ANALYSIS OF DIALLEL CROSS EXPERIMENTS IN A SPLIT-PLOT SITUATION

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Summary

In diallel cross experiments with reciprocal crosses present, crosses with the same maternal line are sometimes planted together or otherwise segregated. The results of Griffing (1956) for the analysis of diallel cross experiments in randomized blocks are extended to give an analysis for this split-plot situation.

I. Introduction

In a diallel cross experiment, p inbred lines are taken and crosses among them are made. The experiment may include the parental lines themselves, and both the $i\times j$ crosses and their reciprocals $j\times i$. In experiments involving plants in which reciprocal crosses are carried out, it sometimes happens that all the crosses with the same maternal line are grown adjacently. This gives rise to a split-plot situation.

In this paper we give a method of analysis for this kind of experiment both for the complete diallel cross and for the modified case in which the parental lines are omitted. We assume that there are no maternal effects, and that the whole plots are chosen at random.

Griffing (1956) has presented the analyses of diallel cross experiments carried out in randomized complete blocks. He considers the cases of both fixed effects (model I) and random effects (model II). We take his estimates of the genetic parameters, noting that these estimates are unbiased if the whole plots can be considered as random variables. The sums of squares for general combining ability (g.c.a.), specific combining ability (s.c.a.), and reciprocal effects are obtained and the expectations of their mean squares calculated with the whole-plot error components. The sum of squares for whole-plot error is taken from the residual sum of squares and the remainder is the sum of squares for subplot error. This approach is analogous to the procedure used in the interblock analysis of incomplete block designs, where the total sum of squares is subdivided into "treatments ignoring blocks" (corresponding to the total of the sums of squares for g.c.a., s.c.a., and reciprocal effects), "blocks adjusted for treatments" (corresponding to whole-plot error), and error (subplot error). Under the normality assumption, all the sums of squares are distributed independently. Variances of differences between estimates of effects are calculated.

An alternative approach would be to consider the whole-plot errors as additional parameters and obtain least squares estimates from the augmented normal equations. This method is complicated by the non-orthogonality introduced by

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TABLE 1

ANALYSIS OF VARIANCE FOR THE COMPLETE DIALLEL CROSS

Source	Degrees of Freedom	Sum of Squares*	Expectation of Mean Squares	
			Model I	Model II
General combining ability	$p-1$	S_g	$\sigma^2+2np\left(\frac{1}{p-1}\right)\sum_i g_i^2+\frac{1}{2}p\sigma_1^2$	$\sigma^2+\frac{2n(p-1)}{p}\sigma_s^2+2np\sigma_g^2+\frac{1}{2}p\sigma_1^2$
Specific combining ability	$p(p-1)/2$	S_s	$\sigma^2+\frac{2n}{p(p-1)}\sum_i\sum_j s_{ij}^2$	$\sigma^2+2n\frac{(p^2-p+1)}{p^2}\sigma_s^2$
Reciprocal effects	$p(p-1)/2$	S_r	$\sigma^2+2n\left(\frac{2}{p(p-1)}\right)\sum_i\sum_j r_{ij}^2+\sigma_1^2$	$\sigma^2+2n\sigma_r^2+\sigma_1^2$
Replicates	$n-1$	S_n	$\sigma^2+p\sigma_1^2+p^2\sigma_2^2$	$\sigma^2+p\sigma_1^2+p^2\sigma_2^2$
Whole-plot error	$(n-1)(p-1)$	$S_{e'}$	$\sigma^2+p\sigma_1^2$	$\sigma^2+p\sigma_1^2$
Subplot error	$p(p-1)(n-1)$	S_e	σ^2	σ^2

*Where $S_g=\frac{1}{2np}\sum_i (X_{i..}+X_{.i.})^2-\frac{2}{np^2}\sum X^2_{...}$,

$$S_s=\frac{1}{2n}\sum_i\sum_j X_{ij.}(X_{ij.}+X_{ji.})-\frac{1}{2np}\sum_i (X_{i..}+X_{.i.})^2+\frac{1}{np^2}X^2_{...} ,$$

$$S_r=\frac{1}{2n}\sum_{i<j}\sum (X_{ij.}-X_{ji.})^2 ,$$

$$S_n=\frac{1}{p^2}\sum_k X^2_{..k}-\frac{1}{np^2}X^2_{...} ,$$

$$S_{e'}=\frac{1}{p}\sum_i\sum_k X^2_{i.k}-\frac{1}{np}\sum_i X^2_{i..}-S_n .$$

the addition of the new parameters (in the same way that Henderson (1948) introduces non-orthogonality with his term for maternal effects).

