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ANALYSIS OF UNBALANCED DIALLEL CROSSES

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ABSTRACT

The estimation process of general and specific combining abilities as well as their corresponding sums of squares obtained from unbalanced diallel systems in which progenitors and/or hybrid combinations were evaluated with an unequal number of replications. As an illustration, the hypothetical data sets of a diallel involving progenitors and the corresponding F_1's and another involving only the F_1's were analysed.

INTRODUCTION

The analysis of diallel crosses is of unquestionable importance for improving plants when one has to make a decision about the breeding method to be used and to select genetic material for breeding.

This method of analysis has also been used successfully in studies involving quantitative genetics. It has helped to better understand the kind of genic action involved in the establishment of quantitative characters (Gardner and Eberhart, 1966).

The general combining ability (GCA) and specific combining ability (SCA) estimates of a diallel cross are used in animal and plant breeding. Several methodologies have been used for obtaining these estimates (Griffing, 1956; Kempthorne, 1957; Geraldi and Miranda Filho, 1988) and they have been applied to the analysis of balanced diallels. However, many data sets are unbalanced, especially for self-fertilizing species for which artificial crossing is difficult and time consuming (England, 1974). Thus, an alternative method for estimating GCA and SCA is desirable.

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We introduce a methodology to analyse a diallel with an unequal number of replications. This procedure involves modifications of the methodology proposed by Griffing, 1956.

METHODOLOGY

General

The unbalanced diallel arises when each progenitor and/or hybrid combination evaluated has a different number of replications. This variation can be caused by the loss of plots, seed restriction, etc. Breeders of some self-fertilizing species sometimes have to deal with this situation because the artificial crosses performed to obtain the F_1's usually generate not only a very low but also a variable number of seeds. Since the effects of combining abilities are estimated from averages derived from progenitor and hybrid combinations, analyses of the unbalanced diallel requires changes in the conventional estimating process. The experimental errors associated with these averages have an independent distribution, with zero mean and variance equal to $D\sigma^2$, whe D is the t x t matrix (t = number of entries in the diallel), whose elements are the reciprocals of the numbers of replications of each entry. This situation generates the need for the application of the weighted least squares method to estimate the effects and the sums of squares of the combining abilities, instead of the ordinary least squares method.

The process for estimating the effects of the combining abilities through the least squares method is described below. Considering,

$$\underset{\sim}{y} = X\beta + \varepsilon, \quad \text{in which}$$

$\underset{\sim}{y}$ = Vector of observed means of each hybrid combination or progenitor included in the diallel.

X = Design matrix whose elements are established by the diallel model used.

β = Vector of parameters (effects of the means and of the general and specific combining abilities) to be estimated.

ε = Vector of the experimental errors, $\varepsilon \sim NID(\Phi, D\sigma^2)$, where Φ is a null vector.

Since D is a symmetrical, real and positive matrix, there exists an F such that $D^{-1} = FF'$ ($D = F'^{-1}F^{-1}$), and since D is diagonal, F is the square root of D^{-1}. The transformation $F'y = F'X\beta + F'\varepsilon$ provides a new equation $z = M\beta + \delta$, in which δ is the vector of independently distributed errors with zero means and $I\sigma^2$ variances.

From $z = M\beta + \delta$, β is estimated from the least squares equations resulting from the minimization of $\delta'\delta$, expressed by:

$$M'M\hat{\beta} = M'z \quad \text{or}$$

$$X'D^{-1}X\hat{\beta} = X'D^{-1}y\,,$$

because

$$M = F'X, \quad z = F'y \quad \text{e} \quad \delta = F'\varepsilon\,,$$

therefore

$$E(\delta) = F'E(\varepsilon) = \Phi, \text{ a null vector and}$$

$$V(\delta) = V(F'\varepsilon) = F'V(\varepsilon)F = F'DF\sigma^2 = I\sigma^2.$$

Description of the unbalanced diallel matrices

The matrices involved in the estimation of the combining abilities of a diallel with p progenitors and p(p-1)/2 F_1 hybrids, following the model proposed by Griffing (1956), are:

$$X = \left[\begin{array}{c:ccccc:cccccccc}
1 & 2 & 0 & . & . & . & 0 & 1 & 0 & . & . & . & 0 & . & . & . & 0 \\
1 & 1 & 1 & . & . & . & 0 & 0 & 1 & . & . & . & 0 & . & . & . & 0 \\
. & . & . & & & & . & . & . & & & & . & & & & . \\
. & . & . & & & & . & . & . & & & & . & & & & . \\
. & . & . & & & & . & . & . & & & & . & & & & . \\
1 & 1 & 0 & . & . & . & 1 & 0 & 0 & . & . & . & 1 & . & . & . & 0 \\
. & . & . & & & & . & . & . & & & & . & & & & . \\
. & . & . & & & & . & . & . & & & & . & & & & . \\
. & . & . & & & & . & . & . & & & & . & & & & . \\
1 & 0 & 0 & . & . & . & 2 & 0 & 0 & . & . & . & 0 & . & . & . & 1
\end{array}\right]_{t \times (t+p+1)}$$

$$\underset{\sim}{y} = \begin{bmatrix} \bar{y}_{11} \\ \bar{y}_{12} \\ \cdot \\ \cdot \\ \cdot \\ \bar{y}_{1p} \\ \cdot \\ \cdot \\ \cdot \\ \bar{y}_{pp} \end{bmatrix}_{t \times 1} ; \quad \beta = \begin{bmatrix} m \\ g_1 \\ \cdot \\ \cdot \\ \cdot \\ g_p \\ s_{11} \\ s_{12} \\ \cdot \\ \cdot \\ \cdot \\ s_{pp} \end{bmatrix}_{(t+p+1) \times 1} ; \quad \varepsilon = \begin{bmatrix} \bar{e}_{11} \\ \bar{e}_{12} \\ \cdot \\ \cdot \\ \cdot \\ \bar{e}_{1p} \\ \cdot \\ \cdot \\ \cdot \\ \bar{e}_{pp} \end{bmatrix}_{t \times 1}$$

The elements of $\underset{\sim}{y}$ are averages remaining from r_{ij} repetition. The D and F matrices are show by:

$$D = \begin{bmatrix} 1/r_{11} & 0 & \cdots & 0 \\ 0 & 1/r_{12} & \cdots & 0 \\ \cdot & \cdot & & \cdot \\ \cdot & \cdot & & \cdot \\ \cdot & \cdot & & \cdot \\ 0 & 0 & \cdots & 1/r_{pp} \end{bmatrix}_{t \times t} \quad F = \begin{bmatrix} (r_{11})^{1/2} & 0 & 0 & \cdots & 0 \\ 0 & (r_{12})^{1/2} & 0 & \cdots & 0 \\ \cdot & \cdot & \cdot & & \cdot \\ \cdot & \cdot & \cdot & & \cdot \\ \cdot & \cdot & \cdot & & \cdot \\ 0 & 0 & 0 & \cdots & (r_{pp})^{1/2} \end{bmatrix}_{t \times t}$$

For diallels which involve only hybrid combinations, the $\bar{y}_{ii}$ values must be excluded from the $\underset{\sim}{y}$ vector; the corresponding elements in the other matrices must also be excluded.

Diallel analysis involving progenitors and F_1 hybrids

A - Estimation of combining ability effects

The estimation of combining ability effects can be determined by solving the $M'M\hat{\beta} = M'z$ equation. When the diallel involves p progenitors and p(p-1)/2 hybrid combinations, the following equation results:

$$M'M = (FX)'FX = X'D^{-1}X, \qquad \text{where}$$

$$M'M = \begin{bmatrix}
N & k_1 & k_2 & \cdots & k_p & r_{11} & r_{12} & \cdots & r_{1p} & r_{22} & \cdots & r_{2p} & \cdots & r_{pp} \\
k_1 & 2r_{11}+k_1 & r_{12} & \cdots & r_{1p} & 2r_{11} & r_{12} & \cdots & r_{1p} & 0 & \cdots & 0 & \cdots & 0 \\
k_2 & r_{21} & 2r_{22}+k_2 & \cdots & r_{2p} & 0 & r_{21} & \cdots & 0 & 2r_{22} & \cdots & r_{2p} & \cdots & 0 \\
\vdots & \vdots & \vdots & & \vdots & \vdots & \vdots & & \vdots & \vdots & & \vdots & & \vdots \\
k_p & r_{p1} & r_{p2} & \cdots & 2r_{pp}+k_p & 0 & 0 & \cdots & r_{p1} & 0 & \cdots & r_{p2} & \cdots & 2r_{pp} \\
r_{11} & 2r_{11} & 0 & \cdots & 0 & r_{11} & 0 & \cdots & 0 & 0 & \cdots & 0 & \cdots & 0 \\
r_{12} & r_{12} & r_{21} & \cdots & 0 & 0 & r_{12} & \cdots & 0 & 0 & \cdots & 0 & \cdots & 0 \\
\vdots & \vdots & \vdots & & \vdots & \vdots & \vdots & & \vdots & \vdots & & \vdots & & \vdots \\
r_{1p} & r_{1p} & 0 & \cdots & r_{p1} & 0 & 0 & \cdots & r_{1p} & 0 & \cdots & 0 & \cdots & 0 \\
r_{22} & 0 & 2r_{22} & \cdots & 0 & 0 & 0 & \cdots & 0 & r_{22} & \cdots & 0 & \cdots & 0 \\
\vdots & \vdots & \vdots & & \vdots & \vdots & \vdots & & \vdots & \vdots & & \vdots & & \vdots \\
r_{2p} & 0 & r_{2p} & \cdots & r_{p2} & 0 & 0 & \cdots & 0 & 0 & \cdots & r_{2p} & \cdots & 0 \\
\vdots & \vdots & \vdots & & \vdots & \vdots & \vdots & & \vdots & \vdots & & \vdots & & \vdots \\
r_{pp} & 0 & 0 & \cdots & 2r_{pp} & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & \cdots & r_{pp}
\end{bmatrix}$$

In which

$$N = \sum_{i \le j}\sum r_{ij} = r_{11} + r_{12} + \ldots + r_{pp}$$

$k_i = r_{ii} + r_{i.}$ (if $i = 1$ then $k_1 = 2r_{11} + r_{12} + \ldots + r_{1p}$)

$r_{ij} = r_{ji}$, and

$$M'z = X'D^{-1}y = \begin{bmatrix}
\sum_{i \le j}\sum y_{ij}\, r_{ij} \\
r_{11}\, y_{11} + \sum_j r_{1j}\, y_{ij} \\
\vdots \\
r_{pp}\, y_{pp} + \sum_j r_{pj}\, y_{pj} \\
r_{11}\, y_{11} \\
r_{12}\, y_{12} \\
\vdots \\
r_{pp}\, y_{pp}
\end{bmatrix}$$

From the $M'M\beta = M'z$ equality the following normal equations may be obtained:

$$\sum_{i \le j}\sum y_{ij} r_{ij} = N\hat{m} + \sum_j k_j \hat{g}_j + 1/2 \sum_i (r_{ii}\hat{s}_{ii} + \sum_j r_{ij}\hat{s}_{ij}) \quad (I)$$

$$r_{ii} y_{ii} + \sum_j r_{ij} y_{ij} = k_i\hat{m} + \sum_j r_{ij}\hat{g}_j + (r_{ii} + k_i)\hat{g}_i + r_{ii}\hat{s}_{ii} + \sum_j r_{ij}\hat{s}_{ij} \quad (II)$$

$$r_{ij} y_{ij} = r_{ij}\hat{m} + r_{ij}(\hat{g}_i + \hat{g}_j) + r_{ij}\hat{s}_{ij} \quad (III)$$

imposing the restrictions:

$$\sum_j k_j \hat{g}_j = 0$$

and

$$r_{ii}\hat{s}_{ii} + \sum_j r_{ij}\hat{s}_{ij} = 0,$$

equation (I) yields:

$$\hat{m} = \frac{\sum_{i \le j} y_{ij} r_{ij}}{N}$$

and equation (II) yields:

$$r_{ii} y_{ii} + \sum_j r_{ij} y_{ij} = k_i\hat{m} + \sum_j r_{ij}\hat{g}_j + (r_{ii} + k_i)\hat{g}_i$$

