THE USE OF REGRESSION METHODS TO STUDY GENOTYPE-ENVIRONMENT INTERACTIONS

EXTENDING GRIFFING'S MODEL FOR DIALLEL CROSS EXPERIMENTS AND TESTING AN EMPIRICAL GROUPING METHOD

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SUMMARY

A model combining features of Griffing's diallel cross analysis with regression analysis for genotype-environment interactions is introduced using carp data of Moav *et al.* (1975) as an example. An analysis of variance based on this model provides information on the combining abilities of genetic effects and the interactions of these effects with environments from which inferences can readily be made on heterosis and heterosis-environment interactions.

Applying the empirical grouping method of Lin and Thompson (1975) to these data (ignoring their diallel cross structure) established groups which were remarkably consistent with their members' crossing backgrounds.

1. INTRODUCTION

REGRESSION techniques for studying genotype-environment (GE) interactions are among the most widely used methods for investigating the response patterns of genotypes. Typically, the linear regression of the data on environmental indices is obtained for each genotype (the indices are usually defined as the differences between the environmental means and the grand mean). The regression slopes and intercepts, the latter simply the genotype means, are considered to be characteristics of the genotypes.

Several recent publications have used this approach on data from diallel cross experiments. These studies generally treated the intercept and slope obtained from the regression analysis as a starting point and then proceeded with a genetic analysis treating the two estimates as if they were independent observations. For example, Hinkelmann (1974) suggested an analysis in which the sum of squares for heterogeneity of slopes was partitioned into general and specific combining ability (g.c.a. and s.c.a.) components to investigate whether heterogeneity of slope can be attributed to " interactions between environments and additive or non-additive gene action ", Moav, Hulata, and Wohlfarth (1975) regarded each slope as being the sum of two components (one proportional to the corresponding intercept and the other equal to the remainder) which they obtained by regressing the slopes on the intercepts; the two components of the slopes, and the intercepts, were then analysed separately using potence ratios to investigate the heterosis of cross-breds. Connolly and Jinks (1975) partitioned the slope into the same two components, but used the approach of Jinks (1954) and Hayman (1954) to the diallel cross to interpret them.

In view of these studies, it seems desirable to develop a single model which specifically relates the regression parameters of the GE interaction

to the appropriate genetic parameters so that the genetic components and their interactions with environment can be examined simultaneously. One such model based on the concept of additivity and dominance was proposed by Perkins (1970), as an extension of Perkins and Jinks (1968). Here we present another model of this type based on Griffing's (1956) combining ability approach, and illustrate its practical value using the carp weight gain data of Moav *et al.* The relationship between this model and other models pertaining to GE interaction are discussed.

Lin and Thompson (1975), working in a more general context, have shown how the genotype-environment interactions can be used empirically to group genotypes with similar response patterns. Since this diallel cross data of Moav *et al.* provide a useful example of GE interactions with known genotypic background, the method of Lin-Thompson has been applied to these data to determine if the resulting groups conform with this background.

2. DATA AND ANALYSES

Data given by Moav *et al.* (1975) for the adjusted weight gain of common carp (*Cyprinus carpio L.*) were used in the present study. Twelve genotypes, including four parental lines—a Chinese strain, Big-Belly (BB), and the European strains, Našice (Nas), Gold (G) and Dor 70 (Dor), six F_1 crossbreds

