# GENE-ENVIRONMENT INTERACTION :

## A RELATIONSHIP BETWEEN DOMINANCE, HETEROSIS, PHENOTYPIC STABILITY AND VARIABILITY

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## 1. GENE ACTION

DARLINGTON and Mather (1949) have classified gene action and interaction in four types :—direct, successive, cooperative and competitive. It is essential for the present study to add duplicate or parallel gene action, in which a particular phenotype is the outcome of two or more genes or alleles working towards the same end but by slightly different synthetic routes.

Enough examples of duplicate major genes are known in higher plants and animals and in micro-organisms to show that they are both widespread and frequent. Duplicate gene action implies that parallel, and therefore alternative, pathways are available between the successive steps from gene to character. Such alternative pathways may be determined either by allelomorphs or by different loci. Which pathway is in operation under a particular set of conditions will depend upon which allele or gene is dominant or epistatic under these conditions. Each gene will have its optimum set of conditions which comprise three components : (*a*) Genetic background (genic environment) ; (*b*) Stage of development (cytoplasmic environment), and (*c*) External conditions (external environment).

The present study is concerned with the effects of the cytoplasmic and external environment on average dominance as it affects a polygenic character and how this in turn affects the stability in external form of an organism.

## 2. THEORETICAL PRINCIPLES

### (*a*) *Homozygotes*

The present attempt to analyse theoretically interactions arising between two pure lines, their $F_1$ and two different environments follows the more manageable analysis of the possible interactions with two genetically different populations in two environments made by Haldane (1947). But to keep the analysis within bounds only some of the extreme possibilities have been selected.

Let us consider a pair of alleles : **A**1, **A**2 affecting a measurable character such as height or flower number in plants or wing length in *Drosophila*. Let us assume that both alleles are positively promoting the expression of the character and that in some environments **A**2

produces twice the effect of $A_1$. We can ascribe character values to individuals such that $A_1A_1 = 1$ and $A_2A_2 = 2$. Furthermore let us assume two environments L.E. and H.E. Consider for simplicity the two extreme environmental effects which might be manifested according to the genotype observed: (1) L.E. and H.E. have the same effect and (2) H.E. produces a phenotype twice as large as that produced by L.E. All intermediate interactions, which are probably the most common, can be ignored without any serious effect on the general conclusions.

When reduced to these artificial but manageable proportions there are four basic situations between the two homozygotes and the two environments (table 1).

TABLE 1

*Basic extreme situations for two homozygotes in two environments. The environmental difference is assumed to have either no effect or a two-fold effect*

I

| | $A_{1.1}$ | $A_{2.2}$ |
|---|---|---|
| L.E. | 1 | 2 |
| H.E. | 2 | 4 |

II

| | $A_{1.1}$ | $A_{2.2}$ |
|---|---|---|
| L.E. | 1 | 1 |
| H.E. | 1 | 2 |

III

| | $A_{1.1}$ | $A_{2.2}$ |
|---|---|---|
| L.E. | 1 | 2 |
| H.E. | 2 | 2 |

IV

| | $A_{1.1}$ | $A_{2.2}$ |
|---|---|---|
| L.E. | 1 | 1 |
| H.E. | 1 | 1 |

In situation I, H.E. has twice the effect of L.E. with both homozygotes; in II the difference is shown only with $A_{2.2}$; in III with $A_{1.1}$ and in IV with neither of the homozygotes. The effect of the genotype is apparent in both environments in situation I, in only one environment in situation II and III, and not observable at all in situation IV.

We can for convenience call L.E. the *low-expression* and H.E. the *high-expression environment*: and since the extent of the environmental effect on the phenotype is one of the main aspects to be considered we must introduce the concept of *phenotypic stability*. This can be defined as the ability of an individual or population to produce a certain narrow range of phenotypes in different environments. It is similar to the concept of *homeostasis* (*cf.* Dobzhansky and Wallace, 1953). A convenient measure of phenotypic stability is the *stability factor*, which can be expressed as :—S.F. $= \frac{\bar{x}\ \text{H.E.}}{\bar{x}\ \text{L.E.}}$ where $\bar{x}$ is the

mean character value. This factor can be applied to : (1) between similar parts of the same individual, (2) to means of similar parts in different samples, (3) means of populations. The maximum phenotypic stability is attained when S.F. = 1, for then the phenotype is unaffected by the environment ; the greater S.F. deviates from unity the less stable is the phenotype.

### (*b*) *Heterozygotes—Dominance*

If there is no dominance of A1 or A2 then the heterozygote has an intermediate value between the two homozygotes in both L.E. and H.E., and we have in situation I the following relationships :—

| Gen. / Env. | A1.1 | A1.2 | A2.2 |
|---|---|---|---|
| L.E. | 1 | 1·5 | 2 |
| H.E. | 2 | 3 | 4 |
| S.F. | 2 | 2 | 2 |

In this example the heterozygote has the same stability factor as the two homozygotes. We are now able to consider the heterozygotes in the four basic homozygotic situations.

If we exclude superdominance, there are nine possible relationships of the heterozygote to the homozygotes : these are shown for situation I in table 2. They have been arranged in columns and rows according to the dominance relationships : the stability factors for heterozygotes given at the base and right side are means for each of the three basic dominance variants which are given at the top and left-hand side of the table.

It should be noted that the stability factor of both parents is 2·0 in situation I and therefore any hybrid with an S.F. below 2 is more stable than its parents and one with S.F. greater than 2 is more variable. The stability factors for the heterozygotes in the nine variants (*a-i*) in the four basic situations (I-IV) are summarised in table 3. The S.F.'s for situation I are taken from table 2 and those for the other situations have been derived in a similar way to those of situation I.

By comparing the hybrid S.F.'s with the mean parental values in table 3 it will be seen that certain generalisations about the interactions can be made.

1. A heterozygote which is more stable than the parental homozygotes is obtained when the gene which is dominant in a particular environment has an effect opposite to that of the environment, *e.g.*

small>large in the high expression environment and large>small in low expression environment.

2. A less stable heterozygote is obtained when the gene which is dominant in a particular environment has an effect which is similar to that of the environment, *e.g.* small>large in the low expression environment and large>small in the high expression environment.

TABLE 2

*The nine possible dominance relationships with the two environments L.E. and H.E. in situation I, in which both homozygotes are affected similarly by the environments. The stability factors (S.F.) are means of the three variants in each column and row*

| Dominance ⟶ / A1..A2 in L.E. | A1....A2 in H.E. | A1>A2 in H.E. | A2>A1 in H.E. | |
|---|---|---|---|---|
| | (a) A1.1 A1.2 A2.2 | (b) A1.1 A1.2 A2.2 | (c) A1.1 A1.2 A2.2 | |
| L.E. | 1 1·5 2 | 1 1·5 2 | 1 1·5 2 | 2·0 |
| H.E. | 2 3 4 | 2 2 4 | 2 4 4 | |
| | (d) | (e) | (f) | |
| A1>A2 in L.E. L.E. | 1 1 2 | 1 1 2 | 1 1 2 | 3·0 |
| H.E. | 2 3 4 | 2 2 4 | 2 4 4 | |
| | (g) | (h) | (i) | |
| A2>A1 in L.E. L.E. | 1 2 2 | 1 2 2 | 1 2 2 | 1·5 |
| H.E. | 2 3 4 | 2 2 4 | 2 4 4 | |
| | 2·0 | 1·3 | 2·6 ← S.F. | |

Note that to get a more stable hybrid the gene which is dominant in a particular environment must have an effect opposite to that of the environment. *E.g.* when small>large in high expression environment S.F. = 1·3 : and when large>small in low expression environment S.F. = 1·5. (All S.F.'s for homozygotes = 2·0.)

