

# The Relation between Hybrid Vigour and Genotype-Environment Interactions

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**Summary.** Consideration was given to the response curves and response surfaces that are obtained when genotypes are grown at various levels of environmental factors. These curves and surfaces were used to illustrate genotype-environment interactions and possible relations between two parents and their  $F_1$ .

When a hybrid had a response exactly intermediate between its parents, the metric values for the hybrid were not intermediate but varied with the environment, exhibiting different degrees of dominance including overdominance (hybrid vigour). A range in dominance for the metric also was found when the response of the hybrid was more similar to one parent than the other.

A hybrid with an intermediate response has a lower phenotypic variance across environments than the mean variance of its parents. In some situations the hybrid's variance is less than that of either parent.

A component of the error variation for a genotype was shown to vary with the environment having a minimal value when the environment was optimal.

An algebraic treatment of response curves and surfaces was presented. In some instances the metric values for two parents and their  $F_1$  in a range of environments may be related in the form of a multiple regression.

## 1. Introduction

Despite the many studies undertaken on hybrid vigour (heterosis), its occurrence is difficult to predict and few generalisations about the phenomenon can be made. In this paper possible reasons for varying results on heterosis will be suggested using as a basis for discussion observed genotype-environment interactions.

Genotype-environment interactions are evident when a ranking of genotypes differs between environments. Attempts have been made to extend the theory of quantitative genetics to account for such interactions across several environments (Haldane 1947, Lewis 1954, Mather and Morley Jones 1958). More recently, interactions in continuous range of environments have been analysed on the supposition that the interactions may be treated as linear functions of the environments (Bucio Alanis 1966; Bucio Alanis and Hill 1966; Perkins and Jinks 1968a, b). For reasons given previously (Knight 1970) it is believed that the treatment of interactions in this way is inappropriate in many instances.

In the past, hypotheses in quantitative genetics have endeavoured to account for hybrid performance using the mid-parent metric value as a base from which to measure the various generations. For instance, dominance or potence is measured as the departure of the  $F_1$  value from the mid-parental value. Attempts are then made to relate the yields of the parents,  $F_1$ , backcross and other generations on an additive scale and transformations may be used in an endeavour to achieve additivity (Mather 1949, Mather and Jinks 1971).

In the present study genotype-environment interactions will be considered in the form of response curves or response surface functions. Consideration will be given to simple genetic situations involving these response functions, in the belief that they are more fundamental than genetic considerations of yield or other metrics which are manifestations of the response. It will be shown that this may result in very different expectations of the metric yield values of  $F_1$ 's and other generations. The transformations that are used often to achieve additivity also will be questioned.

The following discussion is considered relevant to characters such as yield, height, body weight or grain number that are polygenically inherited but the term yield will be used throughout.

## 2. Response Curves and Response Surfaces

When individuals of a genotype are grown under different levels of an environmental factor that affects their growth, their yield response usually shows a continuous curvilinear relation with the environment (Fig. 1). The curve has a steep slope when the level of the environmental factor is low but at higher levels the slope decreases until an optimum is reached and maximum yields are obtained. Subsequently the response curve may have a negative slope at super-optimal levels of the environment. If only a small part of the environmental range was assayed the response might appear linear but a basic assumption in this paper is that the response is curvilinear.

Fig. 1 represents a response to one environmental factor, such as nitrogen when other factors are held

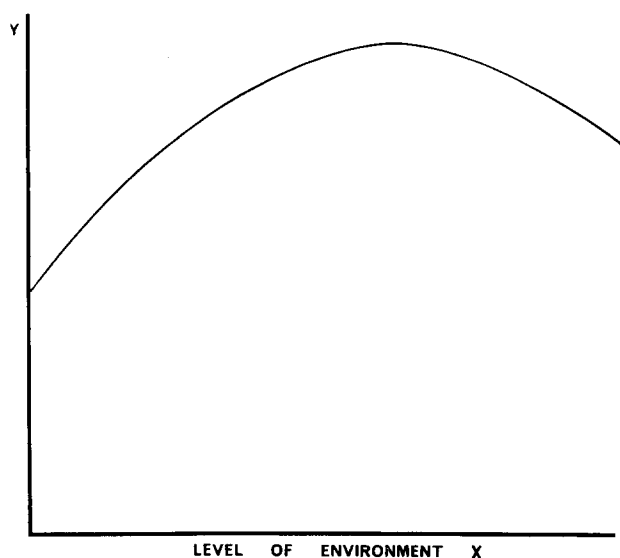


Fig. 1. The response curve obtained from growing individuals of a genotype at various levels of an environmental factor

