interaction, and cultivars for a target region is to conduct experiments at a number of locations (sites) and over a period of years. The cost of finding sites, travel, food, and lodging can make such types of experiments expensive. Obtaining a large number of sites, say 100, could be prohibitively costly. An alternative is to "select" sites that contain the range of conditions to be encountered by growers in the target region. Although this may appear reasonable, probably only the apparently obvious conditions could be selected. This may also be a costly procedure. It should be realized that whatever "sample" of sites is selected, there is the possibility that only a very small range of environments will be encountered. Hence, any regression curves based on this limited range of environments would be unreliable and could even be misleading. Another point to consider is that for some cultivars, plant material in the early stages may be very limited, e.g., sugarcane; because of the lack of plant material, an experiment at several sites may be impossible.

The question is, can these problems be resolved? The answer is definitely in the affirmative. To do this we suggest the following. Select factors that are the major causes of environmental differences such as, for example:

Category 1	Category 2
Water (rainfall) level	Soil type
Fertilizer level	Elevation or altitude
Biological planting and harvesting dates	Temperature
Disease and insect level	Type of farming
Weed level	
Crop density	
Spatial arrangement	
Drought periods	
Soil salt	

1 Whole plot							
Poor conditions	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	xxx	xxx	xxx	xxx	xxx	xxx	xxx
	Optimal conditions	xxx	xxx	xxx	xxx	xxx	xxx

Fig. 3. Experimental units with a range of environments in each speu

Density	Planting date		
	Early	Optimal	Late
Low	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
	x	x	x
Dense	x	x	x

Fig. 4. Experimental unit for one cultivar and varying density and planting date

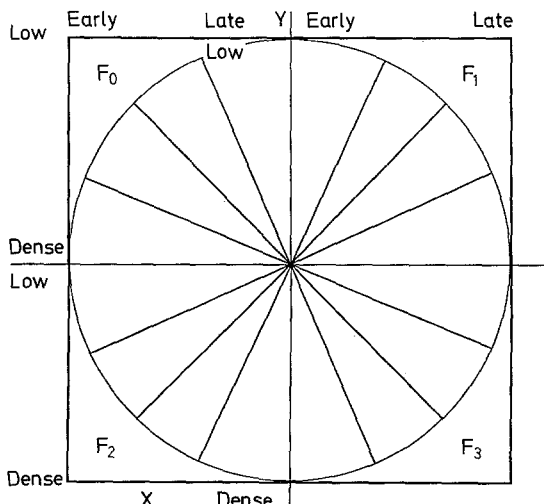


Fig. 5. Experimental units for the three variables: density, time of planting, and four fertilizer levels (F<sub>0</sub>, ..., F<sub>3</sub>)

The factors in category 1 could be varied from low to high within a single experimental unit (a cultivar or treatment), while the factors in category 2 would have to be whole plots at selected sites. Some factors in category 1, e.g., disease and insect level, may need to be set up as whole plots. For those factors which can be varied within a single experimental unit some such arrangement as in Fig. 3 might be used for a whole plot. Note that whole plots need not be adjacent but could be in different parts of a field or even in different fields. Also, there could be replication within a whole plot, e.g., elevations.

A particular whole plot is given in Fig. 3 for *v* cultivars as the split plots. The split plot experimental units, speus, should be long and narrow and should be arranged such that competition between them is eliminated. This can be done by increasing the distance between speus and increasing plant density within speus. This technique can be used to keep density per hectare constant while eliminating competition.

As depicted in Fig. 3, within each split plot the factor(s) to be varied, e.g., water plus fertilizer, would be varied from insufficient water plus fertilizer to optimal water plus fertilizer. This would be done for each split plot in the same manner. The split plots should be as alike as possible. The range of levels of the varied factor(s) should exceed any that would be encountered by a grower of the crop. Providing a wide range of conditions improves the response function estimates. Note that the entire range of environments would be included in each speu and that this should be wider than what would be encountered by selecting a "sample" of sites.

