ENVIRONMENTAL AND GENOTYPE-ENVIRONMENTAL COMPONENTS OF VARIABILITY

V. SEGREGATING GENERATIONS

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1. INTRODUCTION

THE description and estimation of the components of phenotypic expression have been presented for two or more inbred lines and the F_1 crosses between them by Bucio Alanis (1966), Bucio Alanis and Hill (1966) and Perkins and Jinks (1968*a* and *b*), and the approach has been illustrated by the analysis of data from *Nicotiana rustica* grown in different seasons and locations. The most important finding to emerge from these analyses is that the genotype-environmental interaction component is often a linear function of the additive environmental effects. The same relationship has been found in other species grown in a variety of environments using different analytical approaches (*e.g.* Yates and Cochran, 1938; Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Breese, 1969). The advantage of the biometrical genetical aproach which we have developed, however, lies in its predictive value across generations; an important feature which is not a part of any of the alternative analyses currently in use. This aspect will be illustrated by extending the model and analysis to include the F_2 and backcross generations of an initial cross between two inbred lines. In the present paper we will confine our attention to the mean genotype of these segregating generations leaving the variation within the generations for a later paper.

2. MATERIAL AND MODEL

The data consist of final plant height in the inbred lines of *Nicotiana rustica* P_1 and P_5 and the F_1, F_2, B_1 and B_5 generations derived from them. They were collected over a period of 18 years at three locations (see Bucio Alanis, 1966, for details). The generation means for each environment are listed in table 1.

(i) *Generation means*

The expectations for the parental and F_1 generation means in environment j, as developed in the earlier papers, are

$$P_{1j} = \mu - [d] + \epsilon_j - g_{aj}$$

$$P_{5j} = \mu + [d] + \epsilon_j + g_{aj} \quad (\textit{i.e.}, P_5 \text{ greater in height on average.})$$

$$F_{1j} = \mu + [h] + \epsilon_j + g_{hj}$$

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where μ, the origin from which the effects of parameters are measured, is defined as the mean of the two parents averaged over all environments $(j = 1 \text{ to } s)$

$$= \frac{\sum_j (P_{1j} + P_{5j})}{2s}$$

TABLE 1

Plant height in the Nicotiana rustica *experiment*

Year	P_1	P_5	F_1	F_2	B_1	B_5
1946	39·36	49·10	49·74	47·27	46·88	49·20
1947	39·60	50·14	50·87	48·14	45·60	51·55
1948	39·48	48·16	49·15	47·45	45·28	49·08
1950	37·13	41·17	43·33	39·60	39·70	38·43
1951	40·20	42·94	45·66	43·21	42·93	42·40
1952	38·34	37·37	42·63	38·63	40·51	37·80
1953	38·14	40·54	41·56	41·47	40·78	40·56
1954	41·90	44·68	49·78	46·73	43·30	47·20
1956	42·15	42·50	47·11	44·64	44·94	43·48
1957	35·84	32·86	37·42	39·70	38·91	39·56
1958	44·45	47·43	52·40	55·28	48·49	50·05
1959	36·75	44·62	46·75	47·42	44·10	49·25
1960	48·70	60·73	63·63	60·37	59·28	63·77
1961	47·31	57·69	60·11	55·67	52·35	55·64
1962	45·23	53·49	55·31	51·44	49·49	54·08
1964	46·36	60·03	59·51	57·81	53·80	59·67
Performance	41·31	47·09	49·68	47·80	46·02	48·23
Variance	4·01	7·94	7·20	6·73	5·57	7·64

$[d]$ and $[h]$ are the genetic contributions to the generation means averaged over all environments for the additive and dominance effects of the genes, respectively, *i.e.*

$$[d] = \frac{\sum_j (P_{5j} - P_{1j})}{2s}$$

$$[h] = \frac{\sum_j (F_{1j})}{s} - \mu$$

ϵ_j is the additive environmental effect of the jth environment and is the deviation of the mid-parent value in that environment from μ *i.e.*

$$\epsilon_j = \frac{(P_{5j} + P_{1j})}{2} - \mu.$$

From these definitions and the assumption that an additive-dominance model is adequate on the chosen scale *i.e.* there is no epistasis, we can write the expectations for the F_2 and backcross generations in the jth environment as

