ENVIRONMENTAL AND GENOTYPE-ENVIRONMENTAL COMPONENTS OF VARIABILITY

III. MULTIPLE LINES AND CROSSES

JEAN M. PERKINS and J. L. JINKS
Department of Genetics, University of Birmingham, England

1. INTRODUCTION

EXPERIMENTAL and practical breeders have long been aware of the problems arising from the occurrence of environmental variation and genotype-environmental interactions. Attempts to specify, estimate and correct for their effects have recently met with some success. Two main approaches have been used. One is a purely statistical analysis originally proposed by Yates and Cochran (1938) and used by Finlay and Wilkinson (1963) and Eberhart and Russell (1966) to detect and measure the magnitude of genotype-environmental interactions in barley and maize, respectively. The components in this analysis have not been related to parameters in a biometrical genetical model. The other approach is based on fitting models which specify the contributions of genetic, environmental and genotype-environmental interactions to generation means and variances, and which allow for the contributions of additive, dominance and epistatic gene action to the genetic and interaction components (Mather and Jones, 1958; Jones and Mather, 1958; Jinks and Stevens, 1959; Bucio Alanis, 1966; Bucio Alanis and Hill 1966). This approach has been used to investigate genotype-environmental interactions in *Nicotiana rustica*.

The analysis of Yates and Cochran (1938) is applicable to any number of strains or varieties grown in any number of environments. The alternative analysis in its present form (Bucio Alanis, 1966; Bucio Alanis and Hill, 1966) is appropriate only for a pair of inbred lines and the generations that can be derived from an initial cross between them. This analysis, however, leads to more informative conclusions and can be used to predict across generations as well as across environments. Nevertheless, the most important conclusion to emerge from the analysis of data is the same for both kinds of analysis, namely, that the magnitudes of the genotype-environmental interactions are a linear function of the environmental effects. Furthermore, this conclusion also applies to the interactions of the environment with additive and dominance effects of the genes (Bucio Alanis, 1966; Bucio Alanis and Hill, 1966).

In the present paper the gap between the two alternative analyses will be bridged. Expectations of the items in the statistical analysis of Yates and Cochran will be given in terms of standard models of gene and environmental action and genotype-environmental interaction, and the analysis of Bucio Alanis will be extended to cover many inbred lines and the crosses among them. The method will be illustrated by reference to final height in a number of inbred lines of N. *rustica* and the F_1 hybrids obtained from crossing eight of these lines in all possible combinations grown over several seasons and locations within seasons.

2. MODELS

The performance Y_{ij} of the ith line in the jth environment can be written as

1. $$Y_{ij} = \mu + d_i + \varepsilon_j + g_{ij} + e_{ij}$$

where μ = grand mean over all lines and environments;
d_i = additive genetic contribution to the ith line;
ε_j = additive environmental contribution of jth environment;
g_{ij} = genotype-environmental interaction of the ith line in the jth environment;
e_{ij} = experimental error of the ith line in the jth environment.

We will consider d_i, ε_j and g_{ij} as fixed effects so that

$$\sum_i d_i = 0, \quad \sum_j \varepsilon_j = 0 \quad \text{and} \quad \sum_{ij} g_{ij} = 0.$$

In the simple case of two genes at each of two loci, A-a, B-b, equal gene frequencies and random gene distributions, four possible inbred lines will occur with equal frequencies. Their expected phenotypes in each of two environments will be (Mather and Jones, 1958; Bucio Alanis, 1966):

Line Genotypes	Environments		Mean over environments
	1	2	
1. AABB	$\mu + d_a + d_b + \varepsilon_1 + g_a + g_b$	$\mu + d_a + d_b - \varepsilon_1 - g_a - g_b$	$\mu + d_a + d_b$
2. AAbb	$\mu + d_a - d_b + \varepsilon_1 + g_a - g_b$	$\mu + d_a - d_b - \varepsilon_1 - g_a + g_b$	$\mu + d_a - d_b$
3. aaBB	$\mu - d_a + d_b + \varepsilon_1 - g_a + g_b$	$\mu - d_a + d_b - \varepsilon_1 + g_a - g_b$	$\mu - d_a + d_b$
4. aabb	$\mu - d_a - d_b + \varepsilon_1 - g_a + g_b$	$\mu - d_a - d_b - \varepsilon_1 + g_a + g_b$	$\mu - d_a - d_b$
Mean over lines	$\mu + \varepsilon_1$	$\mu - \varepsilon_1$	μ

We can readily estimate $d_1 = d_a + d_b$, $d_2 = d_a - d_b$ etc., $\varepsilon_1 = \varepsilon_1$, $\varepsilon_2 = -\varepsilon_1$ and by substituting in these values we can estimate $g_1 = g_a + g_b$, $g_2 = g_a - g_b$, etc.

Extension to an arbitrary number of lines and an arbitrary number of environments, assuming equal gene frequencies at all loci and random gene distributions, presents no problems. The symbolism, however, can be simplified by writing

$r_i \Sigma d = d_i$ where r_i is the coefficient of dispersion for the ith line (Jinks and Jones 1958) and equals

$$\frac{k - 2k_i'}{k}$$

k being the total number of genes and k_i' the number of genes with decreasing effect in the ith line. Similarly, ε_j is now the sum of the individual ε's for environment j and g_{ij} becomes the sum of individual interactions of each of the genes in line i with each of the environmental factors in environment j. The expectations for t inbred lines in s environments are given in table 1.

TABLE 1

The specification of t inbred lines in s environments assuming equal gene frequencies and random gene distributions

Lines	Environments 1	Environments 2	Environments s	sum	mean
1	$\mu+d_1+\varepsilon_1+g_{11}$	$\mu+d_1+\varepsilon_2+g_{12}$ ...	$\mu+d_1+\varepsilon_s+g_{1s}$	$Y_1.$	$Y_1./s = \mu+d_1$
2	$\mu+d_2+\varepsilon_1+g_{21}$	$\mu+d_2+\varepsilon_2+g_{22}$ ...	$\mu+d_2+\varepsilon_s+g_{2s}$	$Y_2.$	$Y_2./s = \mu+d_2$
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
t	$\mu+d_t+\varepsilon_1+g_{t1}$	$\mu+d_t+\varepsilon_2+g_{t2}$ ...	$\mu+d_t+\varepsilon_s+g_{ts}$	$Y_t.$	$Y_t./s = \mu+d_t$
sum	$Y._1$	$Y._2$	$Y._s$	$Y..$	
mean	$Y._{1}/t = \mu+\varepsilon_1$	$Y._{2}/t = \mu+\varepsilon_2$ ..	$Y._{s}/t = \mu+\varepsilon_s$		$Y../ts = \mu$

