GENOTYPE-ENVIRONMENTAL INTERACTIONS IN *SCHIZOPHYLLUM COMMUNE*

I. ANALYSIS AND CHARACTER

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1. GENERAL INTRODUCTION

ANY genetical investigation of a quantitative character becomes complicated when more than one environment is considered because of the changes in gene expression that may occur with change in environment. These changes, observable as genotype $\times$ environment interactions in a biometrical analysis, have long been recognised as an important source of phenotypic variation (Immer, Hayes and Powers, 1934; Yates and Cochran, 1938; Mather, 1949). Little is known of the inheritance and physiology of these changes, but it has been found empirically that a linear relation frequently exists between phenotype and environment when the latter is measured by its effect on the character under study (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Perkins and Jinks, 1968; Breese, 1969). This linear relation usually accounts for most of the variation over environments of a genotype and as a result it is possible to predict its phenotype under further related environmental conditions (Breese, 1969; Jinks and Perkins, 1970). In addition, this regression of phenotype against environment provides two simple measures—the regression coefficient and the deviations from regression mean square—of the sensitivity of a genotype to environmental change. These two measures, referred to throughout as the linear sensitivity and non-linear sensitivity, respectively, may be used to measure the relative responsiveness of different genotypes to changes in the environment.

The present investigations were designed to provide more information about the description, prediction and inheritance of genotype-environmental interactions. The problems specifically examined are: (a) the proportion of the variation over environments that is linearly related to quantitative assessments of the environment; (b) the advantages of alternative methods of assessing environments; (c) the specificity of the response of a genotype to diverse environmental factors; (d) the relative sensitivities of different components of variation to change in the environment; and (e) the degree of independence of the genetic systems controlling the mean expression and sensitivity aspects of phenotype.

The organism, character, experimental procedures and analytical techniques used to investigate all these questions will be described in the present paper, which thus forms a general introduction to the above specific topics which will be considered in subsequent papers. Most of the data will be presented and discussed in these later papers. Results are given in the present report simply to demonstrate the analysis used and to show the suitability of the character chosen.

2. SELECTION OF A MODEL SYSTEM FOR STUDYING GENOTYPE-ENVIRONMENTAL INTERACTIONS

Investigations of the inheritance of the genotype-environmental component of phenotype and the development of techniques to describe and predict it are most readily performed in the laboratory where defined environmental conditions can be created, maintained and repeated. For such studies a number of individuals of each genotype are required, since each genotype must be grown in each environment. This presents no problem if the organism used is readily propagated clonally. An organism which has this property, which can be grown in numerous well-defined laboratory environments and which has been shown to be suitable for genetical (Raper and Miles, 1958; Raper, 1966) and biometrical-genetical studies (Simchen and Jinks, 1964; Simchen, 1966*a, b*, 1967; Connolly, personal communication) is *Schizophyllum commune*.

This fungus is a heterothallic Basidiomycete with a haploid-dikaryotic life-cycle in which mating is controlled by a tetrapolar incompatibility system. Both monokaryons and dikaryons are capable of indefinite vegetative growth. Hence, once isolated, a particular monokaryotic or dikaryotic genotype can be exactly duplicated, used repeatedly and maintained indefinitely by subculturing. As *S. commune* is a micro-organism relatively large numbers of individuals can be handled in a single experiment, allowing numerous treatments (*i.e.* combinations of genotypes and environments) to be investigated. Furthermore, as these large numbers can be grown in a limited closely controlled area variation due to micro-environmental differences is minimised. This reduces the amount of replication necessary compared to similar experiments with higher organisms and further increases the relative number of treatments that can be compared in a single experiment.

