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METHODOLOGY

Analysis of variance of partial diallel tables

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Abstract

The theory of variance analysis of partial diallel tables, following Hayman's proposal of 1954, is presented. As several statistical tests yield similar inferences, the present analysis mainly proposes to assess genetic variability in two groups of parents and to study specific, varietal and mean heteroses. Testing the nullity of specific heteroses equals testing absence of dominance. Testing equality of varietal heteroses of the parents of a group is equivalent to testing the hypothesis that in the other group allelic genes have the same frequency. Rejection of the hypothesis that the mean heterosis is null indicates dominance. The information obtained complements that provided by diallel analysis involving parents and their F_1 hybrids or F_2 generations. An example with the common bean is included.

INTRODUCTION

The methods of diallel analysis proposed by Jinks and Hayman (1953) and Hayman (1954b, 1958) employ first degree statistics (means) to estimate variances and covariances used to assess adequacy of the additive-dominance model and estimate the genetic components of variation and other genetic parameters. Since fitted linear models use second degree statistics (variances and covariances), the approach is less precise in sampling variation terms than analysis of variance.

Variance analysis of diallel tables allows inferences about the significance of genetic components of variation (Hayman, 1954a) using tests based on statistics with known distributions (Searle, 1971; Graybill, 1976). As for the methods proposed by Griffing (1956) and Gardner and Eberhart (1966), and their adaptations to partial diallels (Miranda Filho and Geraldi, 1984; Geraldi and Miranda Filho, 1988), the diallel analysis corresponds to a variance analysis.

This paper presents variance analysis of partial diallel tables including parents and their F_1 hybrids or F_2 generations, according to Hayman's proposal. Allowing a detailed evaluation of dominance in the polygenic systems under study, the analysis assesses specific, varietal and mean heteroses.

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Partial diallel analysis, which includes assessing the adequacy of the additive-dominance model from variance analysis of the differences between covariance (W) and variance (V) in the arrays and/or from regression analysis of W on V (Mather and Jinks, 1974) in each group of parents, makes variance analysis of the partial diallel table redundant at many points, since they virtually duplicate information. Also, several tests in variance analysis are repetitive, making them appear insignificant. We will show, however, that they can complement each other, mainly regarding specific, varietal and mean heteroses.

Tables I and II show analyses of variance of plot means or totals involving N parents, with n in one group and n' in the other (n + n' = N), and their nn' F_1 hybrids or F_2 generations, arranged in a randomized complete block design. The non-genetic component of the expected mean squares was obtained assuming equal variances for residuals associated with observations of the parents (e_{tj}) and their F_1 hybrids or F_2 generations (e_{rsj}) ($V(e_{tj}) = V(e_{rsj}) = \sigma^2$, for all t, r, s and j; t = 1, ..., N; r = 1, ..., n; s = 1, ..., n', and j = 1, ..., b, where b is the number of replications). The means m_{L0}, m'_{L0}, m_{L1} and m_{L2}, the non-genetic components E, E' and E", the genetic components of the expected mean squares and the other parameters presented throughout the text are defined by Viana *et al.* (1999, in press). The values p and q are, respectively, n/N and n'/N. Note that the additive genetic components $D_{(1)}$, $D_{(2)}$ and $D_{(3)} = (D - p^2D_{(1)} - q^2D_{(2)})/2pq$ are estimable.

The treatment sum of squares is:

$$\text{SSTreatments} = \{b[\sum_{r=1}^{n} y_r^2 - \frac{(y_.)^2}{n}] + b[\sum_{s=1}^{n'} y_s^2 - \frac{(y'_.)^2}{n'}] +$$

$$b[\frac{(y_.)^2}{n} + \frac{(y'_.)^2}{n'} - \frac{(y_. + y'_.)^2}{n+n'}]\} + \{bn'[\sum_{r=1}^{n} \bar{y}_{r.}^2 - \frac{(y_{..})^2}{n(n')^2}] +$$

$$bn[\sum_{s=1}^{n'} \bar{y}_{.s}^2 - \frac{(y_{..})^2}{(n)^2n'}] + b[\sum_{r=1}^{n}\sum_{s=1}^{n'} y_{rs}^2 - n'\sum_{r=1}^{n} \bar{y}_{r.}^2 - n\sum_{s=1}^{n'} \bar{y}_{.s}^2 +$$

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Table I - Analysis of variance of partial diallel involving parents and their F_1 hybrids arranged in a randomized complete block design.