TABLE 1

Weight gain data of 12 genotypes grown under five environments (in grams, adjusted for initial weight) from Moav et al. (1975). The final two columns are estimates of individual regressions on the environmental indices

| Genotype | | Environment | | | | | Regression | |
Cross	*ij-* identification	Density 1 at Dor	Yehiam	Density 2 at Dor	Density 3 at Dor	Density 4 at Dor	Intercept (mean)	Slope
BB	11	264	283	297	367	468	335·8	0·4773
BB × Nas	12	378	395	454	505	725	491·4	0·8030
BB × G	13	321	405	401	495	726	469·6	0·8855
BB × Dor	14	383	386	457	535	740	500·2	0·8490
Nas	22	279	292	352	479	795	439·4	1·2285
Nas × G	23	397	397	520	590	891	559·0	1·1639
Nas × Dor	24	399	403	477	594	918	558·2	1·2406
G	33	301	317	391	478	726	442·6	0·9962
G × Dor	34	353	388	472	587	780	516·0	0·9858
Dor	44	394	403	517	593	874	556·2	1·1238
V		356	416	456	589	877	538·8	1·1910
L (G × Blue-Grey)		360	397	444	551	816	513·6	1·0555
Environmental indices (θ_k)		−144·65	−119·90	−56·90	36·85	284·60		

of these lines, and two commercial crossbreds V and L—were reared under five environmental conditions: two locations, Dor and Yehiam, with four population densities at Dor. The genotype-environment means are presented in table 1. The environmental indices (θ_k) were obtained by subtracting the overall mean from each environmental mean. These values will be regarded as constant and assumed to represent environments in both Analyses I and II. In Analysis I, this is a slight departure from common practice where indices are usually based on the genotypes included in the analysis. However, in order to simplify the presentation of results and to facilitate comparison of the results with those of Moav *et al.*, a single set of θ_k has been used throughout. Analysis I was, in fact, repeated using indices based on the 10 relevant genotypes, but the results differed little from those presented here.

(i) *Analysis I. Joint combining ability and regression analysis*

The 10 genotypes of Moav *et al.* which comprised a diallel cross (*i.e.* excluding V and L) were investigated in Analysis I. Let Y_{ijk} be the weight gain of the ijth genotype (the progeny of the cross between the ith and the jth parental lines) at the kth environment. If the GE interaction can be expressed as a linear function of the environmental indices, the two-way classification model can be written as follows:

$$Y_{ijk} = \mu + \alpha_{ij} + \varepsilon_k + \beta_{ij}\theta_k + \Delta_{ijk} \qquad \text{(Model 1)}$$

where α_{ij} are the genetic effects, ε_k are the environmental effects, β_{ij} are the coefficients of regression of $(Y_{ijk} - \bar{Y}_{ij.} - \bar{Y}_{..k} + \bar{Y}_{...})$ on θ_k and Δ_{ijk} are deviations.

If genetic effects are written in terms of g.c.a. and s.c.a., *i.e.*

$$\alpha_{ij} = g_i + g_j + s_{ij},$$

where g_i and s_{ij} represent g.c.a. and s.c.a. respectively; and if the interaction between these components and environment can be expressed as a linear function of θ_k, Model 1 can be written as follows:

$$Y_{ijk} = \mu + g_i + g_j + s_{ij} + \varepsilon_k + [\beta_{(g)i} + \beta_{(g)j} + \beta_{(s)ij}]\theta_k + \Delta_{ijk} \qquad \text{(Model 2)}$$

where $\beta_{(g)i}$, $\beta_{(s)ij}$ are the regression coefficients of g_i and s_{ij} on θ_k respectively. To be consistent with Griffing's Method 2* (1956), the following restrictions are imposed:

$$\sum_i g_i = \sum_i \beta_{(g)i} = \sum_k \varepsilon_k = 0,$$

and

$$s_{ii} + \sum_j s_{ij} = 0, \quad \beta_{(s)ii} + \sum_j \beta_{(s)ij} = 0,$$

where

$$s_{ij} = s_{ji}, \quad \beta_{(s)ij} = \beta_{(s)ji}.$$

The analysis of variance of the carp data, assuming Model 2, is shown in table 2. Although the same mean squares would be obtained by Hinkelmann's approach, his specification of the model differs from Model 2, a point which will be discussed later. The estimates of g_i and s_{ij} at each environment and their coefficients of regression on θ_k are shown in table 3. Both the g.c.a. and s.c.a. mean squares are highly significant ($P < 0.01$) when tested against the pooled residual mean square (345·4 with 27 d.f.). Most of the $g_i \times E$ interaction is accounted for by heterogeneity of the slopes of g_i. On the other hand, since the mean square for differences among $\beta_{(s)ij}$ (*viz.* 693·4) is not significant, the null hypothesis $\beta_{(s)ij} = 0$, for all i and j, is not unreasonable. It is worth noting that the pooled residual mean square is about the same magnitude as the mean square for the replication-genotype interaction pooled over environments at Dor as reported in the original paper (1563/4 = 390·8).