To incorporate conditions for two factors, or two sets of factors, in a split plot experimental unit, the two factors could be varied as in the experimental unit depicted in Fig. 4. Here plant density is varied from low to high and planting date from early to late. Data taken on individual plants or on individual subunits may be used to fit a response function of yields against known levels of the two factors varied. Combining the ideas of Fig. 4 with those of Mead and Riley (1981, Fig. 5), it may be possible to add another variable like spatial arrangement to Fig. 4. Other schemes are possible, and the type will depend upon the variables, the goals, and the creativity of the experimenter.

If a third factor is introduced, then a plan like Fig. 5 might be appropriate. The four rectangles could be a plan as in Fig. 4, and the different rectangles could be four levels of another variable. Also, instead of a rectangle, a Nelder (1962)-type fan could be placed in each of the four quadrants of a circle as pictured in Fig. 5. Fertilizer level and date of planting could be the two variables for each quadrant. Then, the different quadrants could be different amounts of moisture applied. Alternatively, two variables, as in Fig. 4, could form the experimental unit; then for two or more other variables, a factorial arrangement

(or a fractional replicate) could be used on the experimental units. These would be randomized as usual. If it were desired to study factors individually some sort of split-split plot, split-split-split plot, and/or split-block arrangements would be appropriate.

Various experiment designs may be used. As an example, suppose that slope of land and elevation were two variables that needed consideration in evaluating treatment response for the area in question. Suppose further that planting dates of early, optimal, and late needed to be included and also that water and fertilizer levels were to be varied as in Fig. 4. Then for the  $v$  treatments or genotypes under consideration, the slope types and elevations, either in a fractional or complete factorial, would form the whole plots. Replication of the whole plots may or may not be done. Also, replication of split-plot treatments within each whole plot may or may not be used. The split-split plot treatments would appear in each split plot and each whole plot, and when only one replicate of the whole experiment design was used, components of interaction sums of squares would be used to form an experimental error mean square. If replication of the whole plots were desired, this could be accomplished by using sites and/or years as blocks.

The measurements would be made by either splitting each *speu* into  $n$  subunits or measuring the plants continuously through the *speu*. This would depend upon the method of varying the factor(s) through the *speu*. For each *speu*, a response function would be fitted to the data. The particular regression function fitted would be arbitrary until sufficient data have been collected to ascertain the types of response functions encountered in practice. These could then be used as the response functions. From the data presented by Verma et al. (1978), it would appear that a simple quadratic regression equation,

$$Y_i = \text{response } i = \alpha + \beta X_i + \gamma X_i^2, \quad (1)$$

would suffice in many situations. This is form  $D_1$  and  $D_4$  in Fig. 2. Such a regression equation can only be regarded as an approximation to the true response function. For some situations, the approximation may recover all of the needed information. Note that for responses of type  $D_2$  and  $S_3$ , the approximation would be inappropriate and would not recover the information contained therein.

In lieu of information of the exact nature of cultivar responses to changing environments, it is suggested that the above quadratic regression equation be used as a first approximation. Then, a desirable or acceptable cultivar in Fig. 2 would have the following characteristics:

- 1) The intercept  $\alpha$  would be at or preferably above the minimum acceptable level  $Y_0$ ;
- 2) The linear regression slope  $\beta$  should be positive and a maximum; and

- 3) The quadratic coefficient  $\gamma$  should be as large as possible negatively (response  $D_4$ ). Even positive  $\hat{\gamma}$ 's ( $D_1$ ) may be accepted depending upon the material and goals.

Thus, for each *speu*, an estimated intercept  $\hat{\alpha}$ , estimated slope  $\hat{\beta}$ , and an estimated, quadratic regression coefficient  $\hat{\gamma}$  would be obtained. These would be the measurements to use in selecting cultivars either for parents in a breeding program or for growers.

The statistical design given above (1) minimizes cost, material, and other resources; (2) covers a known range of environments; (3) allows the interpretation of responses over known conditions; (4) assures that a range of environments is present in the experiment; (5) achieves the height of parsimony; (6) is usable for a variety of investigations; and (7) requires the investigator to define "environments". With respect to the next to the last item above, cultivars can be evaluated for yield, quality, tolerance, usefulness as an intercrop, or a variety of other characteristics.

