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METHODOLOGY:

Analysis of diallel tables with reciprocal crosses

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ABSTRACT

The methodology of diallel crosses is extended to provide procedures for the analysis of variance and estimation of effects when the reciprocal crosses are included. The model of Gardner and Eberhart (*Biometrics 22*: 439-452, 1966) was used for the analysis of variety diallel crosses when reciprocal crosses are included. The least square procedure was used to derive the formulas for estimation of effects (components of means) and for the analysis of variance. It was found that the estimates of effects is the same if the analysis is performed according to the original model, with varieties and the average of reciprocal crosses to represent any hybrid combination. The standard errors of the estimates of effects, however, change in the proposed procedure. The sums of squares in the analysis of variance are different from those obtained according to the original model. Some comparisons are made and an example is given for illustration.

INTRODUCTION

The diallel mating scheme is probably the procedure most used for evaluating genotypes in hybrid crosses. Following the concept of general combining ability (gca) and specific combining ability (sca) of Sprague and Tatum (1942), several methods were developed for estimating constants (components of means) and performing the analysis of variance for tests of hypotheses. Griffing (1956) provided detailed procedures for the analysis of variance and estimation of effects under two models (I - fixed; II - random) and four methods, described according to the nature of entries in the diallel analysis: 1. parents, F_1's and reciprocals; 2. parents and F_1's; 3. F_1's and reciprocals; and 4. only the F_1's. For the fixed model in all methods, the analysis of variance is made for testing hypotheses, and estimates are obtained for general combining ability (g_i) and specific combining ability (s_{ii}), that are the only effects with genetic meaning in the statistical models. The random model allows the estimation of variance components and emphasis on testing hypotheses is lessened (Hallauer and Miranda Filho, 1988).

Gardner and Eberhart (1966) and Gardner (1967) presented a method for the analysis of diallel crosses among a fixed set of varieties; actually it is applicable to any fixed set of materials (varieties, composites, families, etc.) provided that they are in Hardy-Weinberg equilibrium. The diallel table includes the mean (or total) over r replications of the parent varieties (diagonal) and the F_1's (off diagonal). The model includes the mean of the variety set (μ), the variety effects (v_i), the average heterosis (h), the variety heterosis effects (h_i), the specific heterosis ($s_{ii'}$) and the error term ($e_{ii'}$), adjusted to the entry means. For the fixed effects, the relation between the model of Gardner and Eberhart (1966) and the method (4) of Griffing (1956)

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is given by: $g_i = 1/2\ v_i + h_i$ and $s_{ii'}$ has the same meaning in both procedures.

The model of Gardner and Eberhart (1966) for diallel crosses is based on the general model for genetic effects where, besides the parents and F_1's, other generations (F_2, backcrosses, selfed populations) can be included and the overall analysis is performed according to the least square procedure (Eberhart and Gardner, 1966). Nevertheless, the formulae for the analysis of variance and for estimation of effects are available only for the diallel cross model, where only the parents and F_1 hybrids are included (Gardner, 1967).

The effect of reciprocal crosses for yield of maize at the population level has been shown to be non-significant in most instances. This cannot be the case for some particular trait in maize or for other crop species. When reciprocal crosses are included, their effect must be considered in the model. Under the hypothesis of no reciprocal effects, the analysis of variance and estimation of effects can be done by averaging the means of reciprocal hybrids. Nevertheless, this situation is valid only when the entries comprise only hybrids and reciprocals, so that averaging pairs of entries implies that all treatments are represented by the same number of experimental plots and consequently are under the same average error.

In variety diallel schemes when parents are included, averaging reciprocal crosses for the analysis of variance is not a correct procedure because the hybrids would be represented by twice as many experimental plots as the parental varieties. This would introduce a bias in the estimates and in the analysis of variance.

MATERIAL AND METHODS

Let's consider a diallel table with n^2 elements (means over r replications), that includes **n** parent varieties, **n(n-1)/2** F_1 hybrid crosses, and **n(n-1)/2** reciprocal crosses. The basic model is an extension of that given by Gardner and Eberhart (1966) for diallel crosses:

$$Y_{ii'k} = m + 1/2\ (v_i + v_{i'}) + \theta\ (\bar{h} + h_i + h_{i'} + s_{ii'} + r_{ii'k}) + e_{ii'k}$$

where $\theta = 0$ for varieties and $\theta = 1$ for hybrids; the sub-index k applies only for hybrids. $Y_{ii'k}$ represents the cross between varieties i and i' where k is used to differentiate between any specific cross and its reciprocal; μ is the mean of varieties; $\bar{h}$ is the average heterosis; h_i is the variety heterosis; $s_{ii'}$ is the specific heterosis; $r_{ii'k}$ is the effect of reciprocal crosses; and $e_{ii'k}$ is the error term adjusted to entry means.