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* Although Analysis I was based on Griffing's Method 2, Model 2 can clearly be used with any of Griffing's other three methods.

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TABLE 2

ANOVA for Model 2 of text

Source	d.f.		MS
Environment (E)	4		287558·8
Genotypes (G)	9		
g.c.a. (g_i)		3	43749·5
s.c.a. (s_{ij})		6	14356·7
$G \times E$	36		
$g_i \times E$		12	(4901·4)
Slopes of g_i		3	18535·9
Residual		9	356·6
$s_{ij} \times E$		24	(428·2)
Slopes of s_{ij}		6	693·4
Residual		18	339·9
Total	49		

TABLE 3

Estimates of combining abilities (g₁, sᵢⱼ) and heterosis (Hᵢⱼ) at each environment and their coefficients of regression on the environmental indices

	Density 1 at Dor	Yehiam	Density 2 at Dor	Density 3 at Dor	Density 4 at Dor	Mean	Regression coefficients
g_1	−20·8	−13·8	−43·8	−57·1	−115·8	−50·2	−0·2308
g_2	−0·4	−9·3	−2·3	5·9	50·4	8·9	0·1313
g_3	−10·3	−1·8	1·0	2·8	4·6	−0·7	0·0252
g_4	31·4	24·8	45·2	48·4	60·8	42·1	0·0744
s_{11}	−41·4	−56·4	−49·1	−41·1	−64·8	−50·6	−0·0365
s_{12}	52·3	51·1	66·4	33·9	26·0	45·9	−0·0728
s_{13}	5·1	53·6	10·0	27·0	72·9	33·7	0·1158
s_{14}	25·4	8·1	21·9	21·4	30·7	21·5	0·0300
s_{22}	−67·1	−56·4	−77·1	−55·1	−70·1	−65·2	−0·0094
s_{23}	60·8	41·1	87·5	59·0	71·7	64·0	0·0321
s_{24}	21·1	20·6	0·4	17·4	42·5	20·4	0·0596
s_{33}	−25·4	−40·4	−44·8	−49·8	−47·5	−42·8	−0·0294
s_{34}	−15·1	−1·9	−8·0	13·5	−49·6	−12·2	−0·0891
s_{44}	−15·7	−13·4	−7·1	−26·1	−11·8	−14·8	−0·0003
H_{12}	106·5	107·5	129·5	82·0	93·5	103·8	−0·0499
H_{13}	38·5	105·0	57·0	72·5	129·0	80·4	0·1488
H_{14}	54·0	43·0	50·0	55·0	69·0	54·2	0·0484
H_{23}	107·0	92·5	148·5	111·5	130·5	118·0	0·0515
H_{24}	62·5	55·5	42·5	58·0	83·5	60·4	0·0644
H_{34}	5·0	28·0	18·0	51·5	−20·0	16·6	−0·0742
θ_k	−144·6	−119·9	−56·9	36·8	284·6	0	

(ii) *Analysis II. Phenotypic grouping of genotypes based on Lin-Thompson's method*