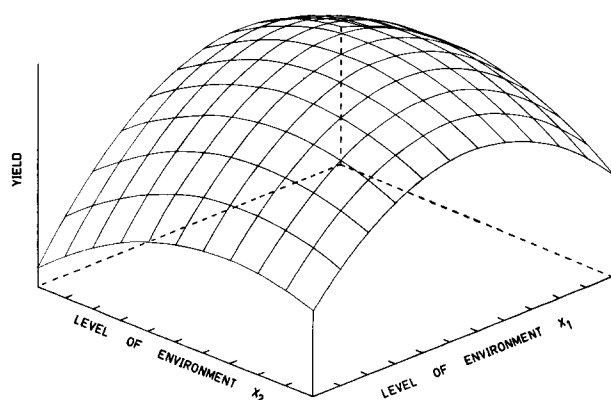


Fig. 2. The response surface for individuals of a genotype grown at various combinations of environmental levels  $x_1$  and  $x_2$

constant. If another effective factor is also varied the response may change and different slopes and optima be obtained. This is illustrated by a response surface (Fig. 2) in which the surface is formed from the many individual response curves. In this three-dimensional diagram the  $x_1$  and  $x_2$  axes are levels of the environmental factors such as nitrogen and phosphorus, and  $y$  is the yield axis. Here the optimal level for  $x_1$  differs with different levels of  $x_2$ .

An alternative presentation of  $x_1$ ,  $x_2$  and  $y$  is in the form of a contour map (Fig. 3) where the contours are equal values of  $y$ . The contours are sometimes referred to as isoquants (Munson and Doll 1959). Examples of response surfaces may be found in the literature (e.g. Goodall *et al.* 1955, Munson and Doll 1959, Heady and Dillon 1961, Hackett 1966, Dillon 1968).

When three environmental factors  $x_1$ ,  $x_2$  and  $x_3$  are varied the response may be depicted also by a three dimensional diagram (Box 1954). The general form

of the response may be visualised if the isoquant diagram Fig. 3 is rotated about a line, normal to either axis and passing through the optimum. The result is an ellipsoid or egg-shaped body whose centre represents the highest yield and optimal levels of the three environmental factors. Successive strata moving outwards from the centre are isoquants of yield. Responses involving three or more factors will not be considered in great detail in this paper.

With our existing knowledge of the growth of organisms it is not possible to formulate equations for response curves and surfaces based on fundamental principles, and the equations are largely empirical. Some are based on the concept of diminishing returns which suggests that there is an upper limit to yield which is achieved at an optimum level of an environmental factor essential for growth. Below the optimum, the level of the factor is inadequate for a full expression of yield whereas above the optimum the factor is in excess and harmful to yield. In either instance, yield is proportionately decreased with departure from the optimum.

A mathematical treatment of the response function was first considered by Mitscherlich (1909, 1928) but there have been several others (reviewed by Heady and Dillon 1961). Functions often used to depict curves and surfaces respectively are

$$y = b_0 + b_1 x - b_{11} x^2 \quad (1)$$

$$y = b_0 + b_1 x_1 + b_2 x_2 - b_{11} x_1^2 - b_{22} x_2^2 + b_{12} x_1 x_2 \quad (2)$$

where  $y$  is the yield response,  $x$  the level of one environmental factor,  $x_1$ ,  $x_2$  the levels of two environmental factors, and the coefficients  $b_0$ ,  $b_1$ ,  $b_2$ ,  $b_{11}$ ,  $b_{22}$  and  $b_{12}$  are constants for any one genotype.