For intercropping investigations, the density, arrangement, and intimacy could be varied through the *speu*. This would be in line with the parsimonious layouts suggested by Nelder (1962), B. N. Okigbo (1978, personal communication), and Mead and Riley (1981) for the investigation of density and spatial arrangements. The Nelder fan design and the Okigbo circle design (see Fig. 5) have proven useful for studying wide ranges of such factors as plant density, plant spacing, orientation, and row spacing for a variety of crops.

### Breeding procedures

In searching for desirable genotypes, breeders commonly evaluate a quantitative trait based on a genotype mean derived from experimental units in different blocks, sites, and years. Those genotypes with the highest means are selected as parents for future crosses and/or are advanced through a breeding program and ultimately developed into cultivars. A high mean, however, does not imply low genotype by environmental interaction (i.e., stability in one sense) for any specified trait. In order to obtain a genotype with the desired form of response (Figs. 1 and 2), an estimated response function for a genotype over a set of environments is characterized by a set of estimates of parameters of the response function. With the parsimonious experiment design (PED) described earlier, an estimated response function for yield or any other quantitative trait to changing environments may be obtained. In lieu of knowing the exact form of a response function, it may be approximated using quadratic regression with the set of estimated parameters for the intercept ( $\alpha$ ), slope ( $\beta$ ), and curvature ( $\gamma$ ). Genotypes may be evaluated and se-

lected for a single component trait such as  $\alpha$ , which may be used to define a minimum desired level of response, or for a combination of all three components or parameters,  $\alpha$ ,  $\beta$ , and  $\gamma$ .

When selection is for all three parameters of the response function, not only the minimum desired value but also the shape of the response curve are considered. Additionally, selection may be practiced on the parameters for more than one quantitative trait. For example, breeders of oats (*Avena sativa* L.) may need to select for the desired form of response of yield to changing environments as well as for a minimum groat (cover on seed next to kernel) level ( $\alpha$ ). In sugarcane (*Saccharum officinarum* L.), breeders may need to select for the desired response function for both yield of sugarcane and percentage of sucrose. This would require selection for two sets of parameters  $\alpha$ ,  $\beta$ , and  $\gamma$  to meet the desired standard.

Any manipulation for a desired response function implies the existence of genetic variability and observable phenotype differences. Oat breeders have been concerned with the genetics of stability, as defined in the literature, and have attempted to estimate heritabilities/repeatabilities of different stability parameters. Fatunla and Frey (1976) estimated the standard unit heritability of the Finlay and Wilkinson (1963) stability parameter for the yield of nine oat populations. They obtained values ranging from  $-0.35$  to  $0.64$  and concluded that the measure of stability was not very heritable. Later, Eagles and Frey (1977) evaluated the genetic basis of Shukla's (1972) stability parameter for the yield of grain and straw in oats. They found heritabilities ranging from  $0.78$  to  $0.85$ , and  $0.81$  to  $0.86$  for the mean yield of grain and straw, respectively. The repeatabilities of stability ranged from  $0.06$  to  $0.12$  for grain and  $0.01$  to  $0.30$  for straw. They concluded that selection for the stability of straw yield was feasible, but not for grain yield. In cowpeas [*Vigna unguiculata* (L.) Walp.], Ntare and Aken'Ova (1985) computed Eberhart and Russell's (1966) stability parameter for a set of  $F_3$ s and their  $F_5$  derived lines and bulks. The correlation between the stability parameters of related  $F_3$  and  $F_5$  lines was  $0.60$ , while the correlation between related  $F_3$  and  $F_5$  bulks was poor. Ntare and Aken'Ova (1985) did not estimate a heritability for stability, but given the genetic covariance between  $F_3$  and  $F_5$  lines, and a correlation of  $0.60$ , an estimate is clearly possible. These investigations on oats and cowpeas suggest that stability has a genetic base upon which selection can be practiced.