$$F_{2j} = \mu + \tfrac{1}{2}[h] + \epsilon_j + \tfrac{1}{2}g_{hj}$$

$$B_{1j} = \mu - \tfrac{1}{2}[d] + \tfrac{1}{2}[h] + \epsilon_j - \tfrac{1}{2}g_{dj} + \tfrac{1}{2}g_{hj}$$

$$B_{5j} = \mu + \tfrac{1}{2}[d] + \tfrac{1}{2}[h] + \epsilon_j + \tfrac{1}{2}g_{dj} + \tfrac{1}{2}g_{hj}$$

On averaging over all environments the expected means for the six generations reduce to their familiar forms (see table 4). Hence we can use the means over environments to estimate μ, $[d]$ and $[h]$ by the usual methods (Jinks, 1956) and hence test the adequacy of the additive-dominance model.

(ii) *Variance of generation means*

The expectations in the jth environment of each of the six generation means namely, P_1, P_5, F_1, F_2, B_1 and B_5 can be used to find their expected variances over environments in terms of the variance components $V\epsilon$, Vg_d and Vg_h and the covariance components $W\epsilon g_d$, $W\epsilon g_h$ and $Wg_d g_h$. For example, the variance over environments of the F_2 generation mean is expected to be

$$VF_2 = V\epsilon + \tfrac{1}{4}Vg_h + W\epsilon g_h$$

since $[h]$ is a constant.

In table 2 the expectations are summarised for the variances over environments for all six generations. The first three have been derived previously by Bucio Alanis (1966), and Bucio Alanis and Hill (1966). The observed values for final height for each generation are given at the foot of table 1.

TABLE 2

Variances of generation means over environments

Generation	Expected variance
VP_1	$V\epsilon + Vg_d - 2W\epsilon g_d$
VP_5	$V\epsilon + Vg_d + 2W\epsilon g_d$
VF_1	$V\epsilon + Vg_h + 2W\epsilon g_h$
VF_2	$V\epsilon + \tfrac{1}{4}Vg_h + W\epsilon g_h$
VB_1	$V\epsilon + \tfrac{1}{4}Vg_d + \tfrac{1}{4}Vg_h - W\epsilon g_d + W\epsilon g_h - \tfrac{1}{2}Wg_d g_h$
VB_5	$V\epsilon + \tfrac{1}{4}Vg_d + \tfrac{1}{4}Vg_h + W\epsilon g_d + W\epsilon g_h + \tfrac{1}{2}Wg_d g_h$

Each of these variances of the generation means may be regarded as a measure of instability over environments. Equally, they can be used in a perfect fit solution to obtain estimates of the six components of the expected variances as in table 3.

TABLE 3

Environmental and genotype-environmental interaction
variances and covariances

$$
\begin{aligned}
V\epsilon &= \tfrac{1}{2}VP_5 + \tfrac{1}{2}VP_1 + 4VF_2 - 2VB_5 - 2VB_1 \\
Vg_d &= 2VB_5 + 2VB_1 - 4VF_2 \\
Vg_h &= VF_5 + VP_1 + 2VF_2 - 4VB_5 - 4VB_1 \\
W\epsilon g_d &= \tfrac{1}{4}VP_5 - \tfrac{1}{4}VP_1 \\
W\epsilon g_h &= 3VB_5 + 3VB_1 - \tfrac{3}{4}VP_5 - \tfrac{3}{4}VP_1 - \tfrac{1}{2}VF_1 - 4VF_2 \\
Wg_d g_h &= VB_5 - VB_1 - \tfrac{1}{2}VP_5 + \tfrac{1}{2}VP_1
\end{aligned}
$$

(iii) *Linear functions*

In the previous papers of this series it was shown that the genotype-environmental interaction components are linear functions of the additive environmental component, that is

$$g_{dj} = \beta_d \epsilon_j$$
$$\text{and} \qquad g_{hj} = \beta_h \epsilon_j$$

