METHODOLOGY
Proposal for applying combined selection to diallel analysis

*Cleso Antônio Patto Pacheco[1], Maria Amélia Gava Ferrão[2], Cosme Damião Cruz[3]
and Roland Vencovsky[4]*

ABSTRACT

The philosophy of intrapopulation combined selection is the search for and identification of individuals with superior genotypic behavior, based on their performance compared to the family mean and, at the same time, of their family mean in relation to the population mean, through the weighting of the phenotypic values represented, respectively, by the within and among families heritability coefficient. The objective of this study was to adapt and apply this philosophy to diallel analysis. The crosses were considered as having fixed effects and selected on the basis of their specific combining ability (SCA), and on the mean performance of the two involved parents, in relation to the general combining ability (GCA). This work was based on Griffing's (*Heredity 10*: 35-50, 1956) method 2, model 1 which involves $p(p + 1)/2$ treatments. The proposed index resulted from the weighting of the effects of GCA (g_i's) and SCA (s_{ij}'s) by the respective determination coefficients of additive and dominant genetic determinations, resulting from the partitioning of the total genotypic determination coefficient. An example is given for illustration.

INTRODUCTION

When individuals are related by a simple family structure, the phenotypic value (P) of an individual, measured as the deviation from the population mean, may be expressed as the sum of two parts: the deviation from its family mean in relation to the population mean (P_f) and the deviation from the individual mean to the family mean (P_w), which is the within family deviation (Falconer, 1981) so that:

$$P = P_f + P_w$$

The selection procedure varies according to the weight given to these two parts. Selection can be based only on the family mean (P_f), totally ignoring the within family deviation (P_w). Selection can also be made only on P_w, totally ignoring P_f. Further, selection can be made considering both components, P_f and P_w, given different weights, chosen to make the best use of the information sources. This is called combined selection. Thus, the individuals are assessed in a single stage, not two, and their individual value is not the only information used for their selection or rejection.

In combined selection, the first step is to find which are the appropriate weights to be used, so that they contain the family and the individual within family contributions. It is, therefore, necessary to estimate the appropriate coefficients for the individual values and for the means of the corresponding families (Cruz, 1995).

[1] EMBRAPA-CNPMS, Caixa Postal 151, 35701-970 Sete Lagoas, MG, Brasil. Send correspondence to C.A.P.P.
[2] EMCAPA-EEL, Caixa Postal 62, 29900-970 Linhares, ES, Brasil.
[3] Departamento de Biologia Geral, UFV, 36570-000 Viçosa, MG, Brasil.
[4] ESALQ-USP, Caixa Postal 83, 13400-970 Piracicaba, SP, Brasil.

In the genotypic study of a metric trait, only the individual phenotypic value can be measured, but it is the genetic value which determines its influence in the next generation. In this context, the heritability (h^2), expressed as the proportion of the total variance which is attributed to the mean genetic effect, predicts the reliability of the phenotypic value as a measure of the genetic value. Therefore, the success of individual selection according to the phenotypic value can only be predicted by knowledge of the degree of correspondence between the phenotypic and the genetic values measured by the heritability.

Taking the heritability as a regression of the genetic values on the phenotypic values, a good estimate of the genetic value of an individual may be obtained by multiplying its phenotypic value by the heritability, h^2P. This idea can be applied, separately, to the two parts of the phenotypic value, as long as they are not correlated and provide independent information on the genetic value.

Thus, taking both parts of the phenotypic value, the best estimate of the genetic value of the individual is given by:

Expected genetic value: $G = h_f^2 P_f + h_w^2 P_w$

The weights which make the most efficient use of the two sources of information are, therefore, the two appropriate heritabilities, that is, the heritability among (h_f^2) and within (h_w^2) families.

The combined selection criteria may be presented in the form of an index model, where:

$$G = h_f^2 P_f + h_w^2 P_w$$

This solution of the problem, that is, the best use of the information provided by the parents, may be precisely molded in the way in which the problem is introduced.