The formulas for the analysis of variance and for estimation of effects were obtained by using the least square procedure in the following matrix equation: $\mathbf{Y = X\beta + \varepsilon}$, where Y is the vector of means representing the diallel table; X is the matrix of coefficients in accordance with the basic model; $\boldsymbol{\beta}$ is the vector of parameters as defined in the basic model, and $\boldsymbol{\varepsilon}$ is the vector of the error term. For constructing the matrix, the basic model was reduced by neglecting the reciprocal effect (r_{ii}), so that it is not directly estimated and its variation is identified as deviations from the model in the analysis of variance. Therefore, the operational model is represented by:

$$Y_{ii'} = \mu + 1/2\ (v_i + v_{i'}) + \theta\ (\bar{h} + h_i + h_{i'} + s_{ii'}) + \delta_{ii'}$$

Following the least square procedure, the solution of the normal equations is given by: $\hat{\beta} = (X'X)^{-1}\ \mathbf{X'Y}$. The following restrictions were considered: $\sum_i \hat{g}_i = 0$; $\sum_i \hat{h}_i = 0$; $\sum_{i \cdot i} \hat{s}_{ii'} = 0$ for each i.

The formulas for the sums of squares in the analysis of variance were obtained by considering sequentially reduced models and the corresponding reduction (R) in the sums of squares (Kempthorne, 1952):

Model 1: $R_1 = R\ (\mu,\ v_i,\ \bar{h},\ h_i,\ s_{ii'})$
Model 2: $R_2 = R\ (\mu,\ v_i,\ \bar{h},\ h_i)$
Model 3: $R_3 = R\ (\mu,\ v_i,\ \bar{h})$
Model 4: $R_4 = R\ (\mu,\ v_i)$
Model 5: $R_5 = R\ (\mu)$

The sums of squares due to each source of variation were obtained by the following set of equations:

Source of variation	Sums of squares
Populations (POP)	$\sum_i Y_{ii}^2 + \sum_{i<i'} Y_{ii'}^2 - \frac{Y_{..}^2}{n^2}$
Varieties	$R_4 - R_5$
Average heterosis	$R_3 - R_4$
Variety heterosis	$R_2 - R_3$
Specific heterosis	$R_1 - R_2$
Deviations (reciprocals)	$S(POP) - R_1$

For illustration of the proposed procedure, the analysis of yield data from a 4x4 diallel cross (Table I) is presented.

Table I - Yield data (kg/5m^2: means over r replications) of four maize varieties (diagonal), F_1 hybrids (above diagonal) and reciprocal crosses (below diagonal)*.

Varieties	Syn-D	Syn-F	SC-01	SC-02
Syn-D	2.414	3.534	3.472	3.314
Syn-F	3.627	3.160	3.400	3.732
SC-01	3.405	3.827	2.392	3.818
SC-02	3.326	3.843	3.806	2.850

*From Aguilar-Morán (1990).

RESULTS AND DISCUSSION

The following results refer to a methodology where the estimates of effects and the analysis of variance are obtained according to the least square procedure, i.e., by minimizing the deviations from the model.

The formulas for estimation of effects and their standard errors in a diallel cross scheme when reciprocals are included are shown in Table II. The formulas for the analysis of variance are shown in Table III.

The analysis of a 4x4 diallel cross with reciprocals, taken as an example, was first performed in the usual way, with partition of the sum of squares for hybrids into general and specific combining ability, according to Model 3 of Griffing (1956), as shown in Table IV. The analysis of the diallel, according to the model of Gardner and Eberhart (1966), is shown in Table V. Some sources of variation show the same sum of squares in both analysis. Populations, varieties vs hybrids, reciprocals and specific combining ability sources of variation (Table IV) are the same as populations, average heterosis, reciprocals and specific heterosis (Table V). Actually, they represent sums of squares of the same corresponding effects. Except for reciprocals, Gardner and Eberhart (1966) have found the same relations when comparing their model with Model 4 (without reciprocals) of Griffing (1956).