The genic systems controlling four quantitative characters of *S. commune*, monokaryotic growth rate, dikaryotic growth rate, fruiting time and weight of fruit bodies, have already been investigated (Simchen and Jinks, 1964; Simchen, 1966*a, b*, 1967; Connolly, personal communication). For the study of dikaryotic characters Simchen and Jinks (1964) developed statistics, analogous to those of the diallel analysis of Jinks (1954), for use with the North Carolina Model 2 (NCM2) mating situation (Comstock and Robinson, 1952; Kearsey, 1965) imposed by the incompatibility system of *S. commune*. Using these it is possible to detect additive, dominance and non-allelic interaction components of variation and to determine whether dominance, if present, is directional (Simchen and Jinks, 1964; Connolly, personal communication).

Studies by Simchen (1966*b*, 1967), involving five wild isolates, indicated that in crosses among monokaryons from single wild isolates dikaryotic growth rate is controlled by genes displaying additivity and dominance only, dominance being ambidirectional. In crosses between monokaryons from different isolates non-allelic interactions are also involved. For his studies Simchen used 2 per cent. malt medium at 25° C. Equivalent crosses among monokaryons from two of Simchen's wild isolates, but grown on 2 per cent. malt at 20° C. and 30° C., showed non-allelic interactions and marginal directional dominance for high growth rate (Connolly, personal communication). Other results, from experiments involving all three

temperatures, suggest that Simchen's and Connolly's results are not contradictory but probably reflect changes in gene expression with change in environment (*i.e.* genotype-environmental interactions).

The other dikaryotic characters, fruiting time and weight of fruit bodies, have only been investigated in crosses among monokaryons from single wild isolates. For all but one (No. 6) of the six isolates studied, non-allelic interactions as well as additivity and dominance were found (Simchen, 1966*b*).

These biometrical studies with *S. commune* have shown that individual wild isolates are highly heterozygous for genes controlling all four quantitative characters. A most important conclusion that emerges is that allelic and non-allelic interactions operate between genomes in two different nuclei (*i.e.* in dikaryons) in a manner similar to that between genomes within a single nucleus (*i.e.* in diploids). It is possible therefore, by studying dikaryotic characters, to simulate the genic properties of diploid organisms while exploiting the technical advantages of micro-organisms.

Some preliminary studies of genotype-environmental interactions in *S. commune* have already been made by Connolly (personal communication). From each of two wild dikaryotic isolates, No. 2 and No. 6 (Simchen and Jinks, 1964), Connolly was able to select a number of inbred dikaryons with extreme high and low growth rates. When their rates of growth in a range of temperatures were analysed using the approach of Perkins and Jinks (1968), most of their genotype-environmental interactions were accounted for by linear regressions on their additive environmental components.

The dikaryotic phase of *S. commune* clearly has many technical advantages for biometrical-genetical studies. In addition, the accumulated information allows selection of a character, growth rate, which is not only conveniently and reliably measured but is known to show predominantly linear genotype-environmental interactions and to be controlled by genes displaying mainly additive and dominance effects. Furthermore, the available evidence suggests that any biometrical-genetical principles that may emerge from investigations of dikaryotic growth rate in *S. commune* should be applicable to diploid organisms.

3. REGRESSION APPROACHES

Three approaches have been used to describe the genotype-environmental interactions of a set of genotypes. The first (Finlay and Wilkinson, 1963; Rowe and Andrew, 1964; Eberhart and Russell, 1966; Breese, 1969) is a purely statistical approach, whereas the second (Perkins and Jinks, 1968; Baker, 1969) and a third derived from it (Freeman and Perkins, 1971) relate the components in the regression analysis to the basic biometrical-genetical model given by Perkins and Jinks (1968). The definitions of the d_i and g_{ij} parameters in this model (No. 1 in table 1) have been modified, as suggested by Connolly (personal communication), to allow for heterozygosity in the genotypes (see also Breese, 1969).

