

EXPERIMENTAL DESIGNS FOR
POPULATION HYBRIDIZATION STUDIES

by

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I. INTRODUCTION

Research in quantitative genetics is based to a large extent upon experimental investigations. The interpretation of results from these investigations is based upon a statistical analysis of the data resulting from the experiment. One way the statistician can contribute to quantitative genetics is to design experiments that will help to provide answers to questions in plant or animal breeding.

One of the current topics being investigated in forest genetics is the evaluation of breeding programs that utilize crosses between trees from different species and subspecies. Based upon research that has been completed in the past, geneticists now know that interspecies, intergroup, and interracial crosses are possible for many types of trees and in some small studies the progeny have demonstrated desirable characteristics.

Once the feasibility of crossing different species of trees is established, more detailed and designed experiments need to be conducted to answer questions of the following type:

- (i) Is there such a thing as population heterosis?
- (ii) Do some populations perform better, on the average, than others in interpopulation crosses?
- (iii) Are some population crosses better than would be expected on the basis of the average performance of the populations involved?

- (iv) Do some individuals perform better than other individuals from the same population when they are involved in inter-population crosses?
- (v) Do some crosses between individuals from different populations perform better than would be expected on the basis of the average performance of the individuals in intrapopulation crosses?

The present investigation is concerned with constructing and analysing experimental designs to answer these types of questions.

In quantitative genetics we have two designs to consider--a mating design that produces offspring to be tested and an environmental design in which to grow these offspring. The analysis of the experiment will depend on the mating design chosen and the environmental design that is used. In this investigation we will be considering mating designs that may be used for population hybridization studies. Since these designs often result in a large number of crosses to be tested we will also investigate incomplete environmental designs and partial mating schemes as methods of reducing the required block size in the environmental design.

To indicate the potential usefulness of designs proposed here, we shall give a brief review of some breeding experiments in forest genetics.

1.1. Population Hybridization in Forest Tree Breeding

Population hybridization is becoming an important technique in forest tree breeding. Crosses between trees from different genera,

species, and subspecies are being made to determine the crossability pattern among the species available, to investigate the characteristics of the hybrids, and to develop new types of trees. Often these crosses are made to induce some new characteristic, say disease resistance, into a species that is already valued for the quality of its wood or its fast growth. Hybrid vigor has been found in the offspring of many population crosses especially when the hybrids were grown in intermediate or disturbed environments. Additional research needs to be conducted to ascertain the breeding potential of different populations and of the individual variations within these populations.

In beginning a population hybridization study the first question to be answered is which crosses will result in viable seed. There have been many studies that have investigated this question for different varieties of trees. Silen, Critchfield, and Franklin (1965) discovered no genetic barriers existed to prevent the crossing of noble and California red firs. In a study of interspecific crosses between three species of sweetgum trees, Santamour (1972 a) found good yields of hybrid seed and seedlings. In other studies Santamour obtained successful crosses between American and oriental planetrees (Santamour, 1972 b), between American and Chinese tuliptrees (Santamour, 1972 d), and between Chinese and September elms (Santamour, 1972 c). Successful interspecies crosses have been obtained using chestnut trees (Diller and Clapper, 1969), poplars (Vincent and Polnar, 1970), and Betula varieties (Johnsson, 1974).

The second question to be investigated in any population hybridization study concerns the characteristics of the offspring. Do the

hybrids possess a trait, say disease resistance, that one of the parents does not? Do the hybrids display more vigor or hardiness than the parents? Many population hybridization studies are being conducted to determine if disease resistance can be bred into a population. For instance, crosses between the American chestnut and the Oriental chestnut are being made to see if the hybrids will possess the forest-tree form of the American tree as well as the resistance to chestnut-blight fungus of the oriental tree (Diller and Clapper, 1969). In a study of hybrid pines, Stark (1964) found the Jeffrey × (Jeffrey × Coulter) backcross had good growth characteristics as well as resistance to damage from insects, snow and porcupines. Hybrids resulting from the cross of Knobcone × Monterey pine were found to have inherited the early growth of the Monterey pine and the drought and frost resistance of the Knobcone pine (Griffin and Conkle, 1967). Vincent and Polnar (1970) report poplar hybrids that show rapid growth as well as a higher level of resistance. Crosses between Platanus occidentalis and P. orientalis are being investigated to determine if the hybrids have the resistance to sycamore anthracnose disease of the oriental plane and the hardiness and growth form of the American planetree (Santamour, 1972 b). Many of the studies discovered that the hybrids were intermediate in characteristics between the two parental varieties (Johnsson (1974), Mergen, Stairs, and Snyder (1965)).

These studies were aimed at discovering whether these species of trees could be successfully crossed and at describing the resulting hybrids. No statistical analyses were performed. In two other studies population hybrids were tested for differences in performance. Shearer

(1966) demonstrated that there existed differences between individual crosses of Rocky Mountain and Pacific coast forms of ponderosa pine. Pollen from a Pinus ponderosa var. scopulorum was used to pollinate trees of P. ponderosa Laws growing at different elevations. Significant differences in height, diameter, and crown width were found between these hybrids. In a study of hybrid poplars in West Virginia, Wendel (1972) found that the clones differed significantly in diameter and total height.

The final stage in developing an effective breeding program utilizing population hybrids is to implement a study that will provide information on how economically important traits are inherited. This will involve an experimental design that will allow one to exploit the genetic variability between populations as well as the variability among individual trees in the same populations. A study is now being conducted at the Pennsylvania State University by Park (1977) that will provide this type of information. In this experiment two female trees selected from each of seven Scotch pine populations were fertilized with pollen bulk from each of the seven populations. This experiment will provide information on heterosis in Scotch pine hybrids, the general and specific combining abilities of the Scotch pine populations, and the general and specific combining abilities of individual trees.

Many studies have now been completed demonstrating that population hybridization is a potentially valuable technique in forest tree breeding. Within many genera of trees it is known that population hybrids can be obtained and that these hybrids may have desirable characteristics. At this point there is a need for more thorough

studies such as Park's mentioned above. These studies would allow one to simultaneously estimate the breeding potential of populations and individuals as well as develop new types of trees. This paper will discuss some proposed mating designs and environmental designs that may help the tree breeder achieve these objectives.

1.2. Intrapopulation Diallel Cross Experiments

1.2.1. General Remarks

An interesting aspect of genetic design of experiments is that there are two models for the observations--the usual statistical model for the experiment and an underlying genetic model. For instance, the phenotypic value (P) of the individual is usually expressed as the sum of a genotypic effect (G) and an effect due to the environment (E), i.e. $P=G+E$. The fact that the genes an individual possesses occur in pairs is used to partition the genotypic effect into an additive effect (A) plus a dominance deviation (D), i.e. $G=A+D$. The additive effect is the sum of the average effects of the genes an individual carries. Representing the portion of the yield not accounted for by the sum of the average effects of the genes is the dominance deviation which is caused by the interaction of genes within pairs (e.g. Kempthorne, 1969).

The object of plant and animal breeding is to obtain individuals with as "high" a genotypic value as possible. Diallel mating designs are used to evaluate an individual based upon the performance of its progeny. In connection with the diallel cross Sprague and Tatum (1942) have defined the concepts of general and specific combining ability.

The general combining ability (g.c.a.) of a line (or individual) is the average performance of the line (or individual) in hybrid combinations. General combining ability contains essentially additive effects and hence may be transmitted to the offspring. Specific combining ability (s.c.a.) refers to those cases in which certain crosses do relatively better or worse than would be expected on the basis of the average performance of the lines (or individuals) involved. Since specific combining ability contains dominance effects, an individual from a cross showing high specific combining ability cannot pass this effect on to its offspring.

1.2.2. The Type I Diallel Cross Experiment

The type I diallel mating designs are used in animal breeding or with dioecious plants in plant breeding. In this design all possible crosses are made between m males and f females for a total of mf crosses. The designation, type I diallel cross, was suggested by Hinkelmann and Stern (1960). This design is also known as design II of Comstock and Robinson (1952) and as the factorial mating design (Cockerham, 1963).

The statistical model usually assumed for this design is

$$y_{ijk} = \mu + s_i + d_j + (sd)_{ij} + \epsilon_{ijk} \quad (1.2.1)$$

where y_{ijk} is the observation from the k th offspring of the cross between the i th male and the j th female, s_i and d_j are the general combining abilities of the i th male and j th female, respectively, and $(sd)_{ij}$ is the specific combining ability of the cross between the i th male and the j th female. These combining abilities will be fixed

effects when all males and females of interest are included in the experiment and random variables when the males and females are a sample from a larger collection about which inferences are to be made.

The number of crosses the breeder can make and study are limited by the available facilities. Often the number of crosses that must be tested needs to be reduced. In this instance, the breeder should consider using an incomplete or partial mating design in which only a sample of the crosses of the complete diallel are made. Assuming that the total number of crosses is fixed, Kempthorne and Curnow (1961) give the following three reasons why partial mating designs are better than the complete design¹:

- (i) the general combining ability variance of the population from which the parents were selected can be estimated with more efficiency,
- (ii) selection can be made among crosses from a wider range of parents, and
- (iii) the general combining abilities of a larger number of parents can be estimated.

In choosing a partial mating design, a desirable characteristic of the design would be that contrasts of the form $s_i - s_i'$, or $d_j - d_j'$, be estimated with at most two different variances. Hinkelmann (1966) has suggested a method for constructing such designs using BIB or PBIB(2) designs whose duals are also BIB or PBIB(2). To construct a partial

¹Although these reasons were given with respect to partial type II diallels, they also apply for partial type I diallels.

type I diallel cross where each male is mated r_m times and each female is mated r_f times, choose one of the above mentioned BIB or PBIB(2) designs with parameters $(t, r, b, k) = (m, r_m, f, r_f)$. Identify the male parents with the m treatments and the female parents with the f blocks. The cross between male i and female j will be made if and only if treatment i occurs in block j . A list of these designs and relevant information may be found in Hinkelmann (1966).

In addition to the mating design there is also an environmental design. For instance, the model (1.2.1) is based upon the assumption that all offspring of the mf crosses are grown in a completely randomized design. Often a need for local control (blocking) makes the use of the completely randomized design as the underlying environmental design infeasible. Since the total number of crosses (mf) is often large, the same objection may be made about a randomized block design. To reduce the required block size, one can reduce the number of crosses made by using a partial mating scheme, or one can use an incomplete block design as the underlying environmental design, or one can combine the partial mating design with the incomplete block design.

To construct an incomplete environmental design for the type I diallel cross, one could choose any incomplete block design for mf treatments and make an analogy between the mf crosses of the diallel and the mf treatments. Since the mating design has the same structure as a factorial experiment, incomplete block designs suitable for factorial experiments may be used such as the group divisible PBIB(2) designs (Kramer and Bradley (1957 a,b)). Another useful class of designs is the PBIB(3) designs given by Vartak (1959).

1.2.3. The Type II Diallel Cross Experiment

The type II diallel mating design is used with crosses between m inbred lines or monoecious parents. Four different forms of this design have been discussed by Griffing (1956). In this paper only the modified diallel (Model 4 of Griffing) will be considered. This design makes all possible crosses $i \times j$ where $i < j$ between the m inbred lines, i.e. excluding selfs and reciprocal crosses.

The statistical model that is usually assumed is

$$y_{ijk} = \mu + g_i + g_j + s_{ij} + \epsilon_{ijk} \quad (1.2.2)$$

where y_{ijk} is the observation from the k th offspring of the cross $i \times j$, g_i is the g.c.a. of line i , and s_{ij} is the s.c.a. of the cross $i \times j$.

For the reasons discussed earlier, the experimenter may not wish to make all the crosses of the complete diallel. Again an analogy can be made with incomplete block designs to determine which crosses to make. Any p -associate class PBIB with m treatments, block size two, and each of the λ_i ($i = 1, 2, \dots, p$) equal to zero or one may be used. Line i will be crossed with line j if and only if treatment i and treatment j occur together in the same block. The analysis is based upon the model in (1.2.2) where the s_{ij} are assumed to be random effects. Details of the analysis may be found in Hinkelmann and Kempthorne (1963).

Circulant partial type II diallels and their analysis may be found in Hinkelmann and Stern (1960) and in Kempthorne and Curnow (1961). Fyfe and Gilbert (1963) suggest still two other methods for constructing partial type II diallels that are in general better balanced than the circulant partial diallels. Tables of partial diallel mating designs

and relevant information concerning the analysis may be found in Curnow (1963) and Hinkelmann and Kempthorne (1963).

Again, the problem frequently arises that as m , the number of inbred lines, increases the required block size becomes far too large to allow the use of a randomized block environmental design. (The block size for a complete diallel cross embedded in a randomized block design is $m(m-1)/2$.) Reducing the number of crosses that are made using a partial diallel mating design is one solution to the problem. Two other ways to reduce the required block size are to use an incomplete environmental design for the complete diallel or to embed a partial diallel in an incomplete environmental design.

To construct an incomplete environmental design for a complete diallel cross one could choose any incomplete block design with $m(m-1)/2$ treatments and make an association between the $m(m-1)/2$ crosses of the diallel and the treatments. Triangular PBIB designs possess the most desirable characteristics. Aggarwal (1973, 1974) noted that there is a natural association between the crosses of the type II diallel and the treatments of a triangular PBIB. A complete list of triangular PBIB designs may be found in Clatworthy (1973).

Finally one may further reduce the required block size by selecting only a sample of the crosses to make and embedding these crosses in an incomplete environmental design. Braaten (1965) discusses three methods for assigning the crosses of a partial diallel to blocks so that each line occurs in exactly t crosses per block.

1.3. Interpopulation Diallel Cross Experiments

The type I and type II diallel cross experiments just discussed are based upon the assumption that the inbred lines or individuals being crossed are all from the same population. The average performance of an individual, for instance, is measured on the basis of the performance of its offspring when the individual is mated to other individuals from the same population. But as noted in section 1.1 the crossing of trees from different populations is becoming an important technique in forest tree breeding. Many tree breeders have demonstrated that interpopulation crosses are feasible (e.g. Santamour, 1972 a, b, c, d) and that the progeny from these crosses may possess desirable characteristics such as disease resistance (e.g. Diller and Clapper, 1969). A need now exists for suitable and statistically sound mating designs that will allow the tree breeder to evaluate the performance of populations in hybrid crosses as well as the performance of individuals within these populations. One such mating design is the two-level diallel cross developed by Hinkelmann (1974).

1.3.1. The Two-Level Diallel Cross Experiment

The two-level diallel cross experiment discussed by Hinkelmann (1974) would allow the breeder to evaluate the performance of populations in interpopulation crosses and to evaluate an individual on the basis of crosses with individuals from other populations. To define a two-level diallel mating design, suppose the experimenter has m populations (denoted by P_1, P_2, \dots, P_m) of trees he wants to test. These populations may be species, races, groups, or other genetically

meaningful collections of individuals. For each of these a sample of n individuals (trees, clones) are available. Denote the n individuals from population P_i by $I_{i1}, I_{i2}, \dots, I_{in}$ where $i = 1, 2, \dots, m$. Then the two-level diallel mating design consists of $m(m-1)/2$ population crosses $P_i \times P_j$, where $i < j$, and of n^2 individual crosses $I_{ik} \times I_{j\ell}$ for each population cross. For $m=4$ and $n=3$ this mating scheme is illustrated in Figure 1.1.

If the offspring from these crosses are grown using a completely randomized environmental design, the following model could be fit to the observations:

$$Y_{(ik)(j\ell)z} = \mu + G_i + G_j + S_{ij} + g_{ik} + g_{j\ell} + s_{(ik)(j\ell)} + \epsilon_{(ik)(j\ell)z}$$

where $Y_{(ik)(j\ell)z}$ is the observation from the z th offspring of the mating of the k th individual from population i with the ℓ th individual from population j , G_i is the general combining ability of population i , and S_{ij} is the specific combining ability of the population cross $P_i \times P_j$. The general combining ability of the k th individual from population i is represented by g_{ik} , and $s_{(ik)(j\ell)}$ is the specific combining ability of the individual cross $I_{ik} \times I_{j\ell}$. Hinkelmann (1974) presents estimators for these effects, comparisons between combining abilities and their variances, the variances for comparisons of average effects, and an analysis of variance with expected mean squares.

1.3.2. The Scope of This Investigation

Even for relatively small values of m and n the number of crosses, $m(m-1)n^2/2$, may be far too large to allow the use of the completely

		Population 1			Population 2			Population 3			Population 4		
		I_{11}	I_{12}	I_{13}	I_{21}	I_{22}	I_{23}	I_{31}	I_{32}	I_{33}	I_{41}	I_{42}	I_{43}
Population 1	I_{11}				X	X	X	X	X	X	X	X	X
	I_{12}				X	X	X	X	X	X	X	X	X
	I_{13}				X	X	X	X	X	X	X	X	X
Population 2	I_{21}							X	X	X	X	X	X
	I_{22}							X	X	X	X	X	X
	I_{23}							X	X	X	X	X	X
Population 3	I_{31}										X	X	X
	I_{32}										X	X	X
	I_{33}										X	X	X
Population 4	I_{41}												
	I_{42}												
	I_{43}												

The X's indicate crosses that are made.

Figure 1.1. The Two-Level Diallel Mating Scheme with $m=4$ and $n=3$.

randomized design or the randomized block design as the underlying environmental design. To reduce the experimental error it may be necessary to use an incomplete environmental design to insure the plots in a block are homogeneous. Chapter II discusses a method of constructing an incomplete environmental design for the two-level diallel mating design.

The available facilities limit the number of crosses the plant breeder can make and study. This in turn will limit the number of populations the breeder may investigate as well as the number of individuals per population. Given a fixed number of crosses that can be tested, more populations and more individuals per population can be tested if only a sample of all possible crosses are made. Chapter III discusses three ways of reducing the number of crosses to be made:

- (i) selecting only a sample of the possible population crosses,
- (ii) selecting only a sample of the individual crosses for each population cross, and
- (iii) selecting only a sample of the population crosses and for each population cross sampled selecting only a sample of the individual crosses.

It may still be impossible to obtain a design with block size small enough even if an incomplete environmental design or incomplete mating design is considered. Under these circumstances a solution would be to reduce the number of crosses made and then embed these crosses in an incomplete environmental design. Chapter IV discusses methods of

embedding a partial two-level diallel cross in an incomplete environmental design.

Finally, variations of the two-level diallel mating design are investigated. Chapter V discusses the two-level diallel that has been augmented with intrapopulation crosses. This design allows the breeder to test for population heterosis as well as obtain estimates of general and specific combining ability based upon intrapopulation and interpopulation crosses. Chapter VI discusses a mating design where pollen bulk from each of m populations is used to fertilize n trees from each of the m populations. This may be an easier and more economical way to fertilize the trees and, in addition, reduce the number of crosses.

II. AN INCOMPLETE ENVIRONMENTAL DESIGN FOR THE TWO-LEVEL DIALLEL MATING DESIGN

Every experiment in quantitative genetics is based upon two designs - a mating design for the plants or animals being studied and an environmental design used for evaluating the offspring resulting from the crosses of the mating design. The two-level diallel mating design makes $m(m-1)/2$ population crosses and n^2 individual crosses for each population cross. The total number of crosses, $m(m-1)n^2/2$, may be large for even relatively small values of m and n . For example, if five populations are to be studied using four individuals from each population, then the offspring from 160 crosses will have to be tested.

The testing of these offspring will take place in some type of environmental design. If all offspring from the crosses are randomly assigned to plots on a test site, the environmental design would be a completely randomized design (CRD). For such a large number of offspring, namely $m(m-1)n^2r/2$, the test site will have to be large and hence generally not homogenous. One might then consider a randomized block design (RBD) as the underlying environmental design. The RBD would randomly assign one offspring from each cross to a plot in each of r fields or in r locations within the same field. But again, the required block size, $m(m-1)n^2/2$, may be so large that the blocks will not be sufficiently homogenous. In this case the breeder may wish to reduce the block size and consider an incomplete block design.

2.1. The Incomplete Environmental Design

A general approach to constructing an incomplete environmental design would be to associate the $m(m-1)n^2/2$ crosses with the treatments of an incomplete block design. It would be best to choose a design that estimates similar contrasts with the same precision. For example, one would want $\text{Var}(\hat{G}_i - \hat{G}_{i'})$ to be equal for all values of i and i' ($i \neq i'$) and $\text{Var}(\hat{g}_{ik} - \hat{g}_{ik'})$ to be equal for all values of i , k , and k' ($k \neq k'$). This will not be true in general for incomplete environmental designs. By choosing a design with a structure that corresponds to the structure of the crosses, however, the experimenter may obtain an incomplete environmental design that possesses this property. This section will discuss how to construct one such design.

Because of the two-level structure of the design, i.e. n^2 individual crosses for each of the $m(m-1)/2$ population crosses, one way to reduce the required block size is to reduce the number of population crosses occurring in each block. Any balanced incomplete block (BIB) design or partially balanced incomplete block (PBIB) design with $m(m-1)/2$ treatments may be used, associating the $m(m-1)/2$ population crosses with the treatments of the incomplete block design as illustrated in Figure 2.1. This triangular array indicates, for example that population cross $P_2 \times P_4$ corresponds to treatment 5, etc. Now one can choose any appropriate BIB or PBIB design with blocks of size k as listed in Cochran and Cox (1957) or Clatworthy (1973). Each block of the resulting incomplete environmental design for the two-level diallel cross contains kn^2 plots with seedlings from kn^2 crosses rather than from the $m(m-1)n^2/2$ crosses as in the RBD.

	P ₁	P ₂	P ₃	P ₄
P ₁	*	1	2	3
P ₂		*	4	5
P ₃			*	6
P ₄				*

Figure 2.1. Correspondence Between Population Crosses and Treatments of an Incomplete Block Design.

Table 2.1. gives an example for $m=4$ populations using BIB plan 11.4 of Cochran and Cox (1959) together with the correspondence set up in Figure 2.1. Each of the $k=3$ "plots" per block contain seedlings from n^2 individual crosses.