In the present study the use of a combined selection criterion was adapted to diallel analyses. For this, the best parents must be known simultaneously, based on their general combining ability (GCA), and within the best hybrids, based on their specific combining ability (SCA).

METHODOLOGY

An estimate of a selection index for diallels, combining the information among parent means, which involve GCA, with the information within the same parents involving SCA was developed, using an approach similar to Falconer's (1981) index for combined selection.

Only balanced diallels involving parents and their F1 crosses were considered, with $p(p + 1)/2$ fixed treatments and Griffing's (1956) method 2, model 1 presented by Cruz and Regazzi (1994), with the following statistical model:

$$Y_{ij} = m + (g_i + g_j) + s_{ij} + \bar{e}_{ij} \qquad (i)$$

where, Y_{ij}: mean value of hybrid ($i \neq j$) or parent ($i = j$) combination; m: general mean; g_i: general combining ability effects of i-th parent ($i = 1, 2, ..., p$); s_{ij}: specific combining ability of the cross between the i-th and j-th parents; $\bar{e}_{ij}$: mean experimental error associated with the ij-th observation.

In this model, the g's refer mainly to the additive genetic effects due to loci in homozygosis in the parents, while $s_{ij's}$ refer to the non-additive genetic effects due to the heterozygous loci. It was taken that non-additive effects are due to dominance, ignoring epistasis. The same weight was given to both types of effects, so that model (i), replaced by the estimates of the effects, can be written as follows:

$$Y_{ij} = \hat{m} + (\hat{g}_i + \hat{g}_j) + \hat{s}_{ij}$$

When the effects are random and calculated within a population, $[(\hat{g}_i + \hat{g}_j) + \hat{s}_{ij}]$ refers to a phenotypic component established by the relationship among the treatment means. Its variance involves an additive genetic part due to $(\hat{g}_i + \hat{g}_j)$ and another dominant genetic part due to $\hat{s}_{ij}$.

Thus, diallel analysis allows the partitioning of the phenotypic variance, leading to a better knowledge of the size and proportion of the variation which is due to the additive gene effect and that which is due to a specific combination of these genes. This information allows a safer decision on the choice of parents and/or hybrids.

The phenotypic nature of the $\hat{g}_{i's}$ and the $\hat{s}_{ij's}$ can be seen through the presence of the environmental variation component, associated with the additive and dominance quadratic components, in the expected values of the mean squares, E(MS), in the respective sources of variation, GCA and SCA, as shown in Table I. Thus, to work only with the genotypic components it would be enough to multiply the $\hat{g}_{i's}$ and the $\hat{s}_{ij's}$ effects by the heritability (h^2) or, in a fixed model, by the genotypic determination coefficient (R_G^2), estimated by the following expression:

$$R_G^2 = \frac{MST - MSR}{MST}$$

Table I - Summary of the Griffing method 2 diallel analysis of variance based on means and mathematical expectations of the mean squares, regarding the treatments as fixed effects.

Source of variation	d.f.	MS	F	E(MS)
Treatments	$\frac{p(p+1)}{2}-1$	MST	MST/MSR	$\sigma_e^2+\frac{p}{p+2}\phi_s+2\phi_g$
GCA	$p-1$	MSG	MSG/MSR	$\sigma_e^2+(p+2)\phi_g$
SCA	$\frac{p(p-1)}{2}$	MSS	MSS/MSR	$\sigma_e^2+\phi_s$
Residue	f	MSR		σ_e^2

Where MS = mean square.

Model (i) can be rewritten as:

$$Y'_{ij} = \hat{m} + R_G^2[(\hat{g}_i + \hat{g}_j) + \hat{s}_{ij}] \quad \text{(ii)}$$

In this new model, the Y'_{ij} value would express a genotypic value, probably more adequate than the first (phenotypic), however still without using all the genetic potential provided by the partition of this genotypic value into its additive and dominant parts.

