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GENOTYPE-ENVIRONMENTAL INTERACTIONS IN *SCHIZOPHYLLUM COMMUNE*

III. THE RELATIONSHIP BETWEEN MEAN EXPRESSION AND SENSITIVITY TO CHANGE IN ENVIRONMENT

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SUMMARY

The relationship between the genetical systems determining mean expression and sensitivity to change in environment has been examined for dikaryotic growth rate in *Schizophyllum commune* by examining the correlation between these aspects of phenotype in a population in which both are segregating simultaneously. For a collection of environments of diverse composition a positive association was found between mean expression and linear sensitivity. The correlation was low, however, and approximately 50 per cent. of the variation in those two aspects was independent. In a more uniform set of environments the association disappeared, demonstrating firstly that different genetical systems act in different environments, and secondly that at least in certain circumstances mean expression and linear sensitivity are determined by separate gene systems. The association between mean expression and non-linear sensitivity also depended on the particular set of environments considered. It is concluded that the relationship between mean expression and sensitivity is markedly influenced by the environments involved, and that each combination of genotypes, environments and character should be treated as a separate case.

1. INTRODUCTION

When a regression approach to the analysis of genotype-environmental interactions is followed the mean performance (y_{ij}) of the ith genotype in the jth environment is described by the model:

$$y_{ij} = \mu + d_i + \beta_i z_j + \delta_{ij},$$

where μ = grand mean over all genotypes and environments,
d_i = genetical contribution of the ith genotype,
β_i = regression coefficient of the ith genotype for the regression of y_{ij} on z_j,
z_j = independent assessment of the effect of the jth environment.
δ_{ij} = deviation from its regression on z_j of the ith genotype in the jth environment.

Following this approach, three aspects of phenotype are recognised: (1) mean expression ($\mu + d_i$), (2) linear sensitivity to change in environment (β_i) and (3) non-linear sensitivity to change in environment (dev. M.S. = $\sum_j \delta_{ij}^2/(s-2)$) (Freeman and Perkins, 1971; Fripp and Caten, 1971). Of the two sensitivity measures the linear sensitivity coefficient is of particular interest since it provides a convenient measure of a genotype's sensitivity

and allows predictions across environments to be readily made (Breese, 1969; Jinks and Perkins, 1970; Samuel, Hill, Breese and Davies, 1970). The importance of the genotype in determining mean expression has long been recognised. More recently a number of studies (Bucio Alanis, Perkins and Jinks, 1969; Jinks and Perkins, 1970; Paroda and Hayes, 1971; Westerman, 1971*a*, *b*, *c*; Fripp, unpublished) have shown that the determination of the sensitivity aspects of phenotype also involves a genetical component. An individual's mean performance in any one environment thus depends on three characters each of which is under genetical control and hence subject to manipulation by the plant or animal breeder.

The desired genotype in many practical situations is one with a high mean performance and low linear and non-linear sensitivities. If these three aspects are controlled by different genetical systems such genotypes, if not available, should be obtainable by standard breeding practices. It is thus important to know whether, with respect to the character of interest, mean expression, linear sensitivity and non-linear sensitivity are independently determined.

If two characters are controlled wholly or partly by the same genes they will show a significant correlation when their association in a number of individuals varying for the characters is examined. Random collections of genotypes within several species have been found to show a significant correlation between $\hat{\mu}+\hat{d}_i$ and b_i (an estimate of β_i) for a number of characters. Examples are yield in maize (Eberhart and Russell, 1966), final height in *Nicotiana rustica* (Perkins and Jinks, 1968*a*), final height, flowering time and leaf number in *Arabidopsis thaliana* (Westerman and Lawrence, 1970; Westerman, 1971*a*). With the exception of final height in *A. thaliana* these correlations are positive, that is as mean expression increases so does the linear sensitivity coefficient. On the other hand, for final height and flowering time in *Nicotiana rustica* (Perkins and Jinks, 1968*b*) and siliqua number in *Arabidopsis thaliana* (Westerman, 1971*a*) mean expression, linear and non-linear sensitivity were all independent.