All 12 genotypes were included in this analysis. The intercepts and slopes of the regression of Y_{ijk} on θ_k for each genotype are shown in table 1; the dendrogram of the cluster analysis is given in fig. 1. Six groups were formed when the clustering was stopped after the dissimilarity index exceeded the critical (5 per cent) F-value (table 4). This grouping, established by numerical means, seems genetically very reasonable: the four parental lines all belong to different groups; three crossbreds between Chinese and
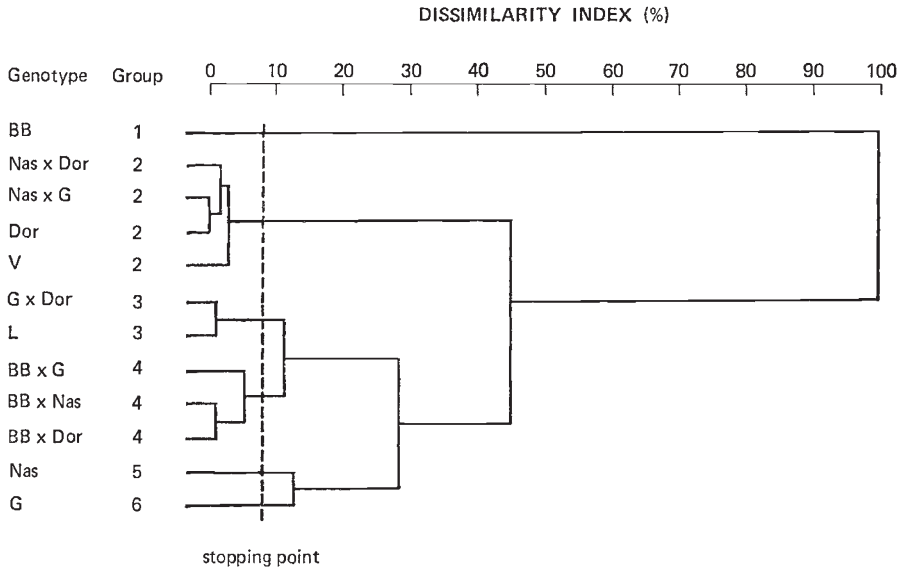
DISSIMILARITY INDEX (%)

FIG. 1.—Dendrogram of clustering process for 12 genotypes, based on the Lin-Thompson method.

European strains are in one group; and European crossbreds fall into two groups. Within each of groups 2, 3, and 4, almost all of the members are half-sibs.

TABLE 4

Intercepts and slopes for the six groups of 12 genotypes

Group	Genotype	Intercept	Slope
1	BB	335·8	0·4773
2	Nas × G, Nas × Dor, Dor, V	553·1	1·1798
3	G × Dor, L (G × Blue-Grey)	514·8	1·0207
4	BB × Nas, BB × G, BB × Dor	487·1	0·8458
5	Nas	439·4	1·2285
6	G	442·6	0·9965

3. DISCUSSION

(i) *Examination of heterosis and heterosis by environment interactions*

When the use of Model 2 is justified, the approach followed in Analysis I can assist considerably in the interpretation of the various genetic relationships suggested by the data. Consider, for example, the question of heterosis.

If we define the heterosis H_{ijk} resulting from crossing the ith and the jth parental line at the kth environment as the expectation of

$$Y_{ijk} - \tfrac{1}{2}(Y_{iik} + Y_{jjk})$$

then under Model 2 (indicating estimates by $^\wedge$), H may be estimated as

$$\hat{H}_{ijk} = \hat{s}_{ij} - \tfrac{1}{2}(\hat{s}_{ii} + \hat{s}_{jj}) + [\hat{\beta}_{(s)ij} - \tfrac{1}{2}(\hat{\beta}_{(s)ii} + \hat{\beta}_{(s)jj})]\theta_k$$

or

$$\hat{H}_{ijk} = \overline{H}_{ij.} + \hat{\beta}_{(H)ij}\theta_k$$

where

$$H_{ij.} = \hat{s}_{ij} - \tfrac{1}{2}(\hat{s}_{ii} + \hat{s}_{jj})$$

and

$$\hat{\beta}_{(H)ij} = \hat{\beta}_{(s)ij} - \tfrac{1}{2}(\hat{\beta}_{(s)ii} + \hat{\beta}_{(s)jj}).$$

These relationships indicate that if heterosis is a linear function of θ_k, the estimated intercept is a linear combination of $\hat{s}_{ij}$ and the estimated slope is a linear combination of $\hat{\beta}_{(s)ij}$.