The following relation can also be shown,

SS(varieties) + SS(GCA) = SS(varieties) + SS(variety heterosis)

where the left side comes from Table IV and the right side comes from Table V. A similar relation was also found by Gardner and Eberhart (1966) for the complete diallel without reciprocals and by Geraldi and Miranda Filho (1988) for the partial diallel when the complete set of varieties is split into two groups, so that the analysis is performed with the varieties and the hybrids between groups following an adaptation of Gardner and Eberhart's (1966) model (Miranda Filho and Geraldi, 1984). The estimates of the effects in the model are shown in Table VI. Another relation found in the present analysis is that $g_i = 1/2\ v_i + h_i$, which is the same as

Table II - Formulas for the estimation of effects and standard errors in a diallel mating scheme with reciprocal crosses.

Effects	Estimators	Standard error
Mean	$\hat{\mu} = \frac{Y_v}{n} = \bar{Y}_v$	$[\frac{1}{n}\sigma^2]^{\frac{1}{2}}$
Variety	$\hat{v}_i = Y_{ii} - \bar{Y}_v$	$[\frac{n-1}{n}\sigma^2]^{\frac{1}{2}}$
Heterosis	$\hat{h}_{ii'} = \frac{1}{2}[Y_{ii'} - Y_{ii} - Y_{i'i'}]$	$[\sigma^2]^{\frac{1}{2}}$
Average heterosis	$\bar{h} = \bar{Y}_H - \bar{Y}_v$	$[\frac{1}{n-1}\sigma^2]^{\frac{1}{2}}$
Variety heterosis	$\hat{h}_i = \frac{n-1}{n-2}(\bar{Y}_{i_H} - \bar{Y}_H) - \frac{1}{2}(Y_{ii} - \bar{Y}_v)$	$[\frac{n-1}{4(n-2)}\sigma^2]^{\frac{1}{2}}$
Specific heterosis	$\hat{S}_{ii'} = \frac{1}{2}Y_{ii'} + \frac{n}{n-2}\bar{Y}_H - \frac{n-1}{n-2}(\bar{Y}_{i_H} + \bar{Y}_{i'_H})$	$[\frac{n-3}{n-1}\sigma^2]^{\frac{1}{2}}$

Table III - Formulas for the analysis of variance in a diallel mating scheme with reciprocal crosses.

Source of variation	d.f.	Sums of squares
Populations	n^2-1	$\sum_{i} Y_{ii}^2 + \sum_{i<i} Y_{ii}^2 - \frac{Y_{..}^2}{n^2}$
Varieties	n-1	$\frac{1}{n}\left[\frac{1}{2}\sum_{i}(Y_{ii}+Y_{i.})^2 - \frac{2}{n}Y_{..}^2\right]$
Heterosis	$\frac{n(n-1)}{2}$	$\sum_{i} Y_{ii}^2 + \frac{1}{2}\sum_{i<i'} Y_{ii'}^2 - \frac{1}{2n}\sum_{i}(Y_{ii}+Y_{i'})^2 + \frac{1}{n^2}Y_{..}^2$
Average heterosis	1	$\frac{1}{n}Y_v^2 + \frac{1}{n(n-1)}Y_H^2 - \frac{1}{n^2}Y_{..}^2$
Variety heterosis	(n-1)	$\sum_{i} Y_{ii}^2 - \frac{1}{n}Y_v^2 + \frac{1}{n-2}\left[\frac{1}{2}\sum_{i} Y_{iH}^2 - \frac{2}{n}Y_H^2\right] - SS(var)$
Specific heterosis	$\frac{n(n-3)}{2}$	$\frac{1}{2}\sum_{i<i'} Y_{ii'}^2 - \frac{1}{n-2}\left[\frac{1}{2}\sum_{i} Y_{iH}^2 - \frac{1}{n-1}Y_H^2\right]$
Deviations	$\frac{n(n-1)}{2}$	$\left[\sum_{i\neq i} Y_{ii'}^2 - \frac{1}{2}\sum_{i<i'} Y_{ii}^2\right]^* = \left[\sum_{ii'k} Y_{ii'k} - \frac{1}{2}\sum_{i<i'} Y_{ii'\cdot}^2\right]^{**}$

Notation used: $\mathbf{Y_{ii}}$ = variety i; $\mathbf{Y_{ii} = Y_{ii'1} + Y_{ii'2}}$ = sum of reciprocal crosses; $\mathbf{Y_v = \sum_i Y_{ii}}$ = sum of varieties; $\mathbf{Y_H = \sum_{i<i'} Y_{ii'}}$ = sum of all crosses and reciprocals; $\mathbf{Y_{..} = Y_v + Y_H}$; $\mathbf{Y_{i.} = \sum_i Y_{ii} + \sum_{i\neq i} Y_{ii}}$ = $Y_{11} + Y_{12} + Y_{21} + Y_{13} + Y_{31} + \ldots$; $\mathbf{Y_{i_H} = \sum_{i\neq i} Y_{ii}}$ = $Y_{12} + Y_{21} + Y_{13} + Y_{31} + \ldots$

*, **: notation according to the operational model and basic model, respectively.

