ENVIRONMENTAL AND GENOTYPE-ENVIRONMENTAL COMPONENTS OF VARIABILITY

II. HETEROZYGOTES

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I. INTRODUCTION

In a previous publication (Bucio Alanis, 1965) the partitioning of the variation observed between two inbred lines when grown under different environmental conditions was discussed. From the results obtained the effect of the genotype-environmental interaction γ was shown to be linearly related to ϵ the environmental effect. Such a relationship could have important practical applications from a breeder's point of view since it can be used as a scale to yield data which is largely free from the effects of genotype-environmental interactions. This in turn should enable the breeder to obtain more reliable estimates of heritability and hence predict with greater accuracy the rate of genetic progress under selection for any given character. From a biometrical standpoint, on the other hand, such a relationship should lead to an increase in the consistency of the estimates of the components of genetic variability made from segregating generations, since it seems generally to be the case that this lack of consistency can be attributed to the effects of genotype-environmental interactions.

In the present paper we shall extend the analyses already described for two inbred lines to the F_1 generation which is both homogeneous and heterozygous. For the purposes of illustration data will be used from an experiment with *Nicotiana rustica*, details of which were given in the earlier paper.

2. DESCRIPTION OF THE F_1 MODEL

From the previous paper we can re-write the expectation of the means of the two inbred lines in a particular environment as

$$\begin{aligned}P_1 &= \mu - [d] + \epsilon - \gamma_d \\P_5 &= \mu + [d] + \epsilon + \gamma_d\end{aligned}$$

where μ is the average mid-parent over all environments, $[d]$ is the mean deviation of P_1 or P_5 from μ , and ϵ is the environmental effect measured as the difference between μ and the mid-parent value in any one environment. The parameter gamma has been written with the subscript " d " to indicate that it relates to the genotype-environment

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interaction of the homozygous genotype, in contrast to γ_h which will be used to specify the genotype-environmental interaction of the heterozygous genotype. Thus the expectation of the F_1 mean will be

$$F_1 = \mu + [h] + \epsilon + \gamma_h \quad \therefore \quad \gamma_h = F_1 - (\mu + [h] + \epsilon)$$

where $[h]$ is the average deviation of the F_1 from μ and can be positive or negative depending upon whether it more nearly resembles P_1 or P_5 . Since both $[d]$ and $[h]$ have been defined as departures from the overall mid-parent value it is clear that the interactions between the genotypes

TABLE 1
Estimates of $[h] + \gamma_h$ obtained for seasons separately

Year	Number of plants	Mean plant height	$F_1 - \mu$	γ	$h + \gamma_h$
1946	100	49.74	6.02	0.51	5.51
1947	100	50.87	7.15	1.15	6.00
1948	99	49.15	5.43	0.10	5.33
1950	96	43.33	-0.39	-4.57	4.18
1951	99	45.66	1.94	-2.15	4.09
1952	98	42.63	-1.09	-5.87	4.78
1953	100	41.56	-2.16	-4.38	2.22
1954	100	49.78	6.06	-0.43	6.49
1956	38	47.11	3.39	-1.40	4.79
1957	99	37.42	-6.30	-9.37	3.07
1958	40	52.40	8.68	2.22	6.46
1959	20	46.75	3.03	-3.04	6.07
1960	80	63.63	19.91	11.00	8.91
1961	75	60.11	16.39	8.78	7.61
1962	80	55.31	11.59	5.64	5.95
1964	59	59.51	15.79	9.48	6.31

which they represent and the environment, γ_d and γ_h , will likewise be related to this origin. From the relationship

$$F_1 - \frac{1}{2}(P_1 + P_5) = [h] + \gamma_h$$

we obtain the values of $[h] + \gamma_h$ given in table 1.

The values of ϵ , the environmental component, are calculated from $\epsilon = \frac{1}{2}(P_1 + P_5) - \mu$ and are of course the same as those used in the previous paper. Now we can obtain the function of ϵ for the heterozygous genotype, *i.e.* γ_h , from the regression of $[h] + \gamma_h$ on ϵ , but a quicker method is to adopt a similar procedure to the one used in the previous paper for estimating γ_d . Thus:

$$V\epsilon = V\frac{1}{2}(P_1 + P_5) = 33.39$$

$$V\gamma_h = \frac{1}{4}V[2F_1 - (P_1 + P_5)] = 0.68.$$

Furthermore, since

$$VF_1 = V\epsilon + V\gamma_h + 2 \text{ cov } \epsilon\gamma_h = 51.90$$

it follows that

$$\text{Cov } \epsilon \gamma_h = \frac{1}{2}(VF_1 - V\epsilon - V\gamma_h) = 8.92.$$

Therefore

$$\beta_h = \frac{\text{COV } \epsilon \gamma_h}{V\epsilon} = 0.27.$$

The function of ϵ for the heterozygous F_1 genotype may then be written as:

$$y = 5.37 + 0.27\epsilon$$

and this is represented in fig. 1.

FIG. 1.—Regression of $[h] + \gamma_h$ on ϵ .