Given this genetic base, a suitable selection technique is required. Because a desired response function may be partitioned into a set of component parts, a multiple trait selection method is needed. The three common methods include: tandem selection, independent culling levels, the selection index, or a modification/combination of these (Falconer 1981). With tandem selection only one parameter trait is selected in a particular generation, and mini-

um levels of trait expression, or truncation points, are preset for each trait in each generation. In the case of  $\alpha$ , the minimum level would be set at  $Y_0$  (Fig. 2), and selection would be applied only for  $\alpha$ . Likewise, truncation points are set for  $\beta$  and  $\gamma$  and selection applied in different generations for each. Independent culling levels require selection for all parameter traits in each generation of selection. Truncation points are set for each trait so that a group of genotypes can be identified as potential parents or breeding materials and subsequently advanced to the next cycle of selection. The independent culling levels approach is probably the easiest and quickest way to identify suitable lines, assuming no genetic relationships among the parameter traits.

The third method, the selection index, is a more elegant procedure because it allows greater control of the shape of the desired response form. However, it requires the estimation of the genetic parameters (heritability and genetic correlation) associated with the three parameter traits and the assignment of economic values to each. Each individual or family line is defined by an index value such that

$$I_j = b_1 \alpha_j + b_2 \beta_j + b_3 \gamma_j \quad (2)$$

where  $I_j$  is the index value of each genotype  $j$ ;  $b_1, b_2, b_3$  are the weights appropriate for each trait; and  $\alpha_j, \beta_j$ , and  $\gamma_j$  are the measured phenotypic means for the intercept, linear, and curvilinear components of a response curve, respectively, for each genotype  $j$ .

The estimated genetic worth, or true value ( $T_j$ ) of each genotype is defined as

$$T_j = e_\alpha G_{\alpha j} + e_\beta G_{\beta j} + e_\gamma G_{\gamma j} \quad (3)$$

where  $e_\alpha, e_\beta$ , and  $e_\gamma$  are the economic values assigned to each of the parameter traits, and  $G_{\alpha j}, G_{\beta j}$ , and  $G_{\gamma j}$  are the unobserved genotypic values for each parameter trait ( $\alpha, \beta, \gamma$ ) based on a given level of gene action.

When  $T$  is equated to  $I$ , the selection index equations given by Henderson (1963) are such that

$$Pb = Ge \quad (4)$$

where  $P$  is a symmetric matrix of phenotypic variances ( $V$ ) and covariances ( $C$ ) among the parameter traits ( $\alpha, \beta, \gamma$ );  $b$  is the vector of unknown weights;  $G$  is a symmetric matrix of genetic variances ( $V_g$ ) and genetic covariances ( $C_g$ ) among the parameter traits; and  $e$  is the vector of economic values assigned to each trait. The matrices appropriate for this example are

$$\begin{bmatrix} V_\alpha & C_{\alpha\beta} & C_{\alpha\gamma} \\ & V_\beta & C_{\beta\gamma} \\ \text{sym} & & V_\gamma \end{bmatrix} \cdot \begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} = \begin{bmatrix} V_{g\alpha} & C_{g\alpha\beta} & C_{g\alpha\gamma} \\ & V_{g\beta} & C_{g\beta\gamma} \\ \text{sym} & & V_{g\gamma} \end{bmatrix} \cdot \begin{bmatrix} e_\alpha \\ e_\beta \\ e_\gamma \end{bmatrix}$$

$$P \quad b \quad = \quad G \quad e$$

Thus,  $\mathbf{b} = \mathbf{P}^{-1} \mathbf{G}_e$  and the  $b_j$ s are substituted back into Eq. 2, and each genotype  $j$  is assigned an index value and ranked (Van Vleck 1979).