It is known that the coefficient of heritability allows the estimation of the part of the total genotypic variation which is of additive genetic nature. The heritability is important because it is a good indicator of the size and the variation of the additive effects, which determines the correlation among relatives. Thus, this coefficient is used to predict the genetic gains in the next generation, from the selection differential estimated from the selected genotypes.

The dominant component, when present in intrapopulation selection, reduces the correlation among the selected progenies and the next generation because of the nature of these effects. However, when there is interest in a certain hybrid combination, this component is very important because it is responsible for heterosis. Therefore, a dominance heritability coefficient or a dominant genetic determination coefficient would allow estimating the success of (F1) hybrid selection.

The quadratic components involved in the GCA and SCA expected mean squares can be isolated by a combination of MS, so that:

$$\hat{\phi}_g = \frac{MSG - MSR}{p+2}$$

$$\hat{\phi}_s = MSS - MSR$$

These quadratic components have been used to determine the magnitude of the additive effects compared to the dominant effects, when both GCA and SCA effects are significant, and help to establish the criteria for selection of parents and/or hybrids.

In the E(MS) for treatments, these two quadratic components are weighted by different coefficients, so that ϕ_g has greater weight than ϕ_s, tending to a 2:1 ratio, when there is a large number of parents.

An orthogonal partition of the genotypic determination coefficient (R_G^2) in its additive (R_g^2) and dominance (R_s^2) parts is possible, so that:

$$R_G^2 = R_g^2 + R_s^2$$

and since:

$$R_G^2 = \frac{\frac{p}{p+2}\phi_s + 2\phi_g}{\sigma_e^2 + \frac{p}{p+2}\phi_s + 2\phi_g}$$

then,

$$R_g^2 = \frac{2\phi_g}{\sigma_e^2 + \frac{p}{p+2}\phi_s + 2\phi_g} \quad \text{or}$$

$$R_g^2 = \frac{2\frac{(MSG-MSR)}{p+2}}{MST} = \frac{2(MSG-MSR)}{(p+2)MST}$$

$$R_s^2 = \frac{\frac{p}{p+2}\phi_s}{\sigma_e^2 + \frac{p}{p+2}\phi_s + 2\phi_g} \quad \text{or}$$

$$R_s^2 = \frac{\frac{p}{p+2}(MSS-MSR)}{MST} = \frac{p(MSS-MSR)}{(p+2)MST}$$

Thus an index based on the weighting of the additive and dominance effects may be determined by their corresponding genetic determination coefficients. This index may be expressed as:

$$I_{ij} = R_g^2(\hat{g}_i + \hat{g}_j) + R_s^2(\hat{s}_{ij})$$

At least three types of relationship between R_g^2 and R_s^2 can be predicted to compare I_{ij} and Y_{ij}, when $i \neq j$:

1 - $R_g^2 > R_s^2$

2 - $R_g^2 < R_s^2$

3 - $R_g^2 \cong R_s^2$

In the first case, the greater the difference between the two determination coefficients, the greater the predominance of the additive effects. Consequently, hybrid prediction based on the parental $g_{i's}$ effects will be reliable.

In the second case, the opposite occurs, and the greater the difference between the two determination coefficients, the greater the predominance of dominant effects. In this situation, where large heterosis effects are expected, the parental g_i values are not good predictors of the hybrids' behavior. Since the importance of the quadratic component due to the dominance effects is large, a significant alteration in the orders of the treatment classification based on I_{ij} and Y_{ij} is expected.

In the two situations described above, the predominance of one effect over the other was considered. However, in practice, several other situations occur between the two extremes (case 3). It is expected that the proposed index will contribute more in these intermediate cases, where there is a small advantage of one effect over another. In these situations, the choice between two parents or two hybrids may be better decided by the combination of small genotypic differences, mainly in cases where the advantage tends to dominance by the weakening of the $g_{i's}$ predictive power.