Generally

$$\mu+\varepsilon_j = Y._{j/t}$$

$$\mu+d_i = Y_{i.}/s$$

$$\mu = Y.._{/ts}$$

from which we may estimate ε_j and d_i and hence g_{ij} as

$$g_{ij} = Y_{ij}-\mu-d_i-\varepsilon_j.$$

For all the data so far analysed the genotype-environmental interactions of any line are a linear function of the environmental values, that is

$$g_{ij} = \beta_i\varepsilon_j+\delta_{ij}$$

where β_i is a linear regression coefficient for the ith line and δ_{ij} is the deviation from the regression line for the ith line in the jth environment. We may therefore write

2. $$Y_{ij} = \mu+r_i\Sigma d+(1+r_i\Sigma\beta)\varepsilon_j+\delta_{ij}+e_{ij}.$$

If we now relax the assumption of equal gene frequencies in the inbred lines so that the frequencies of increasing alleles at the kth locus is u_k and that of decreasing alleles is v_k the expectations must be modified as follows:

Statistic	Gene frequencies Equal	Gene frequencies Unequal
$Y._{j/t}$	$\mu+\varepsilon_j$	$\mu+\Sigma(u-v)d+[1+\Sigma(u-v)\beta]\varepsilon_j$
$Y_{i.}/s$	$\mu+r_i\Sigma d$	$\mu+r_i\Sigma d$
$Y.._{/ts}$	μ	$\mu+\Sigma(u-v)d$
$Y._{j/t}-Y.._{/ts}$	ε_j	$[1+\Sigma(u-v)\beta]\varepsilon_j$
$Y_{i.}/s-Y.._{/ts}$	$r_i\Sigma d$	$r_i\Sigma d-\Sigma(u-v)d$
$Y_{ij}-Y_{i.}/s-Y._{j/t}-Y.._{/s}$	$(r_i\Sigma\beta)\varepsilon_j+\delta_{ij}+e_{ij}$	$[r_i\Sigma\beta-\Sigma(u-v)\beta]\varepsilon_j+\delta_{ij}+e_{ij}$

Thus we may write

3. $$Y_{ij} = \mu'+d'_i+(1+\beta'_i)\varepsilon'_j+\delta_{ij}+e_{ij}$$

where $\mu' = \mu+\Sigma(u-v)d$

$d'_i = r_i\Sigma d-\Sigma(u-v)d$

Z 2

$$\varepsilon_j = [1 + \Sigma(u-v)\beta]\varepsilon_j$$
$$\beta_i' = [r_i \Sigma \beta \Sigma (u-v)\beta]$$

in the general case. This reduces to the earlier form when $u = v = \frac{1}{2}$ at each locus.

To obtain least squares estimates of $(\mu' + d_i')$ and $(1 + \beta_i')$ in equation 3 we must minimise the expression for the ith line

4. $$Q_i = \underset{j}{\Sigma}[Y_{ij} - \mu' - d_i' - (1 + \beta_i')\varepsilon_j' - \delta_{ij}]^2$$

$$\frac{\partial Q_i}{\partial(\mu' + d_i')} = \underset{j}{\Sigma}[Y_{ij} - \mu' - d_i' - (1 + \beta_i')\varepsilon_j' - \delta_{ij}]$$

since $\underset{j}{\Sigma}\varepsilon_j' = 0$ and $\underset{j}{\Sigma}\delta_{ij} = 0$.

5. $$\mu' + d_i' = \frac{\underset{j}{\Sigma}Y_{ij}}{s} = \frac{Y_i.}{s} \text{ as before.}$$

$$\frac{\partial Q_i}{\partial(1+\beta_i')} = \underset{j}{\Sigma}[Y_{ij} - \mu' - d_i' - (1+\beta_i')\varepsilon_j' - \delta_{ij}][\varepsilon_j']$$
$$= \underset{j}{\Sigma}Y_{ij}\varepsilon_j' - (1+\beta_i')\underset{j}{\Sigma}(\varepsilon_j')^2 - \underset{j}{\Sigma}\delta_{ij}\varepsilon_j'$$

Putting $$\underset{j}{\Sigma}\delta_{ij}\varepsilon_j' = 0$$

6. $$1 + \beta_i' = \frac{\underset{j}{\Sigma}Y_{ij}\varepsilon_j'}{\underset{j}{\Sigma}(\varepsilon_j')^2}.$$

For any one line, i, grown in j environments the total sum of squares is

$$\underset{j}{\Sigma}\left(Y_{ij} - \frac{Y_i.}{s}\right)^2 = \frac{(\underset{j}{\Sigma}Y_{ij}\varepsilon_j')^2}{\underset{j}{\Sigma}(\varepsilon_j')^2} + \underset{j}{\Sigma}\delta_{ij}^2$$

where $$\frac{Y_i.}{s} = \mu' + d_i' \text{ and } \underset{j}{\Sigma}\delta_{ij}e_{ij} = 0.$$

We can identify $$\frac{(\underset{j}{\Sigma}Y_{ij}\varepsilon_j')^2}{\underset{j}{\Sigma}(\varepsilon_j')^2}$$

as the regression S.S. and $\underset{j}{\Sigma}\delta_{ij}^2$ as the remainder S.S. for the ith line.

Thus the expected mean squares are:

Item	S.S.	d.f.	M.S.
Regression	$\dfrac{\underset{j}{\Sigma}(Y_{ij}\varepsilon_j')^2}{\Sigma(\varepsilon_j')^2}$	1	$\dfrac{\underset{j}{\Sigma}(Y_{ij}\varepsilon_j')^2}{\Sigma(\varepsilon_j')^2}$
Remainder	$\underset{j}{\Sigma}\delta_{ij}^2$	$(s-2)$	$\dfrac{\underset{j}{\Sigma}\delta_{ij}^2}{(s-2)}$

Each mean square can be compared with σ_e^2 but in order to show that the regression M.S. accounts for a significantly larger proportion of the total variation it should be compared with the remainder M.S.

Since
$$\frac{\sum\limits_{j}(\Upsilon_{ij}\varepsilon_j')^2}{\sum\limits_{j}(\varepsilon_j')^2} = (1+\beta_i')^2\sum\limits_{j}(\varepsilon_j')^2$$

for the regression M.S., it is obvious that we are testing the hypothesis that a significant proportion of the variation of the ith line over environments is accounted for by fitting a regression slope of $(1+\beta_i')$. This, however, accounts both for the additive environmental variation and that part of the genotype-environmental interaction sum of squares that is a linear function of the environmental values. The significance of β_i' can, nevertheless, be tested as the difference between $(1+\beta_i')$ and one. It can also be tested directly by using the approach of Bucio Alanis (1966) in which the $(d_i'+g_{ij}')$ values for each line in each environment are estimated along with the values of ε_j' for each environment as shown earlier (page 341). The linear regression of the $(d_i'+g_{ij}')$'s on the ε_j''s is then calculated for each line. The items in the regression analysis for the ith line are then

Item	d.f.	M.S.
Regression	1	$\beta_i'^2\sum\limits_{j}(\varepsilon_j')^2$
Remainder	$(s-2)$	$\dfrac{\sum\limits_{j}\delta_{ij}^2}{(s-2)}$

and their significance can be tested in the usual way.