Source of variation	Degrees of freedom	e(mean square)
Constant	1	-
Blocks	b - 1	-
Treatments	(N + nn’ - 1)	-
parents	(N - 1)	$\sigma^2 + bD$
parents|group 1	n - 1	$\sigma^2 + bD_{(1)}$
parents|group 2	n’ - 1	$\sigma^2 + bD_{(2)}$
between groups	1	$\sigma^2 + \frac{bnn'}{N}(m_{L0} - m'_{L0})^2$
F_1 hybrids	(nn’ - 1)	$\sigma^2 + \frac{b}{4}(D_{(1)} + D_{(2)} - F_{(1)} - F_{(2)} + H_{1(1)} + H_{1(2)} - H_2)$
arrays|group 1	n - 1	$\sigma^2 + \frac{bn'}{4}(D_{(1)} - F_{(2)} + H_{1(1)} - H_2)$
arrays|group 2	n’ - 1	$\sigma^2 + \frac{bn}{4}(D_{(2)} - F_{(1)} + H_{1(2)} - H_2)$
arrays|group 1 x arrays|group 2	(n - 1)(n’ - 1)	$\sigma^2 + \frac{b}{4(n-1)(n'-1)}[(n'-1)D_{(1)} + (n-1)D_{(2)} -$ $(n-1)F_{(1)} - (n'-1)F_{(2)} + (n'-1)H_{1(1)} +$ $(n-1)H_{1(2)} - (n-1)(n'-1)H_2]$
parents vs. F_1 hybrids	1	$\sigma^2 + \frac{bNnn'}{(N+nn')}(m_{L1} - pm_{L0} - qm'_{L0})^2$
Error	(b - 1)(N + nn’ - 1)	σ^2 (bE = bE’)
error (1)	(b - 1)(N - 1)	bE
error (2)	(b - 1)(nn’ - 1)	bE’
error (3)	(b - 1)	-
Total	b(N + nn’)	

$$\frac{(y_{..})^2}{nn'} \;]\} + b[\frac{(y_{.} + y'_{.})^2}{n+n'} + \frac{(y_{..})^2}{nn'} - \frac{(y_{.} + y'_{.} + y_{..})^2}{N+nn'}]$$

= {SSParents|Group 1 + SSParents|Group 2 + SSBetween Groups} + {SSArrays|Group 1 + SSArrays|Group 2 + SS(Arrays|Group 1 x Arrays|Group 2)} + SS(Parents vs. F_1 Hybrids or F_2 Generations)
= SSParents + SS(F_1 Hybrids or F_2 Generations) + SS(Parents vs. F_1 Hybrids or F_2 Generation),
where y_r and y_s are the means of the rth and sth parents and y_{rs} is the mean of the F_1 hybrid or F_2 generation derived from them.

The error (1) sum of squares is obtained from the analysis of variance considering only the parents. The error (2) sum of squares is obtained considering only the F_1 hybrids or F_2 generations. The sum of squares due to the constant is that attributable to the hypothesis that the expectation of the observed variable is null. The block sum of squares is that due to the hypothesis of equality of the block means. Acceptance of this hypothesis implies that weighted average of the means of the n parents in one group, n’ parents in the other group and nn’ F_1 hybrids or F_2 generations is constant over the b blocks. Consequently, the genetic effects d_a and h_a are constants under the various environmental conditions defined by the blocks. The treatment sum of squares is that attributable to the hypothesis of equality of the means of the N + nn’ treatments, that is, of the N parents and nn’ F_1 hybrids or F_2 generations ($H_0 : p_r = p_s = f_{rs}$ or g_{rs}, for every r and s). Its acceptance shows a lack of genetic variability among the parents ($\theta_{ra} = \theta_{sa}$, for every r, s and a; a = 1, ..., k, where k is the number of loci in the polygenic system under study).

The sum of squares of parents, of parents of group 1 and of parents of group 2 are, respectively, those due to the hypotheses of equality of the means of the N parents ($H_0 : \theta_{ta} = \theta_a$, for every t and a), n parents ($H_0 : \theta_{ra} = \theta_a$, for every r and a) and n’ parents ($H_0 : \theta_{sa} = \theta_a$, for every s and a). Acceptance of these hypotheses also implies lack of genetic variability. The between groups sum of squares is attributable to the hypothesis $H_0 : m_{L0} = m'_{L0}$. Its acceptance shows that the genes are, probably, equally frequent in the two groups of parents ($w_a = w'_a$, for every a) and, therefore, that $D_{(1)} = D_{(2)} = D_{(3)} = D$, $F_{(1)} = F_{(2)} = F$ and $H_{1(1)} = H_{1(2)} = H_{1(3)} = H_1$.