The estimation of $\hat{g}_i$ effects becomes easier under the restriction $\sum_j k_j \hat{g}_j = 0$, by solving the system $\underset{\sim}{Q} = A\,\underset{\sim}{G}$ in which

$$\underset{\sim}{Q} = \begin{bmatrix} r_{11} y_{11} + \sum_j r_{1j} y_{1j} - k_1 \hat{m} \\ r_{22} y_{22} + \sum_j r_{2j} y_{2j} - k_2 \hat{m} \\ \vdots \\ r_{pp} y_{pp} + \sum_j r_{pj} y_{pj} - k_p \hat{m} \end{bmatrix} \quad A = \begin{bmatrix} 2r_{11} + k_1 & r_{12} & \cdots & r_{1p} \\ r_{21} & 2r_{22} + k_2 & \cdots & r_{2p} \\ \vdots & \vdots & & \vdots \\ r_{p1} & r_{p2} & \cdots & 2r_{pp} + k_p \end{bmatrix} \quad \underset{\sim}{G} = \begin{bmatrix} \hat{g}_1 \\ \hat{g}_2 \\ \vdots \\ \hat{g}_p \end{bmatrix}$$

The specific combining ability estimates are obtained using:

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

B - Estimation of the sum of squares of specific and general combining ability effects

The sums of squares of the effects associated with the model are estimated by partitioning the $\hat{\beta}$'M'z product into the sums of squares obtained by multiplying the subspaces of $\hat{\beta}$ and of M'z which correspond to $\hat{m}$, $\hat{g}_i$'s and $\hat{s}_{ij}$'s, resulting in:

$$SS(\hat{m}) = \hat{m} \sum_{i \leq j}\sum y_{ij}\, r_{ij}$$

$$SS(\hat{g}_i) = SS(GCA) = \sum_i \hat{g}_i \,(r_{ii}\, y_{ii} + \sum_j r_{ij}\, y_{ij}) = \underset{\sim}{G}\,'Q$$

$$SS(\hat{s}_{ij}) = SS(SCA) = \sum_{i \leq j}\sum \hat{s}_{ij}\, r_{ij}\, y_{ij}$$

The analysis of variance table would be as follows:

Source	df	MS	F
GCA	p-1	MSG	MSG/MSE
SCA	p(p-3)/2	MSS	MSS/MSE
Error	dfe*	MSE	

* Degree of freedom and mean square associated with the experimental error, from the usual ANOVA, considering the entries as the sole source of genetic variation.

Analysis of diallels involving only F_1 hybrids

A - Estimation of combining ability effects

As was described before, the combining ability effects may be estimated by means of $\hat{\beta} = (M'M)^{-1} M'z$ where, in this case, the following definitions hold:

$$M'M = \begin{bmatrix} N & r_{1.} & r_{2.} & \cdots & r_{p.} & r_{12} & \cdots & r_{1p} & r_{23} & \cdots & r_{p-1,p} \\ r_{1.} & r_{1.} & r_{12} & \cdots & r_{1p} & r_{12} & \cdots & r_{1p} & 0 & \cdots & 0 \\ r_{2.} & r_{21} & r_{2.} & \cdots & r_{2p} & r_{21} & \cdots & 0 & r_{23} & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots & & \vdots & \vdots & & \vdots \\ r_{p.} & r_{p1} & r_{p2} & \cdots & r_{p.} & 0 & \cdots & r_{p1} & 0 & \cdots & r_{p-1,p} \\ r_{12} & r_{12} & r_{21} & \cdots & 0 & r_{12} & \cdots & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots & & \vdots & \vdots & & \vdots \\ r_{1p} & r_{1p} & 0 & \cdots & r_{p1} & 0 & \cdots & r_{1p} & 0 & \cdots & 0 \\ r_{23} & 0 & r_{23} & \cdots & 0 & 0 & \cdots & 0 & r_{23} & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots & & \vdots & \vdots & & \vdots \\ r_{p-1,p} & 0 & 0 & \cdots & r_{p-1,p} & 0 & \cdots & 0 & 0 & \cdots & r_{p-1,p} \end{bmatrix}$$

$$M'M = X'D^{-1}X$$

$$N = \sum_{i<j}\sum r_{ij} = r_{12} + r_{13} + \ldots r_{p-1,p}$$

and,

$$M'z = X'D^{-1}y = \begin{bmatrix} \sum_{i<j}\sum r_{ij}\, y_{ij} \\ \sum_j r_{1j}\, y_{1j} \\ \vdots \\ \sum_j r_{pj}\, y_{pj} \\ r_{12}\, y_{12} \\ \vdots \\ r_{p-1,p}\, y_{p-1,p} \end{bmatrix}$$