In approach 1 (model 2) phenotype (Y_{ij}) is regressed on the additive environmental component (ϵ_j) to give two measures of sensitivity to change in environment. These are the regression coefficient, β_i , and the deviations from linear regression mean square, $(\sum_j \delta_{ij}^2)/(s-2)$. Equivalent sensitivity

measures, β_{di} and $(\sum_j \delta_{ij}^2)/(s-2)$, are obtained in approach 2 (model 3) by the regression of the genotype-environmental component (g_{ij}) on the additive environmental component (ε_j). These two regression approaches are directly related such that x_i , β_i , and δ_{ij} are equal to $(\mu + d_i)$, $(1 + \beta_{di})$

TABLE 1
Models discussed and definition of their parameters

1. *Basic biometrical-genetical model*

$$Y_{ij} = \mu + d_i + \varepsilon_j + g_{ij} \quad \text{Model 1}$$

where:

- Y_{ij} = mean phenotype of the i th genotype in the j th environment.
 μ = grand mean over all genotypes and all environments.
 d_i = genetic contribution of the i th genotype.
 ε_j = additive environmental component of the j th environment.
 g_{ij} = genotype-environmental interaction of the i th genotype in the j th environment.

2. *Regression approach 1*

$$Y_{ij} = x_i + \beta_i \varepsilon_j + \delta_{ij} \quad \text{Model 2}$$

where:

- x_i = mean expression (*i.e.* mean over all environments) of the i th genotype.
 β_i = regression coefficient of the i th genotype for the regression of Y_{ij} on ε_j .
 δ_{ij} = deviation, in the j th environment, of the i th genotype from its linear regression onto ε_j .

3. *Regression approach 2*

$$\begin{aligned} Y_{ij} &= \mu + d_i + \varepsilon_j + \beta_{di} \varepsilon_j + \delta_{ij} \\ &= \mu + d_i + \varepsilon_j (1 + \beta_{di}) + \delta_{ij} \end{aligned} \quad \text{Model 3}$$

where:

- β_{di} = regression coefficient of the i th genotype for the regressions of g_{ij} on to ε_j .

4. *Regression approach 3*

$$Y_{ij} = \mu + d_i + \bar{\beta} z_j + \bar{\delta}_j + \beta_{di} z_j + \delta_{dij} \quad \text{Model 4}$$

$$Y_{ij} = \mu + d_i + \beta_i z_j + \delta_{ij} \quad \text{Model 5}$$

where:

- β_i = regression coefficient of the i th genotype for the regression of Y_{ij} on to z_j .
 $\bar{\beta}$ = combined regression coefficient (equal to the mean of all β_i).
 β_{di} = difference between the regression coefficient of the i th genotype and the combined regression coefficient (*i.e.* $\beta_i - \bar{\beta}$). It is the coefficient for the regression of g_{ij} on to z_j .
 δ_{ij} = deviation, in the j th environment, of the i th genotype from its linear regression on to z_j .
 $\bar{\delta}_j$ = deviation of the mean of all genotypes in the j th environment from the combined regression line (*i.e.* $\varepsilon_j - \bar{\beta} z_j$).
 δ_{dij} = the deviation of the i th genotype from its linear regression on z_j in the j th environment minus $\bar{\delta}_j$ (*i.e.* $\delta_{ij} - \bar{\delta}_j$).

and δ_{ij} , respectively. The relation between β_i and β_{di} occurs because in approach 1 the additive environmental component (ε_j) as well as the genotype-environmental component (g_{ij}) is regressed on the ε_j values and this regression of ε_j on to itself has a slope of unity. Thus, when approach 1 is followed the regression sum of squares contains additive environmental as well as interaction variation and is equal to $(1 + \beta_{di})^2 \sum_j (\varepsilon_j)^2$ where that following approach 2 is $(\beta_{di})^2 \sum_j (\varepsilon_j)^2$ (Perkins and Jinks, 1968). The appro-

appropriate partition of the total degrees of freedom available from t genotypes and s environments is given for each approach in table 2. Because of the relation between the individual regression sums of squares and the equality of the deviations from regression sums of squares, the heterogeneity of regressions and the deviations from regression items of approaches 1 and 2 are equal.