The sum of squares of F_1 hybrids or F_2 generations

Table II - Analysis of variance of partial diallel involving the parents and their F_2 generations arranged in a randomized complete block design.

Source of variation	Degrees of freedom	e(mean square)
Constant	1	-
Blocks	b - 1	-
Treatments	(N + nn'- 1)	-
parents	(N - 1)	$\sigma^2 + bD$
parents|group 1	n - 1	$\sigma^2 + bD_{(1)}$
parents|group 2	n'- 1	$\sigma^2 + bD_{(2)}$
between groups	1	$\sigma^2 + \frac{bnn'}{N} (m_{L0} - m'_{L0})^2$
F_2 generations	(nn'- 1)	$\sigma^2 + \frac{b}{4} (D_{(1)} + D_{(2)} - \frac{1}{2} F_{(1)} - \frac{1}{2} F_{(2)} + \frac{1}{4} H_{1(1)} + \frac{1}{4} H_{1(2)} - \frac{1}{4} H_2)$
arrays|group 1	n - 1	$\sigma^2 + \frac{bn'}{4} (D_{(1)} - \frac{1}{2} F_{(2)} + \frac{1}{4} H_{1(1)} - \frac{1}{4} H_2)$
arrays|group 2	n'- 1	$\sigma^2 + \frac{bn}{4} (D_{(2)} - \frac{1}{2} F_{(1)} + \frac{1}{4} H_{1(2)} - \frac{1}{4} H_2)$
arrays|group 1 x arrays|group 2	(n - 1)(n'- 1)	$\sigma^2 + \frac{b}{4(n-1)(n'-1)} [(n'-1) D_{(1)} + (n-1) D_{(2)} - \frac{(n-1)}{2} F_{(1)} - \frac{(n'-1)}{2} F_{(2)} + \frac{(n'-1)}{4} H_{1(1)} + \frac{(n-1)}{4} H_{1(2)} - \frac{(n-1)(n'-1)}{4} H_2]$
parents vs. F_2 generations	1	$\sigma^2 + \frac{bNnn'}{(N + nn')} (m_{L2} - pm_{L0} - qm'_{L0})^2$
Error	(b - 1)(N + nn'- 1)	$\sigma^2 (bE = bE'')$
error (1)	(b - 1)(N - 1)	bE
error (2)	(b - 1)(nn'- 1)	bE''
error (3)	(b - 1)	-
Total	b(N + nn')	

is due to the hypothesis of equality of the means of the F_1 hybrids or F_2 generations. Testing this hypothesis is equivalent to testing absence of variability in the two groups of parents ($H_0 : \theta_{ra} = \theta_a$ and $\theta_{sa} = \theta'_a$, for every r, s and a). The sum of squares attributable to the hypothesis of equality of the means of the arrays of the parents in group 1 and the sum of squares due to the same hypothesis in group 2 is the sum of squares of the arrays within group 1 and group 2, respectively. The test of the hypothesis of equality of the means of the arrays within a group tests the hypothesis of equality of the parental genotypes in the group ($H_0 : \theta_{ra} = \theta_a$ or $H_0 : \theta_{sa} = \theta'_a$, for every r or s and for every a). The interaction sum of squares is also a sum of squares attributable to the hypothesis of absence of genetic variability in both groups of parents.

The sum of squares of parents versus F_1 hybrids and of parents versus F_2 generations are, respectively, the sums of squares due to the hypotheses:

$$H_0: m_{L1} - \overline{m}_{L0} = \frac{1}{2} \sum_{a=1}^{k} d_a (w_a + w'_a - 2\overline{w}_a) + \frac{1}{2} h = 0$$

$$H_0: m_{L2} - \overline{m}_{L0} = \frac{1}{2} \sum_{a=1}^{k} d_a (w_a + w'_a - 2\overline{w}_a) + \frac{1}{4} h = 0$$

Thus, testing these hypotheses is not equivalent to testing $H_0 : h = 0$. The equivalence only occurs if $w_a = w'_a$ or if p = q.