Thus far the procedure for constructing an incomplete environmental design has been described in general terms, using any available incomplete block design. But the population crosses of the two-level diallel form a type II diallel. As Aggarwal (1973) has pointed out, PBIB designs with a triangular association scheme (T-PBIB) are particularly well suited for type II diallels as they relate in a natural way to the concepts of general and specific combining ability. Using the correspondence between treatments and crosses illustrated in Figure 2.1., two population crosses will be first associates if they have one population in common and second associates if they have no populations in common. Thus $P_1 \times P_2$ and $P_2 \times P_4$ will be first associates and will occur together in λ_1 blocks. $P_1 \times P_2$ and $P_3 \times P_4$ will be second associates and will occur together in λ_2 blocks. For the sake of convenience we define each population cross to be its own zeroth associate and hence λ_0 is the number of times a population cross occurs or $\lambda_0 = r$. Because of this structure, $\text{Var}(\hat{G}_i - \hat{G}_{i'})$ will be the same for all i and i' ($i \neq i'$) and $\text{Var}(\hat{S}_{ij} - \hat{S}_{i',j})$ will be the same for all i, i' , and j , etc. This will be demonstrated later by showing that the eigenvalues of NN' (where N is the incidence matrix of the T-PBIB), θ_1 with multiplicity $m-1$ and θ_2 with multiplicity $m(m-3)/2$, are associated with contrasts in the population g.c.a.'s and s.c.a.'s, respectively. For these reasons only

TABLE 2.1. Example of An Incomplete Environmental Design
(only the population crosses are indicated)

Block	Population crosses
1	$P_1 \times P_2$, $P_1 \times P_3$, $P_2 \times P_4$
2	$P_1 \times P_2$, $P_1 \times P_3$, $P_3 \times P_4$
3	$P_1 \times P_2$, $P_1 \times P_4$, $P_2 \times P_3$
4	$P_1 \times P_2$, $P_1 \times P_4$, $P_3 \times P_4$
5	$P_1 \times P_2$, $P_2 \times P_3$, $P_2 \times P_4$
6	$P_1 \times P_3$, $P_1 \times P_4$, $P_2 \times P_3$
7	$P_1 \times P_3$, $P_1 \times P_4$, $P_2 \times P_4$
8	$P_1 \times P_3$, $P_2 \times P_3$, $P_3 \times P_4$
9	$P_1 \times P_4$, $P_2 \times P_4$, $P_3 \times P_4$
10	$P_2 \times P_3$, $P_2 \times P_4$, $P_3 \times P_4$

T-PBIB designs will be considered as generators of the incomplete environmental designs in the following section.

2.2. Statistical Analysis

Let $Y_{(ik)(j\ell)z}$ denote the observation from the offspring of the cross $I_{ik} \times I_{j\ell}$ (where I_{ik} refers to the k th individual from the i th population) in block z of the environmental design. The basic model underlying the analysis is of the form

$$Y_{(ik)(j\ell)z} = \mu + \tau_{(ik)(j\ell)} + b_z + \epsilon_{(ik)(j\ell)z}, \quad (2.2.1)$$

where

$$\tau_{(ik)(j\ell)} = G_i + G_j + S_{ij} + g_{ik} + g_{j\ell} + s_{(ik)(j\ell)}. \quad (2.2.2)$$

Here $\tau_{(ik)(j\ell)}$ refers to the effect of the cross $I_{ik} \times I_{j\ell}$, and b_z is the effect of the z th block. For the meaning and definition of the other parameters in (2.2.2) we refer to Section 1.3.1. or Hinkelmann (1974). Since we are using an incomplete block design only certain combinations $(ik)(j\ell)z$ occur based on the generating T-PBIB design as outlined in Section 2.1.

Depending on the type of inference that one wishes to make, three models can be distinguished:

- (i) The fixed effects model: G_i , S_{ij} , g_{ik} , and $s_{(ik)(j\ell)}$ are fixed effects with

$$\sum_i G_i = 0, \quad \sum_{\substack{i \\ i \neq j}} S_{ij} = \sum_{\substack{j \\ j \neq i}} S_{ij} = 0 \quad (S_{ij} = S_{ji}),$$

$$\sum_k g_{ik} = 0 \quad \text{for every } i ,$$

$$\sum_{k,\ell} s_{(ik)(j\ell)} = 0 \quad \text{for every } (i,j) ,$$

$$\sum_j \sum_{\ell} s_{(ik)(j\ell)} = 0 \quad \text{for every } (i,k) .$$

- (ii) The random effects model: G_i , S_{ij} , g_{ik} , and $s_{(ik)(j\ell)}$ are random variables, independently distributed with zero means and variances σ_G^2 , σ_S^2 , σ_g^2 and σ_s^2 , respectively.
- (iii) The mixed model: G_i and S_{ij} are fixed effects as in (i) and g_{ik} and $s_{(ik)(j\ell)}$ are random effects as in (ii).

In (i) we are only concerned about the populations and individuals included in the experiment. In (ii) the populations and individuals in the experiment are samples from a larger collection of populations and individuals about which we would like to make inferences. Model (iii) refers to the case where all populations of interest have been included in the study, whereas the individuals represent a sample of all the individuals in the populations.

Estimates of the combining abilities in (2.2.2) are obtained as linear combinations of the estimates of the $\tau_{(ik)(j\ell)}$ from (2.2.1) which in turn are obtained as the intra-block estimates of the cross effects, denoted by $\hat{\tau}_{(ik)(j\ell)}$. These estimates are found by solving the reduced normal equations $C\hat{\tau} = Q$, where the vector $\hat{\tau}$ is of the form

$$\hat{\tau}' = (t'_{12}, t'_{13}, \dots, t'_{1m}, t'_{23}, t'_{24}, \dots, t'_{2m}, \dots, t'_{(m-1)m})$$

with

$$t'_{ij} = (\hat{\tau}_{(i1)}(j1), \hat{\tau}_{(i1)}(j2), \dots, \hat{\tau}_{(i1)}(jn), \hat{\tau}_{(i2)}(j1), \hat{\tau}_{(i2)}(j2), \dots, \hat{\tau}_{(i2)}(jn), \dots, \hat{\tau}_{(in)}(j1), \hat{\tau}_{(in)}(j2), \dots, \hat{\tau}_{(in)}(jn)) ,$$

Q is the vector of adjusted treatment totals or $Q = T - (kn^2)^{-1}N^*B$ and and $C = r I - (kn^2)^{-1}N^*N^{*'}.$ The ordering of the elements in Q and T is the same as in $\hat{\tau}$. In these expressions r is the number of offspring obtained from each cross, kn^2 is the block size, T is the vector of cross totals, and B is the vector of block totals. If N is the incidence matrix of the generating T-PBIB design, then $N^* = N \times J$, where J is a $(n^2 \times 1)$ vector of ones and "x" indicates the direct product operation.

A solution to the reduced normal equations can be written as $\hat{\tau} = C^-Q$, where C^- is a generalized inverse for C. Shah (1959) has proved that $C^- = (C + a J_{v \times v})^{-1}$ is a generalized inverse for C where a is an arbitrary non-zero number and $J_{v \times v}$ is the $v \times v$ matrix of unity elements ($v = m(m-1)n^2/2$ in our case). By the Spectral Decomposition Theorem C may be decomposed into

$$C = \phi_1 A_1 + \phi_2 A_2 + \phi_3 A_3$$

where ϕ_i ($i = 1, 2, 3$) are the non-zero eigenvalues of C with multiplicity v_i and $A_i = \sum_{j=1}^{v_i} x_j x_j'$, where $(x_1, x_2, \dots, x_{v_i})$ is a set of orthonormal eigenvectors associated with ϕ_i . Thus we may express C^- as

$$C^- = \left(\frac{1}{av^2} J_{v \times v} + \phi_1^{-1} A_1 + \phi_2^{-1} A_2 + \phi_3^{-1} A_3 \right) .$$

Since $C = r I - (kn^2)^{-1}N^*N^{*'}.$ we can express the eigenvalues of C, ϕ_i , in terms of the eigenvalues of $N^*N^{*'}$, ω_i , as follows:

$$\phi_i = r - \omega_i / kn^2 .$$

(Note that $\omega_0 = n^2rk$ corresponds to $\phi_0 = 0$.) Since further $N^* = N \times J$, we have for $i = 0, 1, 2$

$$\omega_i = n^2\theta_i,$$

where θ_i are eigenvalues of $N'N$, and $\omega_3 = 0$ (e.g. Raghavarao, 1962).

Let $(t, b, k, r, \lambda_1, \lambda_2)$ be the parameters of the generating T-PBIB design where $t = m(m-1)/2$. Then the eigenvalues of NN' are $\theta_0 = rk$ with $v_0 = 1$, $\theta_1 = r + (m-4)\lambda_1 - (m-3)\lambda_2$ with $v_1 = m-1$, and $\theta_2 = r - 2\lambda_1 + \lambda_2$ with $v_2 = m(m-3)/2$ (Corsten, 1960). A set of independent eigenvectors associated with each θ_i may be found in Corsten (1960). Because $N^* = N \times J$ we have that $z \times J$ is an eigenvector of N^*N^* associated with ω_i ($i = 0, 1, 2$) when z is an eigenvector of NN' associated with θ_i . Thus we may obtain sets of independent eigenvectors for each ω_i ($i = 0, 1, 2$) and after orthonormalizing them obtain the associated idempotent matrix A_i . Since the sum of the A_i 's is the identity matrix, A_3 may be obtained as $A_3 = I - A_0 - A_1 - A_2$.

Let $A_h = \{a_{(ik)(j\ell), (i'k')(j'\ell')}^h\}$, where $h = 0, 1, 2, 3$ and $a_{(ik)(j\ell), (i'k')(j'\ell')}^h$ represents the element of A_h that lies in the $(ik)(j\ell)$ th row and $(i'k')(j'\ell')$ th column. The order of the rows and columns will be the same as that used for $\hat{\tau}$. Using this notation we have $A_0 = (v)^{-1}J_{v \times v}$ where $J_{v \times v}$ is a $(v \times v)$ matrix of unity elements and

$$a_{(ik)(j\ell), (i'k')(j'\ell')}^1 = \begin{cases} \frac{2}{mn^2} & \text{if } P_i \times P_j \text{ and } P_{i'} \times P_{j'} \text{ are 0th associates} \\ \frac{m-4}{m(m-2)n^2} & \text{if } P_i \times P_j \text{ and } P_{i'} \times P_{j'} \text{ are 1st associates} \\ \frac{-4}{m(m-2)n^2} & \text{if } P_i \times P_j \text{ and } P_{i'} \times P_{j'} \text{ are 2nd associates} \end{cases}$$

$$a_{(ik)(j\ell), (i'k')(j'l')}^2 = \begin{cases} \frac{m-3}{(m-1)n^2} & \text{if } P_i \times P_j \text{ and } P_{i'} \times P_{j'} \text{ are 0th} \\ & \text{associates} \\ -\frac{m-3}{(m-1)(m-2)n^2} & \text{if } P_i \times P_j \text{ and } P_{i'} \times P_{j'} \text{ are 1st} \\ & \text{associates} \\ \frac{2}{(m-1)(m-2)n^2} & \text{if } P_i \times P_j \text{ and } P_{i'} \times P_{j'} \text{ are 2nd} \\ & \text{associates} \end{cases}$$

$$a_{(ik)(j\ell), (i'k')(j'l')}^3 = \begin{cases} \frac{n^2-1}{n^2} & \text{if } i=i', j=j', k=k', \ell=\ell' \\ -\frac{1}{n^2} & \text{if } i=i', j=j', \text{ and either } k \neq k', \ell \neq \ell' \\ & \text{or both} \\ 0 & \text{otherwise.} \end{cases}$$

Let

$$Q_{(ik)(j\ell)} = Y_{(ik)(j\ell)} - \frac{1}{kn^2} \sum_{z=1}^b n_{(i,j)z} B_z$$

be the adjusted $(I_{ik} \times I_{j\ell})$ - cross total, where

$$n_{(i,j)z} = \begin{cases} 1 & \text{if } P_i \times P_j \text{ occurs in block } z \\ 0 & \text{otherwise} \end{cases}$$

and B_z is the z th block total. Then

$$\begin{aligned} \hat{\tau}_{(ik)(j\ell)} &= a_{0:0} Q_{(ik)(j\ell)} + a_{0:1} S_{0:1} (Q_{(ik)(j\ell)}) + a_1 S_1 (Q_{(ik)(j\ell)}) \\ &\quad + a_2 S_2 (Q_{(ik)(j\ell)}) \end{aligned} \quad (2.2.3)$$

where

$$a_{0:0} = \frac{1}{av^2} + \frac{2}{mn^2\phi_1} + \frac{m-3}{(m-1)n^2\phi_2} + \frac{(n^2-1)}{n^2r}$$

$$a_{0:1} = \frac{1}{av^2} + \frac{2}{mn^2\phi_1} + \frac{m-3}{(m-1)n^2\phi_2} - \frac{1}{n^2r}$$

$$a_1 = \frac{1}{av^2} + \frac{m-4}{m(m-2)n^2\phi_1} - \frac{m-3}{(m-1)(m-2)n^2\phi_2}$$

$$a_2 = \frac{1}{av^2} - \frac{4}{m(m-2)n^2\phi_1} + \frac{2}{(m-1)(m-2)n^2\phi_2} ,$$

and

$$S_{0:1}(Q_{(ik)(jl)}) = \sum_{\substack{k',l' \\ k' \neq k \\ l' \neq l}} Q_{(ik')(jl')} + \sum_{\substack{k' \\ k' \neq k}} Q_{(ik')(jl)} + \sum_{\substack{l' \\ l' \neq l}} Q_{(ik)(jl')}$$

= sum of all those adjusted cross totals that involve
0th associates of $P_i \times P_j$ excluding $Q_{(ik)(jl)}$

$$S_1(Q_{(ik)(jl)}) = \sum_{j' \neq j} \sum_{k',l'} Q_{(ik')(j'l')} + \sum_{i' \neq i} \sum_{k',l'} Q_{(i'k')(jl')}$$

= sum of all those adjusted cross totals that involve
1st associates of $P_i \times P_j$

$$S_2(Q_{(ik)(jl)}) = \sum_{\substack{i',j' \\ i' < j' \\ (i',j') \neq (i,j)}} \sum_{k',l'} Q_{(i'k')(j'l')}$$

= sum of all those adjusted cross totals that involve
2nd associates of $P_i \times P_j$.

Since $\sum_{\substack{i,j \\ i < j}} \sum_{k,l} Q_{(ik)(jl)} = 0$ we may write

$$S_{0:1}(Q_{(ik)(jl)}) = -Q_{(ik)(jl)} - S_1(Q_{(ik)(jl)}) - S_2(Q_{(ik)(jl)})$$

to obtain from (2.2.3)

$$\hat{\tau} = \frac{1}{r} Q_{(ik)(jl)} - b_1 S_1(Q_{(ik)(jl)}) - b_2 S_2(Q_{(ik)(jl)}) , \quad (2.2.4)$$

where

$$b_1 = [\phi_1^{-1} + (m-3)\phi_2^{-1} - (m-2)]/(m-2)n^2r ,$$

$$b_2 = [2\phi_1^{-1} + (m-4)\phi_2^{-1} - (m-2)]/(m-2)n^2r ,$$

$$\phi_1 = r - \theta_1/kn^2, \text{ and } \phi_2 = r - \theta_2/kn^2 ,$$

and

$$\omega_1 = n^2[r + (m-4)\lambda_1 - (m-3)\lambda_2] ,$$

$$\omega_2 = n^2[r - 2\lambda_1 + \lambda_2] .$$

Using the dot notation

$$\hat{\tau}_{(ik)(\dots)} = \sum_{\substack{j \\ j>i}} \sum_{\ell} \hat{\tau}_{(ik)(j\ell)} + \sum_{\substack{j \\ j<i}} \sum_{\ell} \hat{\tau}_{(j\ell)(ik)}$$

$$\hat{\tau}_{(i\cdot)(j\cdot)} = \sum_{k,\ell} \hat{\tau}_{(ik)(j\ell)}$$

$$\hat{\tau}_{(i\cdot)(\dots)} = \sum_k \hat{\tau}_{(ik)(\dots)}$$

we can then express the estimates of the combining abilities as follows:

$$\hat{G}_i = \hat{\tau}_{(i\cdot)(\dots)}/(m-2)n^2$$

$$\hat{S}_{ij} = \hat{\tau}_{(i\cdot)(j\cdot)}/n^2 - (\hat{\tau}_{(i\cdot)(\dots)} + \hat{\tau}_{(j\cdot)(\dots)})/(m-2)n^2$$

$$\hat{g}_{ik} = \hat{\tau}_{(ik)(\dots)}/(m-1)n - \hat{\tau}_{(i\cdot)(\dots)}/(m-1)n^2$$

$$\begin{aligned} \hat{s}_{(ik)(j\ell)} &= \hat{\tau}_{(ik)(j\ell)} - (\hat{\tau}_{(ik)(\dots)} + \hat{\tau}_{(j\ell)(\dots)})/(m-1)n + (\hat{\tau}_{(i\cdot)(\dots)} \\ &+ \hat{\tau}_{(j\cdot)(\dots)})/(m-1)n^2 - \hat{\tau}_{(i\cdot)(j\cdot)}/n^2 , \end{aligned}$$

Comparisons between combining abilities and associated variances are given in Table 2.2. Also, information about comparisons of average cross performance (at the population as well as at the individual level) is given in Table 2.3. For remarks concerning the nature of σ^2 and its estimate we refer to Hinkelmann (1974). Any modifications should follow from looking at the analysis of variance table and the expected mean squares under the various models, as presented in Tables 2.4. and 2.5., respectively.

The analysis, as presented here, assumes that each field plot contains one seedling from one cross. The modification for $p(>1)$ seedlings per cross per field plot follows the familiar rules.

2.3. Generator T-PBIB Designs

Having described (Section 2.1.) a general method of obtaining one type of incomplete environmental design for the two-level diallel cross experiment, and having given (Section 2.2.) the analysis for such designs generated by T-PBIB designs, we shall comment in this section on some aspects and properties of available T-PBIB designs.

(i) There exist no T-PBIB designs for $m=4$, i.e., $t=6$. One can use instead BIB designs as the generating designs. The analysis as outlined in the previous section can still be applied as now

$\lambda_1 = \lambda_2 = \lambda$, where λ is a parameter of the BIB design; also $\theta_1 = \theta_2 = r - \lambda$, and hence $b_1 = b_2$ in (2.2.4).

(ii) From Table 2.2. we see that

$$\text{Var}(\hat{G}_i - \hat{G}_{i'}) = 2\sigma^2 / (m-2)n^2r(1-\theta_1/rk)$$

TABLE 2.2. Comparisons Between Combining Abilities
and Their Variances for the Two-Level Diallel Cross
Embedded in an Incomplete Environmental Design

Comparison	Variance
(1) $\hat{G}_i - \hat{G}_{i'}$	$2\sigma^2 / [(m-2)n^2r(1-\theta_1/rk)]$
(2) $\hat{S}_{ij} - \hat{S}_{i'j}$	$2(m-3)\sigma^2 / [(m-2)n^2r(1-\theta_2/rk)]$
$\hat{S}_{ij} - \hat{S}_{i'j'}$ ($i \neq i', j \neq j'$)	$2(m-4)\sigma^2 / [(m-2)n^2r(1-\theta_2/rk)]$
(3) $\hat{g}_{ik} - \hat{g}_{ik'}$	$2\sigma^2 / (m-1)nr$
(4) $\hat{s}_{(ik)(jl)} - \hat{s}_{(ik)(jl')}$	$2[(m-1)n-1]\sigma^2 / (m-1)nr$
$\hat{s}_{(ik)(jl)} - \hat{s}_{(ik')(jl')}$ ($k \neq k', l \neq l'$)	$2[(m-1)n-2]\sigma^2 / (m-1)nr$

TABLE 2.3. Comparisons of Average Performance for the Two-Level Diallel Cross
Embedded in an Incomplete Environmental Design

Type of Comparison	Estimator	Variance
(5) $G_i - G_{i'}$	$(\hat{\tau}_{(i\cdot)(\cdot\cdot)} - \hat{\tau}_{(i'\cdot)(\cdot\cdot)}) / (m-2)n^2$	$2\sigma^2 / (m-2)n^2r(1-\theta_1/rk)$
(6) $(G_i + G_j + S_{ij})$ $-(G_{i'} + G_{j'} + S_{i'j'})$	$(\hat{\tau}_{(i\cdot)(j\cdot)} - \hat{\tau}_{(i'\cdot)(j'\cdot)}) / n^2$	$4\sigma^2 / (m-2)n^2r(1-\theta_1/rk)$ $+ 2(m-4)\sigma^2 / (m-2)n^2r(1-\theta_2/rk)$ for $i \neq i', j \neq j'$ $2\sigma^2 / (m-2)n^2r(1-\theta_1/rk)$ $+ 2(m-3)\sigma^2 / (m-2)n^2r(1-\theta_2/rk)$ for $i = i', j \neq j'$
(7) $(G_i + g_{ik}) - (G_{i'} + g_{i'k'})$	$(\hat{\tau}_{(ik)(\cdot\cdot)} - \hat{\tau}_{(i'k')(\cdot\cdot)}) / (m-1)n$ $+ (\hat{\tau}_{(i\cdot)(\cdot\cdot)} - \hat{\tau}_{(i'\cdot)(\cdot\cdot)}) / (m-1)(m-2)n^2$	$2\sigma^2 / (m-2)n^2r(1-\theta_1/rk)$ $+ 2(n-1)\sigma^2 / (m-1)n^2r$ for $i \neq i'$ $2\sigma^2 / (m-1)nr$ for $i = i'$
(8) $(G_i + G_j + S_{ij} + g_{ik})$ $+ g_{j\ell} + s_{(ik)(j\ell)}$ $-(G_{i'} + G_{j'} + S_{i'j'} + g_{i'k'})$ $+ g_{j'\ell'} + s_{(i'k')(j'\ell')}$	$\hat{\tau}_{(ik)(j\ell)} - \hat{\tau}_{(i'k')(j'\ell')}$	$4\sigma^2 / (m-2)n^2r(1-\theta_1/rk) + 2(m-4)\sigma^2 / (m-2)n^2r(1-\theta_2/rk)$ $+ 2(n^2-1)\sigma^2 / n^2r$ for $i \neq i', j \neq j'$ $2\sigma^2 / (m-2)n^2r(1-\theta_1/rk) + 2(m-3)\sigma^2 / (m-2)n^2r(1-\theta_2/rk)$ $+ 2(n^2-1)\sigma^2 / n^2r$ for $i = i', j \neq j'$ $2\sigma^2 / r$ for $i = i', j = j'$

TABLE 2.4. Analysis of Variance for the Two-Level Diallel Cross
Embedded in an Incomplete Environmental Design