The estimate of the environmental component used in approaches 1 and 2 has generally been the mean of all genotypes in each environment, calculated

TABLE 2

Assignment for each of the three regression approaches in table 1 of the degrees of freedom available from t genotypes and s environments

I. Regression approach 1

	Item	d.f.
	1. Between genotypes (G)	$t-1$
	Within genotypes (WG)	$t(s-1)$
WG {	2. Joint regression*	1
	3. Heterogeneity of regressions	$t-1$
	4. Deviations from regression	$t(s-2)$
	Total	$ts-1$

II. Regression approach 2

	Item	d.f.
	1. Between genotypes (G)	$t-1$
	2. Between environments (E)*	$s-1$
	Genotypes $\times$ environments (G $\times$ E)	$(t-1)(s-1)$
G $\times$ E {	3. Heterogeneity of regressions	$t-1$
	4. Deviations from regression	$(t-1)(s-2)$
	Total	$ts-1$

III. Regression approach 3

	Item	d.f.
	1. Between genotypes (G)	$t-1$
	Between environments (E)	$s-1$
E {	2. Combined regression	1
	3. Environmental residual	$s-2$
	Genotypes $\times$ environments (G $\times$ E)	$(t-1)(s-1)$
G $\times$ E {	4. Heterogeneity of regressions	$t-1$
	5. G $\times$ E residual	$(t-1)(s-2)$
	Total	$ts-1$

* Where non-independent environmental values are used the sum of squares of item 2 in approach 1 is equal to that of item 2 in approach 2 but the degrees of freedom assigned are different (see text).

from the actual data analysed for its interaction variation. In these cases the environmental values used on the x axis in the regression analysis have not been independent of the phenotypic variable regressed on them. The only exception to this procedure is the regression of progeny phenotypes on additive environmental components estimated from parental phenotypes. Examples where the performance of F_1 , F_2 or back-cross individuals has been regressed on parental performance may be found in Bucio Alanis and Hill (1966), Perkins and Jinks (1968), Breese (1969), Bucio Alanis, Perkins and Jinks (1969), Perkins (1970), Jinks and Perkins (1970) and Westerman (1971a, b).

Considered individually both approaches described in the preceding paragraphs appear to be statistically valid. However when, as has been the usual procedure, non-independent estimates of ε_j are used, the joint regression sum of squares with one degree of freedom in approach 1 is equal to the environments sum of squares with $(s-1)$ degrees of freedom in approach 2. This ambiguity in assignation of degrees of freedom, noted by Perkins and Jinks (1968), is considered in detail by Freeman and Perkins (*loc. cit.*) in their examination of the use of the statistical theory of regression to describe environmental and genotype-environment variations. They conclude that it is statistically invalid to use non-independent environmental values. This criticism applies, with the exception noted earlier, to all previous work in which approach 1 or approach 2 was followed.

In addition, Freeman and Perkins (*loc. cit.*) criticise the partitioning of the genotype $\times$ environment sum of squares into parts attributable to individual genotypes. This partitioning is implicit in any examination of the individual regression lines with approach 2 and, although possible arithmetically, is not valid statistically as too few degrees of freedom are available. The sensitivities of individual genotypes can only be compared by partitioning the total within genotypes sum of squares, which contains both the between environments and the genotype $\times$ environment components (Freeman and Perkins, 1971).

To correct the statistical shortcomings of the previous approaches Freeman and Perkins (*loc. cit.*) developed approach 3 in which phenotype (X_{ij}) is regressed on to independent environmental values (z_j 's). They suggest that the z_j values be obtained by replication of the genotypes being investigated or use of control genotypes such as the inbred parents used by Bucio Alanis, Perkins and Jinks (*loc. cit.*).