H 2

β_d and β_h being the linear regression coefficients for the interaction of the additive and dominance genetic effects, respectively, with environments. Where the $[d]$ and $[h]$ model adequately accounts for the genetic contributions and the β_d and β_h model accounts for the genotype-environmental interaction contributions, the mean performance for each of the six generations in the jth environment can be rewritten as follows

$$P_{1j} = \mu - [d] + \epsilon_j - \beta_d \epsilon_j$$

$$B_{5j} = \mu + [d] + \epsilon_j + \beta_d \epsilon_j$$

$$F_{1j} = \mu + [h] + \epsilon_j + \beta_h \epsilon_j$$

$$F_{2j} = \mu + \tfrac{1}{2}[h] + \epsilon_j + \tfrac{1}{2}\beta_h \epsilon_j$$

$$B_{1j} = \mu - \tfrac{1}{2}[d] + \tfrac{1}{2}[h] + \epsilon_j - \tfrac{1}{2}\beta_d \epsilon_j + \tfrac{1}{2}\beta_h \epsilon_j$$

$$B_{5j} = \mu + \tfrac{1}{2}[d] + \tfrac{1}{2}[h] + \epsilon_j + \tfrac{1}{2}\beta_d \epsilon_j + \tfrac{1}{2}\beta_h \epsilon_j$$

The expectations for the components of the variances of generation means over environments in the absence of deviations from a linear regression then become (Perkins and Jinks, 1968b)

$$V_{gd} = \beta^2_d V_\epsilon$$

$$V_{gh} = \beta^2_h V_\epsilon$$

$$W_{\epsilon gd} = \beta_d V_\epsilon$$

$$W_{\epsilon gh} = \beta_h V_\epsilon$$

$$W_{gd gh} = \beta_d \beta_h V_\epsilon$$

(V_ϵ remains the same)

The least squares estimates for β_d and β_h, utilising information from all six generations, are

$$\beta_d = \frac{W_{\epsilon gd}}{V_\epsilon} \text{ and } \beta_h = \frac{W_{\epsilon gh}}{V_\epsilon}, \text{ respectively.}$$

In the absence of deviations from a linear regression other variance and covariance relationships would also provide estimates for the β's. For β_d these are

$$\frac{V_{gd}}{W_{\epsilon gd}}, \quad \sqrt{\frac{V_{gd}}{V_\epsilon}} \text{ and } \frac{W_{gd gh}}{W_{\epsilon gh}}$$

and for β_h

$$\frac{V_{gh}}{W_{\epsilon gh}}, \quad \sqrt{\frac{V_{gh}}{V_\epsilon}} \text{ and } \frac{W_{gd gh}}{W_{\epsilon gd}}$$

The linear functions for the genotype-environmental interactions of the F_2 and backcross generations can now be predicted using either the β_d and β_h values derived from the parental and F_1 generations only or from the least squares values derived from information provided by all six generations. The model for the expected linear regression of each generation is given in the second column of table 7.

(iv) *Prediction of the phenotype*

When the $[d]$, $[h]$, β_d and β_h model is adequate the magnitude of these statistics as estimated from the parental and F_1 generations alone can be used to predict the expected mean performance of any other generation derived from the same cross in any environment. These expectations have already been given for the F_2 and backcross generations on page 118. Those for other generations can readily be derived (Bucio Alanis, personal communication).

3. ANALYSIS

(i) *Adequacy of the additive-dominance model using generation means*

The performance of the six generations averaged over environments and their expectations on the additive-dominance model are given in table 4.

TABLE 4

The average performance over all environments for each generation

	Average performance	Expectation
P_1	41·31	$\mu - [d]$
P_5	47·09	$\mu + [d]$
F_1	49·68	$\mu + [h]$
F_2	47·80	$\mu + \frac{1}{2}[h]$
B_1	46·02	$\mu - \frac{1}{2}[d] + \frac{1}{2}[h]$
B_5	48·23	$\mu + \frac{1}{2}[d] + \frac{1}{2}[h]$

The weighted least squares estimates of the three parameters in the model are

$$\hat{\mu} = 44\cdot27 \pm 1\cdot0088$$

$$[d] = 2\cdot84 \pm 0\cdot9937$$

$$[h] = 5\cdot82 \pm 0\cdot9395$$

A test of goodness of fit of the model gives a $\chi^2_{(3)}$ of $0\cdot2744$ which is not significant. Thus the model adequately accounts for the differences in average performance of the six generation means. Since both $[d]$ and $[h]$ are significantly different from zero both are essential components of the model. This result does not rule out the possibility that an additive-dominance model may be inadequate in a particular environment even though it is clearly adequate overall.