A1..A2 = no dominance. A1>A2 = A1 = dominant to A2.

3. In general, complete lack of dominance under all conditions tends to have no differential effect on the stability of the heterozygote as compared with the homozygotes.

### (c) *Superdominance—Heterosis*

It is now left to consider single-locus heterosis or *superdominance*. We must distinguish positive heterosis in which the heterozygotic

phenotypic value is greater than either the homozygotic parental values, and negative heterosis when the heterozygotic value is less than that of the homozygotes. Positive heterosis is exhibited as :—

| $A_{1.1}$ | $A_{1.2}$ | $A_{2.2}$ |
|---|---|---|
| 1 | 3 | 2 |

in L.E. and as

| $A_{1.1}$ | $A_{1.2}$ | $A_{2.2}$ |
|---|---|---|
| 2 | 6 | 4 |

in H.E. The corresponding heterozygotic values with negative heterosis are 0·75 in L.E. and 1·5 in H.E. The effect of positive and negative heterosis on the stability factors is given in table 4.

TABLE 3

*The stability factors obtained in the four basic situations. There are six stability factors for each situation obtained in the same way as shown in table 2. Double squares denote an S.F. lower than the parental mean S.F.*

| | $A_1..A_2$ in H.E. | $A_1>A_2$ in H.E. | $A_2>A_1$ in H.E. | I | II | III | IV | Mean parental S.F. |
|---|---|---|---|---|---|---|---|---|
| | | | | 2·0 | 1·5 | 1·3 | 1·0 | $A_1..A_2$ in L.E. |
| | | | | 3·0 | 1·5 | 2·0 | 1·0 | $A_1>A_2$ in L.E. |
| | | | | 1·5 | 1·5 | 1·0 | 1·0 | $A_2>A_1$ in L.E. |
| I | 2·0 | 1·3 | 2·6 | 2·0 | | | | |
| II | 1·5 | 1·0 | 2·0 | | 1·5 | | | |
| III | 1·3 | 1·3 | 1·3 | | | 1·5 | | |
| IV | 1·0 | 1·0 | 1·0 | | | | 1·0 | |

The effect is similar but more extreme to that of dominance, and the general conclusions 1 and 2 derived from dominance relationship apply also to *superdominance*.

*Application.*—The theoretical interactions based on a pair of alleles is only the model for the types of interaction with a polygenic system. A similar model has proved its worth in the analysis of other genetic characteristics of polygenic systems by Fisher and Mather. The one gene model can be transferred to a polygenic system by using such terms as " average dominance " or potence instead of dominance.

Examples in the literature of changes in dominance of single major genes by environment are not common—this is partly because of the

lack of suitable experiments to reveal such changes but the examples which are known are of the extreme change as shown in situation I (*f*) in table 2, *i.e.* complete reversal of dominance. Examples are Honing's (1928) light requiring seeds of *Nicotiana* in which light requirement is dominant in young seeds but recessive in old; and in *Drosophila*, infrabar eye is dominant to bar eye at 17° C. but recessive at 25° C. (Hersh, 1934).

Since complete reversal of dominance has been found it can be assumed that the less drastic changes, which are the basis of the theoretical analysis, occur.

TABLE 4

*The effect of positive and negative heterosis on the stability factors of the heterozygotes. Note that increased stability (when S.F. = 1·0) is obtained when the direction of the heterotic effect is going against the effect of environment*

Positive heterosis

| | A1.1 | A1.2 | A2.2 |
|---|---|---|---|
| L.E. | 1 | 3 | 2 |
| H.E. | 2 | 3 | 4 |
| S.F. | | 1 | |

| | A1.1 | A1.2 | A2.2 |
|---|---|---|---|
| L.E. | 1 | 1·5 | 2 |
| H.E. | 2 | 6 | 4 |
| S.F. | | 4·0 | |

Negative heterosis

| | A1.1 | A1.2 | A2.2 |
|---|---|---|---|
| L.E. | 1 | 0·75 | 2 |
| H.E. | 2 | 3 | 4 |
| S.F. | | 4·0 | |

| | A1.1 | A1.2 | A2.2 |
|---|---|---|---|
| L.E. | 1 | 1·5 | 2 |
| H.E. | 2 | 1·5 | 2 |
| S.F. | | 1·0 | |

## 3. MATERIAL

### (*a*) *Character-varieties*

The polygenic character used for the experiment is the number of flowers per inflorescence in the cultivated tomato, *Lycopersicon esculentum*. It was chosen because environmental effects on the character expression can be easily controlled. All the material came from two varieties, Kondine Red, which of a large number of varieties had the highest number of flowers and Vetomold which had the lowest number. Kondine Red (K.R. in the text) is an old English greenhouse tomato; Vetomold (V.M.) is a disease-resistant variety which had *Lycopersicon pimpinellifolium* in its ancestry, but which shows only slight evidence of its interspecific origin.

### (*b*) *Inbreeding*

Although English tomato varieties are mainly self-pollinated, K.R. and V.M. were found to be heterozygous for some genes controlling flower numbers because a slight response to selection for low and high number was obtained. Inbreeding by self-pollination was practised until selection failed to give a response: this took three generations.

## 4. METHODS

Seeds were sown in John Innes No. 1 compost and germinated at a constant temperature of $30 \pm 1°$ C. in a glass-sided incubator. Seedlings were transferred to pots of No. 2 compost and at the same time placed in different temperatures. The seedlings were kept in these environments until the initials of the first inflorescence were visible : during this period temperature has a profound effect on size of the first two or three inflorescences. The critical period for the different inflorescences and details of the effects of environment have been described by Lewis (1953).

For important experiments the environments during the critical stage were accurately maintained in specially controlled environment rooms in which the light is entirely artificial from 5 ft. 80 watt daylight fluorescent tubes giving an intensity of 1500 ft. candles at plant height and a day length of 14 hours. The temperature was controlled to within 0·5° : the high expression environment was 13° and the low expression environment was 25°.

Less critical experiments had to be done in environments which were to some extent under the influence of the weather. These were a cold frame and warm greenhouse : in some years it was easy to maintain a satisfactory difference in temperature between them but in others, when high outdoor temperatures prevailed, this was not possible. In all experiments inbred material as standards were grown as a measure of comparison between years. After the period in the critical environments the plants were transplanted to the open ground out-of-doors, where observations, selections and pollinations were made.

Both in the critical environments and in the later outdoor plots, the plants were arranged in randomised blocks.

## 5. PLAN OF THE EXPERIMENT

The experiment consisted of two parts :—

1. A comparison between parents $F_1$, $F_2$, 20 $F_3$ families and backcross generations. The 20 $F_3$ families were derived by selfing $F_2$ plants taken at random in 1951. All these were raised in 1952 in eight randomised blocks : each block contained 28 plants of each family divided between 14 plots. The randomised order of the plants in the critical environments was maintained when planting out in the open ground. Four blocks were raised at 13° C. and four at 25° C. The four blocks at each temperature were sown at different times, following each other through the rooms : the 13° treatments were sown at five-weekly intervals and the 25° at four-weekly intervals, and planted out at corresponding periods. This meant that the environments in the rooms were the same for all replicate blocks but the later environments after planting were different between blocks and the consequences of this will be apparent later.

The critical environment in the controlled rooms during the second to the fifth week after sowing affects the size of the first two or three inflorescences but the fourth and fifth inflorescence will be laid down when the plants are outside. Thus the 1st and 2nd inflorescence will have the same treatment in replicate blocks while the 4th and 5th will have different treatments between the blocks owing to the natural changing temperature and light conditions with the advance of the season.

The comparisons that can be made due to environmental and developmental influences are shown in fig. 1.