The biometrical-genetical model (model 4) and the joint regression analysis (approach 3) proposed by Freeman and Perkins (*loc. cit.*) are given in table 1 and table 2 respectively. The significance of each item in the joint regression analysis can be determined by an F (variance ratio) test against an error mean square obtained from replication. In addition, since these items are orthogonal comparisons can be made between them. Items 2, 3, 4 and 5 provide for the $\bar{\beta}$, $\bar{\delta}_j$, β_{di} and δ_{dij} components in model 4 respectively. When item 4 is significant the regressions are heterogeneous. Whether any two slopes (β_i) are different can be determined by a t -test. If item 3 is non-significant the z_j values provide a statistically adequate assessment of how the additive environmental component of the genotypes being investigated (ε_j) is changing with change in environment. If, in addition, $\bar{\beta}$ is not different from unity the z_j values adequately estimate ε_j and model 4 reduces to that of approach 2 (Freeman and Perkins, *loc. cit.*).

The relationships between the parameters in the various models can be deduced from table 1. To simplify this a simple regression model for approach 3 is given as model 5 in this table. This model would seem to be the more useful one in situations where z_j does not adequately estimate ε_j or where biometrical-genetical interpretation is not required.

In the following text $\hat{\varepsilon}_j$ denotes the mean in a particular environment of the individuals whose interaction with environments is being analysed and is thus a non-independent assessment of the environmental value. In contrast z_j denotes an independent assessment, *i.e.* one not obtained from the data being analysed.

4. MATERIALS AND METHODS

(a) *Genotypes (dikaryons)*

The dikaryons investigated in the present studies were derived from a cross between two selected dikaryons, 3-6L and 3-6H, which were known to be relatively homozygous (Connolly, personal communication) and to differ markedly in both mean growth rate and sensitivity to change in environment (Connolly, personal communication; Fripp, unpublished). These two selections, referred to throughout as the *parental dikaryons*, had been obtained from a single wild isolate, No. 6 of Simchen (1966b), by eight generations of selection for high and low growth rate in a single environment (2 per cent. malt at 30° C.) (Connolly, personal communication).

From each parental dikaryon monokaryons were isolated and their mating types determined as described by Connolly and Simchen (1968). Six monokaryons of $A_{12}B_{11}$ mating type from 3-6L, the low growth-rate parent, and six of $A_{11}B_{12}$ mating type from 3-6H, the high growth-rate parent, were mated in all compatible combinations (*i.e.* 6×6 NCM2) to give 36 F_1 dikaryons. When grown in nine diverse environments these showed low genetic and low genotype-environmental components of variation, confirming that each parental dikaryon was relatively isogenic. Each F_1 dikaryon is thus comparable to an F_1 genotype from a cross between two isogenic selection lines of a diploid species and on selfing should produce a population of genotypes showing a range of growth rates and environmental sensitivities. Hence a single F_1 dikaryon (F_1 122) selected at random was fruited and a sample of its monokaryotic progeny isolated. Six monokaryons of mating-type $A_{11}B_{11}$ and six of $A_{12}B_{12}$ were chosen at random and mated (6×6 NCM2) to produce 36 " F_2 " dikaryons, which will be referred to as the *trial dikaryons*. These were grown in each of fifteen environments. The F_1 dikaryon (F_1 122) from which they were derived was also grown in each environment and is referred to as the *F_1 control dikaryon*. In ten of the environments a second set of 36 " F_2 " dikaryons, referred to as the " F_2 " *control set*, was also grown. The latter was derived at the same time and by the same procedures as the trial set but from a different F_1 dikaryon (F_1 108). The F_1 control dikaryon and the " F_2 " control set have been used to provide independent assessments of the environments.

It should be noted that the " F_2 " dikaryons are not strictly comparable to a standard F_2 generation (*i.e.* generation produced by random mating of an F_1). Rather, they are equivalent to the 36 progenies of a 6×6 NCM2 mating between 12 diploid homozygotes that have been derived by inbreeding without selection from the F_2 progeny of a single F_1 genotype. To emphasise this difference inverted commas have been used when referring to these dikaryons. The derivation of the F_1 and " F_2 " dikaryons used in the present investigation is summarised in fig. 1.