The β_i' values for the different lines can be compared by using a joint regression analysis of the kind proposed by Yates and Cochran (1938). In this analysis based on a comparison of the $(1+\beta_i')$ values,

$$\sum\limits_{i}(\text{regression S.S.})_i = \sum\limits_{i}(1+\beta_i')^2\sum\limits_{j}(\varepsilon_j')^2$$

and since $\Sigma\beta_i' = 0$ this becomes

$$t\sum\limits_{j}(\varepsilon_j')^2+\sum\limits_{i}(\beta_i'^2\sum\limits_{j}(\varepsilon_j')^2$$

$t\sum\limits_{j}(\varepsilon_j')^2$ is the joint regression S.S. which in this analysis equals the environment S.S.

$\sum\limits_{i}(\beta_i')^2\sum\limits_{j}(\varepsilon_j')^2$ is the heterogeneity between regressions S.S. It is also the $\sum\limits_{i}(\text{regression S.S.})_i$ for the regression analysis based on the approach of Bucio Alanis (1966). The expectations of the mean squares in the joint regression analysis are therefore

Item	d.f.	M.S.
Lines (Difference between genotypes)	$(t-1)$	$s\sum_i (d'_i)^2/(t-1)$
Environments (Joint regression)	$(s-1)$	$t\sum_j (\varepsilon'_j)^2/(s-1)$
Lines $\times$ Environments	$(t-1)(s-1)$	
Heterogeneity between regressions	$(t-1)$	$\sum_i (\beta'_i)^2 \sum_j (\varepsilon'_j)^2/(t-1)$
Remainder	$(t-1)(s-2)$	$\sum_{ij} \delta^2_{ij}/(t-1)(s-2)$

There will of course be an additional item, σ^2_e, which is the error mean square from the within line, within environment variation averaged over all lines and environments.

In this analysis the sum over t lines of the regression S.S. is partitioned into the additive environmental item (joint regression S.S.) and that part of the genotype-environmental interactions which are a linear function of the environmental values (heterogeneity between regressions). Both sources of the genotype-environmental interactions, the heterogeneity between regressions M.S. and the remainder M.S., may be significant when compared with σ^2_e. The former item $\sum_i (\beta'_i)^2 \sum_i (\varepsilon'_i)^2$, which is the same as the $\sum_i$(regression S.S.)$_i$ when regressing $(d'_i + g')$ against ε'_j for the ith line, if significant must mean that some of the β_i's are significantly positive and others significantly negative since $\sum_i \beta'_i = 0$.

If either the heterogeneity between regressions M.S., the remainder M.S., or both are significant, genotype-environmental interactions are present. If the heterogeneity M.S. alone is significant we can predict within the limits of the sampling error, all the genotype-environmental interactions for each line from the linear regressions on the environmental values. If the remainder M.S. alone is significant there is either no relationship, or no simple relationship, between the genotype-environmental interactions and the environmental values and hence no predictions can be made by the present approach. If both items are significant the practical usefulness of any predictions will depend on the relative magnitudes of the two M.S.'s. Thus, if the heterogeneity M.S. is significant when compared with the remainder M.S. the predictions of the genotype-environmental interactions based on the linear regression will still have considerable practical value. Indeed, even if the heterogeneity M.S. is not significant when tested against the remainder M.S. this does not rule out the possibility that the regression of $(d'_i + g_{ij})$ on ε'_j for some of the lines taken individually may be highly significant when tested against their remainder M.S. For these particular lines reliable predictions can still be made.

In the above models we have confined our attention to the special case of inbred lines, which is probably the single most important application. However, as Bucio Alanis (1966 and personal communication) has shown models can be derived to cover any generation or population that can be derived from an initial cross between two inbred lines hence we can readily extend the approach to cover the generations that can be derived from pairwise crosses between many inbred lines (see section 3 (c)).

3. Results

(a) Experiment 1. Twenty inbred lines of *Nicotiana rustica* with equal gene frequencies.

The first experiment consists of twenty inbred lines ($t = 20$) derived by selfing and without selection from the F_2 of a cross between varieties 1 and 5 (Mather and Vines, 1952). From the F_7 generation onwards they were regarded as inbred lines and were maintained by selfing for a further 12 generations. From the F_7 generation onwards records of final height are available for nine environments ($s = 9$).

The estimation of the various parameters will be illustrated by reference to line 5. Thus line 5 in environment 1 has a mean height of 32·6 inches hence

$$\mu + d_5 + \varepsilon_1 + g_{51} = 32\cdot6$$

where

$$\mu = 39\cdot85$$

(the mean height of all 20 lines over all 9 environments i.e. $\frac{\Upsilon_{..}}{180}$)

$$d_5 = -9\cdot77$$

(the deviation of the mean height of line 5, over all environments, from μ, i.e. $\frac{\Upsilon_{5.}}{9} - \mu$)

and

$$\varepsilon_1 = 0\cdot16$$

(the deviation of the mean height of all lines in environment 1 from μ, i.e. $\frac{\Upsilon_{.1}}{20} - \mu$)

therefore

$$g_{51} = -2\cdot36$$

(the interaction between line 5 and environment 1)

In order to investigate the relationship between g_{5j} and ε_j it is only necessary to estimate the $(d_5 + g_{5j})$ values by subtracting the $(\mu + \varepsilon_j) = \frac{\Upsilon_{.j}}{20}$ values from the corresponding Υ_{5j} values. Since d_5 is constant the regression of $(d_5 + g_{5j})$ on ε_j is equivalent to regressing g_{5j} on ε_j. The values of $(d_5 + g_{5j})$ and ε_j and the regression analysis are given in table 2.