Table IV - Preliminary analysis of variance with partition of the sums of squares for hybrids according to Model 3 of Griffing (1956).

Source	d.f.	Sums of squares	Mean squares	F
Populations	15	3.2499	0.2167	18.24
Varieties (V)	3	0.4106	0.1369	11.52
Hybrids (H)	5	0.3695	0.0739	6.22
gca	3	0.2615	0.0872	7.39
sca	2	0.1080	0.0540	4.55
V vs H	1	2.3656	2.3656	199.12
Reciprocals	6	0.1040	0.0173	1.46
Error	45	0.5346	0.0118	

Table V - Analysis of variance for ear weight (Kg/5 m^2) in a 4x4 diallel scheme with reciprocals for maize in Piracicaba (1984/85).

Source	d.f.	Sums of squares	Mean squares	F	Analysis-II d.f.	Analysis-II MS
Populations	15	3.2499	0.2167	18.24	9	0.2764
Varieties	3	0.5500	0.1833	15.43	3	0.1533
Heterosis	6	2.5958	0.4326	36.41	6	0.3380
Average het.	1	2.3656	2.3656	199.12	1	1.8925
Variety het.	3	0.1222	0.0407	3.43	3	0.0272
Specific het.	2	0.1080	0.0540	4.55	2	0.0270
Deviations	6	0.1040	0.0173	1.46	-	-
Error	45	0.5346	0.0118			
gca	3	0.2615	0.0872			

Analysis-II: Gardner's (1967) procedure (see text).

that found by Gardner and Eberhart (1966) for the complete diallel and by Geraldi and Miranda Filho (1988) for the partial diallel between groups.

If the analysis of the diallel table with reciprocals is performed with the variety means and the hybrid means obtained by averaging the two reciprocal crosses, the results are changed only in the analysis of variance (see last columm of Table V). However, the estimates of effects are the same as those obtained through the proposed procedure, but their standard

Table VI - Estimates of the variety mean (μ), variety effects (v_i), total heterosis ($h_{ii'}$) average heterosis ($\bar{h}$), variety heterosis (h_i), specific heterosis ($s_{ii'}$) and general combining ability (g_i) for a 4x4 diallel scheme for maize.

#	1	2	3	4	$\hat{v}_i$	$\hat{h}_i$	$\hat{g}_i$
1	-	0.794	1.036	0.688	-0.290	-0.0735	-0.2185
2	0.104	-	0.837	1.782	0.456	-0.1253	0.1027
3	0.021	-0.125	-	1.191	-0.312	0.2000	0.0440
4	-0.125	0.021	0.104	-	0.146	-0.0013	0.0717
					$\hat{\mu}$ = 2.704	$\bar{h}$ = 0.08880 (32.8%)	

g_i: estimate according to Model 3 of Griffing (1956).
#: $h_{ii'}$: above diagonal; $s_{ii'}$: below diagonal.

errors are not. Therefore, when the results of diallel crosses with reciprocals are analyzed only to get information on the estimates of effects, the original procedure (Gardner, 1967) can be used because they are least square estimates. On the other hand, tests of hypotheses about the parameters in the model require the appropriate procedure, as well as the estimates of their standard errors.

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RESUMO

O modelo de Gardner e Eberhart (*Biometrics 22*: 439-452, 1966) foi usado para a análise de cruzamentos dialélicos de variedades quando são incluídos cruzamentos recíprocos. O método de quadrados mínimos foi utilizado para derivar as fórmulas para estimativa dos efeitos (componentes de médias) e para a análise da variância. Constatou-se que as estimativas dos efeitos são as mesmas se a análise for feita segundo o modelo original, com variedades e a média de cruzamentos recíprocos para representar cada combinação híbrida. Entretanto, os erros associados às estimativas alteram com a metodologia proposta, bem como as somas de quadrados na análise da variância. São feitas algumas comparações e um exemplo é dado para ilustração.

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