An important consideration should be added to the proposal of the index in its comparison with the Y_{ij} observed values; the constant presented in the model, the general mean, which is estimated by phenotypic values, corresponds to the mean of the genotypic values, because the other factors of the model are estimated as deviations whose sum is zero. Therefore, the general mean of the Y_{ij} and I_{ij} expressed in the model below corresponds to the constant $\hat{m}$. For $i \neq j$,

$$I_{ij} = \hat{m} + R_g^2 (\hat{g}_i + \hat{g}_j) + R_s^2 (\hat{s}_{ij}) \qquad (iii)$$

Finally, the Griffing model considered in this study, expressed by the parameters of Gardner and Eberhart (1966), as presented by Cruz and Vencovsky (1989), for the cases where i = j, may be written as:

$$Y_{ii} = \hat{m} + (\hat{g}_i + \hat{g}_i) + \hat{s}_{ii}$$

$$Y_{ii} = \hat{m} + \left[\left(\frac{1}{2}\hat{v}_i + \frac{(p-2)}{(p+2)}\hat{h}_i \right) + \left(\frac{1}{2}\hat{v}_i + \frac{(p-2)}{(p+2)}\hat{h}_i \right) \right] +$$

$$+ \left[-\frac{(p-1)}{(p+1)}\hat{\bar{h}} - 2\frac{(p-2)}{(p+2)}\hat{h}_i \right] \qquad (iv)$$

whose simplification leads to the following expression:

$$Y_{ii} = \hat{m} + \hat{v}_i - \frac{(p-1)}{(p+1)}\hat{\bar{h}} \qquad (v)$$

From this expression (v) it can be seen that the mean of the parents is a function only of the variety ($\hat{v}_i$), as the effects of varietal heterosis ($\hat{h}_i$) cancel out and the general mean ($\hat{m}$) and the mean heterosis ($\hat{\bar{h}}$) are constants in each analysis under consideration.

According to the (iv) expression, the index for parent selection may be written in the following way:

$$Y_{ii} = \hat{m} + R_g^2 \left[\left(\frac{1}{2}\hat{v}_i + \frac{(p-2)}{(p+2)}\hat{h}_i \right) + \left(\frac{1}{2}\hat{v}_i + \frac{(p-2)}{(p+2)}\hat{h}_i \right) \right] +$$

$$+ R_s^2 \left[-\frac{(p-1)}{(p+1)}\hat{\bar{h}} - 2\frac{(p-2)}{(p+2)}\hat{h}_i \right] \qquad (vi)$$

whose simplification leads to the following expression:

$$Y_{ii} = \hat{m} + R_g^2 \hat{v}_i + (R_g^2 - R_s^2)\frac{2(p-2)}{(p+2)}\hat{h}_i - R_s^2 \frac{(p-1)}{(p+1)}\hat{\bar{h}} \qquad (vii)$$

where it can be seen that: 1) when the ratio between the two coefficients of determination is unity ($R_g^2 = R_s^2$), one parent will be selected based only on its varietal effect, which would be expected only when the dominance effects were nil; 2) when $R_g^2 < R_s^2$, the index will take into consideration negative values of the varietal heterosis, instead of the desirable positive values.

Thus, the use of the proposed index for parent selection, based on the estimable effects of the Griffing model (1956), should be made with great caution, as the results will only be coherent in cases where R_g^2 is much larger or much smaller than R_s^2, and, in the latter situation, it is necessary to invert the varietal heterosis sign.

APPLICATION

Diallel analyses involving parents and F1's displaying significant varietal or GCA and heterosis or SCA were surveyed in the literature to illustrate the proposed methodology.

The studies originally assessed by Gardner and Eberhart (1966) were re-analyzed using Griffing's (1956) method 2, model 1. In all examples, the additive genetic quadratic components (ϕ_g), the non-additive effects (ϕ_s), the genotypic determination coefficients (R_G^2), additive genetic (R_g^2) and the non-additive genetic (R_s^2) were calculated, following the methodology described in item 2.

Based on the size of these components and coefficients, as well as their ratios, five studies which illustrate the three different proportions were chosen (Table II).