Variance analysis yields detailed assessment of dominance in the polygenic system under study. Consider the following hypothesis:

$H_{0(1)} : f_{rs} - (1/2)(p_r + p_s) = (1/2)h_{rs} = 0$, for every r and s, if parents and F_1 hybrids were evaluated, or

$H_{0(1)} : g_{rs} - (1/2)(p_r + p_s) = (1/4)h_{rs} = 0$, for every r and s, if parents and F_2 generations were evaluated.

If there is evidence of genetic variability among the parents, testing the hypothesis $H_{0(1)}: h_{rs} = 0$, for every r and s (nullity of the specific heteroses), equals testing the hypothesis of absence of dominance in the polygenic system under study ($H_{0(1)}$: $h_a = 0$, for every a). Acceptance of this hypothesis implies that $F_r = F_s = F_{(1)} = F_{(2)} = H_{1(1)} = H_{1(2)} = H_{1(3)} = H_{2r} = H_{2s} = H_2 = h_r = h_s = h = 0$.

Other hypotheses testable in variance analysis are:

$$H_{0(2)}:[f_r - \frac{1}{2}(p_r + m'_{L0})] - [f_{r'} - \frac{1}{2}(p_{r'} + m'_{L0})] = \frac{1}{2}(h_r - h_{r'}) = 0,$$

for every rand r'(r ≠ r'), or

$$H_{0(2)}:[g_r - \frac{1}{2}(p_r + m'_{L0})] - [g_{r'} - \frac{1}{2}(p_{r'} + m'_{L0})] = \frac{1}{2}(h_r - h_{r'}) = 0,$$

for every rand r'(r ≠ r'), and

$$H_{0(3)}:[f_s - \frac{1}{2}(p_s + m_{L0})] - [f_{s'} - \frac{1}{2}(p_{s'} + m_{L0})] = \frac{1}{2}(h_s - h_{s'}) = 0,$$

for every s and s'(s ≠ s'), or

$$H_{0(3)}:[g_s - \frac{1}{2}(p_s + m_{L0})] - [g_{s'} - \frac{1}{2}(p_{s'} + m_{L0})] = \frac{1}{2}(h_s - h_{s'}) = 0,$$

for every s and s'(s ≠ s')

In the presence of genetic variability in the two groups of parents and dominance in the polygenic system under study, with a non-constant h_a value, testing hypothesis $H_{0(2)}$: $h_r = h_{r'}$ for every r and r' (equality of the varietal heteroses of the n parents of a group), is equivalent to testing the hypothesis that in the group with n' parents the allelic genes are as frequent ($H_{0(2)}$: $w'_a = 0$, for every a). In the same way, testing hypothesis $H_{0(3)}$: $h_s = h_{s'}$, for every s and s' (equality of varietal heteroses of n' parents of the other group), is equivalent to testing the hypothesis that in the group with n parents allelic genes are just as frequent ($H_{0(3)}$: $w_a = 0$, for every a). Acceptance of $H_{0(2)}$ implies that $D_{(2)} = D_{(3)}$, $F_{(2)} = 0$, $H_{1(1)} = H_{2s} = H_2$ and $H_{1(2)} = H_{1(3)}$. Acceptance of $H_{0(3)}$ implies that $D_{(1)} = D_{(3)}$, $F_{(1)} = 0$, $H_{1(1)} = H_{1(3)}$ and $H_{1(2)} = H_{2r} = H_2$. If the two hypotheses are accepted, then $D_{(1)} = D_{(2)} = D_{(3)}$, $F_{(1)} = F_{(2)} = 0$ and $H_{1(1)} = H_{1(2)} = H_{1(3)} = H_{2r} = H_{2s} = H_2$.

Expressing the hypotheses $H_{0(1)}$, $H_{0(2)}$ and $H_{0(3)}$ in terms of the components of the statistical model results in:
$H_{0(1)}$: $t_{rs} - (1/2)t_r - (1/2)t'_s = 0$, for every r and s (nn' linear, estimable and independent parametric functions);

$$H_{0(2)}: \frac{1}{n'}\sum_{s=1}^{n'}(t_{rs} - t_{r's}) - \frac{1}{2}(t_r - t_{r'}) = 0,$$

for every r and r'(n - 1 linear, estimable and independent parametric functions);

$$H_{0(3)}: \frac{1}{n}\sum_{r=1}^{n}(t_{rs} - t_{rs'}) - \frac{1}{2}(t'_s - t'_{s'}) = 0,$$

for every s and s' (n'- 1 linear, estimable and independent parametric functions),
where t_{rs} is the effect of the F_1 hybrid or F_2 generation obtained from the cross among the rth and sth parents, t_r is the effect of the rth parent and t'_s is the effect of the sth parent.