From the $M'M\hat{\beta} = M'z$ equality, the normal equations arise:

$$\sum_{i<j}\sum r_{ij}\, y_{ij} = N\hat{m} + \sum_i r_{i.}\,\hat{g}_i + 1/2 \sum_i \Big(\sum_{i \neq j} r_{ij}\,\hat{s}_{ij}\Big) \qquad \text{(I)}$$

$$\sum_j r_{ij}\, y_{ij} = r_{i.}\,\hat{m} + r_{i.}\,\hat{g}_i + \sum_{i \neq i} r_{ij}\,\hat{g}_j + \sum_{j \neq i} r_{ij}\,\hat{s}_{ij} \qquad \text{(II)}$$

$$r_{ij}\, y_{ij} = r_{ij}\,\hat{m} + r_{ij}\,(\hat{g}_i + \hat{g}_j) + r_{ij}\,\hat{s}_{ij} \qquad \text{(III)}$$

imposing the following restrictions:

$$\sum_i r_{i.}\,\hat{g}_i = 0$$

$$\sum_{j \neq i} r_{ij}\,\hat{s}_{ij} = 0, \quad \text{for each } i,$$

$\hat{m}$ can be obtained from equation (I):

$$\hat{m} = \frac{\sum\sum_{i<j} r_{ij}\, y_{ij}}{N}$$

and from equation (II):

$$\sum_j r_{ij}\, y_{ij} = r_{i.}\,\hat{m} + r_{i.}\,\hat{g}_i + \sum r_{ij}\,\hat{g}_i$$

The estimation of $\hat{g}_i$ effects under the restriction $\sum_i r_{i.}\,\hat{g}_i = 0$ is accomplished by solving the system $Q = A\,\underset{\sim}{G}$, where:

$$Q = \begin{bmatrix} \sum_j r_{1j}\, y_{1j} & - & r_{1.}\,\hat{m} \\ \sum_j r_{2j}\, y_{2j} & - & r_{2.}\,\hat{m} \\ & . & \\ & . & \\ & . & \\ \sum_j r_{pj}\, y_{pj} & . & r_{p.}\,\hat{m} \end{bmatrix} \quad A = \begin{bmatrix} r_{1.} & r_{12} & \cdots & r_{1p} \\ r_{21} & r_{2} & \cdots & r_{2p} \\ . & . & & . \\ . & . & & . \\ . & . & & . \\ r_{p1} & r_{p2} & \cdots & r_{p.} \end{bmatrix} \quad \underset{\sim}{G} = \begin{bmatrix} \hat{g}_1 \\ \hat{g}_2 \\ . \\ . \\ . \\ \hat{g}_p \end{bmatrix}$$

The estimates of specific combining ability effects may be found with:

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

B - Estimation of the sums of squares of specific and general combining ability effects

The sums of squares associated with effects of combining abilities may also be estimated by partitioning the $\hat{\beta}$'M'z value into shares corresponding to the products of the multiplication of $\hat{\beta}$ subspaces, corresponding to $\hat{m}$, $\hat{g}_i$'s and $\hat{s}_{ij}$'s, and the M'z subspaces. The sums of squares can be estimated by:

$$SS(\hat{m}) = \hat{m} \sum_{i<j}\sum y_{ij}\, r_{ij}$$

$$SS(\hat{g}_i) = SS(GCA) = \sum_i \hat{g}_i \left(\sum_j r_{ij}\, y_{ij}\right) = \underset{\sim}{G}\,'Q$$

$$SS(\hat{s}_{ij}) = SS(SCA) = \sum_{i<j}\sum \hat{s}_{ij}\, r_{ij}\, y_{ij}$$

The analysis of the variance table is similar to that which was previously defined for a diallel including the parents.

