Two-Level Diallel Cross Experiments')

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(Received January 1974)

1. Introduction

In his recommendations in the "Report of the 1963 World Consultation for Forest Genetics and Tree Improvement" Matthews (1964) puts forward that "progeny tests are vital to any breeding program. To obtain maximum information and to keep costs within tolerable limits, breeders should choose the mating design very carefully." And along the same line Stern (1964) writes: "The tree breeder should choose mating designs carefully. Already at this early stage he is deciding on the kind of information he will get in the future, . . ." The type of information that one should try to obtain from progeny tests is threefold, described by Stern (1964) as follows:

(i) information on general and specific combining ability of parent trees for use in seed orchards;

(ii) reliable estimates of genetic parameters;

(iii) material for further breeding work.

Among the many available mating designs, various forms of diallel crosses have been advocated for (Stern, 1960; Hinkelmann and Stern, 1960; Hinkelmann, 1966) and actually used in forest tree breeding (Libby, Stettler and Seitz, 1969). They are used primarily for evaluating the performance of clones or inbred lines on an intra-population or intra-species basis. However, as population, species and racial hybridization becomes more important (Wright, 1962), there is growing interest with regard to the evaluation of performance on an inter-population or inter-species basis. It is this aspect of progeny tests that we shall address ourselves to, in this paper, proposing yet another variation of a diallel cross experiment.

After defining the two-level mating scheme in Section 2 we outline in Section 3 the different types of combining ability information that can be obtained from such an experiment. This is formalized in Section 4 in terms of a statistical model and based on this model, the analysis is given with detailed information on appropriate and useful comparisons involving the parameters of the underlying model. In Section 5 we comment briefly on the aspects of information on genetic parameters, and in Section 6 we mention some possible and perhaps desirable modifications of the proposed mating scheme.

2. Definition of the two-level diallel mating design

Suppose we have m "diverse" types of trees (clones). These types may be populations, subpopulations, portions of clines, species, races or other genetically meaningful collections of individuals. For the purpose of this paper we shall refer to them as populations and denote them by $P_1, P_2, \ldots, P_m$. For each population we consider n individuals (trees, clones), denoted by $I_{j1}, I_{j2}, \ldots, I_{jn}$ $(j = 1, 2, \ldots, m)$, where these individuals constitute either a random sample from the population or are selected according to some criterion (e. g. plus trees).

The 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 $I_{ik} \times I_{jl}$ $(k, l = 1, 2, \ldots, n)$ for each $P_i \times P_j$;

i. e., it consists of "crosses" at the population level and of crosses at the individual level, hence the name two-level diallel.

For $m = 4$ and $n = 3$ this mating scheme is illustrated in *Fig.* 1.

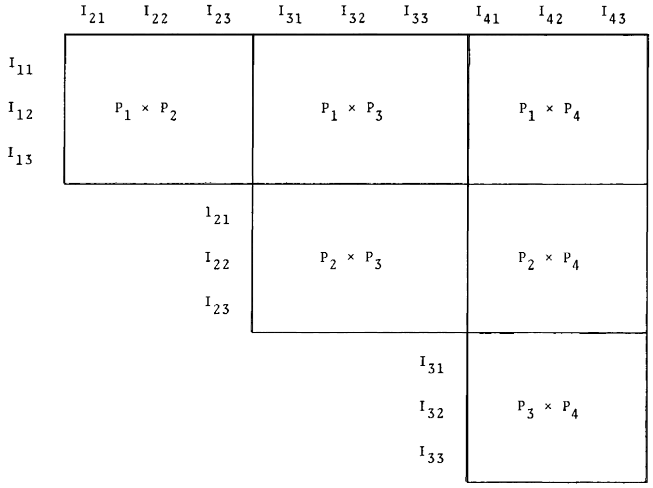

Figure 1. — Example of a two-level diallel mating design.

As a possible practical application we mention interspecies crosses involving $m = 5$ different species of Pinus strobus: P. *parviflora* Sieb. and Zucc., P. peuce Griseb., P. griffithii McClel., P. *monticola* D. Don, and P. strobus L. All these crosses have been successful (Wright, 1959, 1973).

We note that the two-level diallel can be considered as a composite of two types of diallel crosses: The crosses at the population level constitute a diallel of Type II, and the crosses at the individual level within each population cross constitute a diallel of Type I (Hinkelmann and Stern, 1960). This observation will be useful with regard to constructing incomplete two-level diallel mating designs.

3. Combining ability information from two-level diallel

The two-level diallel mating design yields all three types of information mentioned in Section 1, the one most readily available being that listed under (i): general and specific combining abilities. Because of the structure of the mating design we can envisage the following types of combining abilities and comparisons among them:

(1) General combining ability of a population,

(2) general combining ability of an individual tree,

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*) In memoriam Professor Dr. Klaus Stern.