Although the concepts and calculations presented by Perkins (1970) for the diallel cross differ considerably from those presented here, it is interesting to note that $\bar{H}_{ij.}$ is identical to Perkins' estimate of dominance, and if the same environmental indices are used in both methods, $\hat{\beta}_{(H)ij}$ is identical to Perkins' estimate of the linear coefficient of dominance. These points are discussed below.

An interesting feature of Analysis I was that g_i differed significantly among environments but s_{ij} did not; i.e. the $\beta_{(s)ij}$ appeared to be zero under this range of environmental conditions (table 3). Hence, it is apparent from the expression for H_{ijk} above that there was no heterosis by environment interaction. This implies that from the point of view of adaptation, only the g.c.a. was important, or alternatively, that heterosis remained constant over environments.

Again, since the $\beta_{(s)ij}$ were not significantly different from zero, an appropriate model for β_{ij} of Model 1 is $\beta_{ij} = \beta_{(g)i} + \beta_{(g)j}$ which implies that $\beta_{ij} = \tfrac{1}{2}(\beta_{ii} + \beta_{jj})$, since $\beta_{ii} = 2\beta_{(g)i}$, if $\beta_{(s)ii} = 0$. This relationship explains why Moav et al. found the response slopes of crossbreds to be generally intermediate between those of their parents.

(ii) Comparison with Moav's et al. potence ratio analyses

Moav et al. used a potence ratio to compare the weight gains of six crossbreds at six environmental points: three actual points and three hypothetical points (Moav et al., p. 334). The ratio at the kth environment is defined as D_{ijk}/A_{ijk}, where D_{ijk} is equivalent to the present H_{ijk} and A_{ijk} is defined as one-half of the difference between parents. They observed that the mean ratio of all six crosses became smaller as the environments improved, and that in general this held true for each individual cross.

This trend can be interpreted in terms of Model 2 as follows. Since it has already been shown that H_{ijk} (and $\beta_{(s)ij}$) do not appear to change with respect to environments, any change in the potence ratio is due to A_{ijk} which can be written,

$$\hat{A}_{ijk} = \hat{g}_i - \hat{g}_j + \tfrac{1}{2}(\hat{s}_{ii} - \hat{s}_{jj}) + [\hat{\beta}_{(g)i} - \hat{\beta}_{(g)j} + \tfrac{1}{2}(\hat{\beta}_{(s)ii} - \hat{\beta}_{(s)jj})]\theta_k.$$

A change in A_{ijk} due to environment is merely a change in $(\hat{\beta}_{(g)i} - \hat{\beta}_{(g)j})\theta_k$ because $(\hat{\beta}_{(s)ii} - \hat{\beta}_{(s)jj})$ is approximately zero. It can be observed from table 3 that differences among $\hat{g}_i$ increased as θ_k improved, particularly when one parent was BB.

Moav et al. also investigated the potence ratios of the two components of slope mentioned in the first section (the slope, $\hat{\beta}_{ij} + 1$ of Model 1, assuming $\theta_k = \varepsilon_k$, is redefined to be equal to $1 + M\hat{\alpha}_{ij} + N_{ij}$ where M is estimated by the least squares regression of $\hat{\beta}_{ij}$ on $\hat{\alpha}_{ij}$ and N_{ij} is the remainder). They