The comparison L.E. : H.E. which is made *between* individuals, can be calculated only between means of families. The comparisons L.E. : $E_X$ and H.E. : $E_X$, which are made *within* individuals, can be calculated either on individual plants or on the means of the families.

2. The second part of the experiment is the continued selection from the $F_2$

family for high and low numbers under high expression and low expression environments. The two environments for these experiments were provided by the cold frame and heated greenhouse. After some generations of selection, hybrids were made between different lines as a comparison with the original $F_1$ and parents.

## 6. RESULTS OF EXPERIMENTS WITH $P_1$, $P_2$ AND DERIVATIVE GENERATIONS

### *Inflorescence I*

The means of the first inflorescence with their standard errors of the different families in the four blocks of each treatment are given in table 5. The standard errors have been calculated not from between

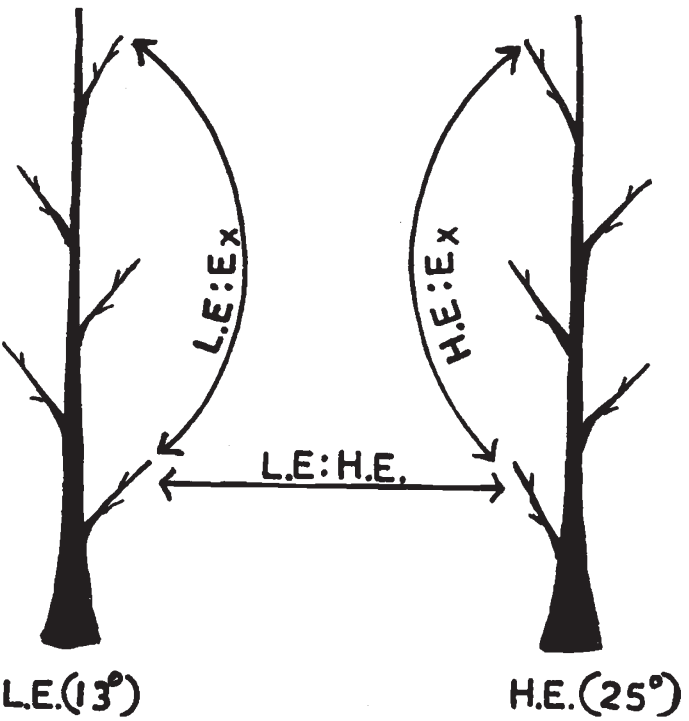


FIG. 1.—Shows the comparisons which can be made between environmental effects. Each plant is allowed to develop five inflorescences, the lower two are formed under the influence of the controlled environments, L.E. and H.E. ; the upper two are formed under the influence of the uncontrolled natural environment, $E_x$.

plots but from between plants by ignoring the subdivision into plots because of the extremely small difference between them.

In general the differences between the blocks are small and not significant, but three significant deviations are found which have technical explanations. Block IV in the H.E. has an abnormally low value for the $P_1$. This was due to the difficulty of counting the flowers in these plants because of their extreme lateness and the bad weather which prevented the younger buds from developing. The same difficulty does not occur with the other

families in this block because the smaller inflorescences finish developing earlier.

Block IV in the L.E. suffers from an abnormally high within family variance in certain families including the $F_1$ which is of major importance in the subsequent analysis. This high variance is reflected in the standard errors given in table 5. Block II in the L.E. has significantly higher mean values for all families. This anomaly was due to a breakdown in temperature control during one day when the temperature rose to 31° C. The result of this rise in temperature was to prevent the formation of the true first inflorescence so that the first on

TABLE 5

*Means of flower numbers in the first inflorescence for parents and derivative generations*

(Abnormal blocks heavily outlined)

| | | Block I | Block II | Block III | Block IV |
|---|---|---|---|---|---|
| H.E. | $P_1$ | 20·68±1·25 | 18·61±1·13 | 18·28±1·09 | 15·29±0·62 |
| | $B_1$ | 14·93±1·17 | 14·61±1·03 | 12·93±0·83 | 14·89±0·91 |
| | $F_1$ | 13·89±0·89 | 13·07±0·61 | 11·43±0·76 | 12·89±0·85 |
| | $F_2$ | 12·28±0·83 | 13·89±0·81 | 13·21±0·94 | 12·19±0·63 |
| | $F_3$ | 12·60±0·56 | 12·46±0·54 | 11·29±0·49 | 11·82±0·51 |
| | $B_2$ | 13·39±0·56 | 12·43±0·55 | 11·50±0·74 | 13·14±0·61 |
| | $P_2$ | 12·28±0·75 | 12·75±0·63 | 11·46±0·65 | 13·96±0·70 |
| L.E. | $P_1$ | 12·43±0·93 | 16·77±2·81 | 11·93±0·73 | 12·85±0·94 |
| | $B_1$ | 11·14±0·75 | 17·82±3·28 | 11·58±0·76 | 10·68±0·63 |
| | $F_1$ | 9·96±0·34 | 14·46±0·76 | 10·67±0·28 | 11·61±0·94 |
| | $F_2$ | 8·46±0·64 | 12·81±1·60 | 9·70±0·95 | 10·89±0·93 |
| | $F_3$ | 8·61±0·39 | 11·99±0·58 | 9·21±0·42 | 8·92±0·40 |
| | $B_2$ | 7·36±0·39 | 9·11±0·65 | 9·29±0·40 | 8·39±0·46 |
| | $P_2$ | 6·96±0·41 | 8·00±0·83 | 6·75±0·33 | 7·61±0·36 |

the plant was produced in the normal position of inflorescence II, *i.e.* above the 12th instead of the 9th leaf. The mean number of flowers in all inflorescences in this block were abnormal due to this displacement.

In all the subsequent analyses on the first inflorescences these three abnormal blocks have been discarded, thus making three blocks in the H.E. and two in the L.E. treatments. It is not legitimate to combine the data of the later inflorescence from different blocks because these inflorescences were laid down under the outdoor conditions. The combined data for inflorescence I are given in fig. 2.

It can be seen that the temperature treatments have an effect on all families but more so on the parents than on the $F_1$ and $F_2$ generations. The dominance of the genes is also changed by the temperature. The small size of the $P_2$ being almost completely dominant in the low temperature as shown by the great disparity between the $F_1$ mean and the Mid parent (M). At the high temperature dominance is absent. This is therefore an example of the theoretical situation I*b* (*cf.* table 2).

Attempts have been made to find the best scale for the data in order to remove interactions (*cf.* Mather, 1949) and hence facilitate the analysis. This has not proved satisfactory because of the different interactions with the different environments. The untransformed data of the L.E. fit the expected values in the scaling tests, while the H.E. shows some significant deviations which are not removed by logarithmic scaling. Thus it is clear that no one scale will fit all the data as was found in *Nicotiana* by Mather and Vines (1952) and in *Lycopersicon* by Powers (1950). Therefore all the analysis has been on untransformed figures.