Source	Degrees of Freedom	Sum of Squares	Mean Square
Blocks ignoring crosses	b-1	$\frac{1}{kn^2} \sum_{z=1}^b B_z^2 - \frac{2G^2}{m(m-1)n^2r}$ *)	
Crosses eliminating blocks	$\frac{m(m-1)}{2} n^2 - 1$	$\sum_{i < j} \sum_{k, \ell} \hat{\tau}_{(ik)(j\ell)} Q_{(ik)(j\ell)}$	
G	m-1	$\frac{(m-2)n^2}{k} (rk - 0_1) \sum_{i=1}^m \hat{G}_i^2$	MS(G)
S	m(m-3)/2	$\frac{n^2}{k} (rk - 0_2) \sum_{\substack{i, j \\ i < j}} \hat{S}_{ij}^2$	MS(S)
g	m(n-1)	$(m-1)nr \sum_{i=1}^m \sum_{k=1}^n \hat{g}_{ik}^2$	MS(g)
s	$\frac{m(m-1)}{2} (n^2 - 1) - m(n-1)$	$r \sum_{\substack{i, j \\ i < j}} \sum_{k, \ell} \hat{s}_{(ik)(j\ell)}^2$	MS(s)
Error	$\frac{m(m-1)}{2} n^2(r-1) - b + 1$	by subtraction	MS(ε)
Total	$\frac{m(m-1)}{2} n^2r - 1$	$\sum_{\substack{i, j \\ i < j}} \sum_{k, \ell} \sum_z Y_{(ik)(j\ell)z}^2 - \frac{2G^2}{m(m-1)n^2r}$	

*) G = grand total

B_z = block total for 2nd block

TABLE 2.5. Expected Mean Squares for the Two-Level Diallel Cross
Embedded in an Incomplete Environmental Design

Mean Square	Model (i)	Model (ii)	Model (iii)
MS(G)	$\sigma_{\epsilon}^2 + \frac{(m-2)n^2}{m-1} \phi_1 \sum_i G_i^2$	$\sigma_{\epsilon}^2 + K_2\sigma_s^2 + nK_1\sigma_g^2 + n^2K_2\sigma_s^2 + n^2K_1\sigma_G^2$	$\sigma_{\epsilon}^2 + K_2\sigma_s^2 + nK_1\sigma_g^2 + \frac{(m-2)n^2}{m-1} \phi_1 \sum_i G_i^2$
MS(S)	$\sigma_{\epsilon}^2 + \frac{2n^2}{m(m-3)} \phi_2 \sum_{i<j} S_{ij}^2$	$\sigma_{\epsilon}^2 + K_4\sigma_s^2 + nK_3\sigma_g^2 + n^2K_4\sigma_s^2 + n^2K_3\sigma_G^2$	$\sigma_{\epsilon}^2 + K_4\sigma_s^2 + nK_3\sigma_g^2 + \frac{2n^2}{m(m-3)} \phi_2 \sum_{i<j} S_{ij}^2$
MS(g)	$\sigma_{\epsilon}^2 + \frac{(m-1)nr}{m(n-1)} \sum_i \sum_k g_{ik}^2$	$\sigma_{\epsilon}^2 + r\sigma_s^2 + (m-1)nr\sigma_g^2$	$\sigma_{\epsilon}^2 + r\sigma_s^2 + (m-1)nr\sigma_g^2$
MS(s)	$\sigma_{\epsilon}^2 + \frac{r}{d} \sum_{i<j} \sum_{k,\ell} s_{(ik)(j\ell)}^2$	$\sigma_{\epsilon}^2 + r\sigma_s^2$	$\sigma_{\epsilon}^2 + r\sigma_s^2$
MS(ϵ)	σ_{ϵ}^2	σ_{ϵ}^2	σ_{ϵ}^2

$$d = \frac{m(m-1)}{2} (n^2-1) - m(n-1)$$

$$K_1 = \frac{m}{(m-2)\phi_1 k^2} \{ (m-1)[rk-r-(m-2)\lambda_1]^2 + [rk-r-3(m-2)\lambda_1 - (m-3)(m-2)\lambda_2]^2 \}$$

$$K_2 = \frac{m}{(m-2)\phi_1 k^2} \{ [rk-r-(m-2)\lambda_1]^2 + \frac{m-2}{2} [2\lambda_1 + (m-3)\lambda_2]^2 \}$$

$$K_3 = \frac{m-1}{(m-3)(m-2)^2\phi_2} [2\phi_1 - \frac{m}{k} (2\lambda_1 + (m-3)\lambda_2)]^2$$

$$K_4 = (m^2-6m+12)\phi_2^2 - \frac{2m}{k} \phi_2 [4\lambda_1 + (m-4)\lambda_2] + \frac{m(m-1)}{2k^2} [4\lambda_1 + (m-4)\lambda_2]^2$$

and

$$\text{Var}(\hat{S}_{ij} - \hat{S}_{i'j'}) = \begin{cases} 2(m-3)\sigma^2/(m-2)n^2r(1-\theta_2/rk) & (i \neq i', j = j') \\ 2(m-4)\sigma^2/(m-2)n^2r(1-\theta_2/rk) & (i \neq i', j \neq j') \end{cases}$$

Compared to the same expressions for the randomized complete block design as given by Hinkelmann (1974) we see that they differ by a factor $1/(1-\theta_1/rk)$ and $1/(1-\theta_2/rk)$, respectively. The efficiencies for comparisons of general and specific combining abilities at the population level using an incomplete environmental design (generated from a T-PBIB design) relative to those using a complete environmental design are then

$$E_G = 1 - \theta_1/rk$$

and

$$E_S = 1 - \theta_2/rk ,$$

respectively. Hence the loss of information (assuming equal σ^2 for both types of designs) is given by θ_1/rk and θ_2/rk , respectively.

This association between θ_1 and the G's and between θ_2 and the S's is a characteristic feature of T-PBIB designs. For this reason we have restricted ourselves to T-PBIB designs (as alluded to in Section 2.1.). It enables the experimenter to identify the most appropriate design, subject only to the constraint of the size of the experiment. For example, if it is desired to incur as little loss of information about the G_i 's as possible one should choose among competing designs the one that has the smallest θ_1/rk , zero if possible. Also, from previous remarks it is obvious that a BIB design will lead to the same loss of

information for G_i 's and S_{ij} 's. Incidentally, no loss of information occurs for the g_{ik} and $s_{(ik)(j\ell)}$.

(iii) For practical purposes, BIB and T-PBIB designs with block size $k=2$ or 3 will generally be the most appropriate, since otherwise the overall block size (kn^2) may still become too large.

In Table 2.6. we present a list of such designs together with their parameters. The numbers of the BIB designs refer the plans given in Cochran and Cox (1957), the T-PBIB designs are labeled as in Clatworthy (1973). These designs are to be used in connection with the correspondence between treatments and population crosses as outlined in Section 2.1.

TABLE 2.6. BIB and T-PBIB Designs Suitable for Constructing
Incomplete Environmental Designs

Type	m	t	k	r	b	λ_1	λ_2	θ_1	θ_2	E_G	E_S
BIB 11.3	4	6	2	5	15	1	1	4	4	.60	.60
BIB 11.4	4	6	3	5	10	2	2	3	3	.80	.80
BIB 11.5	4	6	3	10	20	4	4	6	6	.80	.80
BIB 11.14	5	10	2	9	45	1	1	8	8	.56	.56
T 1	5	10	2	6	30	1	0	7	4	.42	.67
T 2	5	10	2	3	15	0	1	1	4	.83	.33
T 3	5	10	2	6	30	0	2	2	8	.83	.33
T 4	5	10	2	9	45	0	3	3	12	.83	.33
BIB 11.15	5	10	3	9	30	2	2	7	7	.74	.74
T 9	5	10	3	3	10	1	0	4	1	.56	.89
T 10	5	10	3	6	20	2	0	8	2	.56	.89
T 11	5	10	3	9	30	3	0	12	3	.56	.89
T 12	5	10	3	6	20	1	2	3	6	.83	.67
T 13	5	10	3	9	30	1	4	2	11	.93	.59
T 5	6	15	2	8	60	1	0	10	6	.38	.63
T 6	6	15	2	6	45	0	1	3	7	.75	.42
BIB 11.24	6	15	3	7	35	1	1	6	6	.71	.71
T 14	6	15	3	4	20	1	0	6	2	.50	.83
T 15	6	15	3	8	40	2	0	12	4	.50	.83
T 16	6	15	3	3	15	0	1	0	4	1.00	.56
T 17	6	15	3	6	30	0	2	0	8	1.00	.56
T 18	6	15	3	10	50	1	2	6	10	.80	.67
T 19	6	15	3	9	45	0	3	0	12	1.00	.56
T 7	7	21	2	10	105	1	0	13	8	.35	.60
T 8	7	21	2	10	105	0	1	6	11	.70	.45
BIB 11.33	7	21	3	10	70	1	1	9	9	.70	.70
T 20	7	21	3	5	35	1	0	8	3	.47	.80
T 21	7	21	3	10	70	2	0	16	6	.47	.80
T 22	7	21	3	10	70	0	2	2	12	.93	.60

III. PARTIAL MATING DESIGNS FOR THE TWO-LEVEL DIALLEL CROSS EXPERIMENT

Partial mating schemes may be of interest for several reasons. To use the complete diallel mating design the breeder must make $m(m-1)n^2/2$ crosses. For certain species of trees it may be too costly or difficult to make this many crosses. In that case the breeder may want to study only a sample of the crosses. Often the available facilities determine the number of crosses that may be made and tested. Given a fixed number of crosses that can be tested, more populations and more individuals per population may be tested if instead of complete intercrossing only a sample of all possible crosses is taken. And finally the breeder can reduce the required block size of the environmental design by reducing the number of crosses that are made.

These partial mating designs may be constructed in many ways. In this chapter we will discuss three designs that are constructed by exploiting the two-level structure of the mating design. One method of reducing the number of crosses would be to select only a sample of the crosses on the individual level. We will refer to this design as the I-partial two-level diallel mating design. Another method would be to select a sample of the $m(m-1)/2$ population crosses to test. The resulting incomplete mating design will be referred to as the P-partial two-level diallel mating design. Finally we may combine these two methods and sample the crosses on the population and individual levels. We will refer to this design as the PI-partial two-level diallel mating design. We will discuss the PI-partial two-level diallel cross first

since the analysis of the I-partial and P-partial diallels follows naturally from the analysis of the PI-partial diallel.

3.1. The PI-Partial Two-Level Diallel Mating Design

The PI-partial two-level diallel mating design reduces the number of crosses on two levels--first only a sample of the $m(m-1)/2$ population crosses are selected and secondly for each population cross selected only a sample of the n^2 individual crosses are chosen. To insure balance, each population is involved in an equal number of population crosses (c_1) and within each population cross each individual is involved in an equal number of individual crosses (c_2). Such a design is illustrated in Figure 3.1. for $m=5$, $n=4$, $c_1=2$, and $c_2=2$. Note that the total number of crosses has been reduced from 160 for the complete diallel to 40 for the PI-partial diallel.

3.1.1. Construction of the Design

Since the population crosses constitute a type II diallel, one can use the methods discussed in Section 1.2.3. to choose the population crosses to be sampled. The individual crosses to be sampled for each population cross selected will be determined by exploiting the fact that the individual crosses within each population cross constitute a type I diallel. Using the suggestion of Hinkelmann (1966), we make an analogy with a PBIB or BIB design with $t = b = n$ and $r = k = c_2$. For each population cross $P_i \times P_j$ that is sampled, the individual cross $I_{ik} \times I_{j\ell}$ will be made if and only if treatment k occurs in block ℓ of the underlying BIB or PBIB design. Let $V = \{v_{k\ell}\}$ be the incidence matrix of this

		P ₁				P ₂				P ₃				P ₄				P ₅			
		I ₁₁	I ₁₂	I ₁₃	I ₁₄	I ₂₁	I ₂₂	I ₂₃	I ₂₄	I ₃₁	I ₃₂	I ₃₃	I ₃₄	I ₄₁	I ₄₂	I ₄₃	I ₄₄	I ₅₁	I ₅₂	I ₅₃	I ₅₄
P ₁	I ₁₁									X	X			X	X						
	I ₁₂									X		X		X		X					
	I ₁₃										X		X		X		X				
	I ₁₄											X	X			X	X				
P ₂	I ₂₁													X	X			X	X		
	I ₂₂													X		X		X		X	
	I ₂₃														X		X		X		X
	I ₂₄															X	X			X	X
P ₃	I ₃₁																	X	X		
	I ₃₂																	X		X	
	I ₃₃																		X		X
	I ₃₄																			X	X
P ₄	I ₄₁																				
	I ₄₂																				
	I ₄₃																				
	I ₄₄																				
P ₅	I ₅₁																				
	I ₅₂																				
	I ₅₃																				
	I ₅₄																				

Figure 3.1. The PI-Partial Two-Level Diallel Mating Design

design. Then for every population cross $P_i \times P_j$ sampled, individual k of population i will be crossed with individual ℓ of population j if and only if $v_{k\ell} = 1$.

For reasons that will be discussed later, it is preferable to consider designs that are truly self dual, i.e. the dual of the design is the design itself which is equivalent to $V=V'$. Table 3.1. lists self dual BIB and PBIB designs that can be used to determine the individual crosses to be sampled for each population cross selected. In addition, the eigenvalues of the design matrix V are also given. The need for knowing the eigenvalues of V will be discussed later. Except for those designs denoted by asterisks, the BIB designs may be found in Cochran and Cox (1957) and the PBIB designs in Clatworthy (1973). The designs with one asterisk are to be constructed in the following manner: Treatment i will be found in blocks $i, i+d, \dots, i+(n-d)$ where i is always reduced modulo d and c_2 is an integral divisor of n with $d = n/c_2$. For $n=8$ individuals per population and $c_2=2$ the design matrix would be

$$V = \begin{bmatrix} 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 \end{bmatrix} .$$

In some instances a suitable BIB or PBIB self dual design may not be

TABLE 3.1. Self Dual BIB and PBIB Designs Available for Constructing
Partial Two-Level Diallels

n	c ₂	Type	Location	Eigenvalues	n	c ₂	Type	Location	Eigenvalues
4	2	PBIB	***	0,2,±1.4142	16	4	PBIB	*	0,4
4	3	BIB	**	±1,3	16	6	BIB	11.27	±2,6
5	4	BIB	**	±1,4	16	8	PBIB	*	0,8
6	2	PBIB	*	0,2	16	10	BIB	11.29	±2,10
6	3	PBIB	*	0,3	18	3	PBIB	*	0,3
6	4	PBIB	R94	-2,1,4	18	6	PBIB	*	0,6
6	5	BIB	**	±1,5	18	9	PBIB	*	0,9
7	6	BIB	**	±1,6	20	2	PBIB	*	0,2
8	2	PBIB	*	0,2	20	4	PBIB	*	0,4
8	4	PBIB	*	0,4	20	5	PBIB	*	0,5
8	6	PBIB	S19	±2,0,6	20	10	PBIB	*	0,10
8	7	BIB	**	±1,7	21	3	PBIB	*	0,3
9	3	PBIB	*	0,3	21	7	PBIB	*	0,7
9	8	BIB	**	±1,8	22	2	PBIB	*	0,2
10	2	PBIB	*	0,2	24	2	PBIB	*	0,2
10	5	PBIB	*	0,5	24	3	PBIB	*	0,3
10	9	BIB	**	±1,9	24	4	PBIB	*	0,4
11	10	BIB	**	±1,10	24	6	PBIB	*	0,6
12	3	PBIB	*	0,3	24	8	PBIB	*	0,8
12	4	PBIB	*	0,4	24	12	PBIB	*	0,12
12	6	PBIB	*	0,6	25	5	PBIB	*	0,5
14	2	PBIB	*	0,2	26	2	PBIB	*	0,2
14	7	PBIB	*	0,7	26	13	PBIB	*	0,13
15	3	PBIB	*	0,3	27	3	PBIB	*	0,3
15	5	PBIB	*	0,5	27	9	PBIB	*	0,9
16	2	PBIB	*	0,2					

**This design is created by taking all possible combinations of c₂ out of n treatments.

***This design consists of the following crosses: 1×1, 1×2, 2×1, 2×3, 3×2, 3×4, 4×3, 4×4.

available. In this case the breeder may use one of the designs listed in Table 3.2. Again, the BIB designs may be found in Cochran and Cox (1957) and the PBIB designs in Clatworthy (1973). The designs in Table 3.1. and 3.2. were tabulated and discussed by Hinkelmann (1966).

3.1.2. The Statistical Model and Analysis

When the offspring from the PI-partial two-level diallel are grown in a completely randomized environmental design the model for the mean observation from the cross $I_{ik} \times I_{jl}$ will be

$$\bar{Y}_{(ik)(jl)} = \mu + G_i + G_j + g_{ik} + g_{jl} + e_{(ik)(jl)}$$

where G_i and g_{ik} are defined as in Section 2.2. Since an incomplete mating design is being used, not all combinations of $(ik)(jl)$ will occur. The residual $e_{(ik)(jl)}$ may be partitioned into

$$e_{(ik)(jl)} = S_{ij}^* + s_{(ik)(jl)}^* + \frac{1}{r} \sum_z \epsilon_{(ik)(jl)z}$$

where S_{ij}^* and $s_{(ik)(jl)}^*$ are independent random variables representing variation on the population and individual levels, respectively, and $E(e_{(ik)(jl)}) = 0$ with $\text{Var}(e_{(ik)(jl)}) = \sigma^2 = \sigma_{S^*}^2 + \sigma_{s^*}^2 + \sigma_\epsilon^2/r$. Since $\text{Cov}(e_{(ik)(jl)}, e_{(ik')(jl')}) = \sigma_{S^*}^2$ for $k \neq k'$ or $l \neq l'$ or both $k \neq k'$ and $l \neq l'$, the $e_{(ik)(jl)}$'s are correlated. If the e-vector is ordered in the following manner:

$$e' = (e'_{12}, e'_{13}, \dots, e'_{1m}, e'_{23}, e'_{24}, \dots, e'_{2m}, \dots, e'_{(m-1)m})$$

with

TABLE 3.2. BIB and PBIB Designs Available for Constructing Partial Two-Level Diallels

n	c_2	Type	Location	n	c_2	Type	Location
6	3	PBIB	R42	15	3	PBIB	T16
7	3	BIB	11.7	15	4	PBIB	R114
7	4	BIB	11.8	15	7	BIB	11.25
8	3	PBIB	R54	15	8	BIB	11.26
8	4	PBIB	SR36	15	10	PBIB	S104
9	3	PBIB	SR23	16	3	PBIB	LS18
9	4	PBIB	LS26	16	4	PBIB	SR44
9	5	PBIB	LS49	16	8	PBIB	SR92
9	6	PBIB	SR65	17	8	PBIB	C26
10	3	PBIB	T9	17	9	PBIB	C28
10	4	PBIB	T33	18	6	PBIB	SR72
10	6	PBIB	T60	19	9	BIB	11.31
10	7	PBIB	T71	19	10	BIB	11.32
10	8	PBIB	S52	21	5	BIB	11.34
11	5	BIB	11.19	21	9	PBIB	S90
11	6	BIB	11.20	22	10	PBIB	S111
12	4	PBIB	R109	24	5	PBIB	R153
12	6	PBIB	SR68	25	5	PBIB	SR60
12	8	PBIB	S56	25	9	BIB	11.37
12	9	PBIB	S84	26	8	PBIB	S72
12	10	PBIB	S99	27	9	PBIB	SR102
13	3	PBIB	C16	29	7	PBIB	C25
13	4	BIB	11.22	29	8	PBIB	C27
13	9	BIB	11.23				
13	10	PBIB	C29				
14	4	PBIB	R112				
14	6	PBIB	S33				
14	8	PBIB	S60				

$$e'_{ij} = (e_{(i1)(j1)}, e_{(i1)(j2)}, \dots, e_{(i1)(jn)}, e_{(i2)(j1)}, e_{(i2)(j2)}, \dots, e_{(i2)(jn)}, \dots, e_{(in)(j1)}, e_{(in)(j2)}, \dots, e_{(in)(jn)})'$$

then the covariance matrix can be written as

$$E(ee') = \sigma^2 \Sigma$$

with

$$\Sigma = (1-\rho) I + \rho \text{diag}(J, J, \dots, J)$$

where $\rho = \sigma_{S^*}^2 / \sigma^2$ and $\text{diag}(J, J, \dots, J)$ is a block diagonal matrix of order $mc_1 c_2^{n/2} \times mc_1 c_2^{n/2}$ whose diagonal blocks consist of the $nc_2 \times nc_2$ matrix J of unity elements. Since the e 's are correlated a weighted least squares procedure is indicated to obtain best linear unbiased estimates (BLUE). In the appendix, however, the simple least squares estimates are shown to be BLUE.

Let $U = \{u_{ij}\}_{m \times m}$ where $u_{ii} = c_1$ and $u_{ij} = 1$ when the population cross $P_i \times P_j$ ($i \neq j$) is made and zero otherwise. Let V be the incidence matrix of the BIB or PBIB design used to determine which individual crosses to sample. That is, $V = \{v_{kl}\}_{n \times n}$ where $v_{kl} = 1$ if the individual cross $I_{ik} \times I_{jl}$ is sampled whenever the population cross $P_i \times P_j$ is selected and $v_{kl} = 0$ otherwise. Using the dot notation:

$$Y_{(ik)(jl)\cdot} = \sum_z Y_{(ik)(jl)z}$$

$$Y_{(ik)(\cdot\cdot)\cdot} = \sum_{\substack{j \\ j \neq i}} \sum_{\ell} u_{ij} v_{k\ell} Y_{(ik)(j\ell)\cdot}$$

$$Y_{(i\cdot)(\cdot\cdot)\cdot} = \sum_k Y_{(ik)(\cdot\cdot)\cdot}$$

$$Y_{(i\cdot)(j\cdot)\cdot} = \sum_{k,\ell} v_{k\ell} Y_{(ik)(j\ell)\cdot}$$

$$Y_{(\cdot\cdot)(\cdot\cdot)\cdot} = \sum_{\substack{i,j \\ i < j}} u_{ij} Y_{(i\cdot)(j\cdot)\cdot}$$

we obtain the following solution to the NE:

$$\hat{\mu} = \frac{2}{mnc_1c_2r} Y_{(\cdot\cdot)(\cdot\cdot)\cdot}$$

$$\hat{G} = U^{-1}Q$$

and a system of equations for the \hat{g} 's:

$$W\hat{g} = R$$

where $\hat{G}' = (\hat{G}_1, \hat{G}_2, \dots, \hat{G}_m)$ and $Q' = (Q_1, Q_2, \dots, Q_m)$ with

$$Q_i = \frac{1}{nc_2r} Y_{(i\cdot)(\cdot\cdot)\cdot} - \frac{2}{mc_2nr} Y_{(\cdot\cdot)(\cdot\cdot)\cdot}$$

The \hat{g} -vector will be ordered in the following manner:

$$\hat{g}' = (\hat{g}_{11}, \hat{g}_{12}, \dots, \hat{g}_{1n}, \hat{g}_{21}, \hat{g}_{22}, \dots, \hat{g}_{2n}, \dots, \hat{g}_{m1}, \hat{g}_{m2}, \dots, \hat{g}_{mn})$$

The order of the R-vector will follow that of \hat{g} with

$$R_{ik} = \frac{1}{c_1c_2r} Y_{(ik)(\cdot\cdot)\cdot} - \frac{1}{nc_1c_2r} Y_{(i\cdot)(\cdot\cdot)\cdot}$$

U^{-1} is the same as the inverse matrix associated with the partial type II diallel cross selected. The references listed in Section 1.2.3. give partial mating designs and the associated inverse matrix for U. The

matrix W may be expressed as

$$W = I_m \times (I_n - V/c_2) + U \times (V/c_1 c_2)$$

where I_n is the $n \times n$ identity matrix. Let $W = \{w_{ik,jl}\}$ where $w_{ik,jl}$ is the element in the (ik) th row and (jl) th column of W when the rows and columns are ordered following R . Then

$$w_{ik,jl} = \begin{cases} 1 & \text{if } i=j, k=l \\ \frac{1}{c_1 c_2} & \text{if } i \neq j \text{ and } I_{ik} \times I_{jl} \text{ is sampled} \\ 0 & \text{otherwise .} \end{cases}$$

In choosing a PI-partial two-level diallel mating design the breeder should consider only those designs that result in a nonsingular matrix W . In that case we will obtain

$$\hat{g} = W^{-1}R$$

as the estimates of the g_{ik} . There is no explicit form for W^{-1} .