observed that for six crossbreds the potence ratios of the scale function $(1 + M\hat{\alpha}_{ij})$ were all positive, while the potence ratios of the specific responsiveness (N_{ij}) were all negative. The mean potence ratios were 1·30 and −1·12 respectively. From these results, they concluded that both components expressed heterosis of about the same magnitude but in opposite directions giving rise to " additivity of slopes ", that is, the absence of heterosis-environment interactions. Thus Moav *et al.* assume two genetic systems working independently, one controlling the intercept and part of the slope (scale function) and the other controlling the rest of the slope (specific responsiveness), while the present interpretation assumes that one genetic system (g.c.a. and s.c.a.) controls both α_{ij} and β_{ij}. From Moav's *et al.* point of view the additivity of slope arises from the balance of two systems, whereas under the present considerations, additivity is due to nonresponsiveness of s.c.a. It is difficult to determine which of these two interpretations is more in accord with genetic reality. However, it should be noted that the present approach seems easier to comprehend as it is more consistent with the concept of combining ability proposed by earlier workers.

(iii) *Comparison with Moav's* et al. *classification*

In a brief comment, Moav *et al.* suggested four classes for the 12 genotypes, based on the average performance. They included groups 5 and 6 of table 4 in one class and groups 2 and 3 in another class. From fig. 1, it can be seen that groups 5 and 6 are relatively similar, but groups 2 and 3 are considerably different. For comparison ANOVAs based on the four groups of Moav *et al.* and the six groups of fig. 1 are presented in table 5. The analyses show that there were still large proportions of variation in

TABLE 5

ANOVAs based on the two groupings of the genotypes. A refers to the grouping obtained in the text. B refers to the grouping obtained by Moav et al

Source	A d.f.	A MS	B d.f.	B MS
Environments (E)	4	362677·0	4	362677·0
Groups (Gr)	5	45603·2	3	72745·5
Genotype (α)/Gr	6	645·1	8	1706·3
Gr × E	20		12	
slope × Gr	5	12741·2	3	18787·7
dev. × Gr	15	201·0	9	165·9
α × E	24		32	
slope × α/Gr	6	262·9	8	1115·0
dev. × α/Gr	18	414·0	24	373·9

" genotype within groups " and in " slope × α within groups " for Moav's *et al.* classification, indicating that the average performance and slopes within certain groups are not really the same. It may be observed from table 4 that groups 5 and 6 have similar intercepts but they differ in slope, while groups 2 and 3 have similar slopes but they differ in intercept. It should be noted that the relatively clear-cut classification pattern of Analysis II could be, in part, a result of the small heterosis by environment interaction.

(iv) *The interrelationships between Model 2 and other regression models*
for GE interactions

When a diallel cross design is used in a GE experiment, the data can be analysed using a model such as Model 2 which incorporates genetic and regression models, or they can be analysed using a regression model such as Model 1, which ignores the information provided by the genetic structure of the experiment. In a more general context Model 1 can be expressed as a simple regression of Y_{ijk} on θ_k; *i.e.*

$$Y_{ijk} = a_{ij} + b_{ij}\theta_k + \Delta'_{ijk} \qquad \text{(Model 3)}$$

The algebraic relationships among the estimates of the corresponding parameters in each model are summarised below:

(i) The estimates under Model 1 can be expressed in terms of the estimates of Model 3 as

$$\hat{\beta}_{ij} = \hat{b}_{ij} - \sum_k (\overline{Y}_{..k} - \overline{Y}_{...})\theta_k / \sum_k \theta_k^2 = \hat{b}_{ij} - \overline{b}_{..}$$

$$\hat{\alpha}_{ij} = \hat{a}_{ij} - \bar{a}_{..}$$

where $\hat{b}_{..}$ and $\bar{a}_{..}$ are the means of all estimates of b_{ij} and a_{ij} respectively.
When $\theta_k = \overline{Y}_{..k} - \overline{Y}_{...} = \hat{\varepsilon}_k$, the above equations become

$$\hat{\beta}_{ij} = \hat{b}_{ij} - 1$$

$$\hat{\alpha}_{ij} = \hat{a}_{ij} - \overline{Y}_{...}$$

Thus, for example, in Analysis 1 $(\theta_k \neq \hat{\varepsilon}_k)$

$$\hat{\beta}_{11} = 0.4773 - 0.9754 = -0.4981$$

(ii) The β_{ij} of Model 1 and $\beta_{(g)i}$ and $\beta_{(s)ij}$ of Model 2 are related as follows

$$\hat{\beta}_{ij} = \hat{\beta}_{(g)i} + \hat{\beta}_{(g)j} + \hat{\beta}_{(s)ij}$$

e.g. from table 3.