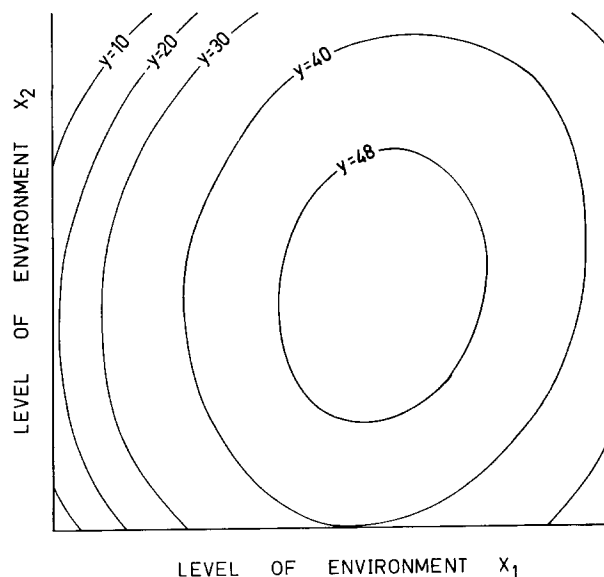


Fig. 3. The same response as in Fig. 2 but represented as an isoquant diagram. Note that the isoquants are closer with distance from the optimum

These functions will be used in the following analyses, however it is believed that similar conclusions would be drawn if other appropriate functions were used.

### 3. Genotypic Differences in Response Curves and Surfaces

Studies on genotypes and their hybrids when grown at various levels of an environmental factor have suggested that within a species there may be different response curves, with optima at different levels of the environment, different yields at the optima, and differences in the range over which the genotypes will grow (Griffing and Langridge 1963). These differences probably reflect the environments under which the genotypes have evolved (Antonovics *et al.* 1967, Knight 1970). Unfortunately, no examples are known to the author in which two parents and their hybrid have been grown at a sufficient number of levels of two environmental factors to derive the three respective response surfaces. However sufficient is known of the response surface of individual genotypes to conjecture on breeding situations involving two parents and a hybrid.

In the following discussion it is accepted that it is more logical for the hybrid to have a response intermediate between its parents than to have a yield that is intermediate. The point will be amplified later.

The hypothetical situation illustrated in Fig. 4 will be discussed. Two parents have similar response surfaces but reach optima at different levels of  $x_2$ . The simplest situation to interpret would be one in which the  $F_1$  hybrid had its optimum between its parents and had a similar shaped response surface. Sections through the response surfaces are presented for one environmental value of  $x_1$  (Fig. 5a) and for five values of  $x_2$  (Fig. 5b, c, d, e, f).

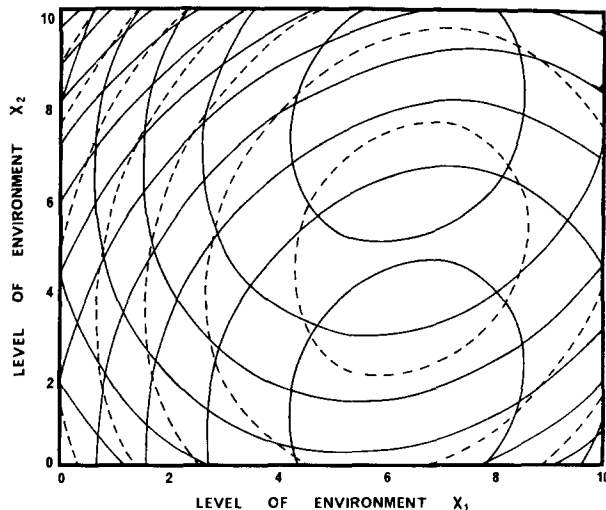


Fig. 4. Isoquants for parents  $P_1$  and  $P_2$  (solid lines) and their  $F_1$  (dotted lines). The  $F_1$  is intermediate between  $P_1$  and  $P_2$  which reach optima at low and high levels of  $x_2$  respectively

In 5a, although the  $F_1$  had a response exactly intermediate between its parents, its yields are not intermediate they exceed the mid parent at all environmental levels of  $x_2$  and at some levels it also exceeds both parents. An algebraic proof is given later. Only this one section needs to be presented for levels of  $x_1$ ; at other levels, although the yield values may be higher or lower, their relationships are similar and the same conclusions would be drawn. The response curves Fig. 5b, c, d, e, f, are a sample of the continuous range of curves that show the changing relation between the  $F_1$ ,  $P_1$  and  $P_2$  at different levels of  $x_2$ . When  $x_2 = 1.0$  (Fig. 5b)  $P_1$  has the highest yield and the  $F_1$  is intermediate whereas when  $x_2 = 8.0$  (Fig. 5f),  $P_2$  has the highest yield and the  $F_1$  is again intermediate. At the other levels (Fig. 5c, d and e), the  $F_1$  exceeds both parents at low levels of  $x_1$ , at all levels, and at high levels respectively.