Table II - Genotypic determination (R_G^2), additive genetic (R_g^2) and dominance (R_s^2) coefficients, additive quadratic genetic (ϕ_g), and quadratic dominance (ϕ_s) components and their relationships in five diallel analyses using Griffing's (1956) method 2.

Source	R_G^2	R_g^2	R_s^2	$\dfrac{R_g^2}{R_s^2}$	ϕ_g	ϕ_s	$\dfrac{\phi_g}{\phi_s}$
1. Miranda (1987)[a]	0.9574	0.8858	0.0716	12.37	36.69	7.91	4.64
2. Delboni et al. (1989)[b*]	0.9038	0.2470	0.6568	0.38	0.039	0.273	0.14
3. Gomide (1980)[b]	0.7820	0.4070	0.3750	1.08	0.226	0.520	0.43
4. Paini (1994) - 1[c]	0.7301	0.3949	0.3352	1.18	320886.0	680887	0.47
5. Paini (1994) - 2[c]	0.7529	0.3078	0.4451	0.69	298515.3	1079253	0.27

[a]Number of fruits per sweet pepper plant.
[b]Maize grain weight in kg/plot of 5.0 m^2.
[c]Maize grain weights in kg/ha.
*Quoted by Cruz and Regazzi (1994).

In Miranda (1987) there was a predominance of R_g^2; in Delboni et al. (1989) of R_s^2; in Gomide (1980) the R_g^2 and R_s^2 values were similar; in Paini (1994)-1, there was a slight superiority of R_g^2 and in Paini (1994)-2, of R_s^2.

The example of Delboni et al. (1989) quoted by Cruz and Regazzi (1994) was chosen from these five examples because it is the most illustrative. Six varieties of maize and their F1 hybrids are involved. Their yield data (kg/ha) was originally analyzed using Gardner and Eberhart (1966) methodology, and the analysis of variance carried out according to Griffing (1956), with a partition of the treatment sum of squares into GCA and SCA, as shown in Table III.

Table III - Analysis of variance of grain weight per plot in a diallel with six varieties of maize and their F1 hybrids. Study by Delboni et al. (1989) quoted by Cruz and Regazzi (1994).

Sources	d.f.	SS	MS	F
Treatments	20	6.2379	0.3119	10.4**
GCA	5	1.6909	0.3382	11.3**
SCA	15	4.5470	0.3031	10.1**
Residual	91	2.7300	0.0300	

Mean = 2.67 kg/plot; coefficient of variation (C.V.%) = 6.49.

According to the literature the conclusion about the type of genic action predominant among the assessed material is normally based on the size of the quadratic components. However, analyzing the E(MS) for treatments (Table I) it can be see that ϕ_g has a participation $2(p + 2)/p$ times greater than that of ϕ_s, thus showing that the ratio 1:1 commonly used may be overestimating the importance of the SCA. The relation between the quadratic components themselves does not seem to be the most appropriate indicator of the predominant gene action, mainly in the intermediate situation, as seen in those represented by cases 3, 4, and 5 in Table II.

In the case of Delboni et al. (1989), where the dominant genetic determination coefficient (R_s^2) was 2.66 times greater than the additive genetic (R_g^2), the great importance that should be given to a hybridization program becomes clear. A similar conclusion is made when the quadratic components are examined, however, it overestimates the tendency with ϕ_s seven times greater than ϕ_g. When this last proportion is not so large, the researcher may arrive at different conclusions by using one or another relationship to infer about the predominance of gene action and make a wrong decision about his breeding program. Table II shows an intermediate situation, as that found in the work of Gomide (1980), where the conclusions are conflicting. When quadratic components are used, a predominance of the dominance effects is found, while when using the determination coefficients a slight tendency of superiority of the additive effects is detected.

Table IV shows the mean values of Y_{ij}, the $\hat{g}_i$, $\hat{g}_j$ and $\hat{s}_{ij}$ effects, the estimated index values (I_{ij}) and the material selected based on the index and the Griffing (1956) methodology.