(ii) *Components of the variances of generation means*

The variances of the generation means over environments, which are a measure of instability, are given for the six generations at the foot of table 1. From these values, estimates for the components of the variances can be derived as described in table 3. These estimates are given in column 2 of table 5 together with the values of the linear functions

$$\beta_d = \frac{W_{\epsilon g d}}{V_\epsilon} \text{ and } \beta_h = \frac{W_{\epsilon g h}}{V_\epsilon}.$$

Column 1 contains the corresponding estimates based upon the parental and F_1 generations only. A comparison between columns 1 and 2 shows that

while the overall picture is the same there are some discrepancies for individual items particularly for those involving dominance effects. There is one important respect in which these estimates could be improved, namely, by making allowances for the differences in the reliability of the different

TABLE 5

*Estimates of the components of the variances of the
generation means over environments*

	Estimates		
Component	1	2	3
V_ϵ	33·39	41·88	32·33
Vg_d	6·20	2·31	6·05
Vg_h	2·73	6·44	2·52
$W_{\epsilon g_d}$	11·76	11·76	11·21
$W_{\epsilon g_h}$	7·89	1·79	7·52
$Wg_d g_h$	*	3·73	2·53
β_d	0·35	0·28	0·35
β_h	0·24	0·04	0·23

* Cannot be estimated from parental and F_1 generations.

generation means by weighting them according to their amounts of information. The procedure then is to estimate by weighted least squares for each environment ($j = 1$ to s) the quantities.

$$(\mu + \epsilon_j), \ ([d] + g_{dj}) \text{ and } ([h] + g_{hj}).$$

Since μ, $[d]$ and $[h]$ are constants it follows that

$$V(\mu + \epsilon_j) = V_\epsilon$$

$$V([d] + g_{dj}) = Vg_d$$

$$V([h] + g_{hj}) = Vg_h$$

$$W([d] + g_{dj})(\mu + \epsilon_j) = W_{\epsilon g_d}$$

$$W([h] + g_{hj})(\mu + \epsilon_j) = W_{\epsilon g_h}$$

$$W([d] + g_{dj})([h] + g_{hj}) = Wg_d g_h$$

Estimates of the six components derived in this way and the values of β_d and β_h based upon them are listed in column 3 of table 5. In general these estimates, which should be more reliable than those in column 2 agree more closely with the estimates from the parental and F_1 generations only (column 1). Indeed the agreement is now remarkably close.

(iii) *Linear functions*

In the previous section we obtained overall estimates for β_d and β_h. We will now examine whether or not a linear function of the additive environmental component (ϵ_j) will account for all the significant genotype-environment interactions in each of the six generations.

The regression analyses of the interaction items on the ϵ_j values are given in table 6 for the six generations along with the observed linear regression

coefficients (β's). The linear regressions are highly significant for P_1, P_5 and F_2 but non-significant for F_2, B_1 and B_5.

This is not surprising on two counts. First, because of the segregation in the F_2 and backcross generations the generation means have larger sampling errors which are reflected in the larger remainder mean squares in the regression analyses. Second, the regression coefficients of the F_2 and B_1 generations are low and indeed they are expected to be low (table 7). In

TABLE 6

Linear regression analyses of the genotype-environmental interactions on the additive environmental values for each of the six generations

		Generation				
Item	df	P_1 and P_2	F_1	F_2	B_1	B_5
Regn. MS.	1	62·1866	28·0251	4·8930	2·4054	29·9234
Rem. MS.	14	2·2020	0·9202	5·3357	2·3220	7·1159
VR		28·2410	30·4554	0·9170	1·0359	4·2051
P		<0·1%	<0·1%	NS	NS	5-10%
β		±0·34±0·07	0·24±0·04	0·10±0·10	−0·07±0·07	0·24±0·12

fact only the regression coefficient for B_5 is expected to approach those of the parental and F_1 generations in magnitude and this is almost significant at the 5 per cent. level (table 6).