All these contrasting yield results are possible therefore from a single relation between the response surface of a hybrid and its two parents and with the simplest possible genetic relation; and  $F_1$  response exactly intermediate between its parents. With more complex genetic situations many different yield relations can be visualised.

One would occur if the  $F_1$  response had an optimum closer to  $P_2$  than  $P_1$ . Now a section for an environmental level of  $x_1$  would be, as in Fig. 6. The  $F_1$  yields show successively negative dominance, no dominance, overdominance and positive dominance. Such a situation illustrates difficulties in the concept of genetic "dominance" or "potence" in quantitative inheritance. As the  $F_1$  response is similar to one of its parents it might be considered an example of dominance, however if the classical definition of dominance is accepted as a deviation from the mid-parental value in terms of yield, then dominance must vary in magnitude and sign with the environment.

The effect on response curves for levels of  $x_2$  when the  $F_1$  optimum is closer to one parent than the other need not be elaborated. Its effect is to alter the relative yield values presented in Fig. 5b–5f without changing the general conclusions.

The great majority of the observed results on parents and their  $F_1$ 's have been encompassed in the above discussion and more complex relations will not be illustrated now. They include instances where the parents have optima differing in both  $x_1$  and  $x_2$ , where the yields are different at the optima, and where  $F_1$  had its optimum outside the range of its parents.

### 4. Algebraic analysis

The first situation to be considered is the one depicted in Fig. 6 in which the parental response curves are of the same form, but  $P_2$  is displaced from  $P_1$  (Fig. 7). The equation for a response curve intermediate be-