II. Presentation of Analysis

(a) Notation

x_{ijk} denotes the observation in the kth replicate of the crossing with the ith maternal and jth paternal lines, and

$$x_{ijk} = m+g_i+g_j+s_{ij}+r_{ij}+t_k+\epsilon_{ik}+e_{ijk};\ \ i, j = 1, \cdots, p;\ \ k = 1, \cdots, n,$$

where m is the population mean, $g_i(g_j)$ is the general combining ability, s_{ij} $(= s_{ji})$ is the specific combining ability, and r_{ij} $(= -r_{ji})$ is the reciprocal effect. These may be either fixed (model I) or random (model II) effects and Griffing gives the expectations of mean squares in both cases. The remaining three parameters t_k, ϵ_{ik}, e_{ijk}, are independently normally distributed with zero means and variances σ_2^2, σ_1^2, σ^2, respectively; t_k is the effect of the kth replicate; ϵ_{ik} is the main-plot or whole-plot error for the whole plot in the kth replicate containing the ith maternal line, and e_{ijk} is the subplot error.

For the complete diallel cross, including the parental lines, we also have

$$x_{iik} = m+2g_i+s_{ii}+t_k+\epsilon_{ik}+e_{ijk}\,.$$

The totals are denoted by

$$X_{\ldots} = \sum_i \sum_j \sum_k x_{ijk};\ \ X_{i\cdot\cdot} = \sum_j \sum_k x_{ijk}, \text{ and so on.}$$

(b) Derivation of Results

The sums of squares for g.c.a., s.c.a., and reciprocal effects are, except for the factor n in the denominator and the changes in symbols for totals, the same as those given by Griffing. In the expectations of these mean squares the coefficients of σ_g^2, σ_s^2, and σ_r^2 differ from Griffing's only by the factor n. The sums of squares for replicates, S_n, whole-plot error, $S_{e'}$, and split-plot error, S_e, are calculated in the usual way. The corresponding mean squares are denoted by M_g, and so on.

We present the calculations of the coefficients of σ_1^2 in some of the mean squares for the modified (x_{iik} absent) diallel and state the remaining results, which are obtained similarly. These coefficients are the same under model I or model II. The coefficients of σ_2^2 are easily obtained.

In these calculations we ignore all the parameters except ϵ_{ik} and write

$$\epsilon_{i\cdot} = \sum_k \epsilon_{ik};$$

then

$$\mathrm{var}(\epsilon_{i\cdot}) = n\sigma_1^2\,.$$

(i) M_g: $\quad 2np(p-2)S_g = \sum_i (X_{i\cdot\cdot}+X_{\cdot i\cdot})\{p(X_{i\cdot\cdot}+X_{\cdot i\cdot})-2X_{\ldots}\}\,.$

$$X_{i\cdot\cdot}-X_{\cdot i\cdot} = (p-1)\epsilon_{i\cdot} - \sum_{j\neq i} \epsilon_{j\cdot};$$