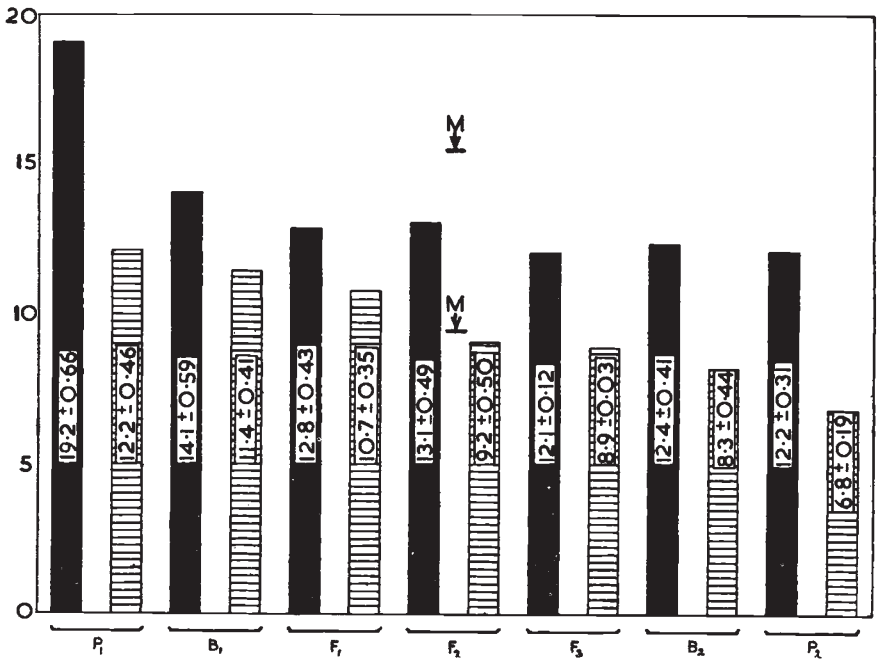


FIG. 2.—Means and standard errors for the two parents and derivative generations raised in different environments :

H.E. (13°). L.E. (25°). M = mid parent value.

Note the almost complete dominance of $P_2$ in the H.E. and the intermediate value of the $F_1$ in the L.E.

To show the reaction of the different families to the two environments the stability factors S.F. $= \left(\frac{\text{mean in H.E.}}{\text{mean in L.E.}}\right)$ have been plotted in fig. 3. The $F_1$ is the least affected by the environments, the two pure line parents the most affected while the other families have intermediate values. It is possible to calculate expected values for these families by assuming that heterozygotes will have the $F_1$ value and the homozygotes will have a value similar to their parents and that there are no interactions.

Thus the expected values are calculated as follows :—

$$B_1 = \frac{P_1+F_1}{2} \quad F_2 = \frac{P_1+P_2+2F_1}{4} \quad F_3 = \frac{P_1+P_2+2F_1+4F_2}{8}$$

$$B_2 = \frac{P_2+F_1}{2}$$

The values compared with observed figures show reasonable agreement as follows

| | $B_1$ | $F_2$ | $F_3$ | $B_2$ |
|---|---|---|---|---|
| Observed . . | 1·23 | 1·42 | 1·35 | 1·49 |
| Expected . . | 1·38 | 1·43 | 1·42 | 1·49 |

The $B_1$ differs by 0·15 from the expected, this is another confirmation of the dominance of the genes from the $P_2$ as shown in fig. 2.

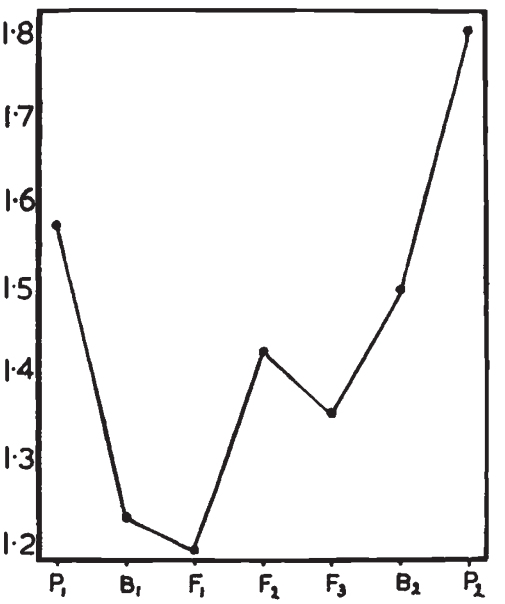


FIG. 3.—Stability factors $\left(\frac{\text{mean in H.E.}}{\text{mean in L.E.}}\right)$ for parents and derivative generations : note the greater stability of the $F_1$ generation.

*Inflorescences I-V*

Of the four randomised blocks only the plants in the first block could be scored for all five inflorescences. The means of the flower numbers for each inflorescence for the two parents, the $F_1$ and back-cross generations are plotted in fig. 4.

It is evident from this figure that the early temperature treatments (L.E. and H.E.) have effects on the first two inflorescences only.

Between the second and third inflorescences there is a switch over so that the treatment producing the highest number in the first and second inflorescences later gives the lowest numbers. There is also a tendency in all families and treatments to have larger inflorescences

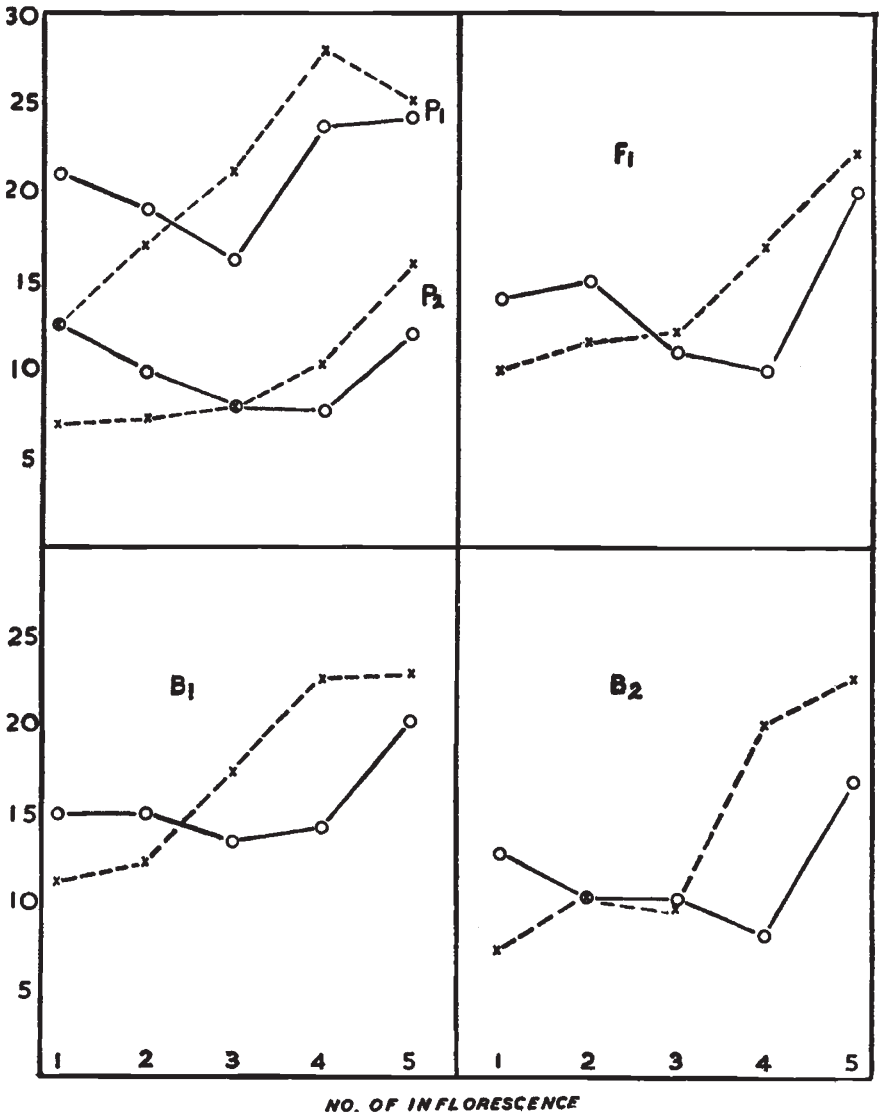


FIG. 4.—Mean number of flowers plotted for the five inflorescences in parents, $F_1$ and backcross generations (data from block I). Note that the effects of the two treatments switch over between the 2nd and 3rd inflorescence : ——— H.E., - - - - - L.E.

in the fifth position. Finally by comparing the parental curves with the $F_1$ it will be seen that the dominance is changed from the first to the fifth inflorescence. In the L.E. lack of dominance in the first is changed to a high degree of dominance of $P_1$ in the fifth, while in

the H.E. dominance of $P_2$ is completely reversed to dominance of $P_1$ in the fifth inflorescence.