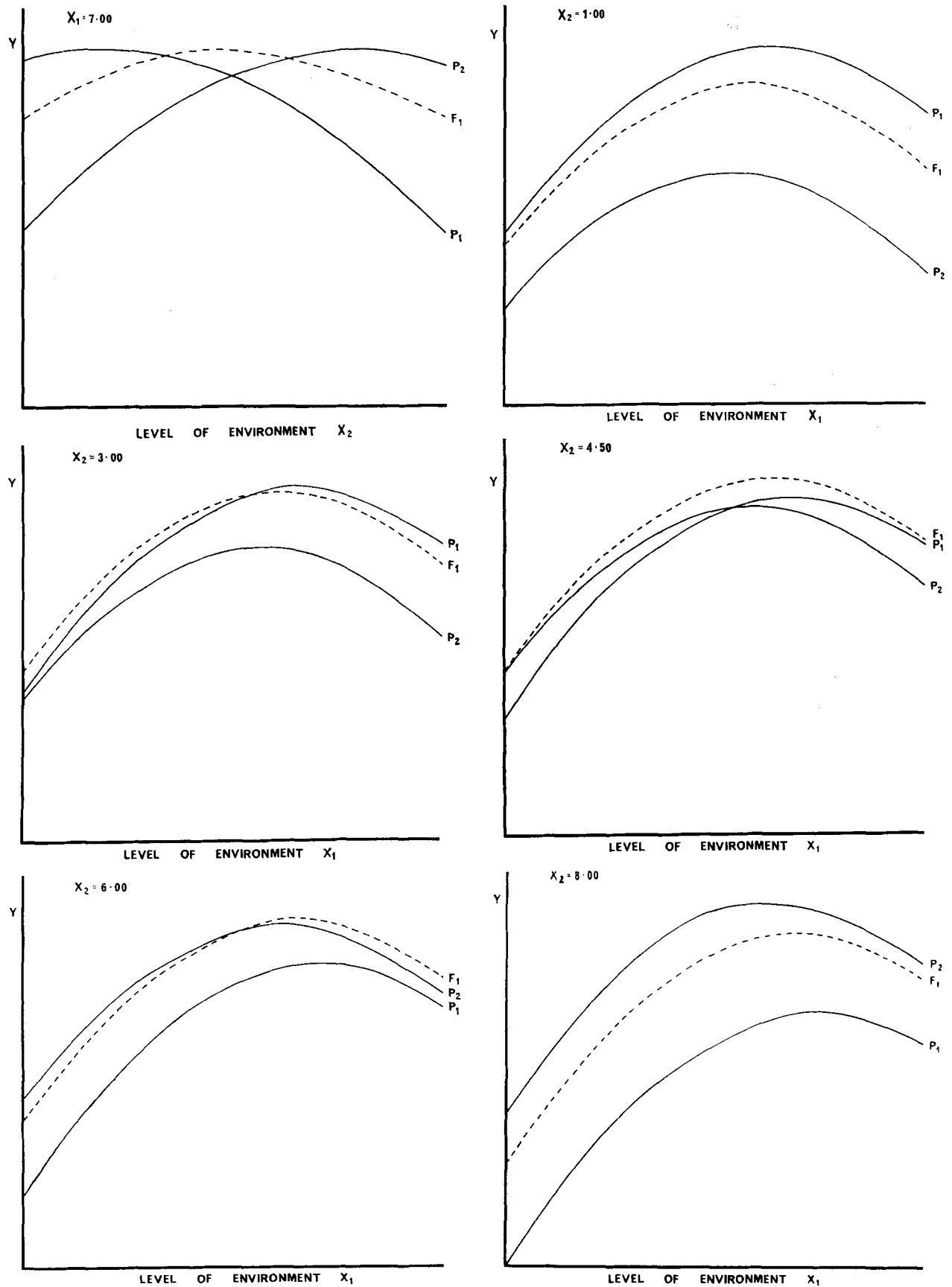


Fig. 5. a. A section through the response surfaces of Fig. 4 at the environmental level  $x_1 = 7.00$   
 b-f. Sections through the response surfaces of Fig. 4 at the environmental levels of  $x_2 = 1.00, 3.00, 4.50, 6.00,$  and  $8.00$

tween the parents, and equations for  $P_1$ ,  $P_2$  and  $F_1$  are

$$I = b_0 + b_1 x - b_{11} x^2$$

$$P_1 = b_0 + b_1 (x + a) - b_{11} (x + a)^2 \quad (3)$$

$$P_2 = b_0 + b_1 (x - a) - b_{11} (x - a)^2 \quad (4)$$

$$F_1 = b_0 + b_1 (x + fa) - b_{11} (x + fa)^2 \quad (5)$$

Where  $I$ ,  $P_1$ ,  $P_2$  and  $F_1$  are the respective yields,  $a$  and  $-a$  are the deviation, in terms of  $x$ , of the  $P_1$  and  $P_2$  responses from the intermediate response, and  $f$  is some function of this deviation shown by the  $F_1$  hybrid. It is possible to eliminate  $x$  algebraically from equations (3), (4) and (5) to give

$$F_1 = b_{11} a^2 (1 - f^2) + P_1 \frac{(1+f)}{2} + P_2 \frac{(1-f)}{2} \quad (6)$$

Thus it is possible to express the relation between the yield of the  $F_1$  and its two parents in the form of a multiple regression without direct reference to the environmental level ( $x$ ). The right hand side of this multiple regression equation may be considered as consisting of a constant  $b_0$  and two regression coefficients  $b_1$  and  $b_2$  pertaining to the respective parents.

It is of interest to consider various values of  $f$ . When the  $F_1$  is intermediate between the parents  $f$  will be zero and equation (6) becomes

$$F_1 = b_{11} a^2 + \frac{(P_1 + P_2)}{2}$$

Therefore when the  $F_1$  has a response exactly intermediate between its parents its yield exceeds the mid-parental yield at all levels of the environment by the constant amount  $b_{11} a^2$ .

When the  $F_1$  is more similar to one parent than the other in its response then  $f$  will have a positive or negative value between 0 and 1. For example if it more nearly resembles  $P_1$ , then  $f$  may have the value  $+0.5$  and equation 6 becomes

$$F_1 = b_{11} a^2 (0.75) + 0.75 P_1 + 0.25 P_2$$

The yield of the  $F_1$  will vary in different environments relative to  $P_1$  and  $P_2$ . When  $P_1$  has a low or high yield value the  $F_1$  will also tend to be low or high yielding.

A further aspect is evident if equation 6 is written as

$$F_1 - \frac{(P_1 + P_2)}{2} = b_{11} a^2 (1 - f^2) + f \frac{(P_1 - P_2)}{2}$$

This shows that the deviations from the mid parent will have their largest values when  $P_1 - P_2$  is large. That is, the deviation from the mid parent will be large in sub and superoptimal environments, so called stress environments and the deviation will be small in optimal, high yielding environments.