We may now compare these observed values in table 6 with the expected linear functions derived from the estimates of β_d and β_h obtained from parents and F_1's only (column 1, table 5) and from the weighted estimates based upon all six generations (column 3, table 5). The model on which the

TABLE 7

Expected and observed linear functions

		Expected		Observed
Generation	Model	Estimates from P_1, P_5, F_1 only	Estimates from all six generations (weighted)	From best fitting linear regression
P_1	$-\beta_d$	−0·35	−0·35	−0·35±0·07
P_5	β_d	+0·35	+0·35	+0·35±0·07
F_1	β_h	+0·24	+0·23	+0·24±0·04
F_2	$\frac{1}{2}\beta_h$	+0·12	+0·12	+0·10±0·10
B_1	$\frac{1}{2}(-\beta_d+\beta_h)$	−0·06	−0·06	−0·07±0·07
B_5	$\frac{1}{2}(\beta_d+\beta_h)$	+0·29	+0·29	0·24±0·12

expectations are based and the two estimates of the expected linear regressions for each generation are given in columns 2, 3 and 4 of table 7 respectively. The last column contains the observed regression values.

There is extremely good agreement between the two expected and the observed values and in no case do they differ significantly.

(iv) *Prediction of the phenotype*

The two components of the phenotype, namely, the genetic component which is constant in magnitude and the genotype-environmental interaction component which in the *N. rustica* data is linearly related to the environmental

value and therefore varies with the environment, have so far been considered separately. For these data a genetic model consisting of μ, $[d]$ and $[h]$ and a genotype-environmental interaction model involving the linear functions β_d and β_h has been shown to give adequate descriptions of these two aspects of the phenotype. We are therefore in a position to predict the phenotypic mean of any generation derivable from P_1 and P_5 grown in any environment. This will be illustrated by predicting the phenotypic means of the F_2 and two backcross generations in each of the 16 environments using information from the parental and F_1 generations only.

TABLE 8

Genetic and genotype-environmental interaction components of generation means

Statistic	Estimates
	P_1, P_5 and F_1*
$\hat{\mu}$	44·20
$[\hat{d}]$	2·89
$[\hat{h}]$	5·49
$\hat{\beta}_d$	0·35
$\hat{\beta}_h$	0·24

* See page 119 and table 7 column 3 for the corresponding weighted estimates from all six generations.

The estimates of the genetic parameters μ, $[d]$ and $[h]$ and of the genotype-environmental interaction parameters β_d and β_h based upon the parental and F_1 generations only are given in table 8. The expected means for the F_2 and two backcross generations in any environment, j, can be predicted by substituting these values into the formulae given in section 2(iii). For example, the formula for B_{5j} is

$$B_{5j} = \mu + \tfrac{1}{2}[d] + \tfrac{1}{2}[h] + \epsilon_j + \tfrac{1}{2}(\beta_d + \beta_h)\epsilon_j$$

Substituting in the estimates this becomes

$$44·20 + 4·19 + 1·30\epsilon_j$$

$$= 48·39 + 1·30\epsilon_j$$

This and the corresponding expressions for the other generations are given in table 9. From these expressions we can predict the mean phenotype in any environment by substituting in the appropriate value of ϵ_j. The reliability of these predictions may be judged from fig. 1 where the observed phenotypic means for the F_2 and backcross generations in each of 16 environments (table 1) are plotted against the environmental values ($\epsilon_j = \tfrac{1}{2}P_{1j} + \tfrac{1}{2}P_{5j}$) The predicted means are represented as a linear regression line superimposed on the observed values. In each generation the agreement between observed and expected is close.