TABLE 2

Illustration of the regression analysis for line 5 of experiment 1

Environments

	1	2	3	4	5	6	7	8	9	d_5
$\Upsilon_{5j} - (\mu + \varepsilon_j)$ $= (d_5 + g_{5j})$	7·41	−5·79	−14·39	−12·13	−9·06	−9·87	−6·07	−7·68	−15·55	−9·77
ε_j	0·16	−0·46	6·04	3·48	−3·19	−1·48	−8·58	−8·37	12·40	

Regression Analysis for $\beta_5 = -0\cdot45$

Item	d.f.	M.S.	V.R. (2)		χ^2 (3)	
1. Regression	1	71·904	17·732	0·1-1·0%	27·518	<0·1%
2. Remainder	7	4·055			10·863	N.S.
3. Error	957	2·613				

The regression M.S. is highly significant against both the remainder M.S. and the error M.S. Furthermore, the remainder M.S. is not significant. Hence, all the significant genotype-environment interaction between line 5 and the nine environments can be accounted for as a linear regression on the additive environmental values where the regression coefficient β_5, is equal to $-0\cdot45$. Since β_5 is large and negative, line 5 is below average in its sensitivity to environmental variation.

TABLE 3

The additive genetic and genotype-environmental interaction components for the 20 inbred lines of experiment 1 in each of nine environments

Environments

Lines	1	2	3	4	5	6	7	8	9	d_i	β_i
1	$-5\cdot81$	$-3\cdot79$	$-3\cdot58$	$2\cdot37$	$6\cdot94$	$2\cdot53$	$0\cdot53$	$-0\cdot28$	$8\cdot75$	$0\cdot85$	$0\cdot19$
2	$0\cdot99$	$-3\cdot59$	$3\cdot11$	$6\cdot07$	$8\cdot44$	$2\cdot33$	$7\cdot53$	$1\cdot32$	$5\cdot45$	$3\cdot52$	$0\cdot01$
3	$-7\cdot20$	$-9\cdot99$	$-3\cdot29$	$-4\cdot73$	$-4\cdot96$	$-1\cdot77$	$-6\cdot27$	$0\cdot72$	$-2\cdot25$	$-4\cdot42$	$0\cdot02$
4	$5\cdot40$	$7\cdot81$	$10\cdot31$	$9\cdot57$	$7\cdot94$	$4\cdot93$	$5\cdot53$	$6\cdot32$	$9\cdot05$	$7\cdot43$	$0\cdot20*$
5	$-7\cdot41$	$-5\cdot79$	$-14\cdot39$	$-12\cdot13$	$-9\cdot06$	$-9\cdot87$	$-6\cdot07$	$-7\cdot68$	$-15\cdot55$	$-9\cdot77$	$-0\cdot45*$
6	$-4\cdot41$	$-6\cdot39$	$-4\cdot98$	$-11\cdot73$	$-8\cdot56$	$-4\cdot57$	$-8\cdot07$	$-8\cdot68$	$-13\cdot25$	$-7\cdot85$	$-0\cdot16$
7	$-3\cdot20$	$-1\cdot19$	$3\cdot31$	$-3\cdot93$	$2\cdot24$	$4\cdot63$	$5\cdot93$	$6\cdot32$	$2\cdot45$	$1\cdot84$	$-0\cdot23$
8	$-5\cdot81$	$-5\cdot59$	$-5\cdot89$	$-10\cdot23$	$-6\cdot36$	$-10\cdot57$	$-5\cdot47$	$-2\cdot48$	$-5\cdot25$	$-6\cdot40$	$-0\cdot09$
9	$-11\cdot71$	$-8\cdot69$	$-10\cdot10$	$-12\cdot13$	$-8\cdot46$	$-4\cdot07$	$-2\cdot77$	$-4\cdot08$	$3\cdot05$	$-6\cdot56$	$0\cdot08$
10	$-0\cdot41$	$0\cdot61$	$-0\cdot19$	$-6\cdot13$	$-1\cdot76$	$-6\cdot17$	$-0\cdot67$	$-1\cdot80$	$0\cdot05$	$-1\cdot75$	$0\cdot02$
11	$-6\cdot81$	$-4\cdot39$	$-5\cdot89$	$-3\cdot63$	$-4\cdot56$	$-2\cdot17$	$-9\cdot77$	$-1\cdot68$	$-10\cdot25$	$-5\cdot46$	$-0\cdot16$
12	$-9\cdot01$	$-9\cdot19$	$0\cdot92$	$2\cdot67$	$-4\cdot86$	$-4\cdot07$	$-7\cdot47$	$-5\cdot68$	$-3\cdot75$	$-4\cdot49$	$0\cdot29$
13	$0\cdot59$	$0\cdot01$	$2\cdot71$	$5\cdot57$	$2\cdot15$	$0\cdot93$	$0\cdot13$	$-1\cdot08$	$0\cdot05$	$1\cdot23$	$0\cdot10$
14	$9\cdot19$	$10\cdot61$	$7\cdot21$	$6\cdot67$	$5\cdot15$	$4\cdot53$	$7\cdot33$	$6\cdot72$	$6\cdot45$	$7\cdot10$	$0\cdot00$
15	$11\cdot40$	$12\cdot11$	$9\cdot11$	$7\cdot77$	$5\cdot94$	$11\cdot03$	$5\cdot93$	$-0\cdot88$	$11\cdot75$	$8\cdot24$	$0\cdot41*$
16	$12\cdot59$	$6\cdot41$	$9\cdot11$	$10\cdot37$	$6\cdot34$	$8\cdot53$	$2\cdot13$	$7\cdot92$	$7\cdot25$	$7\cdot85$	$0\cdot17$
17	$29\cdot99$	$27\cdot41$	$11\cdot11$	$14\cdot57$	$9\cdot44$	$12\cdot23$	$17\cdot73$	$14\cdot12$	$12\cdot75$	$16\cdot60$	$-0\cdot14$
18	$-1\cdot01$	$-0\cdot39$	$-0\cdot89$	$1\cdot97$	$-3\cdot35$	$-4\cdot77$	$-5\cdot27$	$-6\cdot48$	$-7\cdot55$	$-3\cdot08$	$0\cdot07$
19	$4\cdot99$	$1\cdot41$	$0\cdot61$	$2\cdot37$	$3\cdot84$	$1\cdot13$	$3\cdot93$	$-1\cdot88$	$2\cdot05$	$2\cdot05$	$0\cdot02$
20	$-12\cdot41$	$-7\cdot39$	$-8\cdot29$	$-5\cdot33$	$-6\cdot56$	$-4\cdot77$	$-4\cdot87$	$-1\cdot48$	$-11\cdot25$	$-6\cdot93$	$-0\cdot35*$
ε_j	$0\cdot16$	$-0\cdot46$	$6\cdot04$	$3\cdot48$	$-3\cdot19$	$-1\cdot48$	$-8\cdot58$	$-8\cdot37$	$12\cdot40$	$\mu = 39\cdot85$	

* = Significant linear regression.