The occurrence of hybrid vigour may also be postulated for certain environmental and genetic situations. The  $F_1$  will exceed both parents when  $P_1 - P_2 \leq \leq 2 b_{11} a^2 (1 - f)$  that is, it will tend to occur in

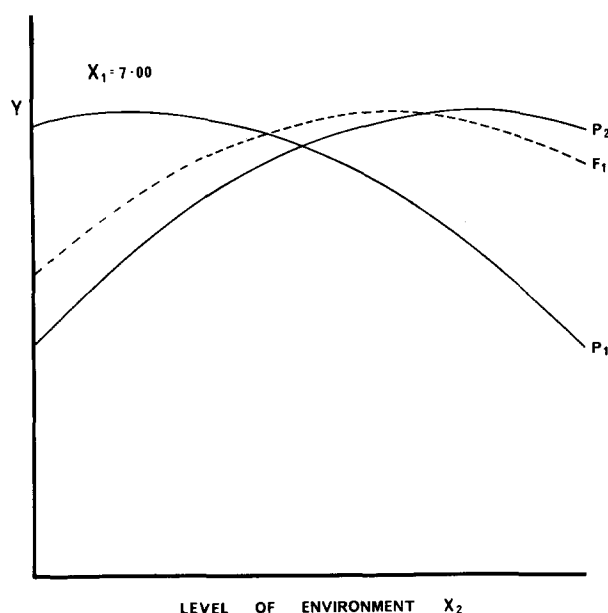


Fig. 6. A section through the response surfaces when the  $F_1$  surface is not intermediate but is closer to  $F_2$

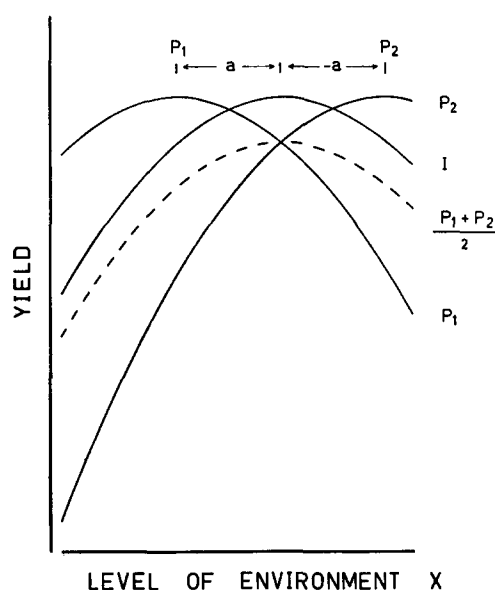


Fig. 7. Diagrammatic representation of models used in algebraic analysis

environments where the difference between the parents is small, when  $b_{11}$  has a large value (an attribute of the curves), when  $a$  the phase separation between the curves is large, and when  $f$  is small and the hybrid response curve approaches intermediacy between its parents.

When the environmental factors  $x_1$ ,  $x_2$ , are influencing the response as in Fig. 4, and the surfaces are of the same form but are displaced relative to each other, the equations for a response intermediate between the parents and for  $P_1$ ,  $P_2$  and the  $F_1$  are

respectively

$$I = b_0 + b_1 x_1 + b_2 x_2 - b_{11} x_1^2 - b_{22} x_2^2 + b_{12} x_1 x_2,$$

$$P_1 = b_0 + b_1 (x_1 + a_1) + b_2 (x_2 + a_2) - b_{11} (x_1 + a_1)^2 - b_{22} (x_2 + a_2)^2 + b_{12} (x_1 + a_1) (x_2 + a_2), \quad (7)$$

$$P_2 = b_0 + b_1 (x_1 - a_1) + b_2 (x_2 - a_2) - b_{11} (x_1 - a_1)^2 - b_{22} (x_2 - a_2)^2 + b_{12} (x_1 - a_1) (x_2 - a_2), \quad (8)$$

$$F_1 = b_0 + b_1 (x_1 + f_1 a_1) + b_2 (x_2 + f_2 a_2) - b_{11} (x_1 + f_1 a_1)^2 - b_{22} (x_2 + f_2 a_2)^2 + b_{12} (x_1 + f_1 a_1) (x_2 + f_2 a_2) \quad (9)$$

where  $I$ ,  $P_1$ ,  $P_2$  and  $F_1$  are the respective yields,  $a_1$  and  $-a_1$  are the displacements in terms of  $x_1$ , and  $a_2$  and  $-a_2$  are displacements in terms of  $x_2$ , of the  $P_1$  and  $P_2$  responses from the intermediate response, and  $f_1$  and  $f_2$  are functions of this deviation shown by the  $F_1$  hybrid. The functions  $f_1$  and  $f_2$  again indicate if the  $F_1$  response is more similar to one parent than the other.