(v) *Potence and Heterosis*

The relative values of the genotype-environmental interaction components g_d (for homozygotes) and g_h (for heterozygotes) will affect both the potence ratio and the degree of heterosis in different environments.
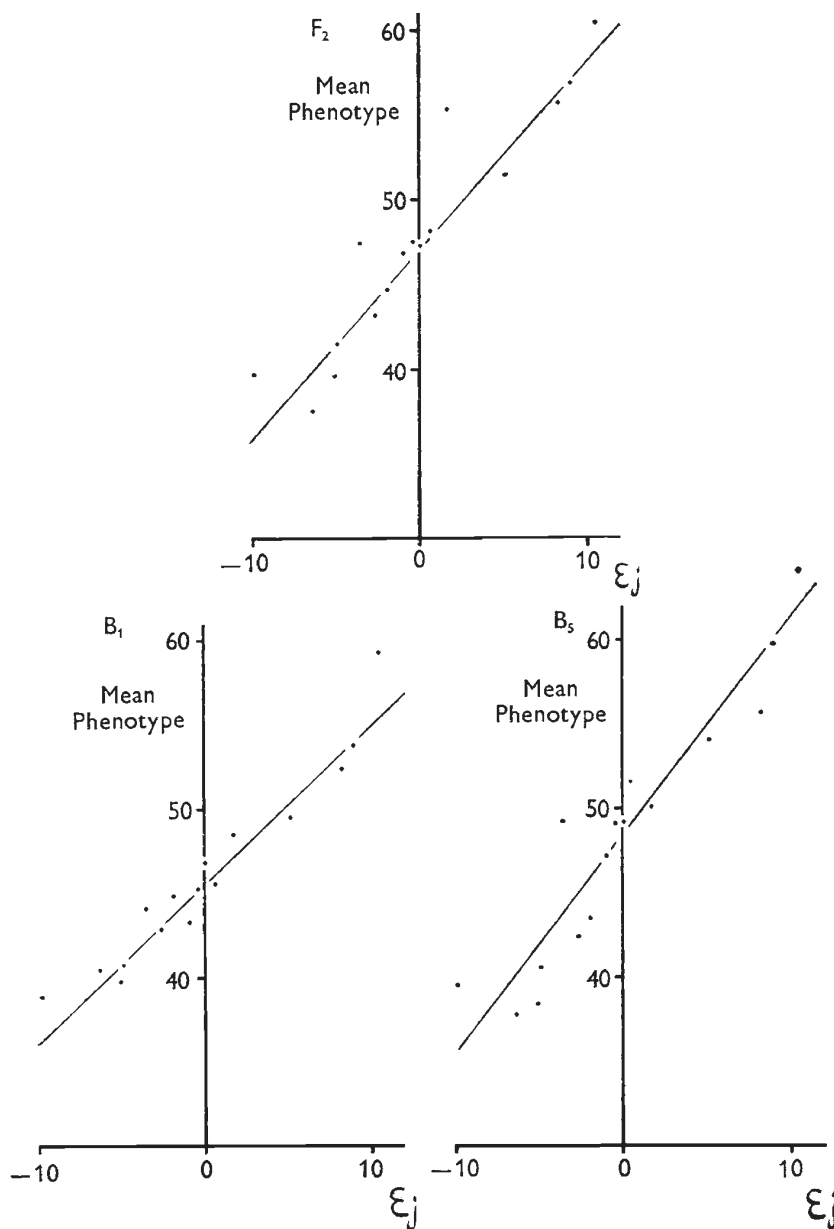
FIG. 1.—The observed phenotypic mean in each of 16 environments is plotted against the corresponding environmental value, ϵ_j, for the F_2 and two backcross generations. In each case the solid line represents the predicted values derived from the formulae in table 9.

In the jth environment the expected potence ratio equals

$$\frac{[h] + g_{hj}}{[d] + g_{dj}} .$$

Heterosis, if positive, equals $[h] + g_{hj} - [d] - g_{dj}$ while, if negative, equals $[h] + g_{hj} + [d] + g_{dj}$.