The parsimonious experiment design is used to estimate the parameters of a response curve for each genotype. An augmented experiment design with the experimental units as in Figs. 3, 4, or 5 may be used to parsimoniously screen genotypes (Federer 1961; Federer and Raghavarao 1975; Federer et al. 1975). The assignment of economic weights ( $e$  values) to these traits is a difficult task and requires a knowledge of the species. In some environments, a minimum yield is the most important aspect of the response curve, and users of the selection index may denote the economic value of  $e_\alpha$  as 1, while  $e_\beta$  and  $e_\gamma$  are set at 0. In this situation, the breeder may need to initially employ tandem selection or independent culling levels to insure a minimum yield level at  $Y_0$  (Fig. 2). In another set of circumstances, minimum yield may not be a problem, but rather the inability of genotypes to improve with improving environments. This would require greater emphasis on the  $\beta$  and  $\gamma$  parameters in Eq. 2 and that emphasis would be reflected in higher values of  $e_\beta$  and  $e_\gamma$  relative to the other  $e$  values. Generally, the selection index provides greater control in the selection for the shape of desired response curve (Fig. 2), allows for the correction of undesirable correlations among the parameter traits, and theoretically provides the greatest gain from selection. Restricted selection indices can also be used to preset desired gains in a given parameter trait (Baker 1986, and included references).

Regardless of the selection technique, gain from selection is a function of the heritability, selection intensity and of the additive genetic relationships of the individuals or families in a breeding program. The choice of a breeding method can affect the estimate of an additive genetic relationship, but this is largely controlled by an organism's reproductive biology. Because the genotype must be grown across an environmental gradient, a large number of related individuals are recommended in order to achieve an accurate evaluation and selection. Breeders should attempt to minimize intra-family variation by increasing the relatedness of individuals within a family and to maximize inter-family variation to improve the probability of finding stable families. This is not to suggest that highly heterogeneous populations are unstable across environments. Clearly, the opposite is true. However, individual genotypes within a given population can vary in their forms of response to changing environments. The purpose of breeding for stability or for a desired form of response is to identify genotypes with the characteristics. These may then be combined (bulked) into heterogeneous populations as a multi-line or open-pollinated cultivar. The ideal situation is found in clonally propagated crops. A family line can be derived from a single plant while variation among lines can be maximized. In self-

pollinated crops, potential parents should be pure lines. If land races are included, pure line selection may be required to reduce intra-line variation. Subsequent to the selection and hybridization of parents, certain breeding procedures would be more desirable than others. As for other characteristics, single seed descent (Brim 1966) is probably the best for selecting for stability in self-pollinated crops because families are not derived and selected until  $F_7$  and  $F_8$ . At this stage the families are composed of virtually identical individuals. The mass selection method is the least desirable because intra-family variation is maintained at a high level. The standard pedigree and bulk methods (Allard 1960) would fall somewhere in between. The pedigree method is perhaps more desirable than the bulk method because individual plant selections in the early generations could be focused on parameter traits other than stability (in the sense of Lin et al. 1986). In later generations when family selection is practiced, stability response would be included as a criterion. In standard bulk breeding, intra-bulk variation is maintained at a high-level until late in the program. Ntare and Aken'Ova (1985) found the use of bulks to be less precise for the identification of stability in early generations. Among the cross-pollinated crops, non-segregating hybrids are clearly the best, while mass-selected open-pollinated cultivars would be hard to evaluate. Generally, it can be speculated that the genotypic methods such as the half-sib, full-sib,  $S_1$ , and  $S_2$  progeny methods are better than the phenotypic methods.

A breeding scheme could be outlined as follows:

- 1) redefine stability as finding a response curve with few parameters and having the desired form;
- 2) evaluate potential parents in the parsimonious experiment design (PED);
- 3) estimate the genetic parameters of the individual parameters of the curve when using a selection index (this is not necessary for tandem selection or independent culling levels);
- 4) identify, select, and inter-mate parents based on a multiple trait selection criteria;
- 5) evaluate progeny with the desired breeding method;
- 6) select those families with the desired stability response; and
- 7) repeat the process if recurrent selection is being practiced.

## Discussion

A statistical design and breeding procedure as described above can greatly accelerate the progress of a program whose goal is to minimize risks for a grower under poor conditions and yet have a cultivar that takes advantage of increasingly more optimal conditions for increased yields. The suggested procedure is feasible and efficient

from a cost and other resource viewpoint. It makes possible what is impossible under some present thinking and presently used procedures and is an extension of other procedures now in use.