$$2\hat{\beta}_{(g)1} + \hat{\beta}_{(s)11} = 2(-0.2308) - 0.0365 = -0.4981$$

which is $\hat{\beta}_{11}$ of Analysis 1.

(iii) The estimates of $\beta_{(g)i}$, $\beta_{(s)ij}$ and their sums of squares (SS) given in tables 2 and 3 can be obtained directly by regressing g_{ik}, s_{ijk} on θ_k, where g_{ik} and s_{ijk} represent the g.c.a. and s.c.a. respectively at the kth environment as shown in the left column of table 6. However, they can also be expressed in terms of $\hat{\beta}_{ij}$ of Model 1, or in terms of $\hat{b}_{ij}$ of Model 3 as shown in the right column of table 6.

When $\hat{b}_{ij}$ are analysed by Griffing's combining ability analysis, the estimates of g.c.a. and s.c.a. for $\hat{b}_{ij}$ are equivalent to $\hat{\beta}_{(g)i}$ and $\hat{\beta}_{(s)ij}$; and the sums of squares for g.c.a. and s.c.a. of $\hat{b}_{ij}$ multiplied by the constant

TABLE 6

Formulae for $\hat{\beta}_{(g)i}$ and $\hat{\beta}_{(s)ij}$ and their sums of squares (p is the number of inbred lines used in the diallel cross)

	In terms of $\hat{g}_{ik}$ and $\hat{s}_{ijk}$	In terms of $\hat{b}_{ij}$

$\hat{\beta}_{(g)i}$ $\sum_k \hat{g}_{ik}\theta_k / \sum_k \theta_k^2$ $\dfrac{1}{p+2}\left(\sum_j \hat{b}_{ij} + \hat{b}_{ii} - \dfrac{2}{p}\sum_{i\leqq j}\sum \hat{b}_{ij}\right) = $ g.c.a. of $\hat{b}_{ij}$

$\hat{\beta}_{(s)ij}$ $\sum_k \hat{s}_{ijk}\theta_k / \sum_k \theta_k^2$ $\hat{b}_{ij} - \dfrac{1}{p+2}\left(\sum_j \hat{b}_{ij} + \hat{b}_{ii} + \sum_i \hat{b}_{ij} + \hat{b}_{jj}\right)$

$$+ \frac{2}{(p+1)(p+2)}\sum_{i\leqq j}\sum \hat{b}_{ij} = \text{s.c.a. of } \hat{b}_{ij}$$

SS (slopes of g_i) $(p+2)\sum_i (\sum_k \hat{g}_{ik}\theta_k)^2 / \sum \theta_k^2$ $\dfrac{1}{p+2}\left\{ \sum_i \left(\sum_j \hat{b}_{ij} + \hat{b}_{ij}\right)^2 - \dfrac{4}{p}\left(\sum_{i\leqq j}\sum \hat{b}_{ij}\right)^2 \right\}\sum_k \theta_k^2$

$$= (\text{SS of g.c.a. of } \hat{b}_{ij})\sum_k \theta_k^2$$

SS (slopes of s_{ij}) $\sum_{i\leqq j}\sum (\sum_k \hat{s}_{ijk}\theta_k)^2 / \sum \theta_k^2$ $\sum_{i\leqq j}\sum (\hat{b}_{ij} - \bar{b}_{..})^2 \sum_k \theta_k^2 - \text{SS (slope of } g_i)$