We have seen that the different temperature treatments also changed the dominance as measured by inflorescence I. These dominance relationships will be discussed later.

## 7. SELECTED LINES

In 1949 selections were begun on $F_2$ families between the K.R. and V.M. pure lines. Single plants which were self-pollinated were

TABLE 6

*Mean flower number of 1st inflorescence for selected $F_6$ lines and their hybrids in two environments—note the negative heterosis in hybrids 3 and 4 expressed only in the H.E.*

| | Parents | | $F_6$ selections | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | K.R. | V.M. | *1 | 2 | *3 | 4 | *5 | *6 | *7 | *8 |
| H.E. | 33·5 | 12·7 | 42·5 | 13·2 | 49·6 | 13·5 | 43·7 | 47·9 | 38·8 | 43·8 |
| L.E. | 9·7 | 6·3 | 11·1 | 6·4 | 12·3 | 7·0 | 12·7 | 11·7 | 11·3 | 11·9 |
| | Hybrids | | 1 | | 2 | | 3 | | 4 | |
| H.E. | | | 20·7 | | 23·3 | | 30·5 | | 25·7 | |
| L.E. | | | 8·7 | | 8·4 | | 12·3 | | 12·0 | |
| | | | Stability factors | | | | | | | |
| S.F. | Parental mean | | 2·9 | | 2·9 | | 3·6 | | 3·9 | |
| | $F_1$ | | 2·3 | | 2·7 | | 2·4 | | 2·1 | |

* High-selection lines.

selected for high and low flower number and in two different environments. These selections have progressed to the $F_6$ generation, and with the method of selfing adopted all the lines became fixed at either the fourth or fifth generation. The details of the results do not warrant publication here but the values obtained with the selected lines and the results of crosses between them are relevant to the subject of this report and are given in table 6.

It should be pointed out that these selected lines were not raised in controlled environment rooms as were the plants in the main experiment. They were raised in a hot greenhouse for the L.E. and in a cool frame for the H.E. The difference in effects of these two environments was greater than that between the corresponding treatments with the main experiment but a comparative check was provided by including the two pure line parents.

It is apparent from table 6 that all the high selections (1, 3, 5, 6, 7 and 8) have many more flowers in the H.E. than the highest parent ; while in the L.E. they have only slightly higher values. The two low selections (2 and 4) on the other hand have values which are the same as those of the low parent.

The two hybrids (3 and 4) between two high lines show that in the L.E. all the parents and the $F_1$'s appear to be identical but in the H.E. the $F_1$'s have values which are much lower than either of their parents. Thus although the lines must have different genes, these are only in operation in the H.E.

These two examples of negative heterosis shown only at the H.E. are another manifestation of the dominance of the small parent which is expressed only in this environment as shown in fig. 2. As with the main experiment the $F_1$ plants are less affected by the two environments than their parents. This is shown by the S.F. values. The theoretical model of this type of heterosis-environment interaction has been considered in table 4.

## 8. EFFECT OF UNCONTROLLED ENVIRONMENTAL DIFFERENCES

Despite the fact that the environment during the sensitive period for flower production was controlled, there were very considerable differences between individual plants within the pure lines and the $F_1$'s which could not be due to genetic differences. They are due to " intangible environmental effects produced by developmental accidents or uncontrolled non-genetic variation with equal probability of affecting any member of a population " (Lerner, 1950). A measure of such effects can be obtained by the variability between plants within a homozygous line or between different parts on the same plant. In the present experiments the different inflorescences on a plant are formed under different experimental environments. Thus if we used the variance between inflorescences on the same plant as a measure, the effects we are looking for would be masked by the gross environmental effects. But differences between plants within any one treatment block will give a valid estimate of these intangible environmental effects.

As a measure of variability the standard deviation and coefficients of variation (c.v. $= \frac{\sqrt{v}}{\text{mean}} \times 100$) have been calculated for parental lines and $F_1$ generations. The coefficient of variation, as pointed out by Day and Fisher (1937), gives a valid comparison only when the standard deviation is proportional to the mean. In the present data the regression coefficients of the standard deviations on the means are only slightly above unity, and therefore their use is unlikely to lead to serious error.

## 9. DOMINANCE AND VARIABILITY

The combined data for the first inflorescence are summarised in table 7. The regression coefficient of standard deviation on the mean is 1·4. Both the standard deviations and the coefficients of variation

TABLE 7

*Means, standard deviation and coefficients of variation for parents and $F_1$ in the two environments L.E. and H.E. Note lower $F_1$ variation only in the L.E.*

| | L.E. mean | Block I and III | | H.E. mean | Block I, II and III | |
|---|---|---|---|---|---|---|
| | | S.D. | C.V. | | S.D. | C.V. |
| $P_1$ | 12·18 | *4·403* | 36·14 | 19·19 | *6·006* | 31·29 |
| $F_1$ | 10·31 | *1·607* | *15·59* | 12·79 | *3·990* | *31·19* |
| $P_2$ | 8·32 | *1·907* | 22·92 | 12·16 | *3·562* | 29·29 |

indicate that in the L.E. the $F_1$ is less variable than its parents while in the H.E. it has equal variability with its parents. In the L.E. the

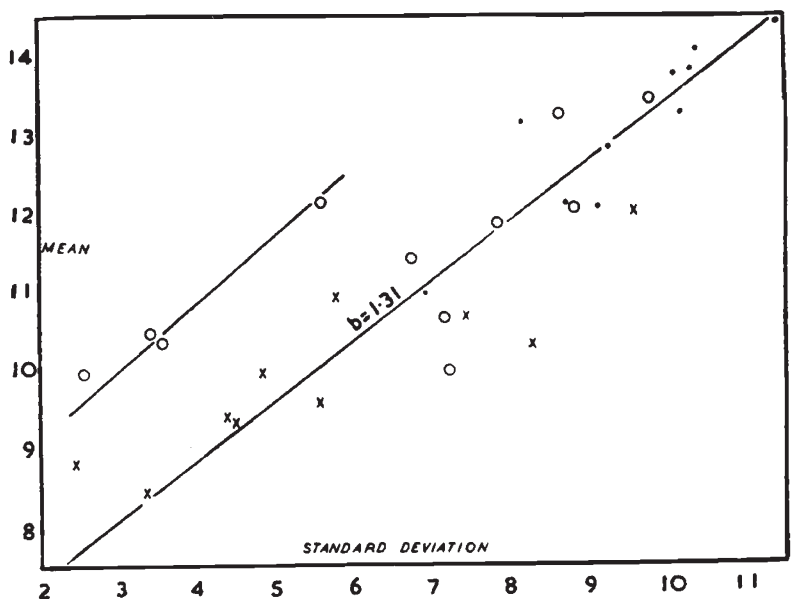


FIG. 5.—The regression of standard deviation, on the mean plotted for parents and $F_1$ for different treatments with different inflorescences. The regression line, $b = 1·31$, is based on parents only. Note the bad fit of the four $F_1$ generations which are indicated by a line estimated from the points: . = $P_1$, x = $P_2$, o = $F_1$, figures transformed to $10 \times \log^{10}$.

mean of the $F_1$ is intermediate between the parents thus showing no dominance, but in the H.E. the small parent ($P_2$) is almost completely dominant.