(3) specific combining ability associated with a population cross,

(4) specific combing ability associated with an individual cross.

This leads one to considering further the following types of comparisons which are of interest in the overall evaluation of the populations and individuals:

(5) Average performance of P_i vs. average performance of P_j,

(6) average performance of hybrid population ($P_i \times P_j$) vs. average performance of hybrid population ($P_{i'} \times P_{j'}$),

(7) average performance of I_{ik} vs. average performance of $I_{i'k'}$,

(8) average performance of hybrid ($I_{ik} \times I_{jl}$) vs. average performance of hybrid ($I_{i'k'} \times I_{j'l'}$).

In other situations we may be interested in the variance components associated with general combining abilities (g.c.a) and specific combining abilities (s.c.a.) mentioned above.

Which type of information is appropriate will depend on what type of inference one is interested to make, which in turn will depend on whether the populations and/or individuals have been drawn from a larger collection or not. This will be obvious from the discussion of the underlying statistical model in the next section.

4. The statistical model and analysis

We shall denote the observation for an offspring of the mating $I_{ik} \times I_{jl}$ by $Y_{(ik)\,(jl)}$ or, in case of several offspring per mating, by $Y_{(ik)\,(jl)z}$ ($z = 1, 2, \ldots, r$). An appropriate linear model, using a completely randomized environmental design, is then given by

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

where G_i = g.c.a of P_i, S_{ij} = s.c.a. of $P_i \times P_j$, g_{ik} = g.c.a. of I_{ik}, $s_{(ik)\,(jl)}$ = s.c.a. of $I_{ik} \times I_{jl}$, and $\varepsilon_{(ik)\,(jl)z}$ is a random error, having mean zero and variance σ_ε^2.

Depending on the type of inference that one wants to make, we distinguish three different models:

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

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

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

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

$$\sum_j \sum_l s_{(ik)\,(jl)} = 0 \text{ for every (i, k).}$$

(ii) The random effects model: G_i, S_{ij}, g_{ik} and $s_{(ik)\,(jl)}$ are random variables, independently distributed with means zero 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 $s_{(ik)\,(jl)}$ are random effects as in (ii).

In (i) inference is made only with respect to the populations and individuals actually included in the experiment. In (ii) inference is made with regard to a larger collection of populations and individuals of which those included in the experiment represent a random sample. Model (iii), finally, refers to the sitution where all populations of interest are included in the experiment, whereas the individuals represent a sample of all the individuals in the populations.

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

$$Y_{(ik)\,(\cdot\,\cdot)\,\cdot} = \sum_{j > i} \sum_l Y_{(ik)\,(jl)\cdot} + \sum_{j < i} \sum_l Y_{(jl)\,(ik)\cdot}$$

$$Y_{(i\,\cdot)\,(j\,\cdot)\,\cdot} = \sum_{k,\,l} Y_{(ik)\,(jl)\,\cdot}$$

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

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

and using constraints on the estimators similar to the conditions used in model (i), we obtain the following least squares estimators for the different effects:

$$\hat{\mu} = Y_{(\cdot\,\cdot)\,(\cdot\,\cdot)\,\cdot}/c \qquad \left(c = \frac{m(m-1)}{2} n^2 r\right)$$

$$\hat{G}_i = \frac{Y_{(i\,\cdot)\,(\cdot\,\cdot)\,\cdot}}{(m-2)n^2r} - \frac{2Y_{(\cdot\,\cdot)\,(\cdot\,\cdot)\,\cdot}}{m(m-2)n^2r}$$

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

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

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

These quantities can be used to estimate the comparisons mentioned in the previous section. Comparisons of types (1) — (4) and their variances are given in *Table 1*, comparisons of types (5) — (8) and their variances are given in *Table 2*. To estimate the variances we note that for the fixed effects model (model (i)) σ^2 stands for σ_ε^2, which is estimated by MS(ε) from *Table 3*. Comparisons (1), (2), and (6) can also be considered for the mixed model (model (iii)). In these cases σ^2 is of the following form:

Comparison (1): $\sigma^2 = \sigma_\varepsilon^2 + r\sigma_s^2 + (m-2)nr\sigma_g^2$, which according to *Table 4* is estimated by (m—2)MS(g) — (m—3) MS(s) with

$$f_1 = \frac{[(m-2)MS(g) - (m-3)MS(s)]^2}{\dfrac{[(m-2)MS(g)]^2}{m(n-1)} + \dfrac{[(m-3)MS(s)]^2}{d}} \text{ d.f.,}$$

with d given in *Table 4*.

Comparison (2): $\sigma^2 = \sigma_\varepsilon^2 + r\sigma_s^2$ which according to *Table 4* is estimated by MS(s).