It is instructive at this point to compare the functions for the homozygous and heterozygous genotypes. The two regressions have been plotted together in fig. 2 from which it is clear in the first place that $[h] > [d]$, implying that plant height shows heterosis under the range of environmental conditions in which estimates of these parameters have been made, with $[h]$ being on average about twice the value of $[d]$. Secondly, any alteration in environmental conditions produces a corresponding change in the estimates of $[d]$ and $[h]$, but since the former changes more rapidly, *i.e.* $\beta_d > \beta_h$ it is apparent that $[d]$ is less stable over environments than is $[h]$. It follows from this that for final height in *N. rustica* heterosis is more pronounced in poorer environments and becomes less when environmental conditions improve. Providing $[h]$ is positive, in those situations when $\beta_d < \beta_h$,

heterosis will obviously be greater in the better environments. It is perhaps worth noting at this point that the vertical axis of the graph is in fact moveable because the origin, μ , along the x axis depends on the frequency with which the different environments occur. Clearly therefore the average values of $[d]$ and $[h]$ will likewise be dependent upon the frequency with which the different environments occur.

FIG. 2.—Comparison of the regressions of γ_d and γ_h on ϵ .

3. GENERAL DISCUSSION OF THE MODEL

There are 13 basic situations in respect of mean and slope which the two regression lines can take in relation to each other. These can be classified into three groups, namely:

(i) $\beta_d = \beta_h = 0$ with three possible situations, $[d] = [h]$, $[d] > [h]$ and $[d] < [h]$

(ii) $\beta_d = \beta_h \neq 0$ with six possible situations, $[d] = [h]$, $[d] > [h]$, $[d] < [h]$, with positive or negative β 's

(iii) $\beta_d \neq \beta_h$ with four possible situations, $\beta_d > \beta_h$, $\beta_d < \beta_h$, again with positive or negative β 's. These major groupings are shown in fig. 3. In the first group the slopes of the two regressions do not differ from zero and hence $[d]$ and $[h]$ do not change over environments or in relation to each other. The relative sizes of the additive and dominance components, measured as the balance of the linear effects of all the genes controlling the character, determine whether there is heterosis, $[d] < [h]$, complete "dominance" $[d] = [h]$ or incomplete "dominance" $[d] > [h]$. (This of course does not refer to the dominance effects of the individual genes, and it only measures true dominance

where there is a single gene difference between the parents.) In the second group the same general conclusions apply with respect to the "dominance" relationship except that now $[d]$ and $[h]$ increase or decrease depending upon the particular environment and the sign of the

FIG. 3.—Graphic representation of the different possible relationships between β_d and β_h .

β 's. However, since the slopes of the two regressions do not differ from one another their rates of change are the same. From purely biological considerations it is the third and final group which is most likely to occur in practice, where the two functions of the environment have slopes which differ from each other, *i.e.* $\beta_a \neq \beta_b$. This in fact is the situation which arises with final height in the *Nicotiana* data, and in such situations the relative values of the additive and "dominance" components will depend upon the specific environment in which they are estimated. Moreover, complete "dominance" will occur only at the point of intersection of the two regression lines. It is generally considered by geneticists and breeders that the better the environment the larger are the differences between genotypes. This leads one to believe that for many of the characters of economic importance the function of ϵ is expected to be positive. However this does not preclude the opposite situation from arising in practice and there are characters known for which a negative function may be anticipated. In man, for example, rachitic individuals who are unable to synthesise vitamin D from solar energy will be at a marked disadvantage as compared to normal individuals in poorer environments and hence large differences will occur between the alternative genotypes. Where the diet is supplemented with vitamin D however, these differences will tend to disappear, since rachitic individuals are able to make better use of this additional source of the vitamin. Similar situations are to be found in biochemical mutants of micro-organisms which cannot survive on minimal media but only on media to which the appropriate constituents have been added. On minimal media differences between mutant and wild type colonies will inevitably be large, though they will disappear when grown upon complete media. It is indeed to be generally expected that negative β 's will occur when the character under observation is one of resistance to adverse environmental conditions, providing of course that genetic differences exist in the first instance. Examples of this occur amongst higher plants for such characters as drought resistance, disease resistance, etc. In fact it is true to say that a breeder selecting for such characters will do so most effectively in the poorer environments when the appropriate agent, such as dry weather or the pathogen, is present, for it is only under such adverse conditions that resistant material can be detected.

Some of the practical applications of adopting a procedure whereby genotype-environment interactions may be examined in greater detail, such as increased accuracy in the estimates of heritability and improved consistency over environments in the estimates of the genetic components of variability, have already been mentioned. However these are by no means the only practical uses to which this analysis can be put. A further and probably more important application stems from a need for adequate control lines against which a breeder may evaluate the performance of any new lines which he is developing. From time to time it will be necessary to eliminate some of the control

lines and replace them with others so that the level of performance of these lines as a whole will bear some relation to that of the lines under test. Clearly in order to establish the true genetic worth of new lines experiments should ideally be carried out over several seasons in different locations. By having suitable controls in these experiments the effect of genotype-environment interactions can be accurately assessed and this in its turn will enable more reliable recommendations to be made as to whether a new variety can be grown generally or only in certain specified types of environments. Before this can be achieved, however, the analytical approach developed so far will have to be extended considerably to cover those situations where more than two inbred lines are involved.

4. SUMMARY

1. A model developed originally to investigate genotype-environment interactions in two inbred lines has been extended to cover their F_1 hybrid generation and applied to data obtained from an experiment carried out for 16 years with *Nicotiana rustica*.

2. The genotype-environment interaction component of the generation means is clearly related linearly to the environmental effect.

3. This approach can lead to improved estimates of performance and of the genetic components of variation from data collected over a number of environments.

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5. REFERENCE

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