However, when the design matrix V used to determine which individual crosses to sample is self dual, more can be said about the structure of W^{-1} . Partition the matrix W^{-1} into

$$W^{-1} = \begin{bmatrix} W^{11} & W^{12} & \dots & W^{1m} \\ W^{21} & W^{22} & \dots & W^{2m} \\ \vdots & \vdots & & \vdots \\ W^{m1} & W^{m2} & \dots & W^{mm} \end{bmatrix} \quad (3.1.1)$$

where W^{ij} is a $n \times n$ matrix corresponding to the population cross $P_i \times P_j$.

Because of the relationship between a partial type II diallel and a PBIB

with s associate classes, W^{-1} will have at most $s+1$ distinct matrices, say W^0, W^1, \dots, W^s , such that if populations i and j are t -th associates then $W^{ij} = W^t$ ($s \leq m-1$). Using $WW^{-1} = I$, a system of $s+1$ sets of equations in the $s+1$ unknown matrices W^0, W^1, \dots, W^s can be written where the coefficients of the t -th equation are obtained from $P_t = \{p_{ij}^t\}$, the parameters of the second kind of a PBIB. If two populations are t -th associates then p_{ij}^t is defined to be the number of populations common to the i th associates of the first and the j th associates of the second. By generalizing the results of Hinkelmann and Kempthorne (1963) for the partial type II diallel, one obtains the following form for this system of equations:

$$\sum_{i=0}^s p_{i0}^t W^i + \frac{1}{c_1 c_2} \sum_{i=0}^s \sum_{j=1}^s \lambda_j p_{ij}^t V W^i = \delta_{t0} I \quad (3.1.2)$$

where δ_{t0} is the Kronecker δ and λ_j is the number of times two j th associates occur together in blocks. (For the designs used in constructing the partial diallels λ_j will be equal to zero or one.)

Let $W^{-1} = \{w^{ik, i'k'}\}$ where $w^{ik, i'k'}$ is the element in the (ik) th row and $(i'k')$ th column. The order of the rows and columns will follow that of R . Further let $U^{-1} = \{u^{ii'}\}$ where $u^{ii'}$ is the element in the i th row and i' th column. Then

$$\text{Var}(\hat{G}_i - \hat{G}_{i'}) = (u^{ii} + u^{i'i'} - 2u^{ii'})\sigma_1^2 \quad (3.1.3)$$

$$\text{Var}(\hat{g}_{ik} - \hat{g}_{i'k'}) = (w^{ik, ik} + w^{i'k', i'k'} - 2w^{ik, i'k'})\sigma_2^2 \quad (3.1.4)$$

where

$$\sigma_1^2 = \sigma_{S^*}^2 + \sigma_{S^*}^2/nc_2 + \sigma_\epsilon^2/nc_2r$$

and

$$\sigma_2^2 = \sigma_{S^*}^2/c_1c_2 + \sigma_\epsilon^2/c_1c_2r .$$

Because of the relationship between the partial type II diallel and a PBIB with s associate classes, U^{-1} will have at most $s+1$ distinct elements, u^0, u^1, \dots, u^s , such that if populations i and i' are t -th associates, then $u^{ii'} = u^t$. Thus (3.1.3) may be rewritten as

$$\text{Var}(\hat{G}_i - \hat{G}_{i'}) = (2u^0 - 2u^t)\sigma_1^2$$

when populations i and i' are t -th associates, and there will be at most s distinct variances for the contrasts $\hat{G}_i - \hat{G}_{i'}$. When V is symmetric, W^{-1} will be composed of at most $s+1$ distinct submatrices, W^0, W^1, \dots, W^s , using the partitioning of (3.1.1). Let $W^t = \{w_{kk'}^t\}$ where $w_{kk'}^t$ is the element in the k th row and k' th column of W^t . Then when populations i and i' are t -th associates (3.1.4) may be written as

$$\text{Var}(\hat{g}_{ik} - \hat{g}_{i'k'}) = (w_{kk}^0 + w_{k'k'}^0 - 2w_{kk'}^t)\sigma_2^2 .$$

The analysis of variance for this design is given in Table 3.3. The sum of squares for S^* and s^* were obtained by partitioning the residual crosses sum of squares or

$$SS(\text{residual}) = r \sum_{\substack{i,j \\ i < j}} \sum_{k,l} u_{ij} v_{kl} (\bar{y}_{(ik)(jl)} - \hat{\mu} - \hat{G}_i - \hat{G}_j - \hat{g}_{ik} - \hat{g}_{jl})^2$$

into a component at the population level or

TABLE 3.3. Analysis of Variance for the PI-Partial Two-Level Diallel Cross Experiment

Source	Degrees of Freedom	Sum of Squares	Mean Square
G	m-1	$\sum_i Y_{(i\cdot)(\cdot\cdot)} \cdot \hat{G}_i$	MS(G)
S*	$m\left(\frac{c_1}{2} - 1\right)$	$\frac{1}{nc_2^r} \sum_{\substack{i,j \\ i < j}} u_{ij} Y_{(i\cdot)(j\cdot)}^2 - \sum_i Y_{(i\cdot)(\cdot\cdot)} \cdot \hat{G}_i - \frac{2}{mnc_1c_2^r} Y_{(\cdot\cdot)(\cdot\cdot)}^2$	MS(S*)
g	m(n-1)	$\sum_i \sum_k Y_{(ik)(\cdot\cdot)} \cdot \hat{g}_{ik}$	MS(g)
s*	$\frac{mc_1}{2} (nc_2 - 1) - m(n-1)$	Difference	MS(s*)
error	$\frac{mc_1c_2^n}{2} (r-1)$	$\sum_{\substack{i,j \\ i < j}} \sum_{k,l} \sum_z u_{ij} v_{kl} Y_{(ik)(jl)z}^2 - \frac{1}{r} \sum_{\substack{i,j \\ i < j}} \sum_{k,l} u_{ij} v_{kl} Y_{(ik)(jl)}^2$	MS(ε)
total	$\frac{mnc_1c_2^r}{2} - 1$	$\sum_{\substack{i,j \\ i < j}} \sum_{k,l} \sum_z u_{ij} v_{kl} Y_{(ik)(jl)z}^2 - \frac{2}{mnc_1c_2^r} Y_{(\cdot\cdot)(\cdot\cdot)}^2$	

$$SS(S^*) = nc_2 r \sum_{\substack{i,j \\ i < j}} u_{ij} (\bar{Y}_{(i\cdot)(j\cdot)} - \hat{\mu} - \hat{G}_i - \hat{G}_j)^2$$

and a component at the individual level or

$$SS(s^*) = r \sum_{\substack{i,j \\ i < j}} \sum_{k,\ell} u_{ij} v_{k\ell} (\bar{Y}_{(ik)(j\ell)} - \bar{Y}_{(i\cdot)(j\cdot)} - \hat{g}_{ik} - \hat{g}_{j\ell})^2 .$$

The expected mean squares are given in Table 3.4. so that appropriate hypotheses about the parameters may be tested and the variance components estimated.

3.2. The P-Partial Two-Level Diallel Mating Design

When the number of populations to be crossed is large and the number of individuals per population is small the breeder may wish to simplify the design by considering the special case of the PI-partial two-level diallel cross in which not all population crosses are sampled but for each population cross sampled all n^2 individual crosses are selected ($c_2=n$). We will call this special case the P-partial two-level diallel cross. The population crosses to be sampled will again be determined using the technique discussed in Section 1.2.3. An illustration of the P-partial two-level diallel cross is given in Figure 3.2. for $m=5$, $n=4$, and $c_1=2$.

The analysis for this design will be the same as that of the PI-partial two-level diallel cross where $c_2=n$ and $v_{k\ell}=1$ for all k and ℓ . The expression for \hat{g}_{ik} when simplified becomes

$$\hat{g}_{ik} = \frac{1}{c_1 nr} Y_{(ik)(\dots)} - \frac{1}{c_1 n^2 r} Y_{(i\cdot)(\dots)} .$$

TABLE 3.4. Expected Mean Squares for the PI-Partial Two-Level Diallel Cross Experiment

Mean Square	Model (i)	Model (ii)	Model (iii)
MS(G)	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2 + nc_2r\sigma_{S^*}^2$ $+ \frac{nc_2r}{m-1} \sum_i \sum_j u_{ij} G_i G_j$	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2 + \frac{(m-2)c_1c_2r}{m-1} \sigma_g^2$ $+ nc_2r\sigma_{S^*}^2 + \frac{(m-2)nc_1c_2r}{m-1} \sigma_G^2$	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2 + nc_2r\sigma_{S^*}^2$ $+ \frac{(m-2)c_1c_2r}{m-1} \sigma_g^2 + \frac{nc_2r}{m-1} \sum_i \sum_j u_{ij} G_i G_j$
MS(S*)	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2 + nc_2r\sigma_{S^*}^2$	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2 + nc_2r\sigma_{S^*}^2$	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2 + nc_2r\sigma_{S^*}^2$
MS(g)	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2$ $+ \frac{c_1c_2r}{m(n-1)} \sum_{i,j} \sum_{k,\ell} w_{(ik)(j\ell)} g_{ik} g_{j\ell}$	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2 + c_1c_2r\sigma_g^2$	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2 + c_1c_2r\sigma_g^2$
MS(s*)	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2$	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2$	$\sigma_{\epsilon}^2 + r\sigma_{S^*}^2$
MS(ε)	σ_{ϵ}^2	σ_{ϵ}^2	σ_{ϵ}^2

		P_1				P_2				P_3				P_4				P_5			
		I_{11}	I_{12}	I_{13}	I_{14}	I_{21}	I_{22}	I_{23}	I_{24}	I_{31}	I_{32}	I_{33}	I_{34}	I_{41}	I_{42}	I_{43}	I_{44}	I_{51}	I_{52}	I_{53}	I_{54}
P_1	I_{11}									X	X	X	X	X	X	X	X				
	I_{12}									X	X	X	X	X	X	X	X				
	I_{13}									X	X	X	X	X	X	X	X				
	I_{14}									X	X	X	X	X	X	X	X				
P_2	I_{21}													X	X	X	X	X	X	X	X
	I_{22}													X	X	X	X	X	X	X	X
	I_{23}													X	X	X	X	X	X	X	X
	I_{24}													X	X	X	X	X	X	X	X
P_3	I_{31}																	X	X	X	X
	I_{32}																	X	X	X	X
	I_{33}																	X	X	X	X
	I_{34}																	X	X	X	X
P_4	I_{41}																				
	I_{42}																				
	I_{43}																				
	I_{44}																				
P_5	I_{51}																				
	I_{52}																				
	I_{53}																				
	I_{54}																				

Figure 3.2. The P-Partial Two-Level Diallel Mating Design

Simpler forms for $SS(g)$ and $SS(s^*)$ are given in Table 3.5. with the expected mean squares in Table 3.6.

3.3. The I-Partial Two-Level Diallel Mating Design

When the number of populations is small, the breeder may wish to use a partial mating design where the crosses are sampled only at the individual level. One such design is the I-partial two-level diallel cross which is the simplification of the PI-partial two-level diallel when $c_1 = m-1$. All $m(m-1)/2$ population crosses will be tested using this design but for each population cross a sample of the n^2 individual crosses will be selected using the method discussed in Section 3.1.1. This design is illustrated in Figure 3.3. for $m=5$, $n=4$, and $c_2=2$.

One advantage of the I-partial two-level diallel cross is that population s.c.a. effects may be estimated. The following model is assumed for the observations:

$$\bar{Y}_{(ik)(j\ell)} = \mu + G_i + G_j + S_{ij} + g_{ik} + g_{j\ell} + e_{(ik)(j\ell)}$$

where the residual $e_{(ik)(j\ell)}$ may be partitioned into an effect representing variation on the individual level and an error term, or

$$e_{(ik)(j\ell)} = s^*_{(ik)(j\ell)} + \frac{1}{r} \epsilon_{(ik)(j\ell)z}$$

The $e_{(ik)(j\ell)}$'s are uncorrelated random variables with mean zero and variance $\sigma^2 = \sigma_{s^*}^2 + \sigma_{\epsilon}^2/r$. For the definition of the other parameters we refer to Section 1.3.1.

Using the dot notation of Section 3.1.2. where $u_{ij} = 1$ for all $i \neq j$, we obtain the following solutions to the normal equations

TABLE 3.5. Analysis of Variance for the P-Partial Two-Level Diallel Cross Experiment

Source	Degrees of Freedom	Sum of Squares	Mean Square
g	m(n-1)	$\frac{1}{nc_1 r} \sum_i \sum_k Y^2_{(ik)(\dots)} - \frac{1}{n^2 c_1 r} Y^2_{(i\cdot)(\dots)}$	MS(g)
s*	$\frac{mc_1}{2} (n^2-1)$ -m(n-1)	$\frac{1}{r} \sum_{i,j} \sum_{k,\ell} u_{ij} Y^2_{(ik)(j\ell)} - \frac{1}{n^2 r} \sum_{i,j} u_{ij} Y^2_{(i\cdot)(j\cdot)}$ $- \frac{1}{nc_1 r} \sum_i \sum_k Y^2_{(ik)(\dots)}$	MS(s*)

The analysis of variance for the other components will be the same as that of Table 3.2. where $c_2 = n$ and $v_{k\ell} = 1$ for all k and ℓ .

TABLE 3.6. Expected Mean Squares for the P-Partial Two-Level Diallel Cross Experiment

Mean Square	Model (i)	Model (ii)	Model (iii)
MS(g)	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + \frac{c_1 nr}{m(n-1)} \sum_i \sum_k g_{ik}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + nc_1 r\sigma_g^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + nc_1 r\sigma_g^2$
MS(s*)	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2$

The expected mean squares for the other components will be the same as that of Table 3.3. where $c_2 = n$.

		P ₁				P ₂				P ₃				P ₄				P ₅			
		I ₁₁	I ₁₂	I ₁₃	I ₁₄	I ₂₁	I ₂₂	I ₂₃	I ₂₄	I ₃₁	I ₃₂	I ₃₃	I ₃₄	I ₄₁	I ₄₂	I ₄₃	I ₄₄	I ₅₁	I ₅₂	I ₅₃	I ₅₄
P ₁	I ₁₁					X	X			X	X			X	X			X	X		
	I ₁₂					X		X		X		X		X		X		X		X	
	I ₁₃						X		X		X		X		X		X		X		X
	I ₁₄							X	X			X	X			X	X			X	X
P ₂	I ₂₁									X	X			X	X			X	X		
	I ₂₂									X		X		X		X		X		X	
	I ₂₃										X		X		X		X		X		X
	I ₂₄											X	X			X	X			X	X
P ₃	I ₃₁													X	X			X	X		
	I ₃₂													X		X		X		X	
	I ₃₃														X		X		X		X
	I ₃₄															X	X			X	X
P ₄	I ₄₁																	X	X		
	I ₄₂																	X		X	
	I ₄₃																		X		X
	I ₄₄																			X	X
P ₅	I ₅₁																				
	I ₅₂																				
	I ₅₃																				
	I ₅₄																				

Figure 3.3. The I-Partial Two-Level Diallel Mating Design

$$\hat{\mu} = \frac{1}{m(m-1)nc_2r} Y_{(\dots)(\dots)}.$$

$$\hat{G}_i = \frac{1}{(m-2)nc_2r} Y_{(i\cdot)(\dots)} - \frac{2}{m(m-2)nc_2r} Y_{(\dots)(\dots)}.$$

$$S_{ij} = \frac{1}{nc_2r} Y_{(i\cdot)(j\cdot)} - \frac{1}{(m-2)nc_2r} (Y_{(i\cdot)(\dots)} + Y_{(j\cdot)(\dots)}) \\ + \frac{2}{(m-1)(m-2)nc_2r} Y_{(\dots)(\dots)}.$$

and a system of equations $W\hat{g} = R$ where now

$$W = I_m \times (I_n - V/(m-1)c_2) + J_m \times (V/(m-1)c_2) .$$

Again the breeder should choose a mating design that results in a nonsingular matrix W so that the estimates of the g_{ik} may be obtained as

$$\hat{g} = W^{-1}R .$$

When the design matrix V is self dual ($V=V'$), an explicit form may be obtained for W^{-1} . Since $s=1$, W^{-1} will be composed of at most two distinct matrices, i.e. $W^{ii} = W^0$ and $W^{ij} = W^1$ for all $i, j (i \neq j)$. Thus (3.1.1) may be written as

$$W^0 + \frac{1}{c_2} VW' = I_n$$

$$\frac{1}{(m-1)c_2} VW^0 + W^1 + \frac{m-2}{(m-1)c_2} VW' = 0_n$$

where 0_n is the $n \times n$ matrix of zero elements. We can then obtain

$$W^0 = I + \frac{1}{(m-1)c_2} V(I + \frac{1}{c_2} V)^{-1} (I - \frac{1}{(m-1)c_2} V)^{-1} V$$

$$W^{-1} = - \frac{1}{(m-1)c_2} \left(I + \frac{1}{c_2} V \right)^{-1} \left(I - \frac{1}{(m-1)c_2} V \right)^{-1} V .$$

The inverse matrix will exist as long as $(m-1)c_2$ and $-c_2$ are not eigenvalues of V . Table 3.1. gives the eigenvalues for each of the self dual designs so that the breeder can choose a design such that $(m-1)c_2$ and $-c_2$ will not be eigenvalues of the design matrix V .

The variances for comparisons among the combining abilities and for comparisons of average performance are given in Table 3.7. For the fixed effects model (model (i)) σ_c^2 stands for $\sigma_\epsilon^2 + r\sigma_{s^*}^2$ which is estimated by $MS(s^*)$ in Table 3.3. For the mixed model (model (iii)) comparisons (1), (2), and (4) will be of interest where σ_c^2 will be of the following form:

$$\text{Comparison 1: } \sigma_c^2 = \sigma_\epsilon^2 + r\sigma_{s^*}^2 + (m-2)c_2r\sigma_g^2 .$$

$$\text{Comparison 2: } \sigma_c^2 = \sigma_\epsilon^2 + r\sigma_{s^*}^2 .$$

$$\text{Comparison 4: } \sigma_c^2 = \sigma_\epsilon^2 + r\sigma_{s^*}^2 + nr\sigma_g^2 \text{ if } i=i', j \neq j', \text{ and}$$

$$\sigma_c^2 = \sigma_\epsilon^2 + r\sigma_{s^*}^2 + 2nr\sigma_g^2 \text{ if } i \neq i', j \neq j' .$$

The analysis of variance is given in Table 3.8. with the expected mean squares in Table 3.9.

TABLE 3.7. Variances of Comparisons Among Combining Abilities and Comparisons of Average Performance for the I-Partial Two-Level Diallel Cross

Comparison	Variance
(1) $\hat{G}_i - \hat{G}_{i'}$	$2\sigma_c^2 / (m-2)nc_2r$
(2) $\hat{S}_{ij} - \hat{S}_{i'j}$	$2(m-3)\sigma_c^2 / (m-2)nc_2r$
$\hat{S}_{ij} - \hat{S}_{i'j'}$ ($i \neq i', j \neq j'$)	$2(m-4)\sigma_c^2 / (m-2)nc_2r$
(3) $\hat{g}_{ik} - \hat{g}_{ik'}$	$2\sigma_c^2 / (m-1)c_2r$
(4) $(\hat{G}_i + \hat{G}_j + \hat{S}_{ij}) - (\hat{G}_{i'} + \hat{G}_{j'} + \hat{S}_{i'j'})$	$\left\{ \begin{array}{l} 2[(m-2)(mn-n+1)+1]\sigma_c^2 / (m-1)^2(m-2)nc_2r \\ \text{when } i \neq i' \\ 2\sigma_c^2 / (m-1)c_2r \text{ when } i = i' \end{array} \right.$

TABLE 3.8. Analysis of Variance for the I-Partial Two-Level Diallel Cross Experiment

Source	Degrees of Freedom	Sum of Squares	Mean Square
G	m-1	$\frac{1}{(m-2)nc_2r} \sum_i Y^2_{(i\cdot)(\cdot\cdot)\cdot} - \frac{4}{m(m-2)nc_2r} Y^2_{(\cdot\cdot)(\cdot\cdot)\cdot}$	MS(G)
S	$\frac{m(m-3)}{2}$	$\frac{1}{nc_2r} \sum_{\substack{i,j \\ i < j}} Y^2_{(i\cdot)(j\cdot)\cdot} - \frac{1}{(m-2)nc_2r} \sum_i Y^2_{(i\cdot)(\cdot\cdot)\cdot} + \frac{2}{(m-1)(m-2)nc_2r} Y^2_{(\cdot\cdot)(\cdot\cdot)\cdot}$	MS(S)

The analysis of variance for the other components will be the same as that of Table 3.2. where $c_1 = m-1$ and $u_{ij} = 1$ for all $i < j$.