(b) *Environments*

The environments were investigated as, and can be conveniently subdivided into, two sets. The first was intended to be an orthogonol set of nine environments, made up three media, Czapek (Smith, 1969), SF and 2 per cent. malt (Simchen and Jinks, 1964) and three incubation temperatures, 20° C., 25° C. and 30° C. Unfortunately the two blocks of the 30° C. Czapek environment were erroneously set up from batches of medium

* The 36 progeny of each 6 × 6 NCM2 mating were numbered systematically one horizontal array after another, so those with a parental monokaryon in common are readily determined using a 6 × 6 checkerboard diagram.

FIG. 1.—Derivation of the F₁ and “F₂” dikaryons from a cross between a low (3-6L) and a high (3-6H) growth rate selection line dikaryon.

TABLE 3
Composition of the environments

	Environment number	Temperature (°C.)	Medium
<i>Set 1</i> (experiment 1)	1	30	SF
	2	30	2% malt
	3	30	Czapek block I
	4	30	Czapek block II
	5	25	SF
	6	25	2% malt
	7	25	Czapek
	8	20	SF
	9	20	2% malt
	10	20	Czapek
<i>Set 2</i> (experiment 2)	11	25	0.04% dextrose*
	12	25	0.20% dextrose
	13	25	0.40% dextrose
	14	25	2.00% dextrose
	15	25	10.00% dextrose

* Percentage is grammes per 100 ml. of medium.

containing different phosphate salts. These gave very different growth rates, and these two blocks have been considered to constitute different environments, making a total of 10 environments in the first set. The second set comprised five environments derived by varying the dextrose concentration in the *S. commune* minimal medium of Raper and Miles (1958). One temperature, 25° C., was used.

The composition of the 15 environments is summarised in table 3. The environments will be referred to by the numbers under which they are listed in this table.

(c) *Experimental procedures*

The growth tube technique of Simchen and Jinks (1964) was used to measure the rate of growth. The inoculum for the tubes was produced by subculturing the required genotypes on plates containing SCM medium (Snider and Raper, 1958) and incubating for 3 days at 25° C. Following Simchen and Jinks (*loc. cit.*), the total growth over a 10-day period is used as the metric in the analyses and is referred to as the "growth rate".

The two sets of environments were studied in separate experiments. In experiment 1, 75 dikaryons, consisting of the 36 trial " F_2 " dikaryons, the 36 " F_2 " control set dikaryons, the F_1 control dikaryon and the two parental dikaryons were grown in each of the set 1 environments. Of these, only the 36 trial " F_2 " dikaryons and the F_1 control dikaryon will be considered in the present paper. In experiment 2, the 36 trial " F_2 " dikaryons, the F_1 control, and the two parental dikaryons were grown in each of the five set 2 environments.

Each experiment was replicated in two blocks. The use of different incubators for the three temperatures meant that blocks could not be completely cross-classified. Within each block there was complete randomisation of the dikaryons and the two blocks within each environment were allocated to different incubator shelves.

5. ANALYSIS AND RESULTS

A Bartlett test showed that the error variances (*i.e.* blocks $\times$ genotypes mean squares) of the 15 environments were heterogeneous. Transformation to the log or the square root scales failed to remove this heterogeneity and appeared to have little effect on the interpretation of the data as a whole. Hence it was decided to consider untransformed data in the present and subsequent studies. The genotype-environmental analysis of Freeman and Perkins (1971) was carried out using the mean performance, over blocks, of the F_1 control dikaryon to provide an independent assessment of the environments. Following Freeman and Perkins (1971) b_i denotes the regression coefficient of the i th genotype in this analysis.