TABLE 4

Joint regression analysis for the 20 inbred lines of experiment 1

Item		d.f.	M.S.	χ^2
Lines		19	$428\cdot239$	$3113\cdot869*$
Environments		8	$896\cdot573$	$2744\cdot960*$
$G \times E$ Int^n	Het. bet. reg.'s	19	$15\cdot638$	$113\cdot709*$
	Remainder	133	$13\cdot714$	$698\cdot042*$
Error		957	$2\cdot613$	—

* $P < 0\cdot1$ per cent.

The corresponding analyses of all the 20 lines are summarised in table 3. The four β_i values which are significant against the error M.S. or against the remainder M.S., where this is itself significant, are indicated in the table.

The joint regression analysis of the data is summarised in table 4. All the items in this analysis are significant against the error M.S. There are, therefore, differences between the lines and between the environments and

there are significant genotype-environmental interactions. However while a significant portion of these interactions (the heterogeneity of regression M.S.) is a linear function of the environmental values this portion is only slightly larger than the portion (remainder M.S.) that is not accounted for by this relationship. This is in agreement with the results obtained from the analyses of the individual β_i's.

(b) Experiment 2. Twenty-nine inbred lines of *Nicotiana rustica* from diverse origins with unequal gene frequencies.

Data are available for the final heights of 29 inbred lines of *N. rustica* grown in 10 environments. Estimates for d_i' and β_i' are given in table 5 and for ε_j' in table 6.

TABLE 5

Estimates of the genetic and regression parameters for final heights of 29 varieties of experiment 2

| | | Estimates | |
Variety	Line	d_i'	β_i'
1	1	−3·47	−0·33+
2	2	−0·90	−0·19+
5	3	−1·03	−0·11
6	4	16·95	0·24+
8	5	−0·38	−0·31+
10	6	−1·05	−0·25+
11	7	1·67	0·17
12	8	11·28	0·10
13	9	6·93	−0·07
15	10	−12·72	−0·21+
16	11	−10·71	0·00
21	12	0·30	−0·19+
22	13	11·43	0·20+
23	14	13·45	0·39+
24	15	−1·54	−0·04
25	16	−3·12	0·15
27	17	−1·90	0·04
28	18	−3·84	0·21+
29	19	−2·90	−0·17
30	20	−1·29	0·00
31	21	0·84	−0·06
32	22	−2·65	−0·31*
33	23	−9·07	−0·22+
34	24	−1·52	−0·05
35	25	7·65	0·48+
36	26	−3·80	−0·25+
38	27	−8·13	−0·02
41	28	−3·61	0·14
42	29	3·25	0·67*

* and +, see text.

The β_i' regression analysis is illustrated by reference to line 29 (variety 42) in table 6. The regression M.S. and the remainder M.S. are significant against the error M.S. Furthermore, the regression M.S. accounts for 83 per cent. of the total variation which can be attributed to the interaction of line 29 with environments and is significant when tested against the remainder M.S. Thus there are significant genotype-environmental inter-

actions and most of the interactions are a linear function of the environmental values with a regression slope of 0·67. The slopes for all the varieties are listed in table 5. Two of the β_i''s (marked by * in table 5) are significant when tested against the error M.S. and against their own significant remainder M.S.'s. A further thirteen β_i''s (marked by +) are significant against the error M.S. but also have significant remainder M.S.'s.

TABLE 6

Illustration of the regression analysis using variety 42 (line 29) of expeirment 2

Environments

	1	2	3	4	5	6	7	8	9	10	d_{29}'
$Y_{29j}-(\mu'+\varepsilon_j')$											
$=(d_{29}'+g_{29j})$	2·40	2·18	2·18	−1·74	−7·84	10·58	6·47	4·63	3·50	10·11	3·25
ε_j'	−3·95	3·17	−9·04	1·19	−5·42	3·17	3·87	−1·28	0·65	7·64	

Regression analysis for $\beta_{29}' = 0·67$

Item	d.f.	M.S.	V.R. (2)		χ^2 (3)	
1. Regression	1	100·893	4·950	5-10%	45·243	<0·1%
2. Remainder	8	20·380	—		73·112	<0·1%
3. Error	1446	2·230	—		—	

TABLE 7

Joint regression analysis for the 29 inbred varieties of experiment 2

Item	d.f.	M.S.	χ^2
Lines	28	487·200	6117·247*
Environments	9	144·553	2908·086*
G × E Int^n {Het. bet. reg.'s	28	13·568	170·357*
{Remainder	224	16·916	1699·141*
Error	1446	2·230	—

* P < 0·1 per cent.

The joint regression analysis is given in table 7. All the items are significant when tested against the error M.S. The conclusions are the same as those obtained from experiment 1, namely, there is an additive environmental component and a significant portion of the genotype-environmental interactions are a linear function of the environmental values but there is an equally large portion that is not. The latter conclusion is in agreement with the analyses of the individual β_i''s.

(c) Experiment 3. Inbred parents and F_1's of an 8 × 8 diallel set of crosses of *Nicotiana rustica*.

The final heights of eight inbred lines of *N. rustica* grown in 14 environments and all possible F_1's between them grown simultaneously with the inbred lines in 6 of these environments are available. Estimates of the various parameters for the inbred lines are summarised in table 8 along with the joint regression analyses for all fourteen environments (table 8A) and for the set of six in which the F_1's were also grown (table 8B). All items in both regression analyses are again highly significant. In these data, however, the linear function (the heterogeneity of regression M.S.'s)

accounts for considerably more of the genotype-environment interactions than the remainder M.S.'s.

The greater importance of the linear component of the genotype-environmental interactions in these data is confirmed by tests of significance on the β_i' values for each of the eight lines. Thus when tested against their

TABLE 8

*8 × 8 diallel Regression results for the diagonal items in
A. 14 environments B. 6 environments*

	A		B	
Parent	d_i'	β_i'	d_i'	β_i'
1	−1·10	0·04	−1·51	0·23*
2	1·80	0·21	2·96	0·56*
3	−2·98	0·03	−5·48	0·22
4	14·10	0·42*	14·47	0·16
5	−2·49	−0·37*	−2·58	−0·31*
6	−0·47	−0·14	2·24	−0·30*
7	−5·90	−0·24	−6·56	−0·49
8	−2·95	0·04	−3·51	−0·08
	$\mu' = 42·14$		$\mu' = 42·26$	

* Significant linear regression.