TABLE 3.9. Expected Mean Squares for the I-Partial Two-Level Diallel Cross Experiment

Mean Square	Model (i)	Model (ii)	Model (iii)
MS(G)	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + \frac{(m-2)nc_2r}{m-1} \sum_i G_i^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + (m-2)c_2r\sigma_g^2$ $+ nc_2r\sigma_S^2 + (m-2)nc_2r\sigma_G^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + (m-2)c_2r\sigma_g^2$ $+ \frac{(m-2)nc_2r}{m-1} \sum_i G_i^2$
MS(S)	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + \frac{2nc_2r}{m(m-3)} \sum_{\substack{i,j \\ i < j}} S_{ij}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + nc_2r\sigma_S^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + \frac{2nc_2r}{m(m-3)} \sum_{\substack{i,j \\ i < j}} S_{ij}^2$
MS(g)	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + \frac{(m-1)c_2r}{m(n-1)} \sum_i \sum_k g_{ik}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + (m-1)c_2r\sigma_g^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2 + (m-1)c_2r\sigma_g^2$
MS(s*)	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s^*}^2$
MS(ε)	σ_{ϵ}^2	σ_{ϵ}^2	σ_{ϵ}^2

IV. AN INCOMPLETE ENVIRONMENTAL DESIGN FOR THE PI-PARTIAL TWO-LEVEL DIALLEL MATING DESIGN

One difficulty in using the two-level diallel mating design is the large block size that is required. Two methods have already been discussed to reduce the necessary block size. Chapter II suggests embedding the complete diallel in an incomplete environmental design so that not all population crosses occur in each block. The block size is reduced from $m(m-1)n^2/2$ to kn^2 using this method where k is equal to the number of population crosses occurring each block. Chapter III suggests that the required block size may be reduced by using a partial mating scheme in a RBD. For instance, using the PI-partial two-level diallel mating design would result in $mc_1c_2n/2$ crosses to be tested. If both of these methods fail to give a block size that is small enough, the experimenter may wish to combine the two and embed the PI-partial two-level diallel cross in an incomplete environmental design.

4.1. Construction of the Design

One method that might be used to create such an incomplete environmental design for the PI-partial two-level diallel would be to distribute the $mc_1/2$ population crosses into blocks so that each population is involved in t crosses per block. Recall that the population crosses of the two-level diallel form a type II diallel. We can easily adapt the methods of Braaten (1965) for blocking partial type II diallels to determine which population crosses to sample and to decide how to

distribute the $mc_1/2$ crosses into blocks. Table 4.1. gives the appropriate method of construction for different values of m , t , and c_1 .

Method A partitions the $mc_1/2$ crosses of a circulant partial type II diallel into blocks such that each population is involved in an equal number, t , of crosses per block. We select any $c_1/2$ groups of crosses as defined in (4.1.1). Group ℓ ($\ell = 1, 2, \dots, q$) contains the population crosses

$$P_i \times P_{i+\ell}, \quad i = 1, 2, \dots, m \quad (4.1.1)$$

where $(i+\ell)$ is reduced modulo m and $q = (m-1)/2$ when m is odd and $q = (m-2)/2$ when m is even. Note that each population occurs in exactly two crosses per group. Use equation (4.1.1) to separate the $mc_1/2$ population crosses into $c_1/2$ groups of size m . Assign the groups to the b blocks at random so that each block will contain $c_1/2b = t/2$ groups. The total number of blocks will be $b = c_1/t$. For example, an incomplete environmental design for the population crosses when $m=8$, $c_1=4$, and $t=2$ could be constructed using groups 1 and 2 as defined in (4.1.1). Assign one group of crosses to each block to obtain the environmental design illustrated in Table 4.2.

Method B is a trial and error technique of assigning the $mc_1/2$ crosses of a circulant partial type II diallel to blocks where each population will be involved in an odd number (t) of crosses per block. When c_1 is even the $mc_1/2$ population crosses to sample will be determined by choosing any $c_1/2$ of the groups defined in (4.1.1). When c_1 is odd group $m/2$ as defined in (4.1.2) will be selected and $(c_1-1)/2$ other groups from (4.1.1). Group $\ell = m/2$ consists of the population crosses

TABLE 4.1. Design Methods Applicable for Construction
of Incomplete Environmental Designs for the
PI-Partial Two-Level Diallel Cross

Design Parameters			Method*
m	t	c_1	
even or odd	even	even	A
even	odd	even	B,C
even	odd	odd	B,C

*Listed in order of preference.

TABLE 4.2. An Incomplete Environmental Design
for the PI-Partial Two-Level Diallel
Cross When $m=8$, $c_1=4$, and $t=2$

Blocks	
1	2
$P_1 \times P_2$	$P_1 \times P_3$
$P_2 \times P_3$	$P_2 \times P_4$
$P_3 \times P_4$	$P_3 \times P_5$
$P_4 \times P_5$	$P_4 \times P_6$
$P_5 \times P_6$	$P_5 \times P_7$
$P_6 \times P_7$	$P_6 \times P_8$
$P_7 \times P_8$	$P_1 \times P_7$
$P_1 \times P_8$	$P_2 \times P_8$

$$P_i \times P_{i+l}, \quad i = 1, 2, \dots, m/2. \quad (4.1.2)$$

Unlike the other groups each population is involved in exactly one cross in group $m/2$. Now we distribute the $mc_1/2$ population crosses selected into blocks so that each population is involved in t crosses per block. An illustration of an environmental design constructed using Method B where $m=8$, $c_1=4$, and $t=1$ is given in Table 4.3.

Should it prove difficult to distribute the $mc_1/2$ crosses of Method B among the blocks, Braaten suggests a third method based upon Gilbert's (1958) method of constructing partial type II diallels. To use Method C, superimpose a $m \times m$ symmetric Latin square with a single letter on the main diagonal on the array of population crosses. Choose c_1 of the off diagonal letters and use these to form c_1 groups of $m/2$ crosses each. Divide the c_1 groups equally among the b blocks. This method is illustrated in Figure 4.1. for $m=6$, $c_1=3$, and $t=1$.

These three methods partition the $mc_1/2$ population crosses of the PI-partial type II diallel into blocks so that each population is involved in t population crosses per block. For each population cross used in a block, we made nc_2 individual crosses. The individual crosses are sampled according to the method discussed in Section 3.1. Finally test r offspring from the crosses in each block.

4.2. The Statistical Analysis

This design results in $mc_1c_2n/2$ crosses to be tested in an incomplete environmental design composed of c_1/t blocks each of size $mtnc_2/2$. Because of the requirement that each population must occur t times in each block, population g.c.a. effects are orthogonal to blocks. Further

TABLE 4.3. An Incomplete Environmental Design
for the PI-Partial Two-Level Diallel
Cross When $m=8$, $c_1=4$, and $t=1$

1	$P_1 \times P_2$	$P_3 \times P_4$	$P_5 \times P_6$	$P_7 \times P_8$
2	$P_2 \times P_3$	$P_4 \times P_5$	$P_6 \times P_7$	$P_1 \times P_8$
3	$P_1 \times P_3$	$P_2 \times P_4$	$P_5 \times P_7$	$P_6 \times P_8$
4	$P_3 \times P_5$	$P_4 \times P_6$	$P_1 \times P_7$	$P_2 \times P_8$

	1	2	3	4	5	6
1	A	B	C	D	E	F
2	B	A	D	F	C	E
3	C	D	A	E	F	B
4	D	F	E	A	B	C
5	E	C	F	B	A	D
6	F	E	B	C	D	A

Symmetric Latin
Square with A
on the Main
Diagonal

	P_1	P_2	P_3	P_4	P_5	P_6
P_1			X	X	X	
P_2			X		X	X
P_3				X		
P_4						X
P_5						X
P_6						

The Population Crosses of
the PI-Partial Two-Level
Diallel Cross

	1	$P_1 \times P_3$	$P_2 \times P_5$	$P_4 \times P_6$
Blocks	2	$P_1 \times P_4$	$P_2 \times P_3$	$P_5 \times P_6$
	3	$P_1 \times P_5$	$P_2 \times P_6$	$P_3 \times P_4$

An Incomplete Environmental
Design for the PI-Partial
Two-Level Diallel Cross

Figure 4.1. The Construction of an Incomplete Environmental Design for a PI-Partial Two-Level Diallel Cross

since each individual from a population is involved in c_2 crosses per population cross, individual g.c.a. effects are also orthogonal to blocks.

Let $Y_{(ik)(jl)wz}$ be the observation for the z th offspring of the cross $I_{ik} \times I_{jl}$ grown in the w th block. (Not all combinations of $(ik)(jl)wz$ will occur.) The model for the experiment is

$$Y_{(ik)(jl)wz} = \mu + G_i + G_j + g_{ik} + g_{jl} + b_w + e_{(ik)(jl)wz}$$

where the residual, $e_{(ik)(jl)wz}$, may be partitioned into

$$e_{(ik)(jl)wz} = S_{ij}^* + s_{(ik)(jl)}^* + \frac{1}{r} \epsilon_{(ik)(jl)wz}$$

and b_w is the effect of the w th block. For the definition of the other parameters see Section 1.3.1. and Section 3.1.2.

The analysis of this design with respect to the genetic parameters will be identical to the analysis of the PI-partial two-level diallel cross. (See Section 3.1.3.) The sum of squares for S_{ij}^* adjusted for blocks is obtained as

$$SS(S^*) = nc^2r \sum_{\substack{i,j \\ i < j}} u_{ij} (\bar{Y}_{(i\cdot)(j\cdot)w} - \hat{\mu} - \hat{G}_i - \hat{G}_j - \hat{b}_w)^2$$

where $\hat{b}_w = 2Y_{(\cdot\cdot)(\cdot\cdot)w} / nc_2 mtr - 2Y_{(\cdot\cdot)(\cdot\cdot)\cdot\cdot} / mc_1 c_2 nr$ and the sum of squares for $s_{(ik)(jl)}^*$ adjusted for blocks is

$$SS(s^*) = r \sum_{\substack{i,j \\ i < j}} \sum_{k,l} u_{ij} v_{kl} (\bar{Y}_{(ik)(jl)\cdot\cdot} - \bar{Y}_{(i\cdot)(j\cdot)\cdot\cdot} - \hat{g}_{ik} - \hat{g}_{jl})^2$$

Table 4.4. presents the analysis of variance for the design. The

TABLE 4.4. Analysis of Variance for the PI-Partial Two-Level Diallel Mating Design
Embedded in an Incomplete Environmental Design

Source	Degrees of Freedom	Sum of Squares	Mean Square
Blocks	b-1	$\frac{2}{mnc_2r} \sum_w Y^2(\dots)(\dots)_w - \frac{2}{mnc_1c_2r} Y^2(\dots)(\dots)\dots$	
G	m-1	$\sum_i G_i Y^2(i\cdot)(\dots)\dots$	MS(G)
S*	$m\left(\frac{c_1}{2} - 1\right)$	$\frac{1}{nc_2r} \sum_{\substack{i,j \\ i < j}} u_{ij} Y^2(i\cdot)(j\cdot)\dots - \sum_i G_i Y(i\cdot)(\dots)\dots - \frac{2}{mnc_2r} \sum_w Y^2(\dots)(\dots)_w$	MS(S*)
g	m(n-1)	$\sum_i \sum_k g_{ik} Y^2(ik)(\dots)\dots$	MS(g)
s*	$\frac{mc_1}{2} (nc_2-1) - m(n-1)$	By subtraction	MS(s*)
error	$\frac{mnc_1c_2}{2} (r-1) - b+1$	$\sum_{\substack{i,j \\ i < j}} \sum_{k,\ell} \sum_w \sum_z u_{ij} v_{k\ell} Y^2(ik)(j\ell)wz - \frac{1}{r} \sum_{\substack{i,j \\ i < j}} \sum_{k,\ell} \sum_w u_{ij} v_{k\ell} Y^2(ik)(j\ell)w$	MS(e)
total	$\frac{mnc_1c_2r}{2} - 1$	$\sum_{\substack{i,j \\ i < j}} \sum_{k,\ell} \sum_w \sum_z u_{ij} v_{k\ell} Y^2(ik)(j\ell)wz - \frac{2}{mnc_1c_2r} Y^2(\dots)(\dots)\dots$	

expected mean squares will be the same as those given in Table 3.3. except for MS(S*) which has expected value

$$E(\text{MS}(S^*)) = \sigma_{\epsilon}^2 + [nc_2r - \frac{2(b-1)nc_2r}{mc_1-2m}] \sigma_{S^*}^2 + [r - \frac{2(b-1)r}{mc_1-2m}] \sigma_{S^*}^2 .$$

These tables indicate how various hypotheses about the combining abilities can be tested or how the combining ability variances can be estimated.

The analysis of this design is based upon the fact that for each individual cross sampled r offspring are tested in each block so that $b = c_1/t$ and $k = mtnc_2r/2$. If the r offspring were grown in different blocks, the model for the experiment would be

$$\bar{Y}_{(ik)(j\ell)\dots} = \mu + G_i + G_j + g_{ik} + g_{j\ell} + \frac{1}{r} \sum_{w \in B(i,j)} b_w + e_{(ik)(j\ell)}$$

where $B(i,j)$ is the set of blocks containing the population cross $P_i \times P_j$. This set consists of r blocks each of size $mtnc_2/2$. The analysis of variance and expected mean squares remain the same.

4.3. Modifications of the Design

When $c_1 = m-1$ and $c_2 = n$ this design provides an alternative method of embedding the complete two-level diallel cross in an incomplete block design. There are, however, three differences between this incomplete environmental design and the design presented in Chapter II based upon the T-PBIB design. In this design each population occurs exactly t times in each block so the population g.c.a. effects are orthogonal to blocks. Hence the efficiency of this design with respect to the RBD for estimating contrasts in the population g.c.a. effects is

one. The efficiency of the design based upon the T-PBIB with respect to the RBD is $1-\theta_1/rk$ where θ_1 is an eigenvalue of NN' . Only when θ_1 equals zero will this efficiency be one. Secondly, using the design discussed in this chapter contrasts between pairs of population s.c.a. effects will be estimated with different variances in general. Using the design based upon the T-PBIB, contrasts between pairs of population s.c.a. effects are estimated with two variances. A third and related difference is that the efficiency of the design based upon the T-PBIB for estimating population s.c.a. effects with respect to the RBD is known to be equal to $E_S = 1-\theta_2/rk$. Since θ_2 , an eigenvalue of NN' , is known, the efficiency, E_S , may be used by the experimenter to choose an appropriate design. The efficiency of the design discussed in this section for estimating contrasts in the population s.c.a. effects will depend on the contrast being estimated. Both designs result in no loss of efficiency for estimating contrasts in the individual g.c.a. and s.c.a. effects.

V. THE AUGMENTED TWO-LEVEL DIALLEL CROSS EXPERIMENT

In planning a two-level diallel cross experiment the plant breeder may wish to include crosses between individuals from the same population as a form of control. For instance, the magnitude of the performance of interpopulation crosses may be determined by comparison to the performance of the intrapopulation crosses. The design discussed in this chapter is the two-level diallel mating design to which $n(n-1)/2$ crosses between individuals from each of the m populations have been added. Using this design the experimenter can test to see if population heterosis exists, i.e. if there is a difference in the average performance of interpopulation and intrapopulation crosses.

Two statistical analyses will be presented for the observations resulting from this design. Section 5.2. discusses an analysis based upon an extension of Harvey's (1960) model for the type II diallel. Using this model, the experimenter will obtain two estimates of general combining ability, one based upon performance in interpopulation crosses and one based upon performance in intrapopulation crosses. Section 5.3. discusses an analysis based upon an extension of Griffing's (1956) model for the two-level diallel. The estimates of general combining ability in this analysis will be based upon performance in both interpopulation and intrapopulation crosses.

5.1. Definition of the Augmented Two-Level Diallel Mating Design

Suppose there are m populations P_1, P_2, \dots, P_m . For each population P_i there are n individuals $I_{i1}, I_{i2}, \dots, I_{in}$. The augmented two-level diallel mating design is then defined as consisting of

- (i) $m(m+1)/2$ population crosses $P_i \times P_j$ ($i < j$)
- (ii) n^2 individual crosses $I_{ik} \times I_{j\ell}$ ($k, \ell = 1, 2, \dots, n$) for each $P_i \times P_j$ where $i < j$, and
- (iii) $n(n-1)/2$ individual crosses $I_{ik} \times I_{i\ell}$ ($k < \ell$) for each P_i .

An illustration of this mating design is given in Figure 5.1. for $m=4$ and $n=3$.

5.2. The Statistical Analysis Using the Generalization of Harvey's Model

A generalization of a model given by Harvey (1960) may be used to analyse the results of the experiment. Assuming r offspring are obtained from each individual cross and grown in a completely randomized environmental design, the statistical model for the observation from the z th offspring of the individual cross $I_{ik} \times I_{j\ell}$ will be

$$Y_{(ik)(j\ell)z} = \mu + a_h + T_{hij} + G_{hi} + G_{hj} + S_{hij} + t_{h(ik)} + t_{h(j\ell)} \\ + g_{h(ik)} + g_{h(j\ell)} + s_{(ik)(j\ell)} + \epsilon_{(ik)(j\ell)z}$$

where $h=1$ for intrapopulation crosses ($i=j$) and $h=2$ for interpopulation crosses ($i \neq j$). This implies that

$$G_{1i} = S_{1ii} = g_{1(ik)} = 0,$$

$$T_{2ij} = t_{2(ik)} = 0,$$

		P ₁			P ₂			P ₃			P ₄		
		I ₁₁	I ₁₂	I ₁₃	I ₂₁	I ₂₂	I ₂₃	I ₃₁	I ₃₂	I ₃₃	I ₄₁	I ₄₂	I ₄₃
P ₁	I ₁₁		X	X	X	X	X	X	X	X	X	X	X
	I ₁₂			X	X	X	X	X	X	X	X	X	X
	I ₁₃				X	X	X	X	X	X	X	X	X
P ₂	I ₂₁					X	X	X	X	X	X	X	X
	I ₂₂						X	X	X	X	X	X	X
	I ₂₃							X	X	X	X	X	X
P ₃	I ₃₁								X	X	X	X	X
	I ₃₂									X	X	X	X
	I ₃₃										X	X	X
P ₄	I ₄₁											X	X
	I ₄₂												X
	I ₄₃												

The X's indicate the crosses that are made.

Figure 5.1. Example of an Augmented Two-Level Diallel Mating Design

and the other effects are defined in the following manner:

a_1 is the average effect of intrapopulation crosses, and

a_2 is the average effect of interpopulation crosses,

where $(n-1)a_1 + (m-1)n a_2 = 0$,

T_{1ii} is the effect of the i th population in intrapopulation crosses,

G_{2i} is the general combining ability of the i th population in interpopulation crosses

S_{2ij} is the specific combining ability of the population cross $P_i \times P_j$,

$t_{1(ik)}$ is the general combining ability of individual I_{ik} in intrapopulation crosses,

$g_{2(ik)}$ is the general combining ability of individual I_{ik} in interpopulation crosses, and

$s_{(ik)(j\ell)}$ is the specific combining ability of the individual cross $I_{ik} \times I_{j\ell}$.

The $\varepsilon_{(ik)(j\ell)z}$ are independent random variables with mean zero and variance σ_ε^2 .

Depending on the inferences that we wish to make about the populations and individuals we may use one of the following three models:

- (i) The fixed effects model: T_{1ii} , G_{2i} , S_{2ij} , $t_{1(ik)}$, $g_{2(ik)}$, and $s_{(ik)(j\ell)}$ are fixed effects with

$$\sum_i T_{1ii} = 0, \quad \sum_i G_{2i} = 0, \quad \sum_{\substack{j \\ j \neq i}} S_{2ij} = 0,$$

$$\sum_k t_{1(ik)} = 0, \quad \sum_k g_{2(ik)} = 0, \quad \sum_{\substack{\ell \\ \ell \neq k}} s_{(ik)(i\ell)} = 0,$$

and when $i \neq j$

$$\sum_{k,\ell} s_{(ik)(j\ell)} = 0, \quad \sum_{\substack{j \\ j \neq i}} \sum_{\ell} s_{(ik)(j\ell)} = 0.$$

- (ii) The random effects model: T_{1ii} , G_{2i} , S_{2ij} , $t_{1(ik)}$, $g_{2(ik)}$, $s_{(ik)(i\ell)}$, and $s_{(ik)(j\ell)}$ ($i \neq j$) are random variables independently distributed with zero means and variances σ_T^2 , σ_G^2 , σ_S^2 , σ_t^2 , σ_g^2 , σ_{s1}^2 , and σ_{s2}^2 , respectively.
- (iii) The mixed effects model: The T_{1ii} , G_{2i} , and S_{2ij} are fixed effects as in (i) and the $t_{1(ik)}$, $g_{2(ik)}$, and $s_{(ik)(j\ell)}$ are random variables as in (ii).

In model (i) inferences will be made with respect to only those populations and individuals actually included in the experiment. Model (ii) assumes that the populations and individuals are random samples taken from larger collections of populations and individuals about which inferences are made. And finally model (iii) refers to the situation in which all populations of interest are included in the experiment but the individuals represent a sample of all the individuals in the population.