The joint regression analysis is given in table 4. All items are greater, at the 0.1 per cent. level, than their appropriate error mean squares, and the combined regression and heterogeneity of regressions mean squares are both greater than their corresponding residual mean squares. The significance of item 1 shows that genetic differences which are independent of the environmental conditions, are present. Items 2 and 3 reveal how adequate the z_j values are as an assessment of the additive environmental component (e_j), when the latter is estimated as the mean performance over

TABLE 4

Joint regression analysis (Freeman and Perkins, loc. cit.) for growth rate of 36 “F₂” dikaryons in 15 environments. F₁ control dikaryon (F₁122) used to provide independent environmental values

Item	d.f.	M.S.	VR†	VR†
1. Genotypes (G)	35	841.733	57.94(7)***	—
2. Combined regression	1	122,287.208	2494.79(6)***	371.86(3)***
3. Environmental residual	13	328.849	6.71(6)***	—
4. Heterogeneity of regressions	35	146.999	10.12(7)***	3.48(5)***
5. G × E residual	455	42.264	2.91(7)***	—
6. Blocks (B) within environments	13††	49.017	3.37(7)***	—
7. (B × G) within environments	455††	14.528	—	—

Significance level: *** < 0.005.

† Item used as denominator given in parentheses.

†† One block only in each of two environments.

FIG. 2.—Frequency distribution of linear sensitivity (b_i) for the 36 “F₂” dikaryons.

the trial replicates of the set of trial genotypes in each environment (*i.e.* $\hat{e}_j$). As item 3 in table 4 is significant (*i.e.* $\bar{\delta}_j \neq 0$) the z_j values do not change, relative to one another, with change in environment, in precisely the same way as the $\hat{e}_j$ values. Furthermore, the combined regression coefficient, 0.871 ± 0.045 , is different from unity. Thus both tests ($\bar{\delta}_j = 0$ and $\bar{\beta} = 1.0$)

of Freeman and Perkins (1971) indicate that the z_j 's do not provide statistically adequate estimates of ε_j in this set of data. Nevertheless, the correlation between z_j and $\hat{\varepsilon}_j$ is very high ($r = 0.983$) and is almost as large as that

FIG. 3.—Relationship between mean growth rate (μd_i) and linear sensitivity (b_i) for the 36 "F₂" dikaryons.

between independent estimates of ε_j obtained from different replicates of the same genotypes in the same environments. The z_j 's are obviously providing extremely satisfactory assessments of the environments and therefore the

partitioning of the genotype $\times$ environment sum of squares and the examination of the regressions for individual genotypes should be meaningful.

Item 4 reveals whether any of the genotype-environmental interactions can be attributed to differences in the linear responses of the genotypes to change in the environment. Item 5 provides a test of whether all the genotype-environmental interactions are so explained, *i.e.* a test for the presence of interaction variation which is not attributable to differences in linear sensitivity. It can be seen from table 4 that items 4 and 5 are both significant, indicating the presence of both *linear* and *non-linear* components of variation in the present data. The heterogeneity of regressions mean square is greater than its residual, indicating that a major part of the interaction variation is accounted for by differences in the regressions of the individual genotypes.

A measure of how much, on average, of the difference between two individuals of the same genotype grown in two different environments, excluding that part attributable to the additive environmental effect, is accounted for by the regression coefficient (b_i) can be derived from items 4 and 5. This measure referred to as the *linear proportion* (l per cent.) is defined as $\frac{l}{l+nl} \times 100$ where l = the heterogeneity of regressions mean square minus the error mean square and nl = the $G \times E$ residual mean square minus the error mean square. Its value in the present analysis is 82.2 per cent.

Considering the 36 dikaryons individually, a linear regression accounted for most of the variation over environments of each dikaryon, but for only four did it account for it all. Whether the linear responses of any two dikaryons are different can be determined by a *t*-test of their b_i 's. The distribution of the 36 b_i values, known to be heterogeneous from the joint regression analysis, is shown in fig. 2. These estimates (b_i) of linear sensitivity vary from 0.507 to 1.139 with a mean ($\bar{b}$) of 0.871. The deviations from regression mean squares of the individual dikaryons are also heterogeneous, with a χ^2_{35} of 269.7 ($P < 0.001$). The dikaryons thus differ in both linear and non-linear sensitivity to environmental change.