Joint regression analyses

	A			B		
Item	d.f.	M.S.	χ^2	d.f.	M.S.	χ^2
Lines	7	524·446	1822·803*	7	272·146	1029·741*
Environments	13	217·976	1406·991*	5	312·264	843·957*
G × E Int.ⁿ { Het. bet. reg.'s	7	22·272	77·411*	7	24·254	91·771*
{ Remainder	84	10·896	454·456*	28	6·598	99·866*
Error	541	2·014	—	256	1·850	—

* P < 0·1 per cent.

own remainder M.S., where this is significant, or the error M.S., where it is not significant, the β_i' values for lines 4 and 5 are significant in the full set of environments (A) and 1, 2, 5 and 6 in the sub-set of environments (B). A further two lines (2 and 7) for (A) and two lines (3 and 7) for (B) have significant regression M.S.'s which are, however, non-significant when tested against their significant remainder M.S.'s.

Before considering the F_1 data we must modify the model and the expectations in the way outlined in section 2. $F_{(il)}$ will denote the F_1 obtained by crossing parents P_i and P_l. In a diallel set of crosses there will be $\frac{1}{2}i(l-1)$ such F_1's, if we ignore reciprocal crosses, grown in j environments. This equals $\frac{1}{2}t(t-1)$ F_1's for t inbred lines. We may write the expected mean of $F_{(il)}$ in environment j as

$$Y_{(il)j} = \mu + h_{(il)} + \varepsilon_j + g_{(il)j} + e_{(il)j}.$$

However, for clarity we will write

$$Y_{ij} = P_{ij}, \ Y_{lj} = P_{lj} \text{ and } Y_{(il)j} = F_{(il)j}.$$

Following Bucio Alanis and Hill (1966) we will redefine μ as

$$\mu = \frac{P_{i.}+P_{l.}}{2s}$$

$h_{(il)} = \dfrac{F_{(il).}}{s} - \mu$ is the dominance contribution to the (il)th F_1.

The environmental values ε_j appropriate for $F_{(il)j}$ is now defined as

$$\varepsilon_j = \tfrac{1}{2}(P_{ij}+P_{lj}) - \mu.$$

This means that the ε_j's are estimated from the particular pair of parents which produced the F_1 and not as previously as the mean of all inbred lines grown in environment j. Hence the ε_j values may differ from one F_1 to another. The $g_{(il)j}$'s, the genotype-environmental interactions are similarly defined around the actual parental means as

$$h_{(il)}+g_{(il)j} = F_{(il)j} - \tfrac{1}{2}(P_{ij}+P_{lj}).$$

Bucio Alanis and Hill (1966) have shown that for the F_1 between the inbred varieties 1 and 5

$$g_{(il)j} = \beta_{(il)}\varepsilon_j + \delta_{(il)j}.$$

Therefore,

$$F_{(il)j} = \mu + h_{(il)} + (1+\beta_{(il)})\varepsilon_j + \delta_{(il)j} + e_{(il)j}.$$

which is a simple variant of the expression for inbred lines.

$\beta_{(il)}$ can be estimated as the regression of $g_{(il)j}$ on ε_j for each $F_{(il)}$ in turn. It is, however, simpler to estimate the $\beta_{(il)}$'s directly as the regressions of $h_{(il)}+g_{(il)j}$ on ε_j.

The analysis will be illustrated by reference to the cross 4×6. The genetic and interaction components of the final height for parents P_4 and P_6 and for the F_1 4×6 in each of the six environments are given in table 9.

TABLE 9

The F_1 obtained by crossing parents 4 and 6 as an example of the regression analysis of an F_1 cross in experiment 3

| | Environments | | | | | | |
	1	2	3	4	5	6	d_i
$P_4-(\mu+\varepsilon_j) = d_4+g_{4j}$	3·6	5·0	5·6	6·2	8·5	7·8	6·12
$P_6-(\mu+\varepsilon_j) = d_6+g_{6j}$	−3·6	−5·0	−5·6	−6·2	−8·5	−7·8	−6·12
ε_j	−3·42	−0·62	−4·82	−5·62	6·88	7·58	—
							$h_{(4.6)}$
$F_{(4.6)}-(\mu+\varepsilon_j) = h_{(4.6)}+g_{(4.6)j}$	13·7	10·5	12·1	11·5	25·7	30·7	17·36

Regression analysis for $\beta_{(4.6)} = 1\cdot36$

Item	d.f.	M.S.	V.R. (2)		χ^2 (3)	
1. Regression	1	317·710	24·316	0·1–1·0%	160·947	<0·1%
2. Remainder	4	13·066	—		26·476	<0·1%
3. Error	1344	1·974	—		—	

The linear regression of the estimates of $(h_{(il)}+g_{(il)j})$ on ε_j has a slope $\beta_{(il)}$ of 1·36 and both the regression M.S. and the remainder M.S. are highly

significant when tested against the error M.S. (table 9). Furthermore, the regression M.S. is highly significant when tested against the remainder M.S. The value of the $\beta_{(il)}$'s and $h_{(il)}$'s for each of the 28 F_1's of the 8×8 diallel (after averaging over reciprocal crosses) are given in table 10. Ten of the

TABLE 10

Genetics and regression statistics for the F_1 crosses of the diallel in experiment 3

		1	2	3	4	5	6	7	8
1	$\beta_{(il)}$	—	0·33+	−0·26+	0·62+	0·16	0·20*	0·35+	0·09
	$h_{(il)}$	—	15·8	4·9	20·5	5·0	0·2	4·8	3·3
2	$\beta_{(il)}$	—	—	0·17+	0·46+	0·81*	1·12*	−0·28+	0·67*
	$h_{(il)}$	—	—	11·7	8·5	11·0	14·7	4·6	9·6
3	$\beta_{(il)}$	—	—	—	0·16+	−0·13	0·00	−0·29+	0·17
	$h_{(il)}$	—	—	—	14·8	5·0	2·4	0·9	2·9
4	$\beta_{(il)}$	—	—	—	—	0·77*	1·36*	0·73*	0·34*
	$h_{(il)}$	—	—	—	—	12·4	17·4	9·8	10·5
5	$\beta_{(il)}$	—	—	—	—	—	0·33+	0·57+	−0·18
	$h_{(il)}$	—	—	—	—	—	2·8	2·2	−1·6
6	$\beta_{(il)}$	—	—	—	—	—	—	1·38*	0·23
	$h_{(il)}$	—	—	—	—	—	—	1·0	1·6
7	$\beta_{(il)}$	—	—	—	—	—	—	—	0·02
	$h_{(il)}$	—	—	—	—	—	—	—	−0·4
8	$\beta_{(il)}$	—	—	—	—	—	—	—	—
	$h_{(il)}$	—	—	—	—	—	—	—	—

* Significant values of $\beta_{(il)}$ (P < 5·0 per cent.), when tested against not only the error M.S. but also against their own remainder M.S.'s where the latter itself is significant.
+ Significant values of $\beta_{(il)}$ (P < 5·0 per cent.), when tested against the error M.S. but non-significant when tested against their own remainder M.S.'s.