Using the dot notation:

$$Y_{(ik)(j\ell)\cdot} = \sum_z Y_{(ik)(j\ell)z}$$

$$Y_{2(ik)(\dots)} = \sum_{\substack{j \\ j \neq i}} \sum_{\ell} Y_{(ik)(j\ell)}$$

$$Y_{2(i\cdot)(\dots)} = \sum_k Y_{2(ik)(\dots)}$$

$$Y_{(i\cdot)(i\cdot)} = \sum_{\substack{k, \ell \\ k < \ell}} Y_{(ik)(i\ell)}$$

$$Y_{(i\cdot)(j\cdot)} = \sum_{k, \ell} Y_{(ik)(j\ell)} \quad (i \neq j)$$

$$Y_{(ik)(i\cdot)} = \sum_{\substack{\ell \\ \ell \neq k}} Y_{(ik)(i\ell)}$$

$$Y_{1(\dots)(\dots)} = \sum_i Y_{(i\cdot)(i\cdot)}$$

$$Y_{2(\dots)(\dots)} = \sum_{\substack{i, j \\ i < j}} Y_{(i\cdot)(j\cdot)}$$

$$Y_{(\dots)(\dots)} = Y_{1(\dots)(\dots)} + Y_{2(\dots)(\dots)}$$

and using the same constraints on the estimators as those used in model (i), one obtains the following least squares estimators for the effects:

$$\hat{\mu} = \frac{2}{mn(mn-1)r} Y_{(\dots)(\dots)}$$

$$\hat{a}_1 = \frac{2}{mn(n-1)r} Y_{1(\dots)(\dots)} - \frac{2}{mn(mn-1)r} Y_{(\dots)(\dots)}$$

$$\hat{a}_2 = \frac{2}{m(m-1)n^2r} Y_{2(\dots)(\dots)} - \frac{2}{mn(mn-1)r} Y_{(\dots)(\dots)}$$

$$\hat{T}_{1ii} = \frac{2}{n(n-1)r} Y_{(i\cdot)(i\cdot)} - \frac{2}{mn(n-1)r} Y_{1(\dots)(\dots)}$$

$$\hat{G}_{2ii} = \frac{1}{(m-2)n^2r} Y_{2(i\cdot)(\dots)} - \frac{2}{m(m-2)n^2r} Y_{2(\dots)(\dots)}$$

$$\hat{s}_{2ij} = \frac{1}{n^2r} Y_{(i\cdot)(j\cdot)\cdot} - \frac{1}{(m-2)n^2r} (Y_{2(i\cdot)(\cdot\cdot)\cdot} + Y_{2(j\cdot)(\cdot\cdot)\cdot})$$

$$+ \frac{2}{(m-1)(m-2)n^2r} Y_{2(\cdot\cdot)(\cdot\cdot)\cdot}$$

$$\hat{t}_{1(ik)} = \frac{1}{(n-2)r} Y_{(ik)(i\cdot)\cdot} - \frac{2}{n(n-2)r} Y_{(i\cdot)(i\cdot)\cdot}$$

$$\hat{g}_{2(ik)} = \frac{1}{(m-1)nr} Y_{2(ik)(\cdot\cdot)\cdot} - \frac{1}{(m-1)n^2r} Y_{2(i\cdot)(\cdot\cdot)\cdot}$$

$$\hat{s}_{(ik)(i\ell)} = \frac{1}{r} Y_{(ik)(j\ell)\cdot} - \frac{1}{(n-2)r} (Y_{(ik)(i\cdot)\cdot} + Y_{(i\ell)(i\cdot)\cdot})$$

$$+ \frac{2}{(n-1)(n-2)r} Y_{(i\cdot)(i\cdot)\cdot}$$

$$\hat{s}_{(ik)(j\ell)} = \frac{1}{r} Y_{(ik)(j\ell)\cdot} - \frac{1}{(m-1)nr} (Y_{2(ik)(\cdot\cdot)\cdot} + Y_{2(j\ell)(\cdot\cdot)\cdot})$$

$$+ \frac{1}{(m-1)n^2r} (Y_{2(i\cdot)(\cdot\cdot)\cdot} + Y_{2(j\cdot)(\cdot\cdot)\cdot})$$

$$- \frac{1}{n^2r} Y_{(i\cdot)(j\cdot)\cdot}$$

Using this model the comparisons between combining abilities and the comparisons of average performance for the interpopulation crosses are estimated with the same variances as those obtained by Hinkelmann (1974). (See Table 5.1.) Table 5.1. gives the variances for comparisons among the following types of combining abilities:

- (i) the general combining ability of a population in interpopulation crosses,
- (ii) the general combining ability of an individual in interpopulation crosses,
- (iii) the general combining ability of an individual in intrapopulation crosses,

TABLE 5.1. The Variances for Comparisons Between Combining Abilities and Comparisons of Average Performance for the Augmented Two-Level Diallel Cross (Harvey's Model)

Comparison	Variance
(i) $\hat{G}_{2i} - \hat{G}_{2i'}$	$2\sigma^2 / (m-2)n^2r$
(ii) $\hat{g}_{2(ik)} - \hat{g}_{2(ik')}$	$2\sigma^2 / (m-1)nr$
(iii) $\hat{t}_{1(ik)} - \hat{t}_{1(ik')}$	$2\sigma^2 / (n-2)r$
(iv) $\hat{S}_{2ij} - \hat{S}_{2ij'}$	$2(m-3)\sigma^2 / (m-2)n^2r$
$\hat{S}_{2ij} - \hat{S}_{2i'j'}$	$2(m-4)\sigma^2 / (m-2)n^2r$
(v) $\hat{s}_{(ik)(j\ell)} - \hat{s}_{(ik)(j\ell')}$	$2[(m-1)n-1]\sigma^2 / (m-1)nr$
$\hat{s}_{(ik)(j\ell)} - \hat{s}_{(ik')(j\ell')}$	$2[(m-1)n-2]\sigma^2 / (m-1)nr$
$\hat{s}_{(ik)(j\ell)} - \hat{s}_{(ik)(i\ell')}$	$2\sigma^2 / r$
$\hat{s}_{(ik)(j\ell)} - \hat{s}_{(ik')(i\ell')}$	$2\sigma^2 / r$
(vi) $\hat{T}_{1ii} - \hat{T}_{1i'i}$	$2\sigma^2 / n(n-1)r$
(vii) $(\hat{G}_{2i} + \hat{G}_{2j} + \hat{S}_{2ij}) - (\hat{G}_{2i'} + \hat{G}_{2j'} + \hat{S}_{2i'j'})$	$2\sigma^2 / n^2r$

TABLE 5.1. Continued.

Comparison	Variance
(viii) $(\hat{a}_2 + \hat{G}_{2i} + \hat{G}_{2j} + \hat{S}_{2ij}) - \hat{a}_1 - \frac{1}{2}(\hat{T}_{1ii} + \hat{T}_{1jj})$	$(3n-1)\sigma^2/n^2(n-1)r$
(ix) $(\hat{G}_{2i} + \hat{g}_{2(ik)}) - (\hat{G}_{2i'} + \hat{g}_{2(i'k')})$	$2[(m-2)(mn-n+1)+1]\sigma^2/(m-1)^2(m-2)n^2r$
(x) $(\hat{T}_{1ii} + \hat{t}_{1(ik)}) - (\hat{T}_{1i'i} + \hat{t}_{1(i'k')})$	$[2n(n-3)(n+1)+10]\sigma^2/n(n-1)(n-2)^2r$
(xi) $(\hat{a}_2 + \hat{G}_{2i} + \hat{g}_{2(ik)}) - (\hat{a}_1 + \hat{T}_{1ii} + \hat{t}_{1(ik)})$	$[(m-2)(mn-2n+2)+1]\sigma^2/(m-1)(m-2)^2n^2r$ $+ (n^2-3)\sigma^2/n(n-1)(n-2)r$
(xii) $(\hat{G}_{2i} + \hat{G}_{2j} + \hat{S}_{2ij} + \hat{g}_{2(ik)} + \hat{g}_{2(jl)} + \hat{s}_{(ik)(jl)})$ $- (\hat{G}_{2i'} + \hat{G}_{2j'} + \hat{S}_{2i'j'} + \hat{g}_{2(i'k')} + \hat{g}_{2(j'l')} + \hat{s}_{(i'k')(j'l')})$	$2\sigma^2/r$
(xiii) $(\hat{T}_{1ii} + \hat{t}_{1(ik)} + \hat{t}_{1(il)} + \hat{s}_{(ik)(il)})$ $- (\hat{T}_{1i'i} + \hat{t}_{1(i'k')} + \hat{t}_{1(i'l')} + \hat{s}_{(i'k')(j'l')})$	$2\sigma^2/r$
(xiv) $(\hat{a}_2 + \hat{G}_{2i} + \hat{G}_{2j} + \hat{S}_{2ij} + \hat{g}_{2(ik)} + \hat{g}_{2(jl)} + \hat{s}_{(ik)(jl)})$ $- \hat{a}_1 - \frac{1}{2}(\hat{T}_{1ii} + \hat{T}_{1jj}) - \hat{t}_{1(ik)} - \hat{t}_{1(jl)}$	$(2n-1)\sigma^2/2(n-1)r$

- (iv) the specific combining ability of a population cross, and
- (v) the specific combining ability of an individual cross.

In addition to the variances for comparisons among the combining abilities, Table 5.1. also gives the variances for the following comparisons of average performance:

- (vi) the average performance of P_i vs. the average performance of P_i , in intrapopulation crosses,
- (vii) the average performance of hybrid population ($P_i \times P_j$) vs. the average performance of hybrid population ($P_i' \times P_j'$),
- (viii) the average performance of hybrid population ($P_i \times P_j$) vs. the average performance of P_i and P_j in intrapopulation crosses,
- (ix) the average performance of individual I_{ik} vs. the average performance of individual $I_{i'k'}$, both with respect to interpopulation crosses,
- (x) the average performance of individual I_{ik} vs. the average performance of individual $I_{i'k'}$, both with respect to intrapopulation crosses,
- (xi) the average performance of I_{ik} in interpopulation crosses vs. the average performance of I_{ik} in intrapopulation crosses,
- (xii) the average performance of hybrid ($I_{ik} \times I_{j\ell}$) vs. the average performance of hybrid ($I_{i'k'} \times I_{j'\ell'}$), and
- (xiii) the average performance of hybrid ($I_{ik} \times I_{j\ell}$) vs. the average performance of I_{ik} and $I_{j\ell}$ in intrapopulation crosses.

The analysis of variance is presented in Table 5.2. with the expected mean squares for the three models given in Table 5.3. These tables indicate how various hypotheses about the combining abilities can be tested or how the combining ability variances can be estimated.

5.3. The Statistical Analysis Using the Generalization of Griffing's Model

A generalization of Griffing's (1956) model for type II diallels may also be used to analyse the results of this experiment. Assuming r offspring are obtained from each individual cross and grown in a completely randomized design, the statistical model for the observation from the z th offspring of the individual cross $I_{ik} \times I_{jl}$ will be

$$Y_{(ik)(jl)z} = \mu + G_i + G_j + S_{ij} + g_{ik} + g_{jl} + s_{(ik)(jl)} + \epsilon_{(ik)(jl)z}$$

For the definition of these effects see Section 1.3.1. or Hinkelmann (1974). Note that the g.c.a.'s will be measured on the basis of average performance in intrapopulation as well as interpopulation crosses. Depending on the inferences to be made, one can distinguish three models--(i) the fixed effect model, (ii) the random effects model, and (iii) the mixed model. For a discussion of these models see Section 2.2. In model (ii) the S_{ij} will be random variables with mean zero and variance σ_{S1}^2 when $i=j$ and σ_{S2}^2 when $i \neq j$. In models (ii) and (iii) the $s_{(ik)(jl)}$ will be random variables with mean zero and variance σ_{s1}^2 when $i=j$ and σ_{s2}^2 when $i \neq j$.

Using the dot notation

$$Y_{(ik)(jl)\cdot} = \sum_z Y_{(ik)(jl)z}$$

TABLE 5.2. The Analysis of Variance for the Augmented Two-Level Diallel Cross (Harvey's Model)

Source	Degrees of Freedom	Sum of Squares	Mean Square
Population Heterosis	1	$\frac{m(m-1)n^2(n-1)r}{2(mn-1)} (\hat{a}_2 - \hat{a}_1)^2$	MS(H)
T_{1ii}	m-1	$\frac{2}{n(n-1)r} \sum_i Y_{(i\cdot)(i\cdot)}^2 - \frac{2}{mn(n-1)r} Y_{1(\cdot\cdot)(\cdot\cdot)}^2$	MS(T)
G_{2i}	m-1	$\frac{1}{(m-2)n^2r} \sum_i Y_{2(i\cdot)(\cdot\cdot)}^2 - \frac{4}{m(m-2)n^2r} Y_{2(\cdot\cdot)(\cdot\cdot)}^2$	MS(G)
S_{2ij}	$\frac{m(m-3)}{2}$	$\frac{1}{n^2r} \sum_{\substack{i,j \\ i < j}} Y_{(i\cdot)(j\cdot)}^2 - \frac{1}{(m-2)n^2r} \sum_i Y_{2(i\cdot)(\cdot\cdot)}^2$ $+ \frac{2}{(m-1)(m-2)n^2r} Y_{2(\cdot\cdot)(\cdot\cdot)}^2$	MS(S)
$t_{1(ik)}$	m(n-1)	$\frac{1}{(n-2)r} \sum_i \sum_k Y_{(ik)(i\cdot)}^2 - \frac{4}{n(n-2)r} \sum_i Y_{(i\cdot)(i\cdot)}^2$	MS(t)
$g_{2(ik)}$	m(n-1)	$\frac{1}{(m-1)nr} \sum_i \sum_k Y_{2(ik)(\cdot\cdot)}^2 - \frac{1}{(m-1)n^2r} \sum_i Y_{2(i\cdot)(\cdot\cdot)}^2$	MS(g)

TABLE 5.2. Continued.

Source	Degrees of Freedom	Sum of Squares	Mean Square
$s_{(ik)(il)}$	$\frac{mn(n-3)}{2}$	$\frac{1}{r} \sum_i \sum_{\substack{k,l \\ k < l}} Y^2_{(ik)(il)\cdot} - \frac{1}{(n-2)r} \sum_i \sum_k Y^2_{(ik)(i\cdot)\cdot}$	$MS(s_1)$
$s_{(ik)(jl)}$	$\frac{m(mn)}{2} (n^2-1) - m(n-1)$	$\frac{1}{r} \sum_{i,j} \sum_{\substack{k,l \\ i < j}} Y^2_{(ik)(jl)\cdot} - \frac{1}{(m-1)nr} \sum_i \sum_k Y^2_{2(ik)(\cdot\cdot)\cdot} + \frac{1}{(m-1)n^2r} \sum_i Y^2_{2(i\cdot)(\cdot\cdot)\cdot} - \frac{1}{n^2r} \sum_{\substack{i > j \\ i < j}} Y^2_{(i\cdot)(j\cdot)\cdot}$	$MS(s_2)$
error	$\frac{mn(mn-1)}{2} (r-1)$	$\sum_{\substack{i,j \\ i < j}} \sum_{k,l} \sum_z Y^2_{(ik)(jl)z} + \sum_i \sum_{\substack{k,l \\ k < l}} \sum_z Y^2_{(ik)(il)z} - \frac{1}{r} \sum_{i,j} \sum_{\substack{k,l \\ i < j}} Y^2_{(ik)(jl)\cdot} - \frac{1}{r} \sum_i \sum_{\substack{k,l \\ k < l}} Y^2_{(ik)(il)\cdot}$	$MS(\epsilon)$
total	$\frac{mn(mn-1)r}{2} - 1$	$\sum_{\substack{i,j \\ i < j}} \sum_{k,l} \sum_z Y^2_{(ik)(jl)z} + \sum_i \sum_{\substack{k,l \\ k < l}} \sum_z Y^2_{(ik)(il)z} - \frac{2}{mn(mn-1)r} Y^2_{(\cdot\cdot)(\cdot\cdot)\cdot}$	

TABLE 5.3. Expected Mean Squares for the Augmented Two-Level Diallel Cross (Harvey's Model)

M.S.	Model (i)	Model (ii)	Model (iii)
MS(H)	$\sigma_{\epsilon}^2 + \frac{m(m-1)n^2(n-1)r}{2(mn-1)} (a_2 - a_1)^2$	$\sigma_{\epsilon}^2 + \frac{m(m-1)n^2(n-1)r}{2(mn-1)} (a_2 - a_1)^2$	$\sigma_{\epsilon}^2 + \frac{m(m-1)n^2(n-1)r}{2(mn-1)} (a_2 - a_1)^2$
MS(T)	$\sigma_{\epsilon}^2 + \frac{n(n-1)r}{2(m-1)} \sum_i T_{lii}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s1}^2 + 2(n-1)r\sigma_t^2$ $+ \frac{n(n-1)r}{2} \sigma_T^2$	$\sigma_{\epsilon}^2 + r\sigma_{s1}^2 + 2(n-1)r\sigma_t^2$ $+ \frac{n(n-1)r}{2(m-1)} \sum_i T_{lii}^2$
MS(G)	$\sigma_{\epsilon}^2 + \frac{(m-2)n^2r}{m-1} \sum_i G_{2ii}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s2}^2 + (m-2)nr\sigma_g^2 + n^2r\sigma_S^2$ $+ (m-2)n^2r\sigma_G^2$	$\sigma_{\epsilon}^2 + r\sigma_{s2}^2 + (m-2)nr\sigma_g^2$ $+ \frac{(m-2)n^2r}{m-1} \sum_i G_{2ii}^2$
MS(S)	$\sigma_{\epsilon}^2 + \frac{2n^2r}{m(m-3)} \sum_{i<j} S_{2ij}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s2}^2 + n^2r\sigma_S^2$	$\sigma_{\epsilon}^2 + r\sigma_{s2}^2 + \frac{2n^2r}{m(m-3)} \sum_{i<j} S_{2ij}^2$
MS(t)	$\sigma_{\epsilon}^2 + \frac{(n-2)r}{m(n-1)} \sum_{i,k} t_{lik}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s1}^2 + \frac{n^2-5n+2}{n-1} r\sigma_t^2$	$\sigma_{\epsilon}^2 + r\sigma_{s1}^2 + \frac{n^2-5n+2}{n-1} r\sigma_t^2$
MS(g)	$\sigma_{\epsilon}^2 + \frac{(m-1)nr}{m(n-1)} \sum_{i,k} g_{2ik}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s2}^2 + (m-1)nr\sigma_g^2$	$\sigma_{\epsilon}^2 + r\sigma_{s2}^2 + (m-1)nr\sigma_g^2$
MS(s ₁)	$\sigma_{\epsilon}^2 + \frac{2r}{mn(n-3)} \sum_i \sum_{k<\ell} s_{(ik)(i\ell)}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s1}^2$	$\sigma_{\epsilon}^2 + r\sigma_{s1}^2$

TABLE 5.3. Continued.

M.S.	Model (i)	Model (ii)	Model (iii)
$MS(s_2)^*$	$\sigma_\epsilon^2 + \frac{r}{d} \sum_{i < j} \sum_{k, l} s^2_{(ik)(jl)}$	$\sigma_\epsilon^2 + r\sigma_{s_2}^2$	$\sigma_\epsilon^2 + r\sigma_{s_2}^2$
$MS(\epsilon)$	σ_ϵ^2	σ_ϵ^2	σ_ϵ^2

$$*d = \frac{m(m-1)}{2} (n^2-1) - m(n-1)$$

$$Y_{(ik)(\dots)} = \sum_{\substack{j \\ j \neq i}} \sum_{\ell} Y_{(ik)(j\ell)} + \sum_{\substack{\ell \\ \ell \neq k}} Y_{(ik)(i\ell)}$$

$$Y_{(i\cdot)(\dots)} = \sum_k Y_{(ik)(\dots)}$$

$$Y_{(i\cdot)(j\cdot)} = \sum_{k, \ell} Y_{(ik)(j\ell)} \quad (i \neq j)$$

$$Y_{(i\cdot)(i\cdot)} = \sum_{\substack{k, \ell \\ k < \ell}} Y_{(i\cdot)(i\cdot)}$$

$$Y_{(\dots)(\dots)} = \sum_{\substack{i, j \\ i \leq j}} Y_{(i\cdot)(j\cdot)}$$

we obtain the following estimates

$$\hat{\mu} = \frac{2}{mn(mn-1)r} Y_{(\dots)(\dots)}$$

$$\hat{G}_i = \frac{1}{(mn-2)nr} Y_{(i\cdot)(\dots)} - \frac{2}{mn(mn-2)r} Y_{(\dots)(\dots)}$$

$$\begin{aligned} \hat{S}_{ii} &= \frac{2}{n(n-1)r} Y_{(i\cdot)(i\cdot)} - \frac{2}{(mn-2)nr} Y_{(i\cdot)(\dots)} \\ &\quad + \frac{2}{(mn-1)(mn-2)r} Y_{(\dots)(\dots)} \end{aligned}$$

$$\begin{aligned} \hat{S}_{ij} &= \frac{1}{n^2r} Y_{(i\cdot)(j\cdot)} - \frac{1}{(mn-2)nr} (Y_{(i\cdot)(\dots)} + Y_{(j\cdot)(\dots)}) \\ &\quad + \frac{2}{(mn-1)(mn-2)r} Y_{(\dots)(\dots)} \end{aligned}$$

$$\hat{g}_{ik} = \frac{1}{(mn-2)r} Y_{(ik)(\dots)} - \frac{1}{(mn-2)nr} Y_{(i\cdot)(\dots)}$$

$$\begin{aligned} \hat{S}_{(ik)(i\ell)} &= \frac{1}{r} Y_{(ik)(i\ell)} - \frac{1}{(mn-2)r} (Y_{(ik)(\dots)} + Y_{(i\ell)(\dots)}) \\ &\quad - \frac{2}{n(n-1)r} Y_{(i\cdot)(i\cdot)} + \frac{2}{(mn-2)nr} Y_{(i\cdot)(\dots)} \end{aligned}$$

$$\hat{s}_{(ik)(j\ell)} = \frac{1}{r} Y_{(ik)(j\ell)\cdot} - \frac{1}{(mn-2)r} (Y_{(ik)(\cdot\cdot)\cdot} + Y_{(j\ell)(\cdot\cdot)\cdot}) \\ - \frac{1}{n^2r} Y_{(i\cdot)(j\cdot)\cdot} + \frac{1}{(mn-2)nr} (Y_{(i\cdot)(\cdot\cdot)\cdot} + Y_{(j\cdot)(\cdot\cdot)\cdot}) .$$

The variances for comparisons between combining abilities and for comparisons of average performance are given in Table 5.4. (See Section 5.2. for a discussion of these comparisons.) The analysis of variance for this design is given in Table 5.5. with the expected mean squares in Table 5.6.

Because intrapopulation crosses are included in the mating design, the breeder may also want to determine if population heterosis exists. One method would be to examine the following contrast

$$h_{ij} = \mu_{ij} - (\mu_{ii} + \mu_{jj})/2$$

where μ_{ij} is the average performance of the population cross $P_i \times P_j$.