The criterium for selection of parents and hybrids by the Griffing (1956) methodology is based on $\hat{g}_{i's}$ and $\hat{s}_{ij's}$. According to Cruz and Regazzi (1994) the estimates of the GCA effect ($\hat{g}_{i's}$) provide information about the additive effects of the genes and have been of great use in indicating parents to be used in breeding programs. The SCA ($\hat{s}_{ij's}$) effects, estimated as deviations of a hybrid in relation to what would be expected based on the GCA of its parents, are a measure of the non-additive genetic effects. Normally, the breeder is interested in a hybrid combination with high $\hat{s}_{ij}$ estimates involving at least one of the parents with a high $\hat{g}_i$ effect.

The $\hat{s}_{ii}$ values have great genetic significance and indicate the existence of unidirectional dominance.

Table IV - Y_{ij} genotypic values, $\hat{g}_i$, $\hat{g}_j$ and $\hat{s}_{ij}$ effects, I_{ij} index value and the rank of the five best materials selected by the index and Griffing's (1956) methodology. Study by Delboni *et al.* (1989), quoted by Cruz and Regazzi (1994).

i x j	Y_{ij}	$\hat{g}_i$	$\hat{g}_j$	$\hat{s}_{ij}$	I_{ij}	Index BP	Index BH	Griffing BP	Griffing BH
1 x 1	2.95	0.377	0.377	-0.473	2.55	1º		1º	
1 x 2	3.32	0.377	-0.121	0.395	2.99		2º		1º
1 x 3	3.08	0.377	-0.207	0.241	2.87				
1 x 4	3.24	0.377	0.018	0.176	2.88				2º
1 x 5	2.99	0.377	-0.102	0.046	2.77				
1 x 6	3.17	0.377	0.035	0.088	2.83				3º
2 x 2	1.23	-0.121	-0.121	-1.198	1.82				
2 x 3	3.10	-0.121	-0.207	0.758	3.09		1º		5º
2 x 4	3.03	-0.121	0.018	0.463	2.95		4º		
2 x 5	2.74	-0.121	-0.102	0.293	2.81				
2 x 6	3.07	-0.121	0.035	0.486	2.97		3º		4º
3 x 3	1.52	-0.207	-0.207	-0.735	2.08				
3 x 4	2.58	-0.207	0.018	0.100	2.69				
3 x 5	2.30	-0.207	-0.102	-0.060	2.55				
3 x 6	2.93	-0.207	0.035	0.432	2.91		5º		
4 x 4	2.25	0.018	0.018	-0.455	2.38				
4 x 5	2.62	0.018	-0.102	0.035	2.67				
4 x 6	2.86	0.018	0.035	0.137	2.77				
5 x 5	2.21	-0.102	-0.102	-0.255	2.45	2º			
5 x 6	2.80	-0.102	0.035	0.197	2.78				
6 x 6	2.07	0.035	0.035	-0.670	2.25			2º	

BP: Best parents; BH: best hybrids.

Table V - Y_{ii} genotypic values, $\hat{v}_i$ and $\hat{h}_i$ effects, index I_{ii} values and parents selected by the proposed index expressed in the form of Gardner and Eberhart effects. Study by Delboni *et al.* (1989), quoted by Cruz and Regazzi (1994).

i x j	Y_{ii}	$\hat{v}_i$	$\hat{h}_i$	I_{ii}	BP
1 x 1	2.95	0.912	-0.158	2.79	2º
2 x 2	1.23	-0.808	0.567	2.84	1º
3 x 3	1.52	-0.518	0.104	2.61	
4 x 4	2.25	0,212	-0.176	2.61	
5 x 5	2.21	0.172	-0.376	2.46	
6 x 6	2.07	0.031	0.039	2.70	

BP: Best parents.

The $\hat{s}_{ii}$ values will be negative when the deviations are predominantly positive, and vice-versa (Cruz and Vencovsky, 1989). The size of $\hat{s}_{ii}$ is indicative of the varietal heterosis and its sum is a linear function of the mean heterosis.