It is possible to express the relation between the  $F_1$  and its two parents in the form of a multiple regression without reference to  $x_1$  or  $x_2$  only if  $f_1 = f_2$ . The regression is then

$$F_1 = (b_{11} a_1^2 + b_{22} a_2^2 - b_{12} a_1 a_2) (1 - f^2) + P_1 \frac{(1+f)}{2} + P_2 \frac{(1-f)}{2} \quad (10)$$

where  $f = f_1 = f_2$ . From this equation it is evident that when the  $F_1$  response is intermediate between its parents so that  $f_1 = f_2 = 0$ , the  $F_1$  yield will again differ from the mid-parental yield value by a constant amount.

When the functions  $f_1$  and  $f_2$  are not equal there is no relation between the parents and the  $F_1$  which can be expressed irrespective of the environment in which they were assessed.

With more than two environmental factors the relation between the  $F_1$  and its two parents can be expressed in the form of a multiple regression if the  $f$  values for each environmental factor are equal and if the other assumptions adopted above also hold. These assumptions are that the response for different genotypes has a similar shape about the optimum and that the difference between genotypes is expressed in their relative displacement in space. In the absence of experimental evidence it is not known to what extent these assumptions hold.

### 5. Phenotypic Stability

Phenotypic stability is a term used for the variation in means over a range of environments or for variation within single environments. The latter is an 'error' variance calculated from the differences between yields of individual plants supposedly in the same environment. Both types of variation will be considered.

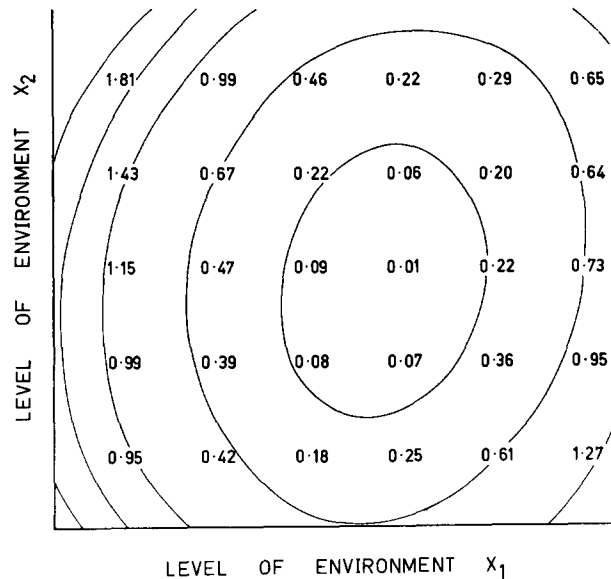


Fig. 8. The surface and isoquants depicted in Fig. 3 with superimposed, at points on the surface, values for a component of the 'error' variance in  $y$ , arising from minor variations in availability of  $x_1$  and  $x_2$

The variation across environments was calculated for each response curve and surface. In the special instance where the surface has circular isoquants or elliptical isoquants normal to the axes (i.e. when the  $b_{12}$  coefficient in equation 2 is zero) the variation is the same for each response curve that makes up the surface and the phenotypic stability of the parents and their  $F_1$  would be identical. The curves have different minimal and maximal values but their ranges are equal. If the isoquants are not of this nature and the coefficient  $b_{12}$  has some value then the variance of an  $F_1$  response curve making up the surface is always less than the mean variance of its parents and may be less than the variance of both parents as in Fig. 5 a.

When the variances of response surfaces are calculated it is found that the variance of a surface increases curvilinearly with displacement of its optimum from a central position in the range of environments. It follows that, if an  $F_1$  surface lies between its parents, then its variance must always be less than the mean variance of its two parents and may be less than the variance of both parents.

An error variation within a single environment is caused by developmental accidents, measuring inaccuracies, and from minor differences in availability of environmental factors such as  $x_1$  and  $x_2$  to the individual plants.

An estimate of the latter component was obtained for the response surface in Fig. 3. For each of a sample of coordinates such as  $(x_1, x_2)$  25 closely surrounding coordinates were considered and the variance of the corresponding yield values ( $y$ ) calculated. The results are in Fig. 8. They show that this error com-

ponent is greatest on the steep slopes of the response surface where minor variations in  $x_1$  and  $x_2$  result in large differences in the yields and it has least value when  $x_1$  and  $x_2$  are optimal.