$\beta_{(il)}$'s (marked by *) are significant not only against the error M.S. but also against their own remainder M.S. where the latter is itself significant. A further ten (marked by +) are significant against the error M.S. only and have significant remainder M.S.'s.

Reference to table 10 shows that the distribution of the significant (*) $\beta_{(il)}$ values is not entirely at random, all crosses with a significant $\beta_{(il)}$ having either 2, 4, 6 or 7 as one or both parents and parent 4 is one parent in half the significant values.

The $\beta_{(il)}$ values can be compared in a joint regression analysis. Since the environmental values are unique to the particular F_1 under consideration the variation between the ε_j's for any one F_1 will be denoted by $\sum_j \varepsilon^2_{(il)j}$. The heterogeneity of regressions sums of squares is then

$$\sum_{(il)} \beta^2_{(il)} \sum_j \varepsilon^2_{(il)j} - \frac{(\sum_{(il)} \beta_{(il)} \sum_j \varepsilon^2_{(il)j})^2}{\sum_{(il)j} \varepsilon^2_{(il)j}}.$$

This is clearly a weighted measure of the sum of the deviation squared of the individual $\beta_{(il)}$ values from their weighted mean value. Hence we can test whether the values of the $\beta_{(il)}$'s differ among the F_1's.

The application of this analysis to the present data is summarised in table 11. The heterogeneity of regression M.S. is significant against both the error M.S. and the significant remainder M.S., hence the $\beta_{(il)}$ values differ among the F_1's. One further significant item in this analysis is of interest because it shows that the $h_{(il)}$ values differ among the crosses.

In conclusion, both the parents and the F_1's of the diallel set crosses show genotype-environmental interactions that are largely linear functions of the environmental values with regression slopes (β's) that differ from one inbred line to another and from one cross to another. Although by definition $\frac{1}{2}(\beta_i + \beta_l)$ equals zero for each pair of parents there is a preponderance of positive $\beta_{(il)}$'s and a significant overall positive mean value of $\beta_{(il)}$ for the F_1's. This has important implications for the relative intensities of the interactions of parents and F_1's with the environment which will be discussed in section 3(d).

TABLE 11

Joint regression of the $\beta_{(il)}$ values for the F_1's of experiment 3

Item	d.f.	M.S.	χ^2
$h_{(il)}$'s	27	216·322	2958·812+
Joint regression	1	679·881	344·418+
Het. bet. reg.'s	27	37·420*	511·825+
Remainder	112	11·142	632·147+
Error	1344	1·974	

* = Significant V.R. (= 3·358, P = <0·1 per cent.) when tested against the remainder M.S.
+ = P < 0·1 per cent.

(d) Correlation between mean performance and sensitivity to environmental change.

It has frequently been observed that the environmental variability of genetically homogenous families are related to their mean performance. Since the additive environmental component of this variation is common to all families it must be the genotype-environment interaction part of the variation that is related to performance. Eberhart and Russell (1966), using the analysis of Yates and Cochran (1938), have found such a correlation for several sets of data on yield in single crosses between inbred lines of maize.

TABLE 12

Correlations between the genetic and regression statistics for experiments 1, 2 and 3

Experiment	Statistics	Correlation coefficient	d.f.	P
(1) 20 inbred lines from the cross $V_1 \times V_5$	d_i and β_i	0·41	18	5–10%
(2) 29 inbred varieties	d'_i and β'_i	0·53	27	0·1–1·0%
(3) 8 × 8 diallel:				
(i) Parents	d'_i and β'_i	0·79	6	1·0–2·0%
(ii) F_1's	$h_{(il)}$ and $\beta_{(il)}$	0·49	26	0·1–1·0%

Similar correlations exist in the present data (table 12). Three of these are significant, namely, the correlation for experiment 2 and that for the parents (when grown in the 14 environments) and F_1's of experiment 3. In general, therefore, the taller genotypes have the greater regression slopes and the shorter genotypes the smaller slopes. This relationship also extends to the parents, varieties 1 and 5, from which the 20 inbred lines of experiment

1 were obtained. Thus variety 1 had a d_i value of $-2 \cdot 79$ and a regression slope of $-0 \cdot 35$ and variety 5 a d_i value of $2 \cdot 79$ and a slope of $0 \cdot 35$ (Bucio Alanis, 1966). The mean of the 20 inbred lines which measures $\mu = 39 \cdot 85$ is quite close to the mid-parent value $\mu = 43 \cdot 72$. The d_i values of the 20 lines range from $-9 \cdot 77$ to $16 \cdot 6$ and hence exceed the difference between the parents. The range in regression slopes $-0 \cdot 45$ to $0 \cdot 41$ is also slightly larger than the difference between the parental slopes. The correlation between d_i and β_i in the two parents is reflected to only a slight degree among the 20 inbred lines which have a correlation of $0 \cdot 41$ ($P = 5 - 10$ per cent.). This is the smallest and the only non-significant correlation in table 12. It appears, therefore, that the correlation between d_i and β_i can be broken down. Hence separate genetic systems are involved in the control of the two aspects of the phenotype. Jinks and Mather (1955) came to a similar conclusion for the mean performance and the sensitivity to the environmental variation within plots for flowering time among inbred lines and F_1's of $\mathcal{N}. rustica$.

Both the parents and the F_1's of the diallel set of crosses show a positive correlation between the genetic control of performance and the value of the regression slope (table 12). Furthermore, this correlation persists across the generations. Thus with six exceptions (the F_1's with negative $h_{(il)}$ or $\beta_{(il)}$ values in table 10) the F_1's have both higher mean performances and higher regression slopes than the mean of their respective parents (table 10). Hence, the heterosis in mean performance exhibited by many of the F_1's (Jinks and Jones, 1958) is in general associated with a greater sensitivity to the environment. On the other hand, the F_1's while on average more sensitive than the parents, are not necessarily more sensitive than would be expected from their higher mean performance.

4. The Incidence of Genotype-Environmental Interactions and Linear Relationships

Examination of each of the lines in experiments 1, 2 and 3 in turn, for the presence of genotype-environmental interactions and for a linear relationship between the latter and the additive environmental values, shows that they fall into one of the following categories:

1. The line exhibits no genotype-environmental interactions. This means that the reaction of the line to the environmental variation does not differ significantly from that of the average of all lines in the experiment.

2. The line exhibits genotype-environmental interactions in which case it falls into one of the following classes:

   (a) There is no linear relationship between this interaction and the additive environmental values, *i.e.* only the regression remainder M.S. is significant against the error M.S.

   (b) There is a linear regression and this accounts for all of the genotype-environmental interactions, *i.e.* the remainder M.S. is not significant.