TABLE 9

*The formulae of the expected generation
means in any environment, j*

Generation	Formula
P_{1j}	$41\cdot31 + 0\cdot65\epsilon_j$
P_{5j}	$47\cdot09 + 1\cdot35\epsilon_j$
F_{1j}	$49\cdot68 + 1\cdot24\epsilon_j$
F_{2j}	$46\cdot94 + 1\cdot12\epsilon_j$
B_{1j}	$45\cdot50 + 0\cdot94\epsilon_j$
B_{5j}	$48\cdot39 + 1\cdot29\epsilon_j$

For the *N. rustica* data g_{hj} can be replaced by $\beta_h\epsilon_j$ and g_{dj} by $\beta_d\epsilon_j$. Substituting the estimated values of $[d]$, $[h]$, β_d and β_h, from the parental and F_1 generations, in these expectations we obtain

$$\text{expected potence} = \frac{5\cdot485 + 0\cdot24\epsilon_j}{2\cdot891 + 0\cdot35\epsilon_j}$$

expected heterosis, which in these data is positive,

$$= 5\cdot485 + 0\cdot24\epsilon_j - 2\cdot891 - 0\cdot35\epsilon_j$$
$$= 2\cdot594 - 0\cdot11\epsilon_j$$

The observed values for potence and heterosis in each of the environments are plotted against the environmental values (ϵ_j's) in figs. 2 and 3, respectively. Superimposed are the expected relationships based on the above formulae. Although the observed potence ratios follow more or less the rather complex expected relationship with the environmental values (fig. 2) the agreement between the observed and expected changes in the magnitude of the heterosis with the environment is considerably better (fig. 3). Indeed the observed linear relationship between heterosis and the ϵ_j values has a regression coefficient of $-0\cdot11$ which is identical with the expected value.

4. DISCUSSION

We have now extended our model of genotype-environmental interactions to the description and estimation of their contribution to the means of segregating generations both in the general case and in the special case where these interactions can be accounted for by a linear function of the environmental values. Application of the model to the F_2 and backcross generations of a cross between two inbred lines of *N. rustica* has shown that the genotype-environmental interactions in these generations, like the interactions in the parental and F_1 generations from which they were derived, are linear functions of the environmental values. Furthermore, the values of the linear functions in the F_2 and backcross generations can be predicted from those of the parents and F_1 generations on the assumption of an additive-dominance model for the genetic component of the interaction with the environment. That is, they can be predicted from two linear functions one
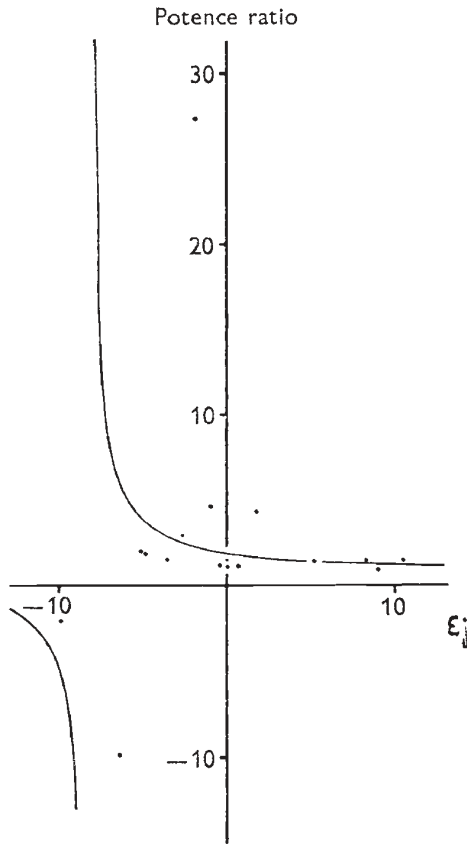
FIG. 2.—The observed potence ratio in each of 16 environments is plotted against the corresponding environmental value, ϵ_j. The solid line represents the expected relationship,

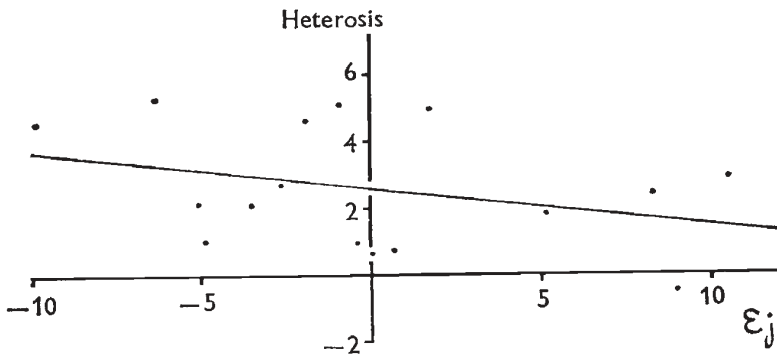$$\text{potence ratio} = \frac{5 \cdot 485 + 0 \cdot 24 \epsilon_j}{2 \cdot 891 + 0 \cdot 35 \epsilon_j}.$$