The sums of squares attributable to the hypotheses $H_{0(1)}$ (sum of squares of the specific heterosis), $H_{0(2)}$ (sum of squares of the varietal heterosis in the group with n parents) and $H_{0(3)}$ (sum of squares of the varietal heterosis in the group with n' parents) may be obtained based on general linear model theory. Let the linear model $Y = X\beta + \varepsilon$ ($\varepsilon \sim N(\Phi, \sigma^2 I)$). The sum of squares due to the hypothesis $H_0 : H\beta = c$ versus $H_a : H\beta \neq c$, where H is a full row rank matrix and $H\beta$ is a set of (rank of H) linear combinations of the parameters, estimable and independent, is (Graybill, 1976; Searle, 1971):

$$SS(H_0) = (H\beta^o - c)'[H(X'X)^G H']^{-1}(H\beta^o - c),$$

with (rank of H) degrees of freedom. A solution of the system of normal equations is β^o and $(X'X)^G$ is any generalized inverse of X'X. The statistic for the test of hypothesis $H_0 : H\beta = c$ is:

$$F = \frac{SQ(H_0)/rank(H)}{\hat{\sigma}^2},$$

which, under H_0, has an F distribution with (rank of H) and [b(N + nn') - (rank of X)] degrees of freedom (Graybill, 1976; Searle, 1971).

Therefore, the sums of squares due to hypotheses $H_{0(1)}$, $H_{0(2)}$ and $H_{0(3)}$ have nn', (n - 1) and (n' - 1) degrees of freedom, respectively. As this approach is unfeasible even for those with knowledge of linear models theory, the following formulae should be used (Miranda Filho and Geraldi, 1984):

$$SS(H_{0(2)}) = \frac{bn'}{4 + n'}\sum_{r=1}^{n}[y_r - \bar{y}. - 2(\bar{y}_{r.} - \bar{y}_{..})]^2$$

$$SS(H_{0(3)}) = \frac{bn}{4 + n}\sum_{s=1}^{n'}[y_s - \bar{y}'. - 2(\bar{y}_{.s} - \bar{y}_{..})]^2$$

$SS(H_{0(1)}) = SS(H_{0(4)}) + SS(H_{0(2)}) + SS(H_{0(3)}) + SS$ (Arrays|Group 1 x Arrays|Group 2)
where $\bar{y}.$ and $\bar{y}'.$ are the means of the groups with n and n' parents and $\bar{y}..$ is the mean of the F_1 hybrids or F_2 generations.

The sum of squares attributable to the hypothesis $H_{0(4)}$: $m_{L1} - (1/2)(m_{L0} + m'_{L0}) = (1/2)h = 0$ or $H_{0(4)}$: $m_{L2} - (1/2)(m_{L0} + m'_{L0}) = (1/4)h = 0$, depending on the populations assessed, is the sum of squares due to the hypothesis that the mean heterosis is null ($H_{0(4)}$: $h = 0$) (sum of squares of the mean heterosis). Rejection of the hypothesis shows the presence of dominance in the polygenic system under study. The sign of the contrast estimate indicates the predominant direction of deviations due to dominance. Expressed in statistical model components the hypothesis is:

$$H_{0(4)}: \frac{1}{nn'}\sum_{r=1}^{n}\sum_{s=1}^{n'} t_{rs} - \frac{1}{2n}\sum_{r=1}^{n} t_r - \frac{1}{2n'}\sum_{s=1}^{n'} t'_s = 0$$

Thus,

$$SS(H_{0(4)}) = \frac{[\bar{y}_{..} - \frac{1}{2}(\bar{y}_{.} + \bar{y}'_{.})]^2}{(\frac{1}{bnn'} + \frac{1}{4bn} + \frac{1}{4bn'})},$$

with one degree of freedom, and

$$E(SS(H_{0(4)})) = \sigma^2 + \frac{(1/4)h^2}{(\frac{1}{bnn'} + \frac{1}{4bn} + \frac{1}{4bn'})},$$

in the case of evaluation of parents and F_1 hybrids, or

$$E(SS(H_{0(4)})) = \sigma^2 + \frac{(1/16)h^2}{(\frac{1}{bnn'} + \frac{1}{4bn} + \frac{1}{4bn'})},$$

in the case of evaluation of parents and F_2 generations.