To see whether this is a general relationship between dominance and variability the data from all inflorescences in block I have been assembled. The mean and standard deviations transformed into $10 \times \text{logarithm}^{10}$ together with the regression line ($b = 1{\cdot}3$) calculated on the parents only are plotted in fig. 5. It will be seen that the parental values fit reasonably well to the regression line, but that while some of the $F_1$ values fit the line others do not. Those which do not fit are less variable than their parental lines. This confirms and extends the data based only on inflorescence I (table 7).

The relationship between dominance and variability suggested in table 7 can be tested if we have valid measures of average dominance and of $F_1$ variability relative to the parents. A measure of average dominance has been devised by Wigan 1944 in the formula $p = \frac{P_1 - F_1}{P_1 - P_2}$ where $P_1$, $F_1$ and $P_2$ are mean values for the respective lines. If we exclude heterosis the value of $p$ may have any value from zero, when $P_1$ is dominant, to unity, when $P_2$ is dominant ($P_1$ being the larger parent) : when there is no dominance, $p = 0{\cdot}5$. With positive heterosis $p$ has a negative value, and with negative heterosis $p$ is greater than unity.

As a measure of $F_1$ variability relative to its parents I propose to use the standard deviation or some appropriate function of it in a *relative variability* function which is obtained as follows :

$$\text{R.V.} = \frac{2F_1 f(v)}{f(v)(P_1 + P_2)}$$

A value of unity is obtained when the $F_1$ is as variable as the mean of the parents, and the lower the value the less variable is the $F_1$ relative to the parents.

The dominance values and the values of R.V. are plotted for the data from the first five inflorescences in both the L.E. and the H.E. from block I in fig. 6.

It is evident from this figure that the $F_1$ relative variability is at its lowest when the dominance value is $0{\cdot}5$, and that it rises as the dominance deviates on either side of the $0{\cdot}5$ value. For dominance values ranging from $0{\cdot}5$ to $1{\cdot}0$ there is a good agreement with a linear relationship. On the other side, from $0{\cdot}5$ to $0{\cdot}0$, the three points are too few to show any general relationship. Some of these points are more reliable than others, those which are obtained from the second inflorescence are of less value than the others because at this inflorescence there is a change over occurring from the early controlled environments to the later condition. If the point $C_2$, which is from the 2nd inflorescence, on the left-hand side of the $0{\cdot}5$ dominance value is discarded the points are not incompatible with a general relationship similar to that on the right side of $0{\cdot}5$.

The data in fig. 6 are from the same parents and $F_1$ in different environments and from different parts of the plant. The $F_6$ selected

lines and their $F_1$'s (table 6) have been analysed in the same way and are in agreement, thus showing that the dominance-variability relationship holds not only with different conditions but with different genotypes.

The two selected lines, which when intercrossed, showed negative heterosis will be referred to later.

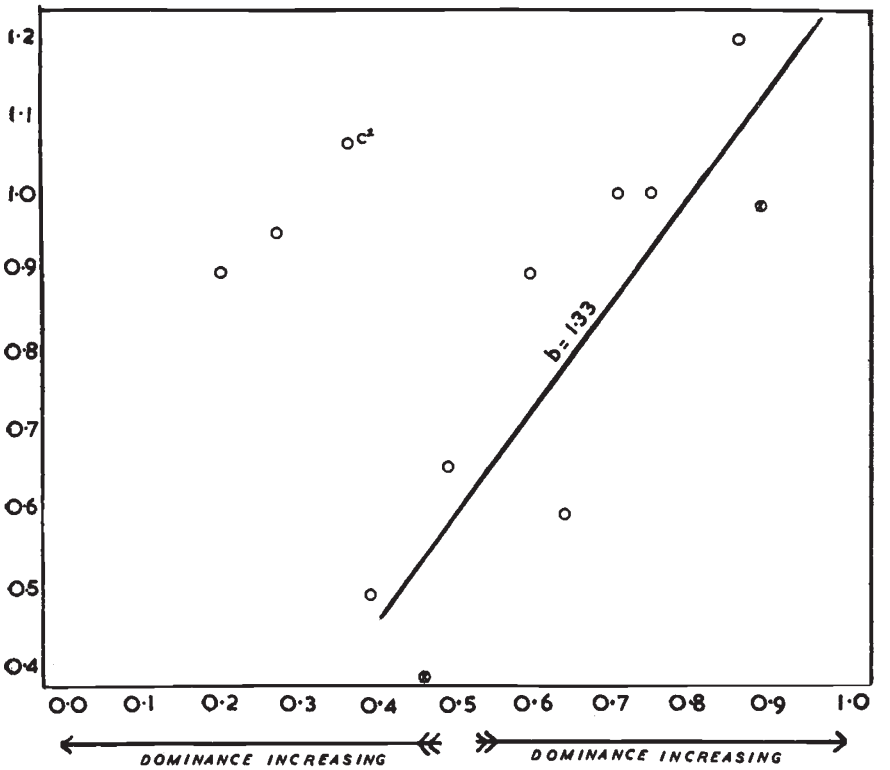


FIG. 6.—Dominance plotted against relative variability based on flower numbers in tomatoes. The o points represent data from different inflorescences and different treatments in block I. The ⊗ points represent the combined data from different treatments on the first inflorescence only. Note that with minimum dominance (0·5) there is a minimum value of the relative variability, and that as dominance increases on either side of the 0·5 value the relative variability increases.

## 10. DOMINANCE AND $F_1$ VARIABILITY IN THE PUBLISHED DATA

Much of the published data on polygenic characters does not include sufficient detail to be able to make a comparison between dominance and $F_1$ variability, but a search has revealed data in *Nicotiana rustica* given in table 10.1, p. 163 by Smith (1952) which can be analysed in the same way as the Tomato data. The *Nicotiana* data are from different genotypes, which make them particularly interesting as a comparison with the Tomato data. The characters analysed are plant height and leaf length in four parental lines and the six hybrids between them. Standard deviations have been calculated from the published variances, and with both height and

leaf length the correlation between the mean and standard deviation is so low that the graphical representation given in fig. 7 is made not on the coefficient of variation as with the Tomato data but on the standard deviation. Only $F_1$ families which do not show heterosis are included in this graph : the others will be considered later.

It is fortunate that the characters in *Nicotiana* tend to show dominance of the large parent, for they give a good relationship of the left side of the dominance value 0·5, thus complementing the

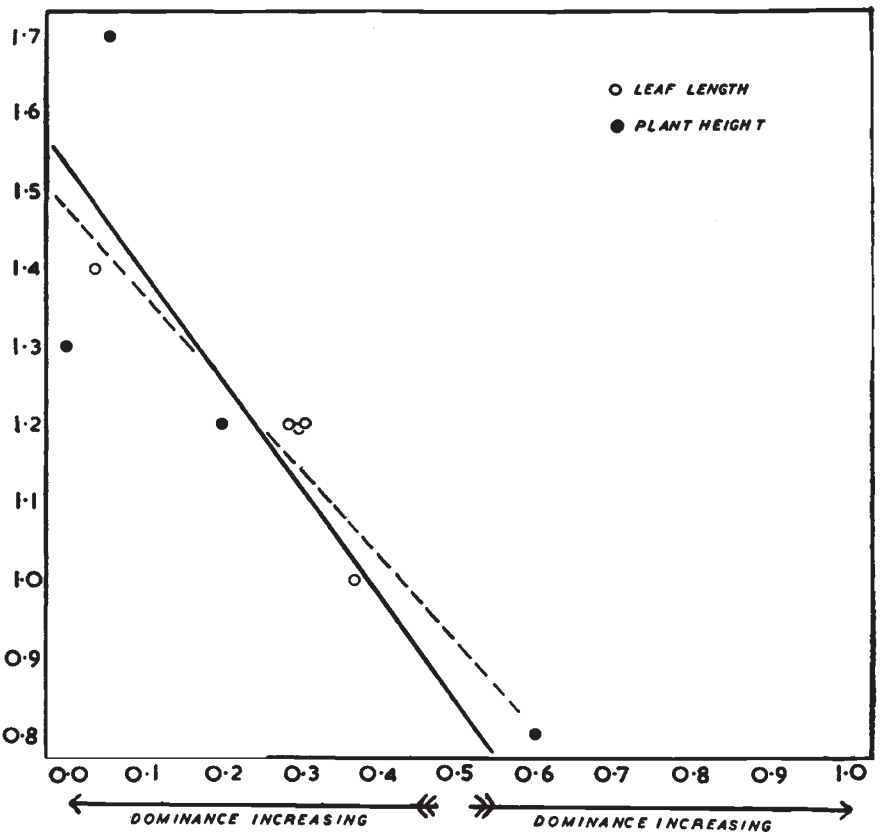


FIG. 7.—Dominance values plotted against relative variability based on *Nicotiana* hybrids (Smith, 1952). Note the low value of the relative variability with the minimum dominance.