This contrast is estimated by

$$\hat{h} = \frac{1}{n^2r} Y_{(i\cdot)(j\cdot)\cdot} - \frac{1}{n(n-1)r} (Y_{(i\cdot)(i\cdot)\cdot} + Y_{(j\cdot)(j\cdot)\cdot}) .$$

One may obtain the sum of squares for heterosis as

$$SS(H) = \hat{h}'D^{-1}\hat{h}$$

where

$$\hat{h}' = (\hat{h}_{12}, \hat{h}_{13}, \dots, \hat{h}_{1m}, \hat{h}_{23}, \hat{h}_{24}, \dots, \hat{h}_{2m}, \dots, \hat{h}_{(m-1)m})$$

and $D\sigma^2$ is the dispersion matrix for \hat{h} , i.e. $\text{Var}(\hat{h}) = \sigma^2 D$. When the individual effects are fixed, $\sigma^2 = \sigma_\epsilon^2$, and when the individual effects are random, $\sigma^2 = \sigma_\epsilon^2 + r\sigma_{s1}^2/2 + r\sigma_{s2}^2/2$. Let $D = \{d_{ij, i'j'}\}$ where

TABLE 5.4. Variances for Comparisons Between Combining Abilities and Comparisons of Average Performance for the Augmented Two-Level Diallel Cross (Griffing's Model)

Comparison	Variance
(1) $\hat{G}_i - \hat{G}_{i'}$	$2[(m-1)n-1]\sigma^2 / (mn-2)^2 nr$
(2) $\hat{g}_{ik} - \hat{g}_{ik'}$	$2\sigma^2 / (mn-2)r$
(4) $\hat{S}_{ij} - \hat{S}_{i'j}$	$2[(mn-2)^2 + (m-1)n^2 - (2mn-3)n]\sigma^2 / (mn-2)^2 n^2 r$
$\hat{S}_{ij} - \hat{S}_{i'j'}$	$2[(mn-2)^2 + 2(m-1)n^2 - 2(2mn-3)n]\sigma^2 / (mn-2)^2 n^2 r$
$\hat{S}_{ii} - \hat{S}_{jj}$	$[4(mn-2)^2 n + (n-1)(8n^2(m-1) - 8n - 16)]\sigma^2 / (mn-2)^2 (n-1)n^2 r$
$\hat{S}_{ij} - \frac{1}{2}(\hat{S}_{ii} + \hat{S}_{jj})$	$(3n^2 - 2n + 1)\sigma^2 / n^2 (n-1)^2 r$
(5) $\hat{s}_{(ik)(j\ell)} - \hat{s}_{(ik)(j\ell')}$	$2(mn-3)\sigma^2 / (mn-2)r$
$\hat{s}_{(ik)(j\ell)} - \hat{s}_{(ik')(j\ell')}$	$2(mn-4)\sigma^2 / (mn-2)r$
(6) $(2\hat{G}_i + \hat{S}_{ii}) - (2\hat{G}_{i'} + \hat{S}_{i'i'})$	$2\sigma^2 / n^2 r$
(7) $(\hat{G}_i + \hat{G}_j + \hat{S}_{ij}) - (\hat{G}_{i'} + \hat{G}_{j'} + \hat{S}_{i'j'})$	$2\sigma^2 / n^2 r$
(8) $(\hat{G}_i + \hat{G}_j + \hat{S}_{ij}) - \frac{1}{2}(2\hat{G}_i + \hat{S}_{ii} + 2\hat{G}_j + \hat{S}_{jj})$	$(2n-1)\sigma^2 / n^2 (n-1)r$
(9) $(\hat{G}_i + \hat{g}_{ik}) - (\hat{G}_{i'} + \hat{g}_{i'k'})$	$2\sigma^2 / (mn-2)r$
(12) $(\hat{G}_i + \hat{G}_j + \hat{S}_{ij} + \hat{g}_{ik} + \hat{g}_j + \hat{s}_{(ik)(j\ell)}) -$ $(\hat{G}_{i'} + \hat{G}_{j'} + \hat{S}_{i'j'} + \hat{g}_{i'k'} + \hat{g}_{j'\ell'} + \hat{s}_{(i'k')(j'\ell')})$	$2\sigma^2 / r$

TABLE 5.5. Analysis of Variance for the Augmented Two-Level Diallel Cross
(Griffing's Model)

Source	Degrees of Freedom	Sum of Squares	Mean Square
G_i	$m-1$	$\frac{1}{(mn-2)nr} \sum_i Y^2_{(i\cdot)(\cdot\cdot)\cdot} - \frac{4}{mn(mn-2)r} Y^2_{(\cdot\cdot)(\cdot\cdot)\cdot}$	$MS(G)$
S_{ii}	m	$\begin{aligned} & \frac{2}{n(n-1)r} \sum_i Y^2_{(i\cdot)(i\cdot)\cdot} - \frac{2}{(mn-2)nr} \sum_i Y_{(i\cdot)(i\cdot)\cdot} \cdot Y_{(i\cdot)(\cdot\cdot)\cdot} \\ & + \frac{2}{(mn-1)(mn-2)r} Y_{(\cdot\cdot)(\cdot\cdot)\cdot} \cdot \sum_i Y_{(i\cdot)(i\cdot)\cdot} \end{aligned}$	$MS_1(S)$
S_{ij}	$\frac{m(m-3)}{2}$	$\begin{aligned} & \frac{1}{n^2r} \sum_{\substack{i,j \\ i < j}} Y^2_{(i\cdot)(j\cdot)\cdot} - \frac{1}{(mn-2)nr} \sum_i Y^2_{(i\cdot)(\cdot\cdot)\cdot} \\ & + \frac{2}{(mn-2)nr} \sum_i Y_{(i\cdot)(i\cdot)\cdot} \cdot Y_{(i\cdot)(\cdot\cdot)\cdot} \\ & - \frac{2}{(mn-1)(mn-2)r} Y_{(\cdot\cdot)(\cdot\cdot)\cdot} \cdot \sum_i Y_{(i\cdot)(i\cdot)\cdot} \\ & + \frac{2}{(mn-1)(mn-2)r} Y^2_{(\cdot\cdot)(\cdot\cdot)\cdot} \end{aligned}$	$MS_2(S)$
g_{ik}	$m(n-1)$	$\frac{1}{(mn-2)r} \sum_i \sum_k Y^2_{(ik)(\cdot\cdot)\cdot} - \frac{1}{(mn-2)nr} \sum_i Y^2_{(i\cdot)(\cdot\cdot)\cdot}$	$MS(g)$

TABLE 5.5. Continued.

Source	Degrees of Freedom	Sum of Squares	Mean Square
$s_{(ik)(i\ell)}$	$\frac{m}{2} (n-2)(n+1)$	$\frac{1}{r} \sum_i \sum_{\substack{k,\ell \\ k < \ell}} Y^2_{(ik)(i\ell)} \cdot - \frac{1}{(mn-2)r} \sum_i \sum_k Y^2_{(ik)(\dots)} \cdot Y_{(ik)(i\cdot)} \cdot$ $- \frac{2}{n(n-1)r} \sum_i Y^2_{(i\cdot)(i\cdot)} \cdot$ $+ \frac{2}{(mn-2)nr} \sum_i Y_{(i\cdot)(i\cdot)} \cdot Y_{(i\cdot)(\dots)} \cdot$	$MS_1(s)$
$s_{(ik)(j\ell)}$	$\frac{m(m-1)}{2} (n^2-1)$ $-m(n-1)$	$\frac{1}{r} \sum_{i,j} \sum_{\substack{k,\ell \\ i < j}} Y^2_{(ik)(j\ell)} \cdot - \frac{1}{(mn-2)r} \sum_i \sum_k Y^2_{(ik)(\dots)} \cdot$ $+ \frac{1}{(mn-2)r} \sum_i \sum_k Y_{(ik)(\dots)} \cdot Y_{(ik)(i\cdot)} \cdot - \frac{1}{n^2r} \sum_{\substack{i,j \\ i < j}} Y^2_{(i\cdot)(j\cdot)} \cdot$	$MS_2(s)$
error	$\frac{mn(mn-1)}{2} (r-1)$	$\sum_{\substack{i,j \\ i < j}} \sum_{k,\ell} \sum_z Y^2_{(ik)(j\ell)z} + \sum_i \sum_{k,\ell} \sum_z Y^2_{(ik)(i\ell)z}$ $- \frac{1}{r} \sum_{\substack{i,j \\ i < j}} \sum_{k,\ell} \sum_z Y^2_{(ik)(j\ell)} - \frac{1}{r} \sum_i \sum_{k,\ell} \sum_z Y^2_{(ik)(i\ell)}$	$MS(\epsilon)$

TABLE 5.5. Continued.

Source	Degrees of Freedom	Sum of Squares	Mean Square
total	$\frac{mn(mn-1)r}{2} - 1$	$\sum_{\substack{i,j \\ i < j}} \sum_{k,l} \sum_z Y^2_{(ik)(jl)z} + \sum_i \sum_{\substack{k,l \\ k < l}} \sum_z Y^2_{(ik)(il)z}$ $- \frac{2}{mn(mn-1)r} Y^2_{(\dots)(\dots)}$	

TABLE 5.6. Expected Mean Squares for the Augmented Two-Level Diallel Cross (Griffing's Model)

Mean Square	Model (i)	Model (ii)	Model (iii)
MS(G)	$\sigma_{\epsilon}^2 + \frac{(mn-2)nr}{m-1} \sum_i G_i^2$	$\sigma_{\epsilon}^2 + \frac{2(n-1)r}{mn-2} \sigma_{s1}^2 + \frac{(m-2)nr}{mn-2} \sigma_{s2}^2 + (mn-2)r\sigma_g^2$ $+ \frac{n(n-1)^2r}{mn-2} \sigma_{S1}^2 + \frac{(m-2)n^3r}{mn-2} \sigma_{S2}^2 + (mn-2)nr\sigma_G^2$	$\sigma_{\epsilon}^2 + \frac{2(n-1)r}{mn-2} \sigma_{s1}^2 + \frac{(m-2)nr}{mn-2} \sigma_{s2}^2 + (mn-2)r\sigma_g^2$ $+ \frac{(mn-2)nr}{m-1} \sum_i G_i^2$
MS ₁ (S)	$\sigma_{\epsilon}^2 + \frac{n(n-1)r}{2m} \sum_i S_{ii}^2$	$\sigma_{\epsilon}^2 + k_1 r \sigma_{s1}^2 + \frac{n(n-1)r}{1} k_1 \sigma_{S1}^2$	$\sigma_{\epsilon}^2 + k_1 r \sigma_{s1}^2 + \frac{n(n-1)r}{2m} \sum_i S_{ii}^2$
MS ₂ (S)	$\sigma_{\epsilon}^2 + \frac{2n^2r}{m(m-3)} \sum_{\substack{i,j \\ i < j}} S_{ij}^2$	$\sigma_{\epsilon}^2 + k_2 r \sigma_{s2}^2 + k_2 n^2 r \sigma_{S2}^2$	$\sigma_{\epsilon}^2 + k_2 r \sigma_{s2}^2 + \frac{2n^2r}{m(m-3)} \sum_{\substack{i,j \\ i < j}} S_{ij}^2$
MS(g)	$\sigma_{\epsilon}^2 + \frac{(mn-2)r}{m(n-1)} \sum_i \sum_k g_{ik}^2$	$\sigma_{\epsilon}^2 + \frac{(m-1)nr}{mn-2} \sigma_{s2}^2 + \frac{(n-2)r}{mn-2} \sigma_{s1}^2 + (mn-2)r\sigma_g^2$	$\sigma_{\epsilon}^2 + \frac{(m-1)nr}{mn-2} \sigma_{s2}^2 + \frac{(n-2)r}{mn-2} \sigma_{s1}^2 + (mn-2)r\sigma_g^2$
MS ₁ (s)	$\sigma_{\epsilon}^2 + \frac{2r}{m(n-2)(n+1)} \sum_i \sum_{\substack{k,\ell \\ k < \ell}} s_{(ik)(i\ell)}^2$	$\sigma_{\epsilon}^2 + r \left[1 - \frac{m(n-1)(n-2)}{(mn-2)d_1} \right] \sigma_{s1}^2$	$\sigma_{\epsilon}^2 + r \left[1 - \frac{m(n-1)(n-2)}{(mn-2)d_1} \right] \sigma_{s1}^2$
MS ₂ (s)	$\sigma_{\epsilon}^2 + \frac{2r}{m(m-1)(n^2-1)-m(n-1)} \sum_{\substack{i,j \\ i < j}} \sum_{k,\ell} s_{(ik)(j\ell)}^2$	$\sigma_{\epsilon}^2 + r \left[1 + \frac{m(n-1)(n-2)}{(mn-2)d_2} \right] \sigma_{s2}^2$	$\sigma_{\epsilon}^2 + r \left[1 + \frac{m(n-1)(n-2)}{(mn-2)d_2} \right] \sigma_{s2}^2$
MS(ε)	σ_{ϵ}^2	σ_{ϵ}^2	σ_{ϵ}^2

$$k_1 = [n(mn-1)(m-2) + n(n-1)] / (mn-1)(mn-2)$$

$$d_1 = m(n-2)(n+1)/2$$

$$k_2 = (m-1) [(mn-1)(mn-2-2n) + 2n^2] / (m-3)(mn-1)(mn-2)$$

$$d_2 = \frac{m(m-1)}{2} (n^2-1) - m(n-1)$$

$d_{ij, i'j'}$ represents the element in the (ij) th row and $(i'j')$ th column.

The order of the rows and columns will follow that of \hat{h} . Then

$$d_{ij, i'j'} = \begin{cases} \frac{2n-1}{n(n-1)r} & \text{if } i=i', j=j' \\ \frac{c}{2n(n-1)r} & \text{if } i=i' \text{ and } j \neq j' \\ & \text{or } i \neq i' \text{ and } j=j' \\ 0 & \text{otherwise,} \end{cases}$$

where

$$c = \begin{cases} 1 & \text{when the individual effects are fixed} \\ \frac{\sigma_\epsilon^2 + r\sigma_{s1}^2}{\sigma^2} & \text{when the individual effects are random.} \end{cases}$$

Let us first consider the case where the individual effects are fixed. Then D^{-1} will be of the following form

$$D^{-1} = \frac{2n^2(n-1)r}{3n-2} I - \frac{n^3(n-1)r}{(mn-1)(3n-2)} J,$$

where J is the $m(m-1)/2 \times m(m-1)/2$ matrix of unity elements. Then the sum of squares used for testing for population heterosis will be

$$SS(H) = \frac{2n^2(n-1)r}{3n-2} \sum_{\substack{i,j \\ i < j}} \hat{h}_{ij}^2 - \frac{n^3(n-1)r}{(mn-1)(3n-2)} \hat{h}_{..}^2,$$

where $\hat{h}_{..} = \sum_{\substack{i,j \\ i < j}} \hat{h}_{ij}$. Under the assumption of normality $SS(H)/\sigma^2$ will

follow a χ^2 distribution with $m(m-1)/2$ degrees of freedom. To test

H_0 : all $h_{ij} = 0$ vs. H_a : not all $h_{ij} = 0$ the test statistic will be

$$F = MS(H)/MS(\epsilon).$$

When the individual effects are random, no explicit form for D^{-1} exists and furthermore $SS(H)$ depends on unknown parameters. Even if they were replaced by their estimates one could not obtain an exact test for heterosis because of the difficulty determining the distribution of $SS(H)$. There is, however, the special case of $\sigma_{s1}^2 = \sigma_{s2}^2$ that leads to $c=1$ and hence to $SS(H)$ as given above. (The breeder must decide if it is reasonable to assume that the two variance components are equal based upon prior knowledge and the data.) When the individual effects are random and $\sigma_{s1}^2 = \sigma_{s2}^2$, the statistic for testing H_0 : all $h_{ij} = 0$ vs. H_a : not all $h_{ij} = 0$ will be

$$F = MS(H)/MS(s)$$

where $MS(s) = 2(SS_1(s) + SS_2(s))/(m^2n^2 - m^2 - 3mn + m)$ with $(m^2n^2 - m^2 - 3mn + m)/2$ degrees of freedom.

If population heterosis is found the breeder may wish to test which crosses show heterosis. To determine if the population cross $P_i \times P_j$ shows heterosis the hypothesis H_0 : $h_{ij} = 0$ vs. H_a : $h_{ij} \neq 0$ may be tested using one of the multiple comparison procedures such as that of Scheffé (1959).

5.4. Comparison of the Two Analyses

The difference between the two models presented in this chapter for the augmented two-level diallel cross is in the way in which general combining ability is defined. In Section 5.2. we discuss an extension of Harvey's (1960) model for the type II diallel in which two estimates of general combining ability are obtained--one based upon average

performance in intrapopulation crosses and one based upon average performance in interpopulation crosses. The model also includes an effect due to the average performance of intrapopulation crosses (a_1) and an effect due to the average performance of interpopulation crosses (a_2) and hence the analysis includes a sum of squares for population heterosis with one degree of freedom.

In Section 5.3. an extension of Griffing's (1956) model for the type II diallel is discussed in which general combining ability is estimated on the basis of performance in both interpopulation and intrapopulation crosses. No effect due to population heterosis is included in the model, but by examining contrasts in the means of the population crosses one can construct a sum of squares for heterosis with $m(m-1)/2$ degrees of freedom when the individual effects are fixed or when the individual effects are random and $\sigma_{s1}^2 = \sigma_{s2}^2$.

5.5. Modifications of the Mating Design

The required block size $(mn(mn-1))/2$ when the mating design is embedded in a randomized block environmental design) may be far too large to be feasible. For each population cross $P_i \times P_i$ the individual crosses form a type II diallel. This suggests three ways of reducing the required block size:

- (i) embedding the complete diallel in an incomplete environmental design. The interpopulation crosses to be included in each block could be determined using the design discussed in Chapter II. All of the intrapopulation crosses would occur in each block.

(ii) selecting only a sample of the crosses to make and test.

The interpopulation crosses to sample could be determined by the methods discussed in Chapter III. All or part of the intrapopulation crosses might be made.

(iii) embedding the partial diallel cross in an incomplete environmental design. The best approach would be to add the intrapopulation crosses to each block of the design suggested in Chapter IV.

The analysis for each of these modifications may be easily generalized from the analyses presented in the relevant chapters cited when the model presented in Section 5.2. is used.

VI. THE MODIFIED TWO-LEVEL DIALLEL CROSS EXPERIMENT

Frequently it is more convenient and economical for the plant breeder to fertilize trees with pollen bulk (a mixture of pollen obtained from many trees). In population hybridization studies where a large number of crosses are to be made, the use of pollen bulk may effectively reduce the cost of the experiment without seriously affecting the amount of information that is available. In addition the number of crosses to be made and tested will be reduced and hence the necessary block size for the environmental design also reduced.

6.1. Definition of the Modified Two-Level Diallel

Cross Mating Design

Suppose the plant breeder has m populations, P_1, P_2, \dots, P_m , that he wishes to test. For each population P_i , there are n individuals, $I_{i1}, I_{i2}, \dots, I_{in}$, that will serve as female parents. The modified two-level diallel mating design will consist of

- (i) m^2 population crosses $P_i \times P_j$ ($i, j = 1, 2, \dots, m$), and
- (ii) for each population cross $P_i \times P_j$, the individuals from P_i will be fertilized with pollen bulk obtained from the j th population. These crosses will be denoted by $I_{ik} \times P_j$ ($k = 1, 2, \dots, n$).

For $m=4$ and $n=3$ this design is illustrated in Figure 6.1.

Male Parents - Pollen Bulk
♂

		P ₁	P ₂	P ₃	P ₄	
♀	P ₁	I ₁₁	X	X	X	X
		I ₁₂	X	X	X	X
		I ₁₃	X	X	X	X
	P ₂	I ₂₁	X	X	X	X
		I ₂₂	X	X	X	X
		I ₂₃	X	X	X	X
	P ₃	I ₃₁	X	X	X	X
		I ₃₂	X	X	X	X
		I ₃₃	X	X	X	X
	P ₄	I ₄₁	X	X	X	X
		I ₄₂	X	X	X	X
		I ₄₃	X	X	X	X

Figure 6.1. The Modified Two-Level Diallel Mating Design

6.2. The Statistical Model and Analysis

Denote the observation from the z th offspring ($z = 1, 2, \dots, r$) of the individual I_{ik} when fertilized by pollen bulk from the j th population by $Y_{(ik)(j-)z}$. Assuming the offspring are grown using a completely randomized environmental design, the statistical model will be

$$Y_{(ik)(j-)z} = \mu + G_i + G_j + S_{ij} + R_{ij} + g_{ik} + s_{(ik)(j-)} + \varepsilon_{(ik)(j\ell)z} \quad (6.2.1)$$

where R_{ij} is the reciprocal effect of the population cross $P_i \times P_j$ with $R_{ij} = -R_{ji}$ and $s_{(ik)(j-)}$ is the specific combining ability of the cross $I_{ik} \times P_j$. For the definition and meaning of the other parameters see Section 1.2.3. As discussed previously (see Section 2.2.), we can distinguish three models, (i) the fixed effects model, (ii) the random effects model, and (iii) the mixed model. In model (ii) and model (iii) R_{ij} will be a random variable with mean zero and variance σ_R^2 .

Unlike the models for the other designs discussed in this paper, model (6.2.1) includes a reciprocal population effect, R_{ij} . Previously we have assumed that no reciprocal effects for population crosses existed, i.e. that there was no effect on the performance of the cross $P_i \times P_j$ based upon which population was serving as the male parent and which as the female parent. However, there may be instances, especially in exploratory investigations, in which the breeder does not wish to make this assumption. Because the structure of the modified two-level diallel cross allows the inclusion of an R_{ij} term in the model without adding to the size of the experiment, the breeder may wish to use this design and test to see if reciprocal population effects exist.

Note that the population crosses form a type II diallel with reciprocal crosses and selfs added (Method 1 of Griffing, 1956). The analysis presented here will be an extension of that given by Griffing.

Using the dot notation:

$$Y_{(ik)(j-)\cdot} = \sum_z Y_{(ik)(j-)z}$$

$$Y_{(ik)(\cdot-)\cdot} = \sum_j Y_{(ik)(j-)\cdot}$$

$$Y_{(i\cdot)(\cdot-)\cdot} = \sum_k Y_{(ik)(j-)\cdot}$$

$$Y_{(\cdot\cdot)(j-)\cdot} = \sum_i \sum_k Y_{(ik)(j-)\cdot}$$

$$Y_{(i\cdot)(j-)\cdot} = \sum_k Y_{(ik)(j-)\cdot}$$

$$Y_{(\cdot\cdot)(\cdot-)\cdot} = \sum_{i,j} \sum_k Y_{(ik)(j-)\cdot}$$

and using constraints on the estimators similar to the conditions of model (i), one obtains the following estimators:

$$\hat{\mu} = \frac{1}{m^2nr} Y_{(\cdot\cdot)(\cdot-)\cdot}$$

$$\hat{G}_i = \frac{1}{2mnr} (Y_{(i\cdot)(\cdot-)\cdot} + Y_{(\cdot\cdot)(i-)\cdot}) - \frac{1}{m^2nr} Y_{(\cdot\cdot)(\cdot-)\cdot}$$

$$\begin{aligned} \hat{S}_{ij} = & \frac{1}{2nr} (Y_{(i\cdot)(j-)\cdot} + Y_{(j\cdot)(i-)\cdot}) - \frac{1}{2mnr} (Y_{(i\cdot)(\cdot-)\cdot} + Y_{(\cdot\cdot)(i-)\cdot} \\ & + Y_{(j\cdot)(\cdot-)\cdot} + Y_{(\cdot\cdot)(j-)\cdot}) + \frac{1}{m^2nr} Y_{(\cdot\cdot)(\cdot-)\cdot} \end{aligned}$$

$$\hat{R}_{ij} = \frac{1}{2nr} (Y_{(i\cdot)(j-)\cdot} - Y_{(j\cdot)(i-)\cdot})$$

$$\hat{g}_{ik} = \frac{1}{mr} Y_{(ik)(\cdot-)} - \frac{1}{mnr} Y_{(i\cdot)(\cdot-)}.$$

$$\begin{aligned} \hat{s}_{(ik)(j\ell)} &= \frac{1}{r} Y_{(ik)(j-)} - \frac{1}{mr} Y_{(ik)(\cdot-)} + \frac{1}{mnr} Y_{(i\cdot)(\cdot-)} \\ &\quad - \frac{1}{nr} Y_{(i\cdot)(j-)}. \end{aligned}$$

Note that the estimates of g.c.a. and s.c.a. effects for populations and individuals are obtained on the basis of performance in intrapopulation and interpopulation crosses.