While at first sight these correlations might be thought to indicate that many of the genes which determine mean expression also affect linear (or non-linear) sensitivity, other interpretations are possible. If the sample of genotypes examined is not representative of all those possible from the segregating alleles, a correlated distribution may arise between two characters controlled by completely separate gene systems. A non-representative sample of genotypes may arise in three ways:

(i) *chance association*, that is by chance alone the genotypes sampled from the population show an association between the two characters;

(ii) *parallel selection*, that is selection for one character has been accompanied by selection (either naturally, or unconsciously or deliberately by man) for the other, with the result that the population sampled consists of genotypes in which the two characters are associated;

(iii) *linkage disequilibrium*, that is the genes controlling the two characters are linked and insufficient generations of recombination and segregation have occurred for the genotypic frequencies to come to equilibrium.

Whether an observed correlation between mean expression and sensitivity is due to pleiotropy or a non-representative sample of genotypes can be determined by allowing recombination and segregation to occur in the absence of selection. If (i) or (ii) is the cause, the association between the two characters will be absent in the resulting population. With (iii), while linkage may retain a degree of association in the progeny, the formation of some recombinant genotypes should lead to a decrease in the magnitude of the correlation compared to that for the parents. A suitable and convenient population for this purpose is provided by the F_2 of a cross between two individuals which show a marked association between the two characters. Perkins and Jinks (1968*a*, *b*) used a random sample of inbred lines derived from such an F_2 population to investigate the cause of the correlations they had observed between mean expression and linear sensitivity for final height in a collection of inbred lines and their F_1 hybrids of *Nicotiana rustica*. From their observations these authors suggested that the correlations may be due to parallel selection and linkage in the past history of the inbreds. A similar conclusion may be drawn from the observation of Paroda and Hayes (1971) that the weak but significant correlation between $\hat{\mu}+\hat{d}_i$ and b_i for rate of ear emergence shown by 10 varieties of spring barley did not persist into the F_1 progenies of a diallel cross between these 10 varieties.

In view of its practical importance it was considered worth while investigating the origin of an observed correlation between mean expression and environmental sensitivity in a further system. The material selected for study was a series of inbred, selection lines of *Schizophyllum commune* which had been found to show a high positive correlation between $\hat{\mu}+\hat{d}_i$ and b_i for linear growth rate (V. Connolly, personal communication).

2. Materials, methods and analysis

When the 10 inbred dikaryons of *S. commune* selected for low and high growth rate by Connolly (1969) were grown in 12 environments, comparable to those described previously (Fripp and Caten, 1971), they gave a correlation between $\hat{\mu}+\hat{d}_i$ and b_i of 0·811 ($P = 0{\cdot}01-0{\cdot}001$). The association of low $\hat{\mu}+\hat{d}_i$ with low b_i and high $\hat{\mu}+\hat{d}_i$ with high b_i was particularly marked for dikaryons 3-6L and 3-6H; the $\hat{\mu}+\hat{d}_i$ and b_i shown by 3-6L were 19·63 and 0·287 respectively, while those for 3-6H were 50·92 and 1·670 respectively. These lines were chosen as contrasting parents to provide a segregating F_2 generation which was examined in a wide range of environments derived by varying growth medium and temperature. Details of the derivation of the F_2 population, the determination of linear growth rate and the 15 environments used have been given elsewhere (Fripp and Caten, 1971). The particular F_2 dikaryons used were those derived from F_1 122 and numbered 201-236 (see fig. 1 of Fripp and Caten, 1971).

The mean expression of each dikaryon was estimated as its mean over environments, that is as $\sum_j y_{ij}/s$. The linear and non-linear sensitivities were estimated following the regression approach of Freeman and Perkins (1971) using the performance of F_1 122 to provide independent environmental values for the regressions. The contribution of the differences in slope of the individual regressions has been estimated both by the linear proportion, l per cent. (Fripp and Caten, 1971) and from the proportion of the $G \times E$ sum of squares that is accounted for by the heterogeneity of regression sum

of squares, after allowing for the contribution of the error source of variation (Finlay and Wilkinson, 1963; R. Knight, personal communication). The latter estimate is referred to as the h per cent.