Comparison (6): For $i = i'$, $j \neq j'$, i.e. the comparison is between two hybrid populations having one parental population in common.

$$\sigma^2 = \sigma_\varepsilon^2 + r\sigma_s^2 + nr\sigma_g^2,$$

which according to *Table 4* is estimated by MS(g). For $i \neq i'$, $j \neq j'$, i.e. the comparison is between two hybrid populations having no parental population in common,

$$\sigma^2 = \sigma_\varepsilon^2 + r\sigma_s^2 + 2nr\sigma_g^2,$$

which is estimated by 2MS(g) — MS(s) with

$$f_2 = \frac{[2MS(g) - MS(s)]^2}{\dfrac{[2MS(g)]^2}{m(n-1)} + \dfrac{[MS(s)]^2}{d}} \text{ d.f.}$$

Table 1. — Comparisons between combining abilities and their variances

Comparison	Variance
(1) $\hat{G}_i - \hat{G}_{i'}$	$2\sigma^2/(m-2)n^2r$
(2) $\hat{S}_{ij} - \hat{S}_{i'j}$ $(i'\neq i)$	$2(m-3)\sigma^2/(m-2)n^2r$
$\hat{S}_{ij} - \hat{S}_{i'j'}$ $\begin{matrix}(i'\neq i)\\(j'\neq j)\end{matrix}$	$2(m-4)\sigma^2/(m-2)n^2r$
(3) $\hat{g}_{ik} - \hat{g}_{ik'}$ $(k'\neq k)$	$2\ \sigma^2/(m-1)nr$
$\hat{g}_{ik} - \hat{g}_{i'k'}$ $(i'\neq i)$	$2[(m-1)(m+1)-2]\sigma^2/(m-1)^2n^2r$
(4) $\hat{s}_{(ik)(j\ell)} - \hat{s}_{(ik)(j\ell')}$ $(\ell'=\ell)$	$2[(m-1)n-1\ ]\sigma^2/(m-1)nr$
$\hat{s}_{(ik)(j\ell)} - \hat{s}_{(ik')(j\ell')}$ $\begin{matrix}(k'\neq k)\\(\ell'\neq \ell)\end{matrix}$	$2[(m-1)n-2]\sigma^2/(m-1)nr$
$\hat{s}_{(ik)(j\ell)} - \hat{s}_{(ik)(j'\ell')}$ $(j'\neq j)$	$2[(m-1)(n^2-1)-(n-3)]\sigma^2/(m-1)n^2r$
$\hat{s}_{(ik)(j\ell)} - \hat{s}_{(ik')(j'\ell')}$ $\begin{matrix}(j'\neq j)\\(k'\neq k)\end{matrix}$	$2[(m-1)(n^2-1)-n]\sigma^2/(m-1)n^2r$
$\hat{s}_{(ik)(j\ell)} - \hat{s}_{(i'k')(j'\ell')}$ $\begin{matrix}(i'\neq i)\\(j'\neq j)\end{matrix}$	$2[(m-1)(n^2-1)-2(n-1)]\sigma^2/(m-1)n^2r$

The analysis of variance is presented in *Table 3* with the expected mean squares for the three different models given in *Table 4*. This table indicates how various hypotheses about the combining abilities can be tested or how the combining ability variances can be estimated.

5. Information on genetic variance components

The analysis given in the previous section exhausts all the information available for model (i). For model (ii), however, it is desirable to give some genetic interpretation to the combining ability variances; i.e. express these variances in terms of genetic variance components. Such interpretation is generally useful for describing the type of gene action present and for deciding upon appropriate selection procedures.

For ordinary diallel cross experiments the genetic interpretation is based on the consideration of covariances among relatives, mainly full-sibs and half-sibs. If we follow this approach for the two-level diallel mating design

Table 2. — Comparisons of average performance

Type of Comparison	Estimator	Variance
(5) $G_i - G_{i'}$	$(Y_{(i\cdot)(\cdot\cdot)} - Y_{(i'\cdot)(\cdot\cdot)\cdot})/(m-2)n^2r$	$2\sigma^2/(m-2)n^2r$
(6) $(G_i + G_j + S_{ij})$ $- (G_{i'} + G_{j'} + S_{i'j'})$	$(Y_{(i\cdot)(j\cdot)\cdot} - Y_{(i'\cdot)(j'\cdot)\cdot})/n^2r$	$2\sigma^2/n^2r$
(7) $(G_i + g_{ik}) - (G_{i'} + g_{i'k'})$	$(Y_{(ik)(\cdot\cdot)\cdot} - Y_{(i'k')(\cdot\cdot)\cdot}/(m-1)nr$ $+(Y_{(i\cdot)(\cdot\cdot)\cdot} - Y_{(i'\cdot)(\cdot\cdot)\cdot})/(m-1)(m-2)n^2r$	$\begin{cases} 2[(m-2)(mn-n+1)+1]\sigma^2/(m-1)^2(m-2)n^2r & (i\neq i') \\ 2\sigma^2/(m-1)nr & (i=i') \end{cases}$
(8) $(G_i + G_j + S_{ij} + g_{ik}$ $+ g_{j\ell} + s_{(ik)(j\ell)})$ $-(G_{i'} + G_{j'} + S_{i'j'} + g_{i'k'}$ $+ g_{j'\ell'} + s_{(i'k')(j'\ell')})$	$(Y_{(ik)(j\ell)\cdot} - Y_{(i'k')(j'\ell')\cdot})/r$	$2\sigma^2/r$