Comparisons between combining abilities and their variances are given in Table 6.1. Also given in Table 6.1. is the variance for comparisons of average cross performance (at the population as well as the individual level). To estimate the variances we note that for the fixed effects model σ^2 stands for σ_{ϵ}^2 , which is estimated by $MS(\epsilon)$ from Table 6.2. Comparisons (1), (2), (5), and (6) can also be considered for the mixed model (model (iii)). In these cases σ^2 is of the following form

$$\text{Comparison (1): } \sigma^2 = \sigma_{\epsilon}^2 + r\sigma_s^2 + mr\sigma_g^2/2,$$

$$\text{Comparison (2): } \sigma^2 = \sigma_{\epsilon}^2 + r\sigma_s^2,$$

$$\begin{aligned} \text{Comparison (5): } \sigma^2 &= \sigma_{\epsilon}^2 + r\sigma_s^2 \text{ if } i=i' \text{ and} \\ &\sigma^2 = \sigma_{\epsilon}^2 + r\sigma_s^2 + r\sigma_g^2 \text{ if } i \neq i', \end{aligned}$$

$$\text{Comparison (6): } \sigma^2 = \sigma_{\epsilon}^2 + r\sigma_s^2 + r\sigma_g^2/3.$$

The analysis of variance for this design is given in Table 6.2. with the expected mean squares in Table 6.3. These tables indicate how various hypotheses about the combining abilities can be tested or how the combining ability variances can be estimated.

TABLE 6.1. Variances of Comparisons Between Combining Abilities and Comparisons of Average Performance for the Modified Two-Level Diallel Cross

Comparison	Variance
(1) $\hat{G}_i - \hat{G}_i$	σ^2/mnr
(2) $\hat{S}_{ij} - \hat{S}_{ij'}$	$(m-1)\sigma^2/mnr$
$\hat{S}_{ij} - \hat{S}_{i'j'}$	$(m-2)\sigma^2/mnr$
(3) $\hat{g}_{ik} - \hat{g}_{ik'}$	$2\sigma^2/mr$
(4) $\hat{s}_{(ik)(j-)} - \hat{s}_{(ik')(j-)}$	$2(m-1)\sigma^2/mr$
(5) $(\hat{G}_i + \hat{G}_j + \hat{S}_{ij} + \hat{R}_{ij}) - (\hat{G}_{i'} + \hat{G}_{j'} + \hat{S}_{i'j'} + \hat{R}_{i'j'})$	$2\sigma^2/nr$
(6) $(\hat{G}_i + \hat{G}_j + \hat{S}_{ij} + \hat{R}_{ij}) - \frac{1}{2}(2\hat{G}_i + \hat{S}_{ii} + 2\hat{G}_j + \hat{S}_{jj})$	$3\sigma^2/2nr$
(7) $(\hat{G}_i + \hat{g}_{ik}) - (\hat{G}_{i'} + \hat{g}_{i'k'})$	$2(n-1)\sigma^2/mnr$ if $i \neq i'$
	$2\sigma^2/mr$ if $i = i'$
(8) $(\hat{G}_i + \hat{G}_j + \hat{S}_{ij} + \hat{R}_{ij} + \hat{g}_{ik} + \hat{s}_{(ik)(j-)}) - (\hat{G}_{i'} + \hat{G}_{j'} + \hat{S}_{i'j'} + \hat{R}_{i'j'} + \hat{g}_{i'k'} + \hat{s}_{(i'k')(j'-)})$	$2\sigma^2/r$

TABLE 6.2. Analysis of Variance for the Modified Two-Level Diallel Cross

Source	Degrees of Freedom	Sum of Squares	Mean Square
G_i	$m-1$	$\frac{1}{2mnr} \sum_i (Y_{(i\cdot)(\cdot-)} + Y_{(\cdot\cdot)(i-)})^2 - \frac{2}{m^2nr} Y_{(\cdot\cdot)(\cdot\cdot)}^2$	MS(G)
S_{ij}	$\frac{m(m-1)}{2}$	$\frac{1}{2nr} \sum_{i,j} Y_{(i\cdot)(j-)} \cdot (Y_{(i\cdot)(j-)} + Y_{(j\cdot)(i-)})$ $- \frac{2}{2mnr} \sum_i (Y_{(i\cdot)(\cdot-)} + Y_{(\cdot\cdot)(i-)})^2 + \frac{1}{m^2nr} Y_{(\cdot\cdot)(\cdot-)}^2$	MS(S)
R_{ij}	$\frac{m(m-1)}{2}$	$\frac{1}{2nr} \sum_{\substack{i,j \\ i < j}} (Y_{(i\cdot)(j-)} - Y_{(j\cdot)(i-)})^2$	MS(R)
g_{ik}	$m(n-1)$	$\frac{1}{mr} \sum_i \sum_k Y_{(ik)(\cdot-)}^2 - \frac{1}{mnr} \sum_i Y_{(i\cdot)(\cdot-)}^2$	MS(g)
$s_{(ik)(j-)}$	$m(m-1)(n-1)$	$\frac{1}{r} \sum_{i,j} \sum_k Y_{(ik)(j-)}^2 - \frac{1}{mr} \sum_i \sum_k Y_{(ik)(\cdot-)}^2$	MS(s)
error	$m^2n(r-1)$	$\sum_{i,j} \sum_k \sum_z Y_{(ik)(j-)z}^2 - \frac{1}{r} \sum_{i,j} \sum_k Y_{(ik)(j-)}^2$	MS(ϵ)
total	m^2nr-1	$\sum_{i,j} \sum_k \sum_z Y_{(ik)(j-)z}^2 - \frac{1}{m^2nr} Y_{(\cdot\cdot)(\cdot-)}^2$	

TABLE 6.3. Expected Mean Squares for the Modified Two-Level Diallel Cross

Source	Model (i)	Model (ii)	Model (iii)
G_i	$\sigma_\epsilon^2 + \frac{2mnr}{m-1} \sum_i G_i^2$	$\sigma_\epsilon^2 + r\sigma_s^2 + \frac{mr}{2} \sigma_g^2 + \frac{2(m-1)nr}{m} \sigma_S^2 + 2mnr \sigma_G^2$	$\sigma_\epsilon^2 + r\sigma_s^2 + \frac{mr}{2} \sigma_g^2 + \frac{2mnr}{m-1} \sum_i G_i^2$
S_{ij}	$\sigma_\epsilon^2 + \frac{2nr}{m(m-1)} \sum_{i,j} S_{ij}^2$	$\sigma_\epsilon^2 + r\sigma_s^2 + \frac{2(m^2-m+1)}{m^2} \sigma_S^2$	$\sigma_\epsilon^2 + r\sigma_s^2 + \frac{2nr}{m(m-1)} \sum_{i,j} S_{ij}^2$
R_{ij}	$\sigma_\epsilon^2 + \frac{2nr}{m(m-1)} \sum_{\substack{i,j \\ i < j}} R_{ij}^2$	$\sigma_\epsilon^2 + r\sigma_s^2 + r\sigma_g^2 + 2nr \sigma_R^2$	$\sigma_\epsilon^2 + r\sigma_s^2 + r\sigma_g^2 + \frac{4nr}{m(m-1)} \sum_{\substack{i,j \\ i < j}} R_{ij}^2$
g_{ik}	$\sigma_\epsilon^2 + \frac{r}{n-1} \sum_{i,k} g_{ik}^2$	$\sigma_\epsilon^2 + r\sigma_s^2 + mr \sigma_g^2$	$\sigma_\epsilon^2 + r\sigma_s^2 + mr \sigma_g^2$
$s_{(ik)(j-)}$	$\sigma_\epsilon^2 + \frac{r}{m(m-1)(n-1)} \sum_{i,j} \sum_k s_{(ik)(j-)}^2$	$\sigma_\epsilon^2 + r\sigma_s^2$	$\sigma_\epsilon^2 + r\sigma_s^2$
error	σ_ϵ^2	σ_ϵ^2	σ_ϵ^2

Since self population crosses are included in the mating design, the breeder may wish to test for population heterosis. One method would be to examine the contrasts $h_{ij} = \mu_{ij} + \mu_{ji} - \mu_{ii} - \mu_{jj}$ ($i < j$) where μ_{ij} is the average performance of the population cross $P_i \times P_j$. We obtain the sum of squares associated with these contrasts as

$$SS(H) = \hat{h}'D^{-1}\hat{h}$$

where $\hat{h}' = (\hat{h}_{12}, \hat{h}_{13}, \dots, \hat{h}_{1m}, \hat{h}_{23}, \hat{h}_{24}, \dots, \hat{h}_{2m}, \dots, \hat{h}_{(m-1)m})$ and $\hat{h}_{ij} = \bar{Y}_{(i\cdot)(j\cdot)} + \bar{Y}_{(j\cdot)(i\cdot)} - \bar{Y}_{(i\cdot)(i\cdot)} - \bar{Y}_{(j\cdot)(j\cdot)}$ and σ^2D is the dispersion matrix (variance-covariance matrix) associated with the \hat{h} 's, i.e. $\text{Var}(\hat{h}) = \sigma^2D$. When individual effects are fixed, $\sigma^2 = \sigma_{\epsilon}^2$ and when individual effects are random, $\sigma^2 = \sigma_{\epsilon}^2 + r\sigma_S^2$. Let $D = \{d_{ij, i'j'}\}$ where $d_{ij, i'j'}$ represents the element in the (ij) th row and the $(i'j')$ th column of D . The order of the rows and columns of D will follow that of \hat{h} . Then

$$d_{ij, i'j'} = \begin{cases} \frac{4}{nr} & \text{if } i=i', j=j' \\ \frac{1}{nr} & \text{if either } i=i' \text{ or } j=j' \text{ but not both} \\ 0 & \text{otherwise} \end{cases}$$

The inverse for the dispersion matrix is then

$$D^{-1} = \frac{nr}{3} I - \frac{nr}{6m} J$$

where J is the $m(m-1)/2 \times m(m-1)/2$ matrix of unity elements. The sum of squares for heterosis will be

$$SS(H) = \frac{nr}{3} \sum_{i < j} \hat{h}_{ij}^2 - \frac{nr}{6m} \hat{h}_{\cdot\cdot}^2,$$

where

$$\hat{h}_{..} = \sum_{\substack{i,j \\ i < j}} \hat{h}_{ij} .$$

Under the assumption of normality $SS(H)/\sigma^2$ will follow a χ^2 distribution with $m(m-1)/2$ degrees of freedom. To test H_0 : all $h_{ij} = 0$ vs.

H_a : not all $h_{ij} = 0$ the test statistic will be

$$F = MS(H)/MS(\epsilon)$$

when the individual effects are fixed and

$$F = MS(H)/MS(s)$$

when individual effects are random. If population heterosis is found the breeder may wish to determine which crosses show heterosis. In this case hypotheses such as H_0 : $h_{ij} = 0$ vs. H_a : $h_{ij} \neq 0$ may be tested using one of the multiple comparison procedures such as that of Scheffé (1959).

6.3. Concluding Remarks

This design has many attractive features. A control for the population and individual hybrids is present in the form of intrapopulation crosses since each individual from population P_i is fertilized with pollen bulk from P_i . As mentioned previously the use of pollen bulk may often be more economical and convenient. In addition, the use of pollen bulk allows the experimenter to reduce the number of crosses to be tested from $mn(mn-1)/2$ for the augmented two-level diallel cross to m^2n for this design. By reducing the number of crosses to be tested the experimenter

has also reduced the necessary block size for the environmental design. Also the efficiency of the modified two-level diallel cross with respect to the augmented two-level diallel cross for estimating contrasts in the combining abilities is not significantly reduced.

VII. SUMMARY

In this investigation, experimental designs were developed that should prove useful in population hybridization studies. The objective of all of these designs was to obtain information about

- (i) the general combining ability of populations,
- (ii) the specific combining ability of population crosses,
- (iii) the general combining ability of individuals, and
- (iv) the specific combining ability of individual crosses.

These concepts were first introduced by Hinkelmann (1974) in relationship to the two-level diallel mating design.

Suppose one has m populations, P_1, P_2, \dots, P_m , and for each population P_i , n individuals, $I_{i1}, I_{i2}, \dots, I_{in}$, that one wants to test. Then the two-level diallel mating design consists of

- (i) $m(m-1)/2$ population crosses $P_i \times P_j$ where $i < j$, and
- (ii) n^2 individual crosses $I_{ik} \times I_{j\ell}$ for each population cross $P_i \times P_j$.

The population crosses form a type II diallel cross and within each population cross the individual crosses compose a type I diallel cross. When the offspring resulting from this mating design are grown in a randomized block environmental design, the blocks must be of size $m(m-1)n^2/2$.

Even for moderate values of m and n the required block size may be far too large. Three methods to reduce the necessary block size were investigated:

- (i) using an incomplete environmental design to grow the offspring from the complete diallel cross,
- (ii) selecting only a sample of the $m(m-1)n^2/2$ total crosses to test, and
- (iii) selecting only a sample of $m(m-1)n^2/2$ crosses to test and using an incomplete environmental design to grow the offspring from these crosses.

Chapter II discussed a method for apportioning the population crosses to blocks so that k population crosses occur per block (versus $m(m-1)/2$ for the complete environmental design) and all n^2 individual crosses occur for each population crosses included in a block. To decide which population crosses are to be included in each block a natural analogy is made between the crosses and the treatments of a triangular PBIB with block size k . A consequence of this natural relationship is that the efficiencies of the design for estimating population g.c.a. and s.c.a. will be determined by the eigenvalues of the NN' matrix. Hence the experimenter may choose a design with the efficiencies in mind.

Another way of reducing the required block size is to reduce the number of crosses that are made. Three ways of constructing a partial two-level diallel were investigated in Chapter III:

- (i) selecting a sample of the population crosses to make,
- (ii) selecting a sample of the individual crosses to make for each population cross, or
- (iii) selecting a sample of the population crosses to make

and further selecting a sample of the individual crosses to make for each population cross sampled.

The two-level structure of the mating design (population cross form a type II diallel cross and individual crosses within each population cross form a type I diallel) was exploited to produce these designs.

Finally, one may combine these two techniques of reducing the block size and embed a partial two-level diallel cross in an incomplete environmental design. In Chapter IV methods for constructing partial two-level diallel mating designs are discussed and instructions are given for apportioning the crosses to blocks so that each population occurs in t crosses in each block. All or part of the n^2 individual crosses will be made for each population cross occurring in a block. When $c_1 = m-1$ this design represents another method for embedding the complete diallel in blocks.

In addition to these designs intended to reduce the required block size, two modifications of the two-level diallel mating design were suggested that would include intrapopulation crosses. First the two-level diallel cross to which $n(n-1)/2$ individual crosses, $I_{ik} \times I_{j\ell}$ ($k < \ell$), were added was investigated in Chapter V. This augmented design has the advantage that the general and specific combining ability of the populations and individuals can be measured on the basis of intrapopulation and interpopulation crosses. In addition this design allows the experimenter to check for population heterosis.

The second modification suggested for the two-level diallel cross was to use pollen bulk for the male parent. In this mating design n females from each of the m populations will be fertilized with pollen bulk from each of the m populations. Besides including intrapopulation crosses as a control, this design also reduces the number of crosses to be made and tested. The two-level diallel cross augmented with intrapopulation crosses makes $mn(mn-1)/2$ crosses. Using pollen bulk for the male parent reduces the number of crosses to be tested to m^2n . Depending on the size of m and n , this can prove to be a significant savings of time and resources.

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APPENDIX

A Proof That the Simple Least Squares Estimates of the Effects in the PI-Partial Two-Level Diallel Cross Experiment Are BLUE

Suppose we have the general linear model $y = X\beta + e$ where y is an $N \times 1$ vector of observable values, X is a known $N \times p$ matrix of rank r , β is a $p \times 1$ vector of parameters, and e is an $N \times 1$ vector of residuals with expectation $E(e) = 0$ and variance $E(ee') = \sigma^2 \Sigma$, where $\sigma^2 > 0$ is unknown and Σ is an $N \times N$ matrix with a known structure. Zyskind (1967) shows that the simple least squares estimates are best linear unbiased estimates (BLUE) if and only if the column space of X is an invariant subspace of the matrix Σ , i.e. for every $a \in C(X)$ the vector $\Sigma a \in C(X)$.

In the PI-partial two-level diallel cross experiment we have the model

$$\bar{Y}_{(ik)(j\ell)} = \mu + G_i + G_j + g_{ik} + g_{j\ell} + e_{(ik)(j\ell)}$$

or written in matrix notation $\bar{Y} = X\beta + e$ where

$$\bar{Y}' = (\bar{Y}'_{12}, \bar{Y}'_{13}, \dots, \bar{Y}'_{1m}, \bar{Y}'_{23}, \bar{Y}'_{24}, \dots, \bar{Y}'_{2m}, \dots, \bar{Y}'_{(m-1)m})$$

with

$$\begin{aligned} \bar{Y}'_{ij} = & (\bar{Y}_{(i1)(j1)}, \bar{Y}_{(i1)(j2)}, \dots, \bar{Y}_{(i1)(jn)}, \bar{Y}_{(i2)(j1)}, \bar{Y}_{(i2)(j2)}, \\ & \dots, \bar{Y}_{(i2)(jn)}, \dots, \bar{Y}_{(in)(j1)}, \bar{Y}_{(in)(j2)}, \dots, \bar{Y}_{(in)(jn)}) \end{aligned}$$

Since we are using an incomplete mating design, not all combinations of $(ik)(j\ell)$ will occur. X will be a $mc_1c_2n/2 \times mc_1c_2n/2$ matrix of rank mn .

The vector of parameters, β , will be ordered in the following manner:

$$\beta' = (\mu, G_1, G_2, \dots, G_m, g_{11}, g_{12}, \dots, g_{1n}, g_{21}, g_{22}, \dots, g_{2n}, \dots, \\ g_{m1}, g_{m2}, \dots, g_{mn})$$

The vector of residuals will have expectation $E(e) = 0$ and variance $E(ee') = \sigma^2 \Sigma$ where

$$\Sigma = (1-p)I + p \text{diag}(J, J, \dots, J)$$

where I is the $mc_1c_2n/2 \times mc_1c_2n/2$ identity matrix and $\text{diag}(J, J, \dots, J)$ is the $mc_1c_2n/2 \times mc_1c_2n/2$ block diagonal matrix whose diagonal entries are the $nc_2 \times nc_2$ matrix J of unity elements.

To prove that the simple least squares estimates are BLUE, we will show that for every column vector x_i of X , $\Sigma x_i \in C(X)$ which is equivalent to proving that $C(X)$ is an invariant subspace of Σ . Label the columns of X -- $x_\mu, x_1, \dots, x_m, x_{11}, \dots, x_{mn}$ -- where x_μ is the vector of ones corresponding to the parameter μ , x_i is the column vector corresponding to G_i , and x_{ik} is the column vector corresponding to g_{ik} . For example if $m=5, c_1=2, n = c_2 = 2$, then the X matrix would be

$$X = \begin{matrix} & x_{\mu} & x_1 & x_2 & x_3 & x_4 & x_5 & x_{11} & x_{12} & x_{21} & x_{22} & x_{31} & x_{32} & x_{41} & x_{42} & x_{51} & x_{52} \\ \left[\begin{array}{cccccccccccccccc}
 1 & 1 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
 1 & 1 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
 1 & 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
 1 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
 \\
 1 & 1 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
 1 & 1 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
 1 & 1 & 0 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
 1 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
 \\
 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 \\
 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
 \\
 1 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
 1 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
 1 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 \\
 1 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
 \\
 1 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 \\
 1 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 \\
 1 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 1 & 0 & 0 \\
 1 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1
 \end{array} \right] .
 \end{matrix}$$

Then, based on the general structure of X ,

$$\Sigma_{x_{\mu}} = (1 + (nc_2 - 1)\rho)x_{\mu} \in C(x)$$

$$\Sigma_{x_i} = (1 + (nc_2 - 1)\rho)x_i \in C(x)$$

$$\Sigma_{x_{ik}} = c_2 \rho x_i + (1 - \rho)x_{ik} \in C(x)$$

for all i and k . Q.E.D.

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EXPERIMENTAL DESIGNS FOR POPULATION HYBRIDIZATION STUDIES

by

Brenda G. Cox

(ABSTRACT)

In this investigation, experimental designs were developed for population hybridization studies. The objective of all of these designs was to obtain information about

- (i) the general combining ability of populations,
- (ii) the specific combining ability of population crosses,
- (iii) the general combining ability of individuals, and
- (iv) the specific combining ability of individual crosses.

These concepts were first introduced by Hinkelmann (1974) in relationship to the two-level diallel mating design.

With m populations, P_1, P_2, \dots, P_m , and n individuals for the i th population, $I_{i1}, I_{i2}, \dots, I_{in}$ ($i = 1, 2, \dots, m$), to be evaluated, the two-level diallel mating design consists of

- (i) $m(m-1)/2$ population crosses $P_i \times P_j$ where $i < j$, and
- (ii) n^2 individual crosses $I_{ik} \times I_{j\ell}$ for each population cross $P_i \times P_j$.

When the offspring from this design are grown in a randomized block environmental design, the blocks will be of size $m(m-1)n^2/2$. Even for moderate values of m and n the required block size may be far too large. Three methods are proposed that will either reduce the block size or the

size of the total experiment or both. These are obtained by

- (i) using an incomplete environmental design to grow the offspring from the complete diallel cross,
- (ii) selecting only a sample of the $m(m-1)n^2/2$ total crosses, either at the population level or at the individual level, to be tested,
- (iii) selecting only a sample of the $m(m-1)n^2/2$ crosses to be tested and using an incomplete environmental design.

Two modifications of the two-level diallel cross were suggested that would include intrapopulation crosses. First the two-level diallel mating design to which, for each population P_i , $n(n-1)/2$ intrapopulation crosses, $I_{ik} \times I_{i\ell}$ ($k < \ell$), were added, was investigated. This augmented design has the advantage that the general and specific combining ability of the populations and individuals can be measured on the basis of intrapopulation and interpopulation crosses. In addition this design allows the experimenter to test for population heterosis.

The second modification suggested was to use pollen bulk as the male parent. In this mating design n females from each of m populations are fertilized with pollen bulk from each of the m populations. Besides including intrapopulation crosses as a control, this design also reduces the number of crosses to be made and tested. The two-level diallel cross with intrapopulation crosses added makes $mn(mn-1)/2$ crosses. Using pollen bulk as the male parent reduces the number of crosses to be tested to m^2n .

For all cases considered, the construction and analysis of appropriate mating and environmental designs have been given.