FIG. 3.—The observed magnitude of heterosis in each of 16 environments is plotted against the corresponding environmental value, ϵ_j. The solid line represents the expected relationship, heterosis $= 2 \cdot 594 - 0 \cdot 11 \epsilon_j$.

of which describes the interaction between the additive gene effects and the environment (β_d) and another which describes the interaction between the dominance effects of the genes and the environment (β_h). Or to put it another way, the magnitude of the linear function in all generations is determined by a gene system which displays both additive and dominance effects but no epistasis. It follows, therefore, that the rate of change with the environment of the mean phenotype of any population derivable from these inbred lines can be predicted if the composition of the population in terms of the relative frequencies of homozygotes and heterozygotes is known.

Where, as in the *N. rustica* data, all the genotype-environmental interactions in all generations can be accounted for by the linear functions of the environmental values (β's), these functions provide a simple measure of the relative abilities of the generations or genotypes to increase or reduce their phenotypic expression in different environments. These relative abilities can be assessed as the ratio of their β's. For example, $\dfrac{\beta_{B5}}{\beta_{P5}}$ represents the ability of the environment to alter the phenotypic expression of the B_5 generation relative to that of parent P_5.

Heterosis, measured as the superiority of an F_1 heterozygote over its better homozygous parent, must vary in magnitude with the environment wherever homozygotes and heterozygotes differ in their response to changes in the environment, *i.e.* wherever $g_d \neq g_h$ or $\beta_d \neq \beta_h$. Where, as in the *N. rustica* data there is positive heterosis, $F_1 > P_5$ and $\beta_d > \beta_h$, the magnitude of the heterosis falls off linearly as the environment improves at a rate equal to $\beta_d - \beta_h$. Hence, the greater stability of the heterozygote to changes in the environment leads to a lower response to an improving environment than is shown by its better parent. But, equally, the heterozygote is less affected by a worsening environment. On the other hand, the more stable parent (P_1) is even more resistant to environmental change than the F_1. Nevertheless, the F_1 is the best overall phenotype in that it combines the highest generation mean with an intermediate sensitivity to the environment.

In the introduction it was claimed that the description and estimation of genotype-environmental interactions we have developed is superior to the alternatives in use in that it allows us to predict across generation as well as across environments. This claim has been amply justified both in theory and in practice. Indeed we have shown that the genetic, environmental and genotype-environmental interaction components of the phenotypes of the F_2 and backcross generations of a cross between two inbred lines of *N. rustica* grown in 16 environments can be individually predicted, within the sampling error of the experiment, from estimates of these components obtained from the parental and F_1 generations. This illustrates once more the value of defining the parameters in a biometrical model according to the concepts of Mendelian Genetics, thus endowing them with the predictive powers of Mendelian laws, rather than defining them on purely statistical grounds, largely dictated by the experimental design and hence having little, if any, relevance to genetical theory or practice.

5. SUMMARY

1. The method of describing, analysing and estimating the genotypic, environmental and genotype-environmental interaction components of

phenotypic expression for inbred lines and their F_1 crosses has been extended to the F_2 and first backcross generations.

2. The procedures are illustrated by the analysis of parental, F_1, F_2 and backcross generations of a cross between two inbred lines of *Nicotiana rustica* grown in each of sixteen locations and seasons.

3. In all generations the genotype-environmental interaction component is a linear function of the additive environmental effects. Furthermore, the functions in the F_2 and backcross generations can be predicted from those in the parental and F_1 generations by assuming that the genotypic contribution to the genotype-environmental interaction component is confined to additive and dominance gene effects.

4. On the same assumption the relationship between potence, heterosis and the additive environmental effects has been predicted and the prediction shown to hold for the *N. rustica* data.

5. The results of the analyses illustrate the advantages of the biometrical genetical approach in that it allows prediction over generations as well as over environments.

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