$$X_{\ldots} = (p-1)\sum_i \epsilon_{i\cdot}\,.$$

TABLE 2

ANALYSIS OF VARIANCE FOR THE MODIFIED DIALLEL CROSS

Source	Degrees of Freedom	Sum of Squares*	Expectation of Mean Squares	
			Model I	Model II
General combining ability	$p-1$	S_g	$\sigma^2+2n(p-2)\left(\frac{1}{p-1}\right)\sum_i g_i^2+\frac{1}{2}(p-2)\sigma_1^2$	$\sigma^2+2n\sigma_s^2+2n(p-2)\sigma_g^2+\frac{1}{2}(p-2)\sigma_1^2$
Specific combining ability	$p(p-3)/2$	S_s	$\sigma^2+2n\left(\frac{2}{p(p-3)}\right)\sum_i\sum_j s_{ij}^2$	$\sigma^2+2n\sigma_s^2$
Reciprocal effects	$p(p-1)/2$	S_r	$\sigma^2+2n\left(\frac{2}{p(p-1)}\right)\sum_i\sum_j r_{ij}^2+\sigma_1^2$	$\sigma^2+2n\sigma_r^2+\sigma_1^2$
Replicates	$(n-1)$	S_n	$\sigma^2+(p-1)\sigma_1^2+p(p-1)\sigma_2^2$	$\sigma^2+(p-1)\sigma_1^2+p(p-1)\sigma_2^2$
Whole-plot error	$(p-1)(n-1)$	$S_{e'}$	$\sigma^2+(p-1)\sigma_1^2$	$\sigma^2+(p-1)\sigma_1^2$
Subplot error	$p(p-2)(n-1)$	S_e	σ^2	σ^2

*Where $S_g = \frac{1}{2n(p-2)}\sum_i (X_{i..}+X_{.i.})^2-\frac{2}{np(p-2)}X^2_{...}\,,$

$$S_s = \frac{1}{2n}\sum_{i<j}\sum (X_{ij.}+X_{ji.})^2-\frac{1}{2n(p-2)}\sum_i (X_{i..}+X_{.i.})^2+\frac{1}{n(p-1)(p-2)}X^2_{...}\,,$$

$$S_r = \frac{1}{2n}\sum_{i<j}\sum (X_{ij.}-X_{ji.})^2\,,$$

$$S_n = \frac{1}{p(p-1)}\sum_k X^2_{..k}-\frac{1}{np(p-1)}X^2_{...}\,,$$

$$S_{e'} = \frac{1}{p-1}\sum_i\sum_k X^2_{i.k}-\frac{1}{n(p-1)}\sum_i X^2_{i..}-S_n\,.$$

Then

$$\begin{aligned} E(X_{i..}-X_{.i.})\{p(X_{i..}-X_{.i.})-2X_{...}\} &= E[(p-1)\epsilon_{i.}-\sum_j \epsilon_{j.}][(p-1)(p-2)\epsilon_{i.}-\{p-2(p-1)\}\sum_j \epsilon_{j.}] \\ &= (p-1)^2(p-2)n\sigma_1^2-(p-1)(p-2)n\sigma_1^2 \\ &= (p-1)(p-2)^2 n\sigma_1^2 . \end{aligned}$$

Hence

$$E[2np(p-2)S_g] = np(p-1)(p-2)^2\sigma_1^2 ,$$

and

$$E(M_g) = (p-2)\sigma_1^2 .$$

(ii) M_r:

$$2nS_r = \sum_{i<j}\sum (X_{ij.}-X_{ji.})^2 ,$$

and

$$X_{ij.}-X_{ji.} = \epsilon_{i.}-\epsilon_{j.} ,$$

so that

$$E(X_{ij.}-X_{ji.})^2 = 2n\sigma_1^2 .$$

Hence

$$E(2nS_r) = 2n\sigma_1^2\{\tfrac{1}{2}p(p-1)\} ,$$

and

$$E(M_r) = \sigma_1^2 .$$

III. The Complete Diallel Cross

The analysis of variance is given in Table 1. To test for s.c.a. and replicate effects in either model I or model II, we have the usual F ratios, M_s/M_e and $M_n/M_{e'}$.

