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METHODOLOGY
Analysis of diallel crosses with F_2 generations

José B. de Miranda Filho[1] *and Lázaro J. Chaves*[2]

ABSTRACT

The model of Gardner and Eberhart (*Biometrics* 22: 439-452, 1966) was used for the analysis of variety diallel crosses, in which the F_2 generations, instead of the F_1 hybrids, are used. The least square procedure was used to derive the formulas for estimation of effects (components of means) and for the analysis of variance. The estimators of the mean (μ) and variety effects (v_i) did not differ from the original model; but the estimators of the heterosis components for F_2 data were twice those obtained from the original model. In the same way, the standard errors of the estimates were different only for the heterosis components, when compared with formulas from the original model, while the formulas for the analysis of variance were the same.

INTRODUCTION

After the concepts of general combining ability (GCA) and specific combining ability (SCA) were introduced by Sprague and Tatum (1942), the methodology of diallel crosses has been extensively used in plant breeding. The diallel scheme is based on all possible crosses between a set of lines or genotypes, and the parents can be included or not. 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 used 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 ($\bar{h}$), the variety heterosis effects (h_i), the specific heterosis (s_{ii}') and the error term ($\bar{e}_{ii}'$), 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) is given by: $g_i = \frac{1}{2} v_i + h_i$ 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 (Eberhart and Gardner, 1966) where, besides the

[1] Departamento de Genética, Escola Superior de Agricultura "Luiz de Queiróz", Universidade de São Paulo, Caixa Postal 83, 13400-900 Piracicaba, SP, Brasil. Send correspondence to J.B.M.F.
[2] Departamento de Agricultura, Universidade Federal de Goiás, Caixa Postal 131, 74001-970 Goiânia, GO, Brasil.

parents and F_1's, other kinds of crosses (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 formulas 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). In some species, where crosses for the obtention of F_1 seeds are difficult, the use of the F_2 generation may be indicated.

The objective of this paper is to extend the methodology of diallel crosses to provide handy procedures for the analysis of variance and estimation of effects in which the means of the F_2 generations are used instead of the F_1's.

MATERIAL AND METHODS

The model of Gardner and Eberhart (1966) for diallel crosses includes heterosis as a component of the hybrid mean. The heterosis ($h_{ii'}$) is, by definition, the difference between the hybrid means ($Y_{ii'}$) and the average of the parental means; i.e., $h_{ii'} = Y_{ii'} - \frac{1}{2}(Y_{ii} + Y_{i'i'})$. Therefore, the basic model of Gardner and Eberhart (1966) is:

$$Y_{ii'} = \mu + \tfrac{1}{2}(v_i + v_{i'}) + \theta h_{ii'} + \bar{e}_{ii'}$$

where $\theta = 0$ for varieties and $\theta = 1$ for hybrids; μ is the mean of varieties; v_i is the effects of varieties, and $\bar{e}_{ii'}$ is the error term adjusted to entry means. The heterosis effect is then partitioned into the following components: $\bar{h}$, the average heterosis; h_i, the variety heterosis, and $s_{ii'}$, the specific heterosis. Eberhart and Gardner (1966) also showed that in the F_2 generation the total heterosis is decreased by half, so that the model for diallel crosses with parents and F_2's is:

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

When the parents are completely inbred lines the variety effects (v_i) expresses only the contribution of the homozygotes, so that it makes no difference if the F_2 generation is obtained by selfing or random mating the F_1's. Nevertheless, when the parents are open-pollinated varieties, the expressions for v_i in the F_2 generation are $\mathbf{v_i = a_i + d_i}$ for random mating, and $\mathbf{v_i = a_i + \frac{1}{2} d_i}$ for selfing; **a** and **d** are the overall contributions of homozygotes and heterozygotes, respectively, to the parent mean (Eberhart and Gardner, 1966). For the purpose of this paper we will consider that the F_2 generation is obtained by selfing when the parents are completely inbred lines, and random mating when the parents are open-pollinated varieties.

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: $\mathbf{Y} = \mathbf{X}\beta + \varepsilon$, where $\mathbf{Y}$ is the vector of means representing the diallel table; $\mathbf{X}$ is the matrix of coefficients in accordance with the basic model; β is the vector of parameters as defined in the basic model; and ε is the vector of the error term.

Following the least square procedure, the solution of the normal equations is given by: $\hat{\beta} = (\mathbf{X'X})^{-1}\mathbf{X'Y}$. The following restrictions were considered: $\sum_i \hat{v}_i = 0$; $\sum_i \hat{h}_i = 0$; $\sum_{i<i'} \hat{s}_{ii'} = 0$ 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	$R_1 - R_2$

For illustration of the proposed procedure, the analysis of yield data from a 6 x 6 diallel cross (Table I) is presented.