In experiments where response curves only are obtained and not the surface, it follows that the error component is larger at sub and superoptimal values than at the optimum and also that there will be differences between individual response curves in their error values.

As two genotypes may have surfaces displaced relative to each other, the slopes of the response surface will be different at the same yield value for the respective genotypes. One genotype will then have an error variation greater than another although their mean yields are identical.

The above results represent only one component of the error variation. If the other components are random and are large, the total error will not show differences of the same proportion. In addition error variation tends to increase with the mean as a consequence of the multiplicative nature of growth and this may also reduce the differences.

## 6. Discussion

It is necessary to highlight the conclusions that have arisen as a result of considering genotype-environment interactions as response functions.

### *Average Dominance or Potence*

The present study revealed difficulties in the interpretation of average dominance or potency. When the  $F_1$  was precisely intermediate between its parents in its response, its yield values varied between negative, positive and overdominance depending on the environment. When the  $F_1$  had a response more similar to one parent than another thus exhibiting "dominance" in its response, its yield values again showed a range from negative to overdominance depending on the environment.

If previous analyses were followed, for the situation depicted in Fig. 4 and the mid-parental yield values were calculated, a surface would be produced similar and intermediate between the parents but overall with lower yields. The optimum for the hybrid would be at a lower yield value than for either parent. In addition these approaches provide no *a priori* reasoning to suggest under what environmental conditions the  $F_1$  would depart from the mid-parental value.

### *Scales and Transformations*

It was accepted here that the phenotypic expression over environments is curvilinear and that genotypes have overlapping response curves depending on the natural selection under which they have evolved. It follows that no simple transformation will lead to additivity and will eliminate the interactions demonstrated by different genotypes. If a very limited

range of environments is studied these interactions may appear linear and be eliminated by transformation but this will not be a common result. There are many examples in which no scale was found that would provide additivity (Smith 1952, Mather and Vines 1952, Powers 1950, Lewis 1954).

Neither can it be expected that the scale change will lead to homogeneity in the error variation, although such homogeneity is required in genetic analyses dependent on least square procedures in tests of significance. From the present results it would be concluded that a component of the error variation would be expected to vary with different genotypes and environments and to attempt to make the errors uniform by transformation of the data may be concealing useful information about the response. A lack of homogeneity of the error variation even among apparently homozygous parents has been noted (Williams and Gilbert 1960). In addition Griffing and Langridge (1963) and Gustafsson and Dormling (1972) found that the error was minimal in an optimal environment and increased in sub and super optimal environments. It is pertinent that both these studies were conducted in controlled environments where other components of the error variation would be expected to be minimal.

### *Phenotypic Stability*

(Variation in mean value over a range of environments.) From a consideration of response curves and surfaces it was found that the  $F_1$  may frequently show a greater phenotypic stability than the mean stability of its parents. This comes about merely as a result of the mathematical relations implicit in response surfaces. It is separate from any possibility that heterozygotes are more stable than homozygotes as a result of intra or inter-allelic gene action.

Other matters relevant to quantitative genetics also arise. Reference was made previously to the ellipsoid shape of the response if three environmental factors are varied. Genotypes differing in their optima will occupy different positions in space and their strata will be interwoven. In the simplest genetic situation the  $F_1$  would have an optimum in space midway between its parents. An elaboration to more than three factors cannot be depicted graphically but the concept of optimal levels for each factor and a position in multidimensional space where maximum yields are obtained can be imagined. In such a complex situation it will be necessary to resolve the genetics of single crosses before attempting to interrelate many crosses. In this context it seems unlikely that diallel analyses that seek to estimate a parameter for a common parent (e.g. a general combining ability effect) will provide a clear picture of the genetic situation. The mathematical function relating  $P_1$ ,  $P_2$  and their  $F_1$ , and  $P_1$ ,  $P_3$  and their  $F_1$  are unlikely to provide similar effects for  $P_1$ , when  $P_2$  and  $P_3$  occupy different positions in space.

An additional shortcoming of many diallel estimates is that they are made in a single environment that is at one point only in the multidimensional space of possible environments.

An experiment that was conducted to assess single hybrid combinations, revealed that the parameter for a parent varied markedly with the parent with which it was crossed (Knight 1971). It is noteworthy that the multiple regression function referred to in the present algebraic analysis was used in this experiment and that it accounted for a very high proportion of the variation found in the hybrid.

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