3. Results

Examination of the regression analyses of the individual dikaryons and the joint regression analysis (table 1*a*) shows: (1) that for all 36 F_2 dikaryons a linear regression exists between y_{ij} and z_j, (2) that these regressions are heterogeneous, and (3) that deviations from regression are present. The l per cent. and h per cent. for the joint regression analysis are 82 and 27 per cent. respectively. The $\hat{\mu}+\hat{d}_i$ values of the F_2 dikaryons, which range from 25·80 to 56·37 with a mean of $39{\cdot}13 \pm 1{\cdot}25$, and the b_i values, which

TABLE 1

Joint regression analyses for the data for all 15 environments (analysis a) and the environments of subset 1 (analysis b) and subset 2 (analysis c)

	Source of variation	Analysis (*a*) d.f.	Analysis (*a*) M.S.†	Analysis (*b*) d.f.	Analysis (*b*) M.S.†	Analysis (*c*) d.f.	Analysis (*c*) M.S.†
1.	Between genotypes	35	841·73**(6)	35	530·14**(6)	35	493·67**(6)
2.	E: Combined regression	1	122,287·21**(6,3)	1	11,962·86**(6,3)	1	36,870·46**(6,3)
3.	E: Environmental residual	13	328·85**(6)	4	41·05**(6)	3	92·52*(6)
4.	G×E: Heterogeneity of regressions	35	147·00**(6,5)	35	51·97**(6,5)	35	60·71**(6) N.S. (5)
5.	G×E residual	455	42·26**(6)	140	26·53**(6)	105	56·91**(6)
6.	Error	468	15·49	175	9·76	175	25·41

† Items used as error terms in the variance ratio tests are given in brackets. Significance levels N.S. $P>0{\cdot}05$; *$P = 0{\cdot}01$-$0{\cdot}05$; **$P<0{\cdot}005$.

vary from 0·507 to 1·139 with a mean of 0·871, are plotted in fig. 1. The values for the parental dikaryons 3-6L and 3-6H grown in the same 15 environments are also shown. The F_2 dikaryons as well as 3-6L and 3-6H show a positive association between b_i and $\hat{\mu}+\hat{d}_i$. However, the association for the F_2 dikaryons is clearly not absolute and dikaryons with a high sensitivity were recovered covering most of the growth rate range. The correlation between $\hat{\mu}+\hat{d}_i$ and b_i for the F_2 dikaryons is 0·688. Although significant ($P<0{\cdot}001$) this correlation is less than that shown by the original population and indicates that more than 50 per cent. of the variation in b_i is independent of that for $\hat{\mu}+\hat{d}_i$. While this independence could result from the same genes acting in different ways with respect to the two aspects of phenotype, it is more likely that it reflects the action of different genes. That is genes exist which are specific to each aspect of phenotype.

For non-linear sensitivity and mean expression the same picture emerges (see table 2); 3-6L and 3-6H show a positive association and the F_2 dikaryons show a low correlation with approximately 50 per cent. of the variation in the dev. M.S. independent of that in $\hat{\mu}+\hat{d}_i$.

Genotype-environmental interactions can result from the action of different genes in different environments, *i.e.* environment specific genes, as