Tomato graph. The probable straight line relationship for both these characters indicates that it may be of general occurrence.

In *Galeopsis* Hagberg (1952) has analysed the dry weights of many parental lines and their hybrids and has plotted the mean dry weights against the standard deviations in fig. 31, p. 225. All these hybrids either show complete dominance of the larger parent or positive heterosis. The graph shows that the $F_1$ families are as variable as the parents. This is in complete agreement since there is no lack of dominance in any of the hybrids.

In barley, Gustafsson (1946) has shown that plants which are heterozygous for a lethal gene are more variable than the homozygotes : this again is in complete accord since the normal allele is dominant.

All these examples are with inbreeding species, but an example from an outbreeding species is found in Mather's (1949) species cross between *Petunia axillaris* and *P. violacea*. The mean of the corolla length of the hybrid was intermediate between the two parents and the variability was much lower than the parents. This is again in agreement.

## 11. HETEROSIS AND $F_1$ VARIABILITY

Two of the Tomato hybrids between selected $F_6$ lines showed negative heterosis. Three of Smith's *Nicotiana* families showed positive heterosis : three of Hagberg's *Galeopsis* families also showed positive heterosis. In all these examples with heterosis the variability quotient is never below one and is generally slightly above one.

Therefore the three species examined all agree in showing lower $F_1$ variability only in the absence of dominance, and that heterosis either negative or positive like dominance results in an $F_1$ which is slightly more variable than the parents.

It is unfortunate that, although the majority of the work published on quantitative characters and heterosis is in naturally outbreeding organisms, the extensive data are not in a form fit for analysis on the dominance-variability relationship. For it would be extremely interesting to see whether the relationship holds with outbreeding organisms.

All the published results on the variability of the $F_1$ relative to their parents has not taken dominance into account. Many of the results give only the coefficients of variation without the means. Mather (1950) has shown that in the outbreeder *Primula sinensis* the variation in style length is lower in $F_1$'s than in pure lines. Rasmusson (1951) and Robertson and Reeve (1952) found lower $F_1$ variabilities in *Drosophila melanogaster*. In four *Drosophila* species a lower $F_1$ variability for fertility has been found by Dobzhansky and Wallace (1953).

Dobzhansky and Wallace have related the reduced $F_1$ variability to the type of balance an organism has attained by its breeding system. They argue that an outbreeding organism will be more balanced physiologically in the heterozygous condition while an inbreeder will be more balanced as a homozygote. The increased $F_1$ variability of the inbreeding barley (Gustafsson, *loc. cit.*) and the decreased $F_1$ variability in outbreeders such as *Primula* and *Drosophila* are quoted to support this view. There is no doubt that the degree of heterozygosis which is optimum for fitness will be higher in an outbreeder than in an inbreeding organism. But the present results with Tomato and the quoted results from *Nicotiana* throw considerable doubt on

the conclusion that this difference in optimum heterozygosity is the cause of the different $F_1$ variabilities—if a difference there is between outbreeders and inbreeders.

## 12. THEORY OF ALTERNATIVE GENETIC PATHWAYS

The present approach to the problem of $F_1$ phenotypic stability and reduced variability is through gene action. In its simplest form we may assume a single biochemical change from a substrate (S) to a product (P). This may be performed by one gene **A**; a homozygote $\mathbf{A_1A_1}$ will have only one genetic pathway between S and P while a heterozygote $\mathbf{A_1A_2}$ may have one or two pathways according to the action of the alleles. This will also apply to different loci A and B having duplicate effects. The essential point is that the actions

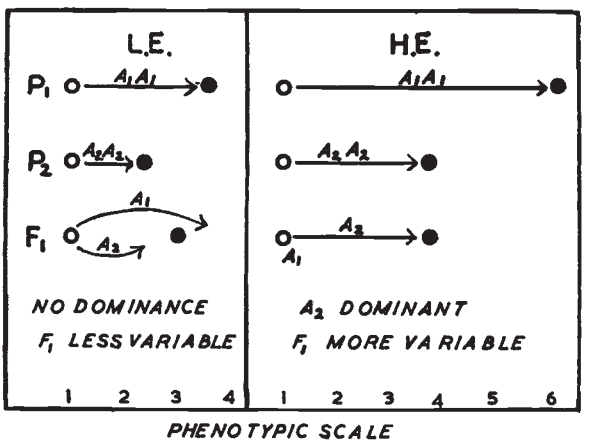


FIG. 8.—Diagram to illustrate the hypothesis of alternative genetic pathways to explain (1) the greater phenotypic stability of heterozygotes to different environments (L.E. and H.E.) and (2) the relationship between high $F_1$ variability, due to minute uncontrolled developmental effects, and dominance. Note that a less variable $F_1$ is obtained only when alternative pathways are in operation.

are in parallel which implies similarity but not identity of the genes. This is shown by their similar but not identical phenotypic expressions. If one of the alleles or duplicate genes is dominant or epistatic then it is assumed that the recessive gene pathway is not in operation; if there is no dominance then both pathways are in operation.

This concept of dominance requires that one dose of the dominant allele is able to perform the full function of the two dominant alleles: this has been found to be so for the $\mathbf{R^+}$ gene in *Drosophila* (Stern, MacKnight and Kodani, 1946) where it was possible to compare a hemizygote $\mathbf{R^+}$ with a homozygote $\mathbf{R^+R^+}$. In autotetraploid plants, the general rule is that a gene which is dominant in the diploid is also fully dominant in the simplex form (**Aaaa**) of the tetraploid, thus showing that there is a great margin of safety with dominant genes.

It is also assumed that different genes will in general but not

always have different optima of conditions—temperature, developmental and cytoplasmic environments, etc.—for their operation.

Thus with alternative genetic pathways the effects of changing conditions will be damped ; this will be manifest in greater phenotypic stability to extremes of environment and reduced variability caused by unknown developmental differences. This scheme is illustrated in fig. 8.