According to Griffing (1956), the materials which should be selected were varieties 1 and 6 and the hybrid combinations 1 x 2, 1 x 4, 1 x 6, 2 x 6, and 2 x 3. With the proposed index, the best materials were varieties 1 and 5, while the best hybrid combinations were 2 x 3, 1 x 2, 2 x 6, 2 x 4, and 3 x 6. Little agreement was observed between the two methods, which may be attributed to the weight given by the Griffing method to the $\hat{g}_i$ effects. Since in this case the dominant gene effects were more important, the index provided a more desirable selection because it was not solely based on the parental performance. The $\hat{g}_{i's}$ were poor predictors of the parents superiority in this case because the parents were not good performers *per se* but were in crosses.

Our data were originally analyzed using Gardner and Eberhart's (1966) method. The varieties

($\hat{v}_i$) and heterosis effects were significant at the 1% level of probability, showing that the varieties did not make up a homogeneous group and there was heterosis in the crosses. The partition of the heterosis effect detected a significant mean ($\hat{\bar{h}}$) and varietal heterosis ($\hat{h}_i$), indicating that the heterosis was not the same for all the varieties, although the variation of this effect on these varieties was not caused by specific heterosis ($\hat{s}_{ij}$). Table V shows the effects of Gardner and Eberhart (1966) for the parents and the index estimates using expression (vii) presented in item 2, with an inversion of the varietal heterosis sign because $R_g^2 < R_s^2$.

Using the $\hat{v}_i$ values Delboni *et al.* (1989) concluded that varieties 1, 4 and 5 have greater potential for *per se* use. Heterotic combinations were obtained with the use of parents 2, 3 and 6, which had the largest $\hat{h}_i$ values. They also emphasized that hybrid combination among divergent parents with good genetic potential should be preferred. Therefore, variety 1, for its performance, and variety 2, for its divergence in relation to the other parents, would be the best options.

The comparison of the values obtained by the index for the parents in Tables IV and V shows, as already pointed out in the methodology, that the proposed index should only be favored for selecting parents when R_g^2 is much greater than R_s^2. Since in the example under consideration this did not happen, the parents should be selected based on the data in Table V.

As in the Gardner and Eberhart (1966) and the Griffing (1956) methods, the superiority of variety 1 was also recognized by the index, in part because it carried the greatest number of favorable alleles among the six varieties analyzed. Because of the highly favorable condition for exploitation of heterosis, the index also selected variety 2 as having great potential for a hybrid program because, in spite of having a lower phenotypic mean, it was the most divergent and had the best gene complementation towards the others.

The main difference between the index and the other two methods for hybrid selection is in the selection of the cross 2 x 3 by the index and 1 x 2 by the other two. Looking at the Y_{ij} values in Table IV it is, at first sight, difficult to understand how a mean of 3.10 (2 x 3) can be better than one of 3.32 (1 x 2). However, taking into consideration that the proposed index expresses the components according to their determination coefficients, it can be seen how an inversion in the means classification can occur. The means became 3.09 for the cross 2 x 3 and 2.99 for 1 x 2. In fact, the 2 and 3 parents were more divergent, as can be seen by the size of the $\hat{h}_i$ and $\hat{s}_{ii}$ values (both had the greatest $\hat{h}_i$ or smallest $\hat{s}_{ii}$) coupled with the best gene complementation, shown by the greater $\hat{s}_{ij}$ value.

Finally, the good agreement between the results obtained with the index and the Gardner and Eberhart (1966) method for the example under consideration is probably due to the strong genotypic determination coefficient (90.38% of the phenotypic variation was due to the genetic effects), so that the phenotypic values were good estimators of the genotypic values.