The mean performances of the dikaryons (*i.e.* $\hat{\mu} + \hat{d}_i$) varied from 25.800 to 56.367 with a mean ($\hat{\mu}$) of 39.130 ± 1.248 . In fig. 3 the linear sensitivity of each genotype is plotted against its mean performance. It is obvious that these two aspects of phenotype are positively associated ($r = 0.688$, $P < 0.001$). This association is not absolute, however, since there are a few dikaryons with low growth rate and high linear sensitivity, and vice versa.

6. DISCUSSION

The results and their interpretation are quite straightforward and need only be discussed with respect to whether or not the stated aims of the present series of investigations are likely to be achieved using the particular regression approach and biological material described.

The results confirm that genotype-environmental interactions are involved in the phenotypic variation in rate of growth of dikaryons of *S. commune* grown in different environments. Following the approach of Freeman and Perkins (*loc. cit.*) most of the variation over environments of each dikaryon can be accounted for by its linear regression on to the environmental values. Furthermore, a significant part, but not all, of the genotype-

environmental interactions of the set of dikaryons can be accounted for by differences in the slopes of their linear regressions, that is by differences in linear sensitivity. The 36 dikaryons differ also in their non-linear sensitivity to environmental change.

The present investigations are the first where genotype-environmental interactions have been analysed using the regression approach of Freeman and Perkins (*loc. cit.*). The example given by these authors is, in fact, taken from the present set of data. The findings, though, agree with those in previous studies encompassing a wide variety of different characters and organisms and in which the performances of some or all genotypes in a set are regressed on to non-independent environmental values (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Perkins and Jinks, 1968; Breese, 1969; Connolly, personal communication; Westerman, 1971*a, b*). This agreement is of considerable practical importance. It suggests that the use of independent environmental values will not alter the general conclusions that have been drawn from previous investigations, even though in certain instances tests of significance which are not strictly reliable have been made (Freeman and Perkins, *loc. cit.*). It also shows that assessments of the environments which are adequate for the regression approach to genotype-environmental interactions can be provided by a single control genotype. While this conclusion is perhaps not surprising in the present instance where the control genotype is closely related to the trial genotypes, similar results have been obtained using an unrelated control (Frapp, in preparation). Agreement between studies using independent (z_j) and non-independent ($\hat{e}_j$) environmental values would be expected in the ideal situation where the z_j values used do not differ from the $\hat{e}_j$ values. This ideal situation will not always be achieved. Thus, the crucial result in the present study is that an interpretable picture, consistent with the previous work in this field, emerges even when the z_j and $\hat{e}_j$ values differ. Various methods by which z_j values may be obtained will be compared and discussed in a subsequent paper.

A positive correlation between mean performance and linear sensitivity has been found in a number of previous studies (Eberhart and Russell, 1966; Perkins and Jinks, 1968; Westerman, 1971*a*). The origin of the relationship between these two characters in the present material will be examined in a subsequent paper.

Finally, the present results demonstrate the suitability for investigations of genotype-environmental interactions of the material chosen. Particularly relevant are: (i) the finding that a significant part of the genotype $\times$ environment variation is accounted for by differences in linear sensitivity, (ii) the agreement between the present and previous studies, (iii) the ability to use a single control genotype to assess the environments, and (iv) the correlation between mean performance and linear sensitivity to environmental change.

7. SUMMARY

1. The properties, technical and genetical, of dikaryotic growth rate in *Schizophyllum commune* which make it a suitable character for studies of genotype-environmental interactions are summarised. The various regression approaches that have been used for the analysis of this source of variation in a set of genotypes are described and compared.

2. The rates of growth of 36 dikaryons, progeny of a single F_1 dikaryon, in each of 15 environments are analysed following the regression approach of Freeman and Perkins. The performance of the parental F_1 dikaryon is used to provide environmental values that are independent of the data being regressed.

3. Most of the variation with change in environment can be accounted for by the linear regressions on these environmental values and a significant part, but not all, of the genotype-environmental variation can be accounted for by heterogeneity of these regressions.

4. Two findings of considerable practical significance emerge. Firstly, the single control genotype provides an extremely good assessment of the environments. Secondly, the present results differ little from those of previous studies where non-independent environmental values were used.

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