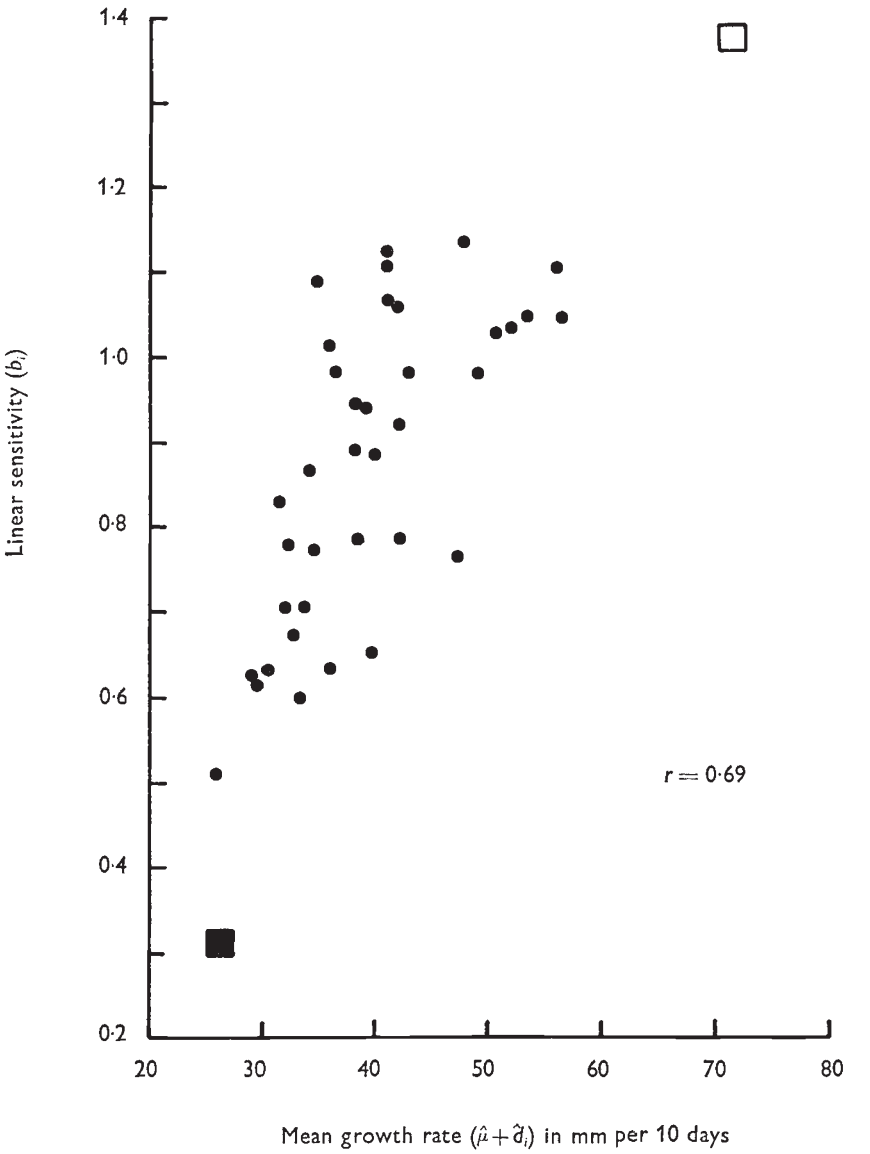

FIG. 1.—Relationship between mean expression ($\hat{\mu}+\hat{di}$) and linear sensitivity (b_i) for the 36 F_2 dikaryons (●) and the parental dikaryons, 3-6L(■) and 3-6H(□) grown in 15 environments. Note that a positive association is shown by both 3-6L and 3-6H, and the F_2 dikaryons.

well as from differential changes in the activity of genes common to all environments, *i.e.* general genes (Perkins and Jinks, 1971). Where two characters are concerned such changes in the spectrum of genes acting may lead to a shift in the proportion of independent to non-independent genes and hence change the correlation between the two characters. Unfortunately the present set of genotypes has not been grown in a further set of environments and it is not possible to examine this effect of the environment

directly. However, the 15 environments included in the full analysis (table 1*a*) comprise a number of groups of related environments, and it is possible that the relationship between environmental mean and sensitivity may differ between these subsets of environments.

A principal components analysis was performed on the present data with the aim of recognising environments producing similar biological effects. Similarities were indicated between environments 4, 8, 11, 12, 13 and 14 (subset 1) and between 1, 2, 5, 6 and 9 (subset 2) while environments 3, 7, 10 and 15 showed no affinity with each other or the other environments (see Fripp and Caten, 1971 for details of these environments). Subsets 1 and 2 have been used to examine the consistency of the relationships between $\hat{\mu}+\hat{d}_i$, b_i and dev. M.S. with change in the environments concerned.