APPLICATION

The application of the above described methodology will be shown using two hypothetical examples. In the first example the unbalanced diallel involves five progenitors and it's ten hybrid combinations; in the second example the diallel involves only the six hybrid combinations of four progenitors.

A - Diallels with parents and F_1's (Example I)

The hypothetical data in Table I is used to illustrate the case of a diallel with F_1's, parents included. No reciprocal effect is considered, so $y_{ij} = y_{ji}$ and $r_{ij} = r_{ji}$.

Table I - Averages and replications (between parentheses) of five progenitors and the corresponding hybrid combinations (hypothetical data).[1]

Parents	1	2	3	4	5	k_i[2/]	w_i[3/]	q_i[4/]
1	2.2182	1.4857	2.8545	2.5077	3.2399	63	155.5989	9.0381
	(11)	(7)	(11)	(13)	(10)			
2	1.4857	1.0000	1.7199	1.3333	1.0846	51	61.0990	-57.5454
	(7)	(10)	(5)	(6)	(13)			
3	2.8545	1.7199	3.8999	2.7937	3.3667	58	182.8964	47.9674
	(11)	(5)	(10)	(16)	(6)			
4	2.5077	1.3333	2.7937	2.3778	1.9428	60	141.6991	2.1174
	(13)	(6)	(16)	(9)	(7)			
5	3.2399	1.0846	3.3667	1.9428	2.4200	56	128.6986	-1.5776
	(10)	(13)	(6)	(7)	(10)			

[1/] $y_{ij} = y_{ji} \; (r_{ij} = r_{ji})$

[2/] $k_i = r_{ii} + r_{i.}$

[3/] $w_i = r_{ii} Y_{ii} + \Sigma r_{ij} Y_{i.}$

[4/] $q_i = w_i - k_i \hat{m}$

By using the mathematical expressions previously shown the following estimates are obtained:

- Over all mean ($\hat{m}$)

$$\hat{m} = \frac{\sum\sum_{i \leq j} r_{ij}\, y_{ij}}{N}$$

where

$$\sum\sum_{i \leq j} r_{ij}\, y_{ij} = (11 \times 2.2182) + \ldots + (10 \times 2.4200) = 334.9900$$

$$N = 11 + 7 + \ldots + 10 = 144$$

Therefore,

$$\hat{m} = \frac{334.9960}{144} = 2.3264$$

- General combining ability effects ($\hat{g}_i$)

They are estimated by means of $\underset{\sim}{G} = A^{-1}Q$, in which

$$Q = \begin{bmatrix} 9.0381 \\ -57.5454 \\ 47.9674 \\ 2.1174 \\ -1.5776 \end{bmatrix} ; \qquad A = \begin{bmatrix} 85 & 7 & 11 & 13 & 10 \\ 7 & 71 & 5 & 6 & 13 \\ 11 & 5 & 78 & 16 & 6 \\ 13 & 6 & 16 & 78 & 7 \\ 10 & 13 & 6 & 7 & 76 \end{bmatrix}$$

The sum of the elements of the Q vector is null ($\Sigma q_i = 0$), thus

$$\underset{\sim}{G} = \begin{bmatrix} \hat{g}_1 \\ \hat{g}_2 \\ \hat{g}_3 \\ \hat{g}_4 \\ \hat{g}_5 \end{bmatrix} = 10^{-3} \begin{bmatrix} 12.3884 & -0.7655 & -1.2668 & -1.6339 & -1.2486 \\ & 14.6766 & -0.5141 & -0.6890 & -2.3057 \\ & & 13.5869 & -2.4835 & -0.5893 \\ & & & 13.6212 & -0.7349 \\ & & & & 13.8308 \end{bmatrix} \begin{bmatrix} 9.0381 \\ -57.5454 \\ 47.9674 \\ 2.1174 \\ -1.5776 \end{bmatrix} = \begin{bmatrix} 0.0937 \\ -0.8740 \\ 0.6655 \\ -0.0640 \\ 0.0697 \end{bmatrix}$$

- Specific combining ability effects ($\hat{s}_{ij}$)

They are estimated by means of: $\hat{s}_{ij} = Y_{ij} - (\hat{m} + \hat{g}_i + \hat{g}_j)$. Thus

$$\hat{s}_{11} = 2.2182 - (2.3264 + 0.0937 + 0.0937) = -0.2967$$

likewise, the other estimates are:

$\hat{s}_{12} = -0.0604$
$\hat{s}_{13} = -0.2312$
$\hat{s}_{14} = 0.1516$
$\hat{s}_{15} = 0.7500$
$\hat{s}_{22} = 0.4216$
$\hat{s}_{23} = 0.3980$

$\hat{s}_{24} = -0.0551$
$\hat{s}_{25} = -0.4375$
$\hat{s}_{33} = 0.2425$
$\hat{s}_{34} = -0.1342$
$\hat{s}_{35} = 0.3050$
$\hat{s}_{44} = 0.1795$
$\hat{s}_{45} = -0.3893$
$\hat{s}_{55} = -0.0459$

The sums of squares are estimated by

$$SS(GCA) = \sum_i \hat{g}_i (r_{ii}\, y_{ii} + \sum_j r_{ij}\, y_{ij}) = \underset{\sim}{G}\,'Q$$

$$= (0.0937 \times 9.0381) + \ldots - (0.0697 \times 1.5776) = 82.8190$$

$$SS(SCA) = \sum_{i \le j} \sum \hat{s}_{ij}\; y_{ij}\, r_{ij}$$

$$= 2.2182 \times (-0.2967) \times 11 + \ldots + 2.4200 \times (-0.0495) \times 10 = 15.3817$$

It is demonstrated that those sums of squares become an orthogonal decomposition of the sums of squares of entries, that is:

$$SS\ Entries = SS(GCA) + SS(SCA) = 98.2007$$

The summary of the analysis of variance is presented in Table II.

Table II - Variation analysis summary with decomposition of the sums of squares of entries in combining ability effects.

Source	df	SS	MS	F
Entries	14	98.2007	7.0143	5.81
GCA	4	82.8190	20.7047	17.13
SCA	10	15.3817	1.5381	1.27
Error	-	-	1.2082*	

* Mean square of residue obtained in preliminary analysis of variance taking into account all the experimental data.

B - Diallel with F_1's only (Example II)

The hypothetical data in Table III is used to illustrate the method of analysis of a diallel with F_1's, parents excluded, and no reciprocal effects considered. In this case again $y_{ij} = y_{ji}$ and $r_{ij} = r_{ji}$.

Table III - Averages and replications (between parentheses) of the hybrid combinations of four progenitors (hypothetical data).[1/]

Parents	1	2	3	4	$r_{i.}$	C_i[2/]	D_i[3/]
1	-	5.8	6.4	7.2	14	91.4	15.968
	-	(5)	(3)	(6)			
2	5.8	-	3.6	4.3	12	56.3	-8.356
	(5)		(4)	(3)			
3	6.4	3.6	-	4.0	11	49.6	-9.668
	(3)	(4)		(4)			
4	7.2	4.3	4.0	-	13	72.1	2.056
	(6)	(3)	(4)				

[1/] $y_{ij} = y_{ji}$ ($r_{ij} = r_{ji}$)
[2/] $C_i = \Sigma r_{ij} y_{ij}$
[3/] $D_i = \sum_j r_{ij} y_{ij} - r_{i.} \hat{m}$

The estimates of the effects are:

- Over all mean ($\hat{m}$)

$$\hat{m} = \frac{\sum\sum_{i<j} r_{ij} y_{ij}}{N}$$

where

$$\sum\sum_{i<j} r_{ij} y_{ij} = 5 \times 5.8 + \ldots + 4 \times 4.0 = 134.7$$

$$N = 5 + 3 + \ldots + 4 = 25$$

Therefore,

$$\hat{m} = \frac{134.7}{25} = 5.3880$$

- Effects of the general combining ability ($\hat{g}_i$)

They are estimated by means of $\underset{\sim}{G} = A^{-1}Q$

$$Q = \begin{bmatrix} 15.968 \\ -8.356 \\ -9.668 \\ 2.056 \end{bmatrix} \quad ; \quad A = \begin{bmatrix} 14 & 5 & 3 & 6 \\ 5 & 12 & 4 & 3 \\ 3 & 4 & 11 & 4 \\ 6 & 3 & 4 & 13 \end{bmatrix}$$