   (c) There is a linear regression but this does not account for all the genotype-environmental interactions since the remainder M.S. is also significant. This last category can be subdivided on the basis of whether the regression M.S. is significant, c (i) or not significant, c (ii) when tested against the remainder M.S.

2 A

The proportion of lines falling into each of these categories is listed for experiments 1, 2 and 3 in table 13. The first five columns in this table correspond in order with the five categories listed above. The last two columns contain the variances of the environmental values $\left(\dfrac{\Sigma \varepsilon_j^2}{s-1}\right)$ and the variance within environments $(\hat{\sigma}_e^2)$.

The larger proportion of significant remainder M.S.'s (columns 2a and 2c (i) in table 13) and fewer satisfactory linear regressions (2b and 2c (ii)) in experiment 2 can be attributed to the greater genetic diversity of the lines used in this experiment relative to those of experiment 1 (Perkins and Jinks,

TABLE 13

The proportion of lines exhibiting the five possible relationships in respect of their genotype-environmental interactions for each experiment and the estimates of the environmental variables

| Experiment | 1. G × E int.[n] absent | 2. G × E int.[n] present | | | | $\dfrac{\Sigma \varepsilon_j^2}{(s-1)}$ | $\hat{\sigma}_e^2$ |
		a. Rem	b. Regn	c. (i) Regn = Rem	c. (ii) Regn > Rem		
1	0·15	0·35	0·10	0·30	0·10	44·829	2·613
2	0·00	0·48	0·00	0·45	0·07	25·740	2·454
3 (i)a	0·00	0·50	0·125	0·25	0·125	27·247	2·014
(i)b	0·25	0·00	0·375	0·25	0·125	39·033	1·850
(ii)	0·04	0·25	0·18	0·36	0·18	43·061*	1·974

Row headings as in table 12, and column headings as in text.

$$ * \quad \frac{\Sigma \varepsilon_j^2}{(s-1)} \text{ becomes } \frac{\sum\limits_{(il)\,j} \Sigma \varepsilon^2(il)j}{\frac{1}{2}t(t-1)(s-1)} \text{ for the } F_1\text{'s in experiment 3 (ii).} $$

1968). Such extreme diversity is however unlikely to exist when comparisons are made between the commercial varieties of a crop plant which often have a similar history of past selection and immediate ancestors in common. On the other hand the varieties of *N. rustica* have no past history of unidirectional selection or immediate common ancestry.

In experiment 3 there is a marked difference in the frequency of significant remainder M.S.'s between the eight inbred parents when grown in 14 environments, 3 (i) a, and when grown in 6 environments, 3 (i) b. Since the genotypes were identical in these two comparisons and the environmental variation between and within environments are very similar (last two columns of table 13) this difference is surprising. The only explanation we can offer is that the data for the eight environments for which experiments 3 (i) a and 3 (i) b differ were obtained during the routine maintenance of the departmental collection of inbred varieties and therefore likely to yield less precise estimate of ε_j' compared with the six environments in common which were part of a controlled experiment.

5. PRACTICAL IMPLICATIONS OF THE LINEAR REGRESSIONS

Where the linear regression coefficient β_i' accounts for all or most of the genotype-environmental interactions it is a convenient measure of the relative sensitivity of a genotype to the environment. A genotype with an average sensitivity will have a $(1 + \beta_i')$ value of 1·00 (Yates and Cochran, analysis) and a β_i' value of zero (Bucio Alanis, analysis). Such a genotype

will be classified as showing no genotype-environmental interaction. A genotype which is unusually sensitive to the environment will have a $(1+\beta_i')$ value greater than 1·00 and have a β_i' value greater than zero. Such a genotype will be undersirable in so far as its performance will show an above average variation between environments. On the other hand, it will show an above average response to any improvement in the environment and hence may be useful if its growth is confined to the better environments.

A genotype which is relatively indifferent to variation in the environment will have a $(1+\beta_i')$ value significantly less than 1·00 and hence a β_i' value which is significantly negative. Where β_i' approaches $-1\cdot00$ in value the $(1+\beta_i')$ value may well be non-significant, *i.e.* there will be no regression of performance (Y_{ij}) in each environment on the additive environmental value (ε_j'). Such a genotype is desirable in so far as its performance is maintained over all environments including the poorer environments.

There are, however, two aspects of the phenotype that must be considered jointly in deciding which is the best genotype, namely the genetic component of performance, d_i', and the sensitivity to the environmental variation as measured by β_i'. As we have seen (section 3 (d)) these two aspects of the phenotype are positively correlated both in the original collection of inbred varieties (experiments 2 and 3) and in the F_1's derived from crosses between eight of these (experiment 3 (ii)). Thus in this material a higher d_i' or $h_{(il)}$ value is in general accompanied by a greater sensitivity to the environment. Nevertheless, while these correlations are significant they are not so large that varieties cannot be found which have an above average mean performance and an average regression slope. Furthermore, from a cross between two varieties (1 and 5) in which the correlation is present, inbred lines have been extracted in which d_i is no longer significantly correlated with β_i (experiment 1, section 3 (d)). It is possible, therefore, to select genotypes which are better for both aspects of the phenotype, especially after crossing (experiment 1), *i.e.* have higher relative mean performances and lower sensitivities to the environment.

In order to select for the simultaneous improvement of both aspects of the phenotype it is essential that the breeding material be assessed at the outset for relative mean performance and sensitivity to the environment and reassessed at appropriate stages throughout the selection programme. It is also essential that the sensitivity be measured for those environmental factors, whether seasonal, locational or deliberately imposed, that are likely to be the most critical for the material under the conditions in which it will ultimately be grown. Our own results suggest that relatively small controlled experiments involving few environments will provide reliable information on both aspects of the phenotype. In fact the smallest experiment, namely experiment 3 (i) b, gave the best estimates of the regression slopes which measure the sensitivity to the environment.

6. SUMMARY

1. The analysis of genotype-environmental interaction developed in earlier papers in this series for a pair of inbred lines and their F_1 has been extended to many inbred lines and the F_1's produced by crosses between them.

2. The analysis is illustrated by data on final height for three experiments

involving a number of lines of *N. rustica* grown in different seasons and locations and the outcome is compared with that from statistical analyses.

3. The analyses show that most of the lines exhibit genotype-environmental interaction and for some of the lines the interaction is wholly or partly accounted for by a linear regression on to the environmental values.

4. In the inbred varieties the sensitivity to the environment as measured by the linear regression is correlated with the relative mean performance. This correlation, however, has been broken in the progeny of a cross between two of the varieties.

5. The practical implications of breeding for the simultaneous improvement of both the sensitivity to the environment and the relative mean performance are discussed.

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