The sum of squares of the specific heterosis is not orthogonal to the sums of squares of varietal heterosis in groups with n and n' parents and to the sum of squares of the mean heterosis, although the last three are orthogonal among themselves.

APPLICATION

In the following variance analyses the data refer to the grain yield per plant, in grams, of nine lines of common beans, six in group 1 and three in group 2, and their 18 F_1 hybrids or F_2 generations, obtained from the partial diallel. Table III shows a summary of analysis of variance of parents and their F_1 hybrids, containing only mean squares supplying informative and non-repetitive tests. Table IV shows the estimates of specific, varietal and mean heteroses. Variance analysis shows presence of genetic variability among parents in group 1. The evidence that the genes determining grain yield are fixed in group 2 is not consistent with results of the diallel analysis considering the additive-dominance model. When there is no genetic variability in one or both groups of parents ($w_a^2 = 1$ and, or, $w_a'^2 = 1$), no relationship exists between covariance and variance in the arrays, as $V(F_r)$ and/or $V(F_s)$ are equal to zero. However, analysis of adequacy of the additive-dominant model shows a functional relation between W and V (Viana *et al.*, 1999).

The parents in group 2 should not have the same genotype, for genes determining grain yield. Magnitudes of their observed means (6.10, 4.48 and 9.54, for BAT-304, FT-84-835 and Batatinha, respectively), specific and varietal heteroses show differences. Evidence of absence of variability in group 2 must stem from high experimental error, revealed by high magnitude of the coefficient of variation. Accentuated variation among treatment replications results from the presence, in the same plot, of many-poded plants with well-developed seeds together with plants with few pods with well-formed seeds and several pods without seeds or with undeveloped seeds. This, most probably, owes to low daytime temperatures observed during plant development. Due to large experimental error, grain yield of the parents in group 2 will be considered different, with approximately 0.19 probability.

Variance analysis indicates, furthermore, that genes determining grain yield are not equally frequent in the two parent groups. Estimate of contrast m_{L0} - m_{L0} (3.32) reveals that genes increasing grain yield are more frequent in group 1. Tests of hypothesis for specific and mean heteroses show, as expected, dominance in the polygenic system determining grain yield. Estimate of mean heterosis shows that dominance effects are predominantly positive, contributing to trait expression increase. The tests of varietal heteroses equality show that, in each parent group, allelic genes are equally frequent. However, their different magnitudes in group 1 and the high experimental error demonstrate that varietal heteroses in this group are not a constant, indicating that the allelic genes are not equally frequent in group 2. When the hypothesis of equality of

Table III - Summary of the analysis of variance of partial diallel including nine lines of common beans and their F_1 hybrids, for grain yield, in grams.

Source of variation	Degrees of freedom	Mean square
Parents|group 1	5	46.89*
Parents|group 2	2	26.71^{++}
Between groups	1	87.74*
Specific heterosis	18	48.97**
Varietal heterosis|group 1	5	28.28^{++}
Varietal heterosis|group 2	2	12.37^{++}
Mean heterosis	1	357.67**
Error	81	15.73
CV (%)	35.34	

**P < 0.01. *0.01 < P < 0.05. $^{++}$P > 0.10.

Table IV - Estimates of specific (central values), varietal in group 1 (vertical marginal values), varietal in group 2 (horizontal marginal values) and mean (lower right hand side) heteroses, for grain yield of common beans, in grams, and significance levels for tests of the hypotheses $H_0 : h_{rs} = 0$, $H_0 : h_r = 0$ and $H_0 : h_s = 0$[1].

Parent	BAT-304	FT-84-835	Batatinha	
Ricopardo 896	4.87^{++}	1.17^{++}	14.34**	6.79*
Ouro Negro	4.64^{++}	10.64*	14.01**	9.76**
Antioquia 8	15.06**	17.64**	6.28^{++}	12.99**
DOR. 241	-4.06^{++}	1.14^{++}	8.15^{+}	1.74^{++}
RAB 94	9.81*	6.82^{++}	0.98^{++}	5.87^{+}
Ouro	3.67^{++}	12.12*	17.37**	11.05**
	5.66*	8.25**	10.19**	8.04

[1] Using the F-statistic. **P < 0.01. *0.01 < P < 0.05. $^{+}$0.05 < P < 0.10. $^{++}$P > 0.10.

varietal heterosis in group 1 is rejected, probability of a type I error is approximately 0.12. It may be considered, therefore, that in group 1, contrary to what happens in group 2, allelic genes affecting grain yield are equally frequent.