RESULTS AND DISCUSSION

The estimates of effects and the analysis of variance are obtained according to the least square procedure.

Table I - Weight of 100 kernels (means in grams over r replications)# of six common bean varieties (diagonal) and the F_2 generations of all possible crosses (above diagonal).

Varieties	1	2	3	4	5	6
1	17.67	19.16	18.80	20.50	20.84	20.36
2		19.39	19.20	21.78	21.72	21.68
3			18.48	20.73	20.76	19.84
4				21.61	21.52	22.86
5					21.94	22.47
6						21.75

Winter season under high level of fertility, from Antunes (1991).

The formulas for estimation of effects and their standard errors in a diallel table with parents and the F_2 generations of the respective crosses are shown in Table II. The formulas for the mean (μ) and variety effects (v_i) are the same as those given by Gardner (1967) for the original model. However, the estimates of the heterosis components ($\bar{h}$, h_i and $s_{ii'}$) are twice those obtained by using Gardner's (1967) formulas. The estimates of general combining ability (g_i) and specific combining ability ($s_{ii'}$) effects according to Griffing's (1956) method 4 are not true estimates and therefore are symbolized here by g_i^* and $s_{ii'}^*$, respectively. From the model presented here, the true estimate of the general combining ability effect is obtained by $\hat{g}_i = \frac{1}{2}\hat{v}_i + \hat{h}_i$, while $g_i^* = \frac{1}{2} v_i + \frac{1}{2} h_i$. In the same way $s_{ii'}^* = \frac{1}{2} s_{ii'}$, as already shown.

Table II - Formulas for estimation of effects and standard errors in a diallel table with parents and F_2 generations.

Effects	Estimators	Standard error
Mean	$\hat{\mu} = \frac{Y_v}{n} = \bar{Y}_v$	$\left[\frac{1}{n}\sigma^2\right]^{\frac{1}{2}}$
Variety	$\hat{v}_i = Y_{ii} - \bar{Y}_v$	$\left[\frac{n-1}{n}\sigma^2\right]^{\frac{1}{2}}$
Heterosis	$\hat{h}_{ii'} = [\,2Y_{ii'} - Y_{ii} - Y_{i'i'}\,]$	$[6\sigma^2]^{\frac{1}{2}}$
Average heterosis	$\bar{h} = 2\,[\,\bar{Y}_H - \bar{Y}_v\,]$	$\left[\frac{4(n+1)}{n(n-1)}\sigma^2\right]^{\frac{1}{2}}$
Variety heterosis	$\hat{h}_i = 2\left[\frac{n-1}{n-2}\right](\bar{Y}_{i_H} - \bar{Y}_H) - (Y_{ii} - \bar{Y}_v)$	$\left[\frac{(n-1)(n+2)}{n(n-2)}\sigma^2\right]^{\frac{1}{2}}$
Specific heterosis	$\hat{s}_{ii'} = 2\left[Y_{ii'} + \frac{n}{n-2}\bar{Y}_H - \frac{n-1}{n-2}(\bar{Y}_{i_H} + \bar{Y}_{i'_H})\right]$	$\left[\frac{4(n-3)}{n-1}\sigma^2\right]^{\frac{1}{2}}$
GCA	$\hat{g}_i = \frac{1}{2}\hat{v}_i + \hat{h}_i = \frac{2(n-1)}{n-2}(\bar{Y}_{iH} - \bar{Y}_H) - \frac{1}{2}(Y_{ii} - \bar{Y}_v)$	$\left[\frac{(n-1)(n+14)}{4n(n-2)}\sigma^2\right]^{\frac{1}{2}}$
Contrasts:	$v_i - v_{i'}$	$(2\sigma^2)^{\frac{1}{2}}$
	$h_i - h_{i'}$	$\left[\frac{2(n+2)}{n-2}\sigma^2\right]^{\frac{1}{2}}$
	$s_{ii'} - s_{ii''}$	$\left[\frac{8(n-3)}{n-2}\sigma^2\right]^{\frac{1}{2}}$
	$s_{ii'} - s_{i''i'''}$	$\left[\frac{8(n-4)}{n-2}\sigma^2\right]^{\frac{1}{2}}$
	$g_i - g_{i'}$	$\left[\frac{n+14}{2(n-2)}\sigma^2\right]^{\frac{1}{2}}$

$\hat{\sigma}^2$: estimate of the error variance.