In the special case of heterosis there are two main types of gene action to consider based on two different theories of heterosis. There

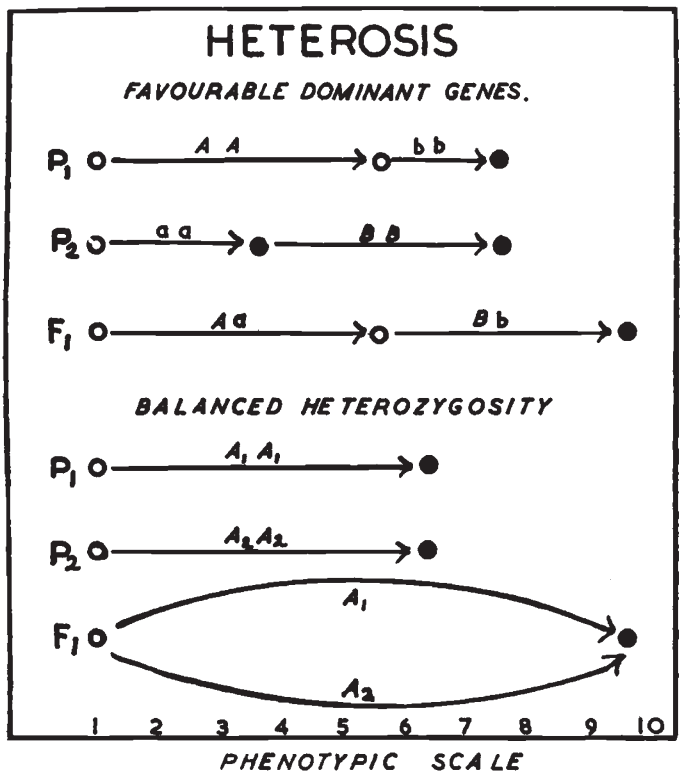


FIG. 9.—Illustrates the two main types of hypothetical gene action which have been postulated for heterosis, only the alternative gene action (balanced heterozygosity) is expected to lead to reduced $F_1$ variability.

is the theory of *favourable dominant* genes generally attributed to Jones (1917) and there is the *heterozygosity* theory of East (1936) which has been more suitably transformed into the *physiological balance* theory of Rendel (1953).

With the favourable dominant gene theory, the dominant genes concerned in heterosis are working in series. With the physiological balance (heterozygosity) theory they are working in parallel. These two types of action are illustrated in fig. 9.

Thus we would expect $F_1$ hybrids showing heterosis based on these two methods of gene action to have different relative variabilities.

In the Tomato, *Nicotiana* and *Galeopsis* data, the heterotic hybrids are not less variable than their parents, indicating that heterosis for the characters studied in these plants is due to favourable dominant genes working in series. Evidence of quite a different kind for this type of gene action in heterosis can be found in the results of Smith (*loc. cit.*) in *Nicotiana*, and in *Galeopsis* by Müntzing (1930) where it was shown that heterosis could be fixed in inbred lines. This should be impossible with the physiological balance action without invoking balanced lethals.

Since all the plants quoted which show high variability in heterotic $F_1$'s are inbreeders, it is tempting to think that the favourable dominant type of heterosis may be common in inbreeding species where balanced heterozygosis would be rare. In outbreeding species on the other hand the physiological balance type of heterosis would probably be more frequent.

A model for alternative gene pathways has been demonstrated with major genes in the flagellar antigenic system in *Paramecium* by Beale (1952). Different antigen-controlling genes come into operation under different conditions.

The parallel between the alternative gene pathways and the alternative biochemical synthesis invoked by Hinshelwood to explain biochemical " adaptation " in micro-organisms is obvious. The adaptation can only occur if there are the alternative genetic pathways to carry out the different syntheses.

## 13. SUMMARY

1. From a simple theoretical model based on a pair of alleles affecting a polygenic character in two environments it is concluded that a heterozygote which is more stable than the homozygotes in respect of the two environments is obtained when one allele is dominant in a particular environment, and when this allele has an effect opposite to that of the environment.

2. Using *Lycopersicon esculentum* as the organism and flower number as the character in two temperature environments, H.E. (High character expression) and L.E. (Low character expression), an experiment with parents, $F_1$, $F_2$, $F_3$, $B_1$ and $B_2$ generations has been analysed.

3. Dominance of genes affecting low flower number is almost complete in the H.E. but absent in the L.E. As predicted from the model, this is expressed as greater $F_1$ phenotypic stability in respect of the two environments.

4. Non-genetic variability of individuals within a single controlled environment due to " intangible environmental effects produced by developmental accidents " is expressed for the $F_1$ as *relative variability*. This is the standard deviation or the coefficient of variation of the $F_1$ divided by the mean value of the standard deviation or the coefficient of variation of the parents. A low $F_1$ relative variability

occurs only when dominance is absent or incomplete. There is a positive linear relationship between $F_1$ relative variability and the degree of dominance.

5. Published data from *Nicotiana rustica* have been analysed for $F_1$ relative variability and dominance, and the same relationship is found.

6. $F_1$ variability is discussed in relation to heterosis, and a theory of *alternative genetic pathways* is advanced which gives some degree of unity to the present data on non-genetic variability, phenotypic stability, dominance and heterosis.

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## 14. REFERENCES

BEALE, G. H. 1952. Antigenic variation in *Paramecium aurelia*, variety 1. *Genetics*, *37*, 62-74.

DARLINGTON, C. D., AND MATHER, K. 1949. *The Elements of Genetics*. Allen & Unwin, London.

DAY, B., AND FISHER, R. A. 1937. The comparison of variability in populations having equal means. *Ann. Eugen.*, *7*, 333-348.

DOBZHANSKY, TH., AND WALLACE, B. 1953. The genetics of homeostasis in *Drosophila*. *P.N.A.S.*, *39*, 162-171.

EAST, E. M. 1936. Heterosis. *Genetics*, *21*, 375-397.

GUSTAFSSON, A. 1946. The effect of heterozygosity on variability and vigour. *Hereditas, Lund.*, *32*, 263-286.

HAGBERG, A. 1952. Heterosis in $F_1$ combinations in *Galeopsis*. II. *Hereditas, Lund.*, *38*, 221-245.

HALDANE, J. B. S. 1947. The interaction of nature and nurture. *Ann. Eugen.*, *13*, 197-205.

HERSH, A. H. 1934. On mendelian dominance and the serial order of phenotypic effects in the bar series of *Drosophila melanogaster*. *Amer. Nat.*, *68*, 186-189.

HONING, J. A. 1927. Dominanzewechzel bei der lichtkeimung. *Verh. 5. Int. Kongr. Vererb. Berlin*, 1927, Bd. 2, 861-865, 1928.

JONES, D. F. 1917. Dominance of linked factors as a means of accounting for heterosis. *Genetics*, *2*, 466-479.

LERNER, I. M. 1950. *Population Genetics and Animal Improvement*. Univ. Press, Cambridge.

LEWIS, D. 1953. Some factors affecting flower production in the tomato. *J. Hort. Sci.*, *28*, 207-220.

MATHER, K. 1949. *Biometrical Genetics*. Methuen, London.

MATHER, K. 1950. The genetical architecture of heterostyly in *Primula sinensis*. *Evolution*, *4*, 340-352.

MATHER, K., AND VINES, A. 1952. The inheritance of height and flowering time in a cross of *Nicotiana rustica*. *Quantitative Inheritance*. H.M. Station. Off., London, pp. 49-79.

MÜNTZING, A. 1930. Outlines to a genetic monograph of the genus *Galeopsis*. *Hereditas, Lund.*, *13*, 185-341.

POWERS, L. 1950. Determining scales and the use of transformations in studies on weight per locule of tomato fruit. *Biometrics*, *6*, 145-163.

RENDEL, J. M. 1953. Heterosis. *Amer. Nat.*, *87*, 129-138.

ROBERTSON, F. W., AND REEVE, E. C. R. 1952. Heterozygosity, environmental variation and heterosis. *Nature, 170,* 286.

SMITH, H. H. 1952. Fixing transgressive vigour in *Nicotiana rustica*. *Heterosis.* Ed. J. W. Gowen, Iowa State College Press, U.S.A.

STERN, C., MACKNIGHT, R. H., AND KODANI, M. 1946. The phenotypes of homozygotes and hemizygotes of position alleles and of heterozygotes between alleles in normal and translocated positions. *Genetics, 31,* 598-619.

WIGAN, L. G. 1944. Balance and potence in natural populations. *J. Genet., 46,* 150-160.