Table V is a summary of variance analysis of the partial diallel considering data from parents and F_2 generations. Results indicate, as expected, genetic variability in group 1. In group 2 genetic variation is nil or reduced ($P = 0.15$), indicating that allelic frequencies in the polygenic system defined by the parents in this group are close to 1 and 0. Estimate of the difference between the means of the two groups (2.00) reveals that genes increasing grain yield occur in greater frequency in group 1. Analysis of dominance in the polygenic system indicates irrelevance of such genic effects. Therefore, one generation of self-pollination sufficed to markedly reduce the contribution of dominance effects for grain yield. Heterosis manifested in the hybrids is nil or negligible in the F_2 generations. These results agree with those from the diallel analysis (Viana *et al.*, in press).

Table V - Summary of the analysis of variance of the partial diallel including nine lines of common beans and their F_2 generations, for grain yield, in grams.

Source of variation	Degrees of freedom	Mean square
parents|group 1	5	16.15**
parents|group 2	2	3.56^{++}
between groups	1	32.16**
specific heterosis	18	1.59^{++}
varietal heterosis|group 1	5	2.36^{++}
varietal heterosis|group 2	2	1.90^{++}
mean heterosis	1	4.50^{++}
error	78	1.87
CV (%)	22.32	

** $P < 0.01$. $^{++}P > 0.10$.

RESUMO

Com base no trabalho de Hayman de 1954, este artigo discute a análise de variância de tabelas de dialelos parciais. Em razão de muitos dos testes proporcionarem as mesmas inferências, os principais objetivos da análise apresentada são a avaliação da variabilidade genética nos dois grupos de pais e o estudo das heteroses específica, varietal e média. Testar a nulidade das heteroses específicas é testar a hipótese de ausência de dominância. O teste de igualdade das heteroses varietais em relação aos pais de um grupo é o teste de igualdade das freqüências alélicas no outro grupo. A rejeição da hipótese de nulidade da heterose média indica que há dominância. As informações geradas complementam as resultantes da análise dialélica, envolvendo os genitores e seus híbridos F_1 ou suas gerações F_2. Um exemplo com feijoeiro comum é incluído.

REFERENCES

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

Geraldi, I.O. and **Miranda Filho, J.B. de** (1988). Adapted models for the analysis of combining ability of varieties in partial diallel crosses. *Rev. Bras. Genet. 11*: 419-430.

Graybill, F.A. (1976). *Theory and Application of the Linear Model*. Duxbury Press, North Scituate, Massachusetts.

Griffing, B. (1956). Concept of general and specific combining ability in relation to diallel crossing system. *Aust. J. Biol. Sci. 9*: 463-493.

Hayman, B.I. (1954a). The analysis of variance of diallel tables. *Biometrics 10*: 235-244.

Hayman, B.I. (1954b). The theory and analysis of diallel crosses. *Genetics 19*: 789-809.

Hayman, B.I. (1958). The theory and analysis of diallel crosses. II. *Genetics 43*: 63-85.

Jinks, J.L. and **Hayman, B.I.** (1953). The analysis of diallel crosses. *Maize Genet. Cooperation NewsL. 27*: 48-54.

Mather, K. and **Jinks, J.L.** (1974). *Biometrical Genetics*. 2nd edn. Cornell University Press, Ithaca, New York.

Miranda-Filho, J.B. de and **Geraldi, I.O.** (1984). An adapted model for the analysis of partial diallel crosses. *Rev. Bras. Genet. VII*: 677-688.

Searle, S.R. (1971). *Linear Models*. John Wiley and Sons, New York.

Viana, J.M.S., Cruz, C.D. and **Cardoso, A.A.** (1999). Theory and analysis of partial diallel crosses. *Genet. Mol. Biol. 22*: 591-599.

Viana, J.M.S., Cruz, C.D. and **Cardoso, A.A.** Theory and analysis of partial diallel crosses. Parents and F_2 generations. *Bragantia* (in press).

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