$$= (\text{SS of s.c.a. of } \hat{b}_{ij})\sum_k \theta_k^2$$

value $\Sigma\theta_k^2$, are equivalent to the sums of squares for " slope of g_i " and for " slope of s_{ij} " respectively in table 2. Furthermore, the sum of these two sums of squares is

$$\sum_i \sum_j (\hat{b}_{ij} - \bar{b}_{..})^2 \sum_k \theta_k^2,$$

which is the sum of squares for heterogeneity of slope under Model 1 and Model 3. Thus, when data from a diallel cross are analysed according to Model 3 or Model 1, the sum of squares for heterogeneity of slope can be partitioned into g.c.a. and s.c.a. components as suggested by Hinkelmann. Algebraically, as stated earlier, the present analysis and Hinkelmann's analysis yield the same results. The difference is that by relating regression parameters to the parameters of combining ability model, Model 2 allows a direct biological interpretation.

In contrast to the above three models which are generally described in terms of phenotypic parameters, the model of Perkins is directly related to the underlying gene action, in particular, to additive and dominance effects. However, the application of Perkins' (1970) model requires the satisfaction of certain restrictive assumptions concerning the genetic background of the material (*e.g.* the parental lines, unlike Moav's, must be pure-breeding). In situations where the assumptions can be justified and the researcher is interested in investigating the nature of the underlying gene action and its interaction with the environment, Perkins' analysis may be more informative. It is interesting to note that where Perkins' model is appropriate the parameter estimates are algebraically related to those of Model 2. In the

particular form presented by Perkins, the following relationships hold (using Perkins' notation to the left of the equality sign):

$$\text{additive:} \quad \hat{d}_i = 2\hat{g}_i + \hat{s}_{ii} - \sum_{i=1}^{p} \hat{s}_{ii}/p$$

$$\text{dominance:} \quad \hat{h}'_{(ij)} = \hat{s}_{ij} - \tfrac{1}{2}(\hat{s}_{ii} + \hat{s}_{jj}) = \bar{H}_{ij}.$$

and if $\theta_k = \varepsilon'_k$, (where ε'_k are the environmental indices used by Perkins and are based on parental lines only)

$$\text{additive} \times \text{Env.:} \quad \hat{\beta}'_d = 2\hat{\beta}_{(g)i} + \hat{\beta}_{(s)ii} - \sum_{i=1}^{p} \hat{\beta}_{(s)ii}/p$$

$$\text{dominance} \times \text{Env.:} \quad \hat{\beta}'_{h(ij)} = \hat{\beta}_{(s)ij} - \tfrac{1}{2}(\hat{\beta}_{(s)ii} + \hat{\beta}_{(s)jj})$$

$$= \hat{\beta}_{(H)ij}$$

4. CONCLUSION

The main advantage of using Model 2 for studying GE interactions in a diallel cross experiment is that both the combining abilities of genetic effects and the linear function of combining ability components by environment interaction can be studied simultaneously. Since the parameters representing the regression model are directly related to the corresponding parameters representing the combining abilities analysis, the model provides a direct and easy biological interpretation. Furthermore, from the results, both heterosis and heterosis by environment interactions can be easily assessed by examining linear combinations of s_{ij} and $\beta_{(s)ij}$ respectively.

It has been shown that the regression coefficients of g.c.a. and s.c.a. components on environmental indices are algebraically equivalent to the g.c.a. and the s.c.a. of $\hat{b}_{ij}$ (Model 3) or $\hat{\beta}_{ij}$ (Model 1). Thus, it can be said that Model 2 provides both a structural as well as a biological base for what may be termed a joint combining ability analyses for both intercept and slope.

The close agreement between groups obtained numerically using Lin-Thompson's method and the parental association of genotypes reflects the importance of GE interactions as classification criteria in biological studies. This example suggests that the grouping method is a useful tool not only in simplifying the interpretation of complicated interactions but also in identifying underlying biological relationships among genotypes in the resulting groups.

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