In each subset of environments all F_2 dikaryons show a linear regression of y_{ij} on z_j and these regressions are heterogenous. Substantial deviations from regression are present however, especially in subset 2 where the

TABLE 2

Statistics used to examine the independence of the genetical systems controlling the mean expression, linear sensitivity and non-linear sensitivity aspects of phenotype

Parental dikaryons		All 15 env.	Subset 1	Subset 2
		Estimates of the aspects of phenotype		
3-6L	$\hat{\mu}+\hat{d}_i$	26·47	26·67	29·30
	b_i	0·317	0·796	0·237
	dev. M.S.	30·17	15·61	26·22
3-6H	$\hat{\mu}+\hat{d}_i$	71·33	74·08	87·60
	b_i	1·383	1·651	1·625
	dev. M.S.	195·19	134·56	2·22
F_2 dikaryons		Correlation values between the aspects of phenotype		
$\hat{\mu}+\hat{d}_i$ and b_i		0·688**	−0·283 N.S.	0·810**
$\hat{\mu}+\hat{d}_i$ and dev. M.S.		0·709**	0·700**	0·127 N.S.
b_i and dev. M.S.		0·349*	−0·097 N.S.	0·244 N.S.

Significance levels: N.S. P > 0·05; * P = 0·05-0·01; ** P = 0·005-0·01.

heterogeneity of regressions M.S. is not greater that the G × E residual M.S. (table 1*b* and *c*). The *l* per cent. values are 72 and 53 per cent. for subsets 1 and 2 respectively, and the *h* per cent. values 39 and 27 per cent. respectively.

The statistics necessary to examine the relationships between the genetical systems controlling the three aspects of phenotype are summarised in table 2. Considering the data for subset 1, the correlation value between b_i and $\hat{\mu}+\hat{d}_i$ in the F_2 dikaryons is low and non-significant. These two statistics still show a positive association in the parent dikaryons, however. The b_i values for the F_2 dikaryons and for 3-6L and 3-6H grown in the environments of this subset are plotted against the corresponding $\hat{\mu}+\hat{d}_i$ values in fig. 2. The complete scatter of points in this figure should be compared with the positive association observed when all 15 environments are considered together (fig. 1). In this subset of environments completely separate gene systems seem to determine b_i and $\hat{\mu}+\hat{d}_i$, and the positive association shown by 3-6L and 3-6H must have arisen through chance association or parallel selection as opposed to pleiotropy or linkage disequilibrium.