The formulas for the analysis of variance are shown in Table III. The analysis of a 6 x 6 diallel cross with parents and F_2's, 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 analysis III of Gardner and Eberhart (1966), as shown in Table IV. The analysis of the diallel, according to the model for variety diallel crosses of Gardner and Eberhart (1966), is shown in Table V. Some sources of variation show the same sum of squares in both analyses. Populations, varieties vs. hybrids, and specific combining ability sources of variation (Table IV) are the same as populations, average heterosis and specific heterosis (Table V). Actually, they represent sums of squares of the same corresponding effects. Gardner and Eberhart (1966) found the same relations when comparing their model with model 4 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 with parents and F_1's and by Geraldi and

Table III - Formulas for the analysis of variance in a diallel table with parents and F_2 generations.

Source of variation	d.f.	Sums of squares
Populations	$\frac{n(n+1)}{2} - 1$	$\sum_i Y_{ii}^2 + \sum_{i<i'} Y_{ii'}^2 - \frac{2Y_{..}^2}{n(n+1)}$
Varieties	n-1	$\frac{1}{n+2}\left[\sum_i (Y_{ii} + Y_{i.})^2 - \frac{4}{n} Y_{..}^2\right]$
Heterosis	$\frac{n(n-1)}{2}$	---
Average heterosis	1	$\frac{1}{n} Y_V^2 + \frac{2}{n(n-1)} Y_H^2 - \frac{2}{n(n+1)} Y_{..}^2$
Variety heterosis	(n-1)	$\sum_i Y_{ii}^2 - \frac{1}{n} Y_V^2 + \frac{1}{n-2}\left[\sum_i Y_{i_H}^2 - \frac{4}{n} Y_H^2\right] - SS(var)$
Specific heterosis	$\frac{n(n-3)}{2}$	$\sum_{i<i'} Y_{ii'}^2 - \frac{1}{n-2}\left[\sum_i Y_{i_H}^2 - \frac{2}{n-1} Y_H^2\right]$

Table IV - Analysis of variance for 100-kernel weight in common bean in a 6 x 6 diallel cross, according to analysis III of Gardner and Eberhart (1966).

Source	d.f.	Sums of squares	Mean squares	F
Populations	20	39.9545	1.9977	6.77
Varieties (V)	5	17.4120	3.4824	11.80
Hybrids (H)	14	20.5918	1.4708	4.98
GCA	5	18.3940	3.6788	12.47
SCA	9	2.1977	0.2442	< 1
V vs H	1	1.9507	1.9507	6.61
Error	70	---	0.2951	---
Varieties + GCA:		35.8060		

Table V - Analysis of variance for 100-kernel weight in common bean in a 6 x 6 diallel cross, according to the complete diallel model of Gardner and Eberhart (1966).

Source	d.f.	Sums of squares	Mean squares	F
Populations	20	39.9545	1.9977	6.77
Varieties	5	35.3662	7.0732	23.97
Heterosis	15	4.5873	0.3058	1.04
Average heterosis	1	1.9507	1.9508	6.61
Variety heterosis	5	0.4388	0.0878	< 1
Specific heterosis	9	2.1977	0.2442	< 1
Error	70	---	0.2951	
Varieties + Var. heterosis:		35.8060		

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) in a 6 x 6 diallel cross.

#	1	2	3	4	5	6	$\hat{v}_i$	$\hat{h}_i$	$\hat{g}_i$	$\hat{g}_i$*
1	---	1.26	1.45	1.72	2.07	1.30	-2.47	0.263	-0.972	-1.103
2	-0.836	---	0.53	2.56	2.11	2.22	-0.75	0.483	0.108	-0.133
3	0.549	-0.591	---	1.37	1.10	-0.55	-1.66	-0.712	-1.542	-1.186
4	-0.081	0.539	0.544	---	-0.51	2.36	1.47	0.188	0.923	0.829
5	0.639	0.459	0.644	-1.866	---	1.25	1.80	-0.182	0.718	0.809
6	-0.271	0.429	-1.146	0.864	0.124	---	1.61	-0.042	0.763	0.784
								$\hat{\mu}=20.140$	$\bar{h}=1.349$ (6.7%)	

$g_i = \frac{1}{2} v_i + h_i$; $\hat{g}_i$*: estimates from Griffing (1956)'s method 4.

#: $h_{ii'}$: above diagonal; $s_{ii'}$: below diagonal.

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 (1966)'s model (Miranda Filho and Geraldi, 1984). The estimates of the effects in the model are shown in Table VI.

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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 os parentais e as gerações F_2 dos cruzamentos. O método de quadrados mínimos foi utilizado para derivar as fórmulas para estimação dos efeitos (componentes de médias) e para a análise da variância. Constatou-se que as estimativas dos componentes de médias não diferem do modelo original para a média das variedades (μ) e para os efeitos de variedades (v_i), mas são diferentes para os componentes da heterose. Do mesmo modo, os erros associados às estimativas diferem do modelo original somente para os componentes da heterose. As fórmulas da análise da variância são as mesmas do modelo original.

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