The area selected for the experiment using a PED should be such that levels of factors are added rather than subtracted. Thus a non-fertile, arid, insect-free, and disease-free area would be ideal for a PED. Such areas are found in many parts of the world. Changes in length of drought periods could easily be made when selecting for sorghum-like drought period tolerance for a crop.

To vary insect and disease populations within one speu may require creativity on the part of the investigator. If diseases and insects spread uniformly throughout the season, a disease and/or insect source could be put at one end of the speus in Fig. 3. Plants closest to the source would be most heavily infected, while those most distance would be least infected. If this cannot be done then the level of disease and/or insects may have to be a whole plot treatment, perhaps even in different fields.

As noted above, many types of characteristics could be used. For example, lodging, fiber content, protein level, tolerance, etc. could be used as a basis for comparing cultivars using the statistical design described above. Such as goal suggests use of a selection index. Farming systems involving levels of factors could be evaluated in intercropping research in much the same manner.

It has been suggested that a response curve with a set of parameters be used. As an alternative, an experimenter may wish simply to find the area under the response curve obtained for an experimental unit. These areas would then serve as the data points for a statistical analysis. Also, the minimum and maximum values obtained, as well as their differences, may be used as the data values in lieu of fitting a quadratic or other regression equation. Computer programs may be written to obtain these statistics from the original data if desired.

A number of abiotic stress investigations have successfully determined genotypic responses across an imposed environmental gradient. In rice (*Oryza sativa* L.), IRRI (1979, 1980, 1981) screened 750 genotypes for cold tolerance using an experimental unit of the form in Fig. 3. Cold water (17°C) was pumped into the field, and temperatures slowly increased to ambient (27°C) as water flowed across the paddy. Genotypes with the ability to tolerate cold were easily distinguished by plant height, tiller number, spikelet fertility, and other morphological traits. In Nigeria, upland rice genotypes were tested for drought tolerance using this same basic design (B.N. Okigbo, 1978, personal communication). In drought research, the line source sprinkler system designed by Hanks et al. (1976) is ideally suited for the selection and breeding procedure presented above. In California, Epstein and collaborators (Epstein and Norlyn 1977; Kingsbury and Epstein 1984; Kelly et al. 1979; Norlyn and

Epstein 1982; Richards et al. 1982) have evaluated the salt tolerance of small grains (barley, triticale, and wheat) and tomatoes (*Lycopersicon esculentum* L.). Using sites with natural salinity gradients, as in Fig. 3, they evaluated genotypes to determine their adaptability to stress. Genotypes were compared and judged by response curve similar to those of Figs. 1 and 2 (Jones and Qualset 1984). Salt tolerance of barley (*Hordeum vulgare* L.) was also evaluated by irrigating genotypes with proportions of sea and fresh water. Genotypes were evaluated for yield and biomass.

In most of these examples, estimates of the response curve parameters were not computed. However, each investigator was keenly aware of the response function of each genotype or the genotype by environment interaction. From these investigations, it appears that a form of the parsimonious design is an integral part of most abiotic stress research. We urge that a response curve methodology be incorporated into these evaluations. Selection could then be applied not only for a threshold level, but also for a particular form of desired response.

## Conclusion

The present concept of stability as described in the literature should be discarded and replaced by the use of a response curve over a known range of conditions. It would appear inappropriate to denote the cultivars that gave responses in Fig. 2 as "stable". A name for these responses was not found except to denote them as desired responses, curves, or functions. The concept of stability as found in the literature does not appear to be useful in a breeding program for maximizing returns. Cultivars meeting the present criteria of low variance and low linear slope would not meet the criteria in Fig. 2 and the criterion suggested by Verma et al. (1978) and Pooni and Jinks (1980). In fact, the most "stable" genotype is one which yields zero in every environment!

This parsimonious design has the advantage of flexibility and is an inexpensive method for determining a response to changing environments, selecting parents, and evaluating progeny. It further describes a genotype's response not just as a single value, but rather as a set of component traits based on fitting a regression equation to the data. These component traits can then be selected and manipulated to meet the requirements of the environment and cropping system using a selection index approach.

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