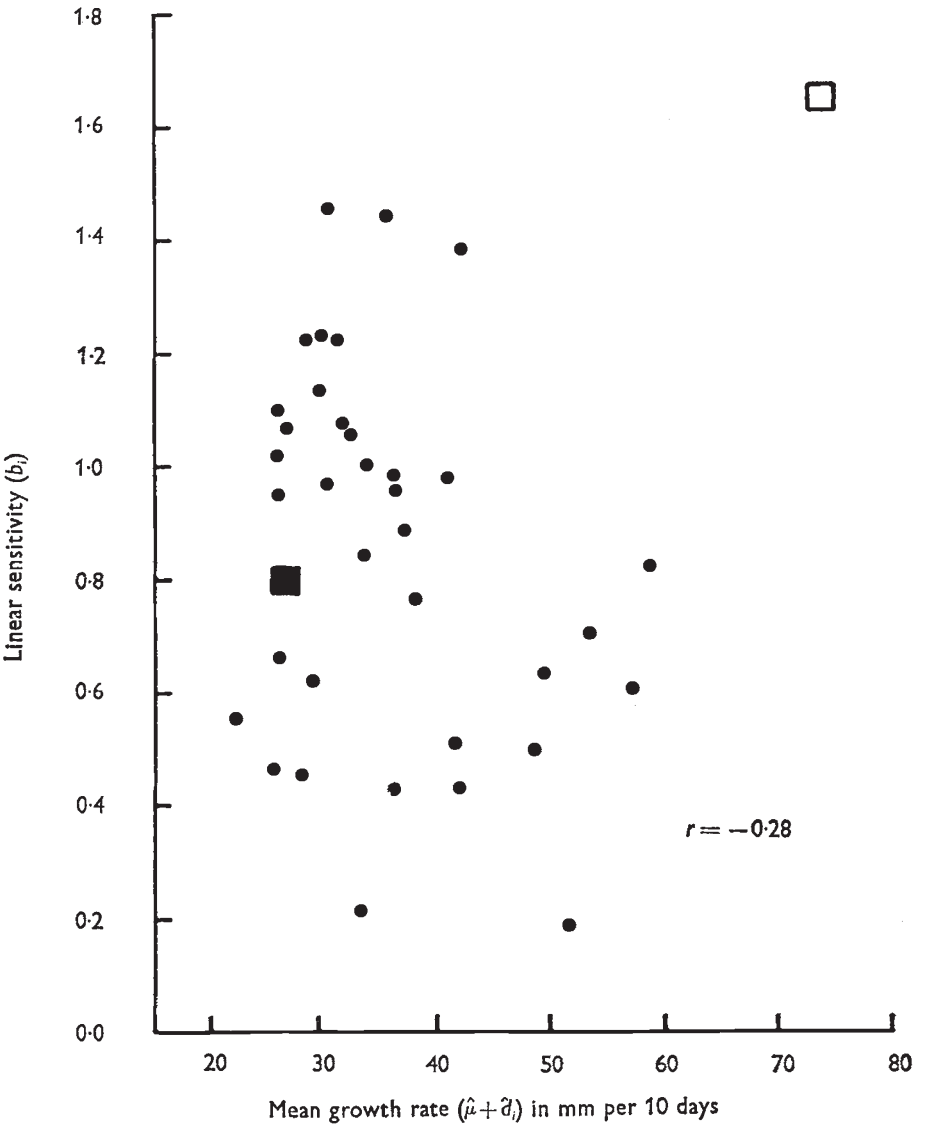

FIG. 2.—Relationship between mean expression ($\hat{\mu}+\hat{d}_i$) and linear sensitivity (b_i) for the 36 F_2 dikaryons (●) and the parental dikaryons, 3-6L(■) and 3-6H(□) in the environments of subset 1. Note that the F_2 dikaryons no longer show a positive association whereas 3-6L and 3-6H still do. This scatter diagram should be compared to that in fig. 1.

In contrast to these results, the correlation between b_i and $\hat{\mu}+\hat{d}_i$ for the F_2 population growing in the environments of subset 2 remains high (greater in fact than for all 15 environments), with approximately 66 per cent. of the variation common to both aspects of phenotype (table 2). In this subset of environments however, in contrast to the subset 1 environments, there is no correlation between the dev. M.S. and $\hat{\mu}+\hat{d}_i$ values of the F_2 genotypes,

indicating that under these conditions separate genetical systems determine mean expression and non-linear sensitivity.

Examination of the $\hat{\mu}+\hat{d}_i$, b_i and dev. M.S. values for the F_2 population in table 2 shows that a physiological correlation which cannot be broken at least under certain environmental conditions does not exist between any two of these three aspects of phenotype.

4. Discussion

The marked effect of the environmental groupings on the relationship between mean expression, linear sensitivity and non-linear sensitivity suggests that the genes determining these aspects of phenotype are not consistent across environments. While the specific effects of environment on mean expression have long been recognised, the occurrence of similar effects on the sensitivity parameters has only recently been demonstrated (Perkins and Jinks, 1971; Fripp, unpublished). As a result of these environmental effects the relationship found between mean performance and the sensitivity parameters will depend upon the set of environments considered. In as much as under the conditions of the subset 1 environments mean expression and linear sensitivity were not correlated, this investigation has shown that there is no immutable physiological reason why high mean expression and high linear sensitivity should be associated, despite the fact that such an association has frequently been found (Eberhart and Russell, 1966; Perkins and Jinks, 1968*a*; Westerman and Lawrence, 1970; Westerman, 1971*a*). The conclusion that mean expression and linear sensitivity may be determined by separate gene systems is in agreement with the findings of Perkins and Jinks (1968*b*), Westerman and Lawrence (1970) and Paroda and Hayes (1971). At the same time the persistence of the correlation when other groups of environments were considered suggest that this is not always the case, and in these instances joint selection for high performance and low sensitivity may be limited by an association between high expression of these two characters. The consequences of this finding for the plant breeder faced with a choice between the development of specifically or generally adapted varieties will depend upon the particular environments with which he has to contend. This investigation clearly reveals the dangers inherent in attempting to draw general conclusions about the genetical basis of the relationship between two characters without regard to the environments used, and emphasises the importance of using realistic rather than contrived environments whenever the findings are to be applied to a practical situation.

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