The sum of the elements of the Q vector is null ($\Sigma q_i = 0$). Therefore,

$$\underset{\sim}{G} = \begin{bmatrix} \hat{g}_1 \\ \hat{g}_2 \\ \hat{g}_3 \\ \hat{g}_4 \end{bmatrix} = 10^{-3} \begin{bmatrix} 99.2892 & -31.2311 & -1.8905 & -38.0369 \\ & 106.5487 & -29.8699 & -0.9830 \\ & & 111.9934 & -26.6939 \\ & & & 102.9189 \end{bmatrix} \begin{bmatrix} 15.968 \\ -8.356 \\ -9.668 \\ 2.056 \end{bmatrix} = \begin{bmatrix} 1.7865 \\ -1.1022 \\ -0.9182 \\ -0.1295 \end{bmatrix}$$

- Effects of specific combining ability ($\hat{s}_{ij}$)

They are estimated by means of

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

Therefore,

$$\hat{s}_{12} = 5.8 - (5.388 + 1.7865 - 1.1022) = -0.2722$$
$$\hat{s}_{13} = 6.4 - (5.388 + 1.7865 - 0.9182) = 0.1437$$
$$\hat{s}_{14} = 7.2 - (5.388 + 1.7865 - 0.1295) = 0.1550$$
$$\hat{s}_{23} = 3.6 - (5.388 - 1.1022 - 0.9182) = 0.2325$$
$$\hat{s}_{24} = 4.3 - (5.388 - 1.1022 - 0.1295) = 0.1437$$
$$\hat{s}_{34} = 4.0 - (5.388 - 0.9182 - 0.1295) = -0.3403$$

The sums of squares are given by:

$$SS(GCA) = \underset{\sim}{G}'Q$$

$$= 1.7865 \times 15.968 + \ldots - 0.1295 \times 2.056 = 46.3483$$

$$SS(SCA) = \sum_{i<j}\sum y_{ij}\, \hat{s}_{ij}\, r_{ij}$$

$$= 5.8 \times (-0.2722) \times 5 + \ldots + 4.0 \times (-0.3403) \times 4 = 1.3181$$

Since SS(GCA) and SS(SCA) are the orthogonal decomposition of the sum of squares for entries:

$$SSEntries = SS(GCA) + SS(SCA) = 47.6664$$

The analysis of variance summary is given in Table IV.

Table IV - Analysis of variance summary with decomposition of the sum of squares of entries for the effects of combining ability.

Source	df	SS	MS	F
Entries	5	47.6664	9.5333	18.33
GCA	3	46.3483	15.4494	29.71
SCA	2	1.3181	0.6590	1.27
Error	-	-	0.5200*	

* Mean square of residue obtained in preliminary analysis of variance, taking into account all the experimental data.

CONCLUDING REMARKS

For the fixed effect models, the approach we have given may suffice because the interest is in estimating the effects and their contrasts. However, for random effect models, it would be necessary to estimate the variance components associated with the general and the specific combining abilities. These are associated with the additive and non-additive effects of the genes, respectively. In the last case we recommend England's (1974) approach.

The relevance of having a simple process of analysis of unbalanced diallels is emphasized by the facts that the genetic information provided by the diallel analysis is important and that self-fertilizing species breeding programs, in which artificial pollination generally generates a low and variable number of hybrid seeds, are frequently used.

RESUMO

Apresentou-se estimadores da capacidade geral e específica de combinação, e respectivas somas de quadrados, obtidos de sistema dialélico desbalanceado, nos quais os progenitores e/ou combinações híbridas são avaliados por meio de um número desigual de repetições.

Foi avaliada, como ilustração, a capacidade combinatória de dois conjuntos hipotéticos de dados provenientes de um dialelo envolvendo progenitores e respectivos F_1's e de outro envolvendo apenas os F_1's.

REFERENCES

England, F. (1974). A general approximate method for fitting additive and specific combining abilities to the diallel cross with unequal numbers of observation in the cells. *Theoret. Appl. Genetics 44*: 378-380.

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

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

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

Kempthorne, O. (1957). *An introductiond to genetic statistics*. John Wiley and Sons, New York, 545 p.

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