For g.c.a. and reciprocal effects we have to use approximate F tests (cf. Scheffé 1959, p. 247). Under either model the approximate test for reciprocal effects is

$$F_{[\frac{1}{2}p(p-1),\, f]} = pM_r/[(p-1)M_e+M_{e'}],$$

where

$$f = p(p-1)(n-1)[(p-1)M_e+M_{e'}]^2/[(p-1)^2M_e^2+pM_{e'}^2].$$

For the g.c.a. effect under model I we have

$$F_{[\frac{1}{2}p(p-1),\, f]} = 2M_g/(M_e+M_{e'}),$$

where

$$f = p(p-1)(n-1)(M_e+M_{e'})^2/(M_e+pM_{e'}).$$

Under model II the test ratio for the hypothesis $\sigma_g^2 = 0$ is

$$F_{[p-1,\, f]} = 2(p^2-p+1)M_g/K,$$

where

$$K = 2p(p-1)M_s+(p^2-p+1)M_{e'}-(p^2-p-1)M_e ,$$

and

$$f = p(p-1)(n-1)K^2/[8p^2(p-1)^2(n-1)M_s^2+p(p^2-p+1)^2M_{e'}^2+(p^2-p-1)^2M_e^2].$$

IV. The Modified Diallel Cross

The analysis of variance is given in Table 2. The test ratios for s.c.a. and replicate effects are again M_s/M_e and $M_n/M_{e'}$. Under either model the approximate test for reciprocal effects is

$$F_{[\frac{1}{2}p(p-1),\, f]} = (p-1)M_r/[(p-2)M_e+M_{e'}],$$

where

$$f = p(p-1)(n-1)[(p-2)M_e+M_{e'}]^2/[(p-1)(p-2)M_e^2+pM_{e'}^2].$$

For g.c.a. effects under model I we have

$$F_{[p-1,\, f]} = 2S_g/(pM_e+(p-2)M_{e'}),$$

where

$$f = (n-1)(p-1)(p-2)[pM_e+(p-2)M_{e'}]^2/[p(p-1)M_e^2+(p-2)^3M_{e'}^2].$$

Under model II the ratio for testing $\sigma_g^2 = 0$ is

$$F_{[p-1,\, f]} = 2S_g/K,$$

where

$$K = 2(p-1)M_s+(p-2)(M_{e'}-M_e),$$

and

$$f = K^2/A,$$

where

$$A = \frac{8(p-1)^2M_s^2}{p(p-3)}+\frac{(p-2)^2M_{e'}^2}{(p-1)(n-1)}+\frac{(p-2)M_e^2}{p(n-1)}.$$

V. Variances of Estimates

In both the complete and modified crosses the estimates of the effects under model I are the same as those given by Griffing. His results for the variances of

Table 3

VARIANCES OF ESTIMATES FOR BOTH COMPLETE DIALLEL AND MODIFIED DIALLEL CROSSES

Estimate	Variance	
	Complete Diallel	Modified Diallel
$\hat{g}_i$	$\frac{p-1}{2p^2n}\sigma^2+\frac{p-1}{4pn}\sigma_1^2$	$\frac{(p-1)\sigma^2}{2np(p-2)}+\frac{(p-1)}{4pn}\sigma_1^2$
$\hat{g}_i-\hat{g}_j \quad (i\neq j)$	$\frac{1}{pn}\sigma^2+\frac{1}{2n}\sigma_1^2$	$\frac{1}{n(p-2)}\sigma^2+\frac{1}{2n}\sigma_1^2$
$\hat{r}_{ij} \quad (i\neq j)$	$\frac{1}{2n}(\sigma^2+\sigma_1^2)$	$\frac{1}{2n}(\sigma^2+\sigma_1^2)$
$\hat{r}_{ij}-\hat{r}_{ik} \quad (i\neq j\neq k)$	$\frac{1}{n}\sigma^2+\frac{1}{2n}\sigma_1^2$	$\frac{1}{n}\sigma^2+\frac{1}{2n}\sigma_1^2$
$\hat{r}_{ij}-\hat{r}_{kl} \quad (i\neq j\neq k\neq l)$	$(\sigma^2+\sigma_1^2)/n$	$(\sigma^2+\sigma_1^2)/n$

estimates of specific combining abilities and their differences are also valid for this split-plot situation (with a factor n in the denominator). The component σ_1^2 does, however, occur in the variances of $\hat{g}_i$ and $\hat{r}_{ij}$. The variances of these estimates and of their differences are given in Table 3.

VI. References

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