CONCLUSIONS

Combined selection is a procedure adopted in family selection (random model). The adaptation of this breeding philosophy to data produced by diallel analysis, with a fixed model, in the form of the proposed index, produced results which allow the following conclusions: a) the proposed index allowed the partitioning of the genetic determination coefficient into its additive and dominant parts and introduced these coefficients as determining factors in the choice of crosses, because of the relationship between the two types of gene action which these coefficients represent in a diallel analysis; b) the total phenotypic variation (100%) was partitioned into environmental, additive and dominant genetic variations, allowing the breeder to assess with greater confidence the relative importance of each factor in the selection process; c) the concept of immediate heritability or determination coefficient of the dominant effects, whose use is similar to that of the narrow sense heritability, is introduced. It gives an idea of the success the breeder will have, on the average, with heterosis in the F1 hybrid generation, and d) the proposed index was shown to be adequate for hybrid selection. However, the selection of parents should be made cautiously, as its construction is dependent on the relationship between the additive and dominant genetic determination coefficients.

RESUMO

A filosofia da seleção combinada intrapopulacional é a busca e identificação de indivíduos de comportamento genotípico superior com base no seu desempenho em relação à média de sua família e, ao mesmo tempo, de sua família em relação à média da população, através da ponderação dos valores fenotípicos por pesos apropriados, representados pelos coeficientes de herdabilidade dentro e entre famílias, respectivamente. O objetivo desse trabalho foi o de adaptar e aplicar essa filosofia à análise dialélica, onde os cruzamentos, considerados como de efeitos fixos, são selecionados com base no seu comportamento específico (SCA) e no desempenho médio em cruzamentos dos dois progenitores envolvidos, em relação à média geral (GCA). O desenvolvimento foi feito com base no método 2, modelo 1 de Griffing (*Heredity 10*: 31-50, 1956), que considera $p(p + 1)/2$ tratamentos. O índice proposto resultou da ponderação dos efeitos da capacidade geral de combinação ($g_{i}'s$) e da capacidade específica de combinação ($s_{ij}'s$), pelos respectivos coeficientes de determinação genético aditivo e genético dominante, provenientes do desdobramento do coeficiente de determinação genotípico. Um exemplo de aplicação é dado para ilustração.

REFERENCES

Cruz, C.D. (1995). Seleção combinada. In: *Notas de Aulas do Curso de Genética Quantitativa Aplicada ao Melhoramento de Plantas - FIT 770*. UFV, Viçosa, MG (mimeografado).

Cruz, C.D. and **Regazzi, A.J.** (1994). *Modelos Biométricos Aplicados ao Melhoramento Genético*. UFV, Impr. Univ., Viçosa, MG, pp. 390.

Cruz, C.D. and **Vencovsky, R.** (1989). Comparações de alguns métodos de análise dialélica. *Rev. Bras. Genet. 12*: 425-438.

Falconer, D.S. (1981). *Introdução à Genética Quantitativa*. UFV, Impr. Univ., Viçosa, MG, pp. 279.

Delboni, J.S., Silva, J.C., Cruz, C.D. *et al.* (1989). Análise de cruzamentos dialélicos entre variedades de milho braquítico usando o método de Gardner e Eberhart. R. *Ceres, 36*: 365-372.

Gardner, C.O. and **Eberhart, S.A.** (1966). Analysis and interpretation of the variety cross diallel and related populations. *Biometrics 22*: 439-452.

Gomide, B.G. (1980). Cruzamentos dialélicos entre variedades de milho (*Zea mays* L.). Master's thesis, UFV, Viçosa, MG, pp. 71.

Griffing, B.A. (1956). A generalized treatment of the use of diallel crosses in quantitative inheritance. *Heredity 10*: 31-50.

Miranda, J.E.C. (1987). Análise genética de um cruzamento dialélico em pimentão (Capsicum annuum L.). Doctoral

thesis, Escola Superior de Agricultura Luiz de Queiroz, Piracicaba, SP, pp. 159.

Paini, J.N. (1994). Capacidade combinatória e heterose em oito variedades de milho (*Zea mays* L.), avaliadas sob condições climáticas da região sul do Brasil. Master's thesis, UFV, Viçosa, MG, pp. 125.