Table 3. — Analysis of variance

Source	d.f.	Sum of squares	Mean squares
G_i	$m-1$	$\frac{1}{(m-2)n^2r}\sum_i Y^2_{(i\cdot)(\cdot\cdot)\cdot} - \frac{4}{m(m-2)n^2r}Y^2_{(\cdot\cdot)(\cdot\cdot)\cdot}$	MS(G)
S_{ij}	$m(m-3)/2$	$\frac{1}{n^2r}\sum_{\substack{i,j\\i<j}} Y^2_{(i\cdot)(j\cdot)\cdot} - \frac{1}{(m-2)n^2r}\sum_i Y^2_{(i\cdot)(\cdot\cdot)\cdot}$ $+\frac{2}{(m-1)(m-2)n^2r}Y^2_{(\cdot\cdot)(\cdot\cdot)\cdot}$	MS(S)
g_{ik}	$m(n-1)$	$\frac{1}{(m-1)nr}\sum_{i,k} Y^2_{(ik)(\cdot\cdot)\cdot} - \frac{1}{(m-1)n^2r}\sum_i Y^2_{(i\cdot)(\cdot\cdot)\cdot}$	MS(g)
$s_{(ik)(j\ell)}$	$\frac{m(m-1)}{2}(n^2-1)-m(n-1)$	$\frac{1}{r}\sum_{\substack{i,j\\i<j}}\sum_{k,\ell} Y^2_{(ik)(j\ell)\cdot} - \frac{1}{(m-1)nr}\sum_{i,k} Y^2_{(ik)(\cdot\cdot)\cdot}$ $+\frac{1}{(m-1)n^2r}\sum_i Y^2_{(i\cdot)(\cdot\cdot)\cdot} - \frac{1}{n^2r}\sum_{\substack{i,j\\i<j}} Y^2_{(i\cdot)(j\cdot)\cdot}$	MS(s)
ε	$\frac{m(m-1)}{2}n^2(r-1)$	$\sum_{\substack{i,j\\i<j}}\sum_{k,\ell}\sum_z Y^2_{(ik)(j\ell)z} - \frac{1}{r}\sum_{\substack{i,j\\i<j}}\sum_{k,\ell} Y^2_{(ik)(j\ell)\cdot}$	MS(ε)

Table 4. — Expected mean squares

Mean Squares	Model (i)	Model (ii)	Model (iii)
MS(G)	$\sigma_\varepsilon^2 + \frac{(m-2)n^2r}{m-1} \sum_i G_i^2$	$\sigma_\varepsilon^2 + r\sigma_s^2 + (m-2)nr\sigma_g^2$ $+ n^2r\sigma_S^2 + (m-2)n^2r\sigma_G^2$	$\sigma_\varepsilon^2 + r\sigma_s^2 + (m-2)nr\sigma_g^2$ $+ \frac{(m-2)n^2r}{m-1} \sum_i G_i^2$
MS(S)	$\sigma_\varepsilon^2 + \frac{2n^2r}{m(m-3)} \sum_{i<j} S_{ij}^2$	$\sigma_\varepsilon^2 + r\sigma_s^2 + n^2r\sigma_S^2$	$\sigma_\varepsilon^2+r\sigma_s^2+ \frac{2n^2r}{m(m-3)} \sum_{i<j} S_{ij}^2$
MS(g)	$\sigma_\varepsilon^2 + \frac{(m-2)^2nr}{m(m-1)(n-1)} \sum_{i,k} g_{ik}^2$	$\sigma_\varepsilon^2 + r\sigma_s^2 + nr\sigma_g^2$	$\sigma_\varepsilon^2 + r\sigma_s^2 + nr\sigma_g^2$
MS(s)[1]	$\sigma_\varepsilon^2 + \frac{r}{d} \sum_{i<j} \sum_{k,\ell} s_{(ik)(j\ell)}^2$	$\sigma_\varepsilon^2 + r\sigma_s^2$	$\sigma_\varepsilon^2 + r\sigma_s^2$
MS(ε)	σ_ε^2	σ_ε^2	σ_ε^2

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

we find the following non-zero covariances among offspring:

$$\mathrm{Cov}(Y_{(ik)\,(jl)z}, Y_{(ik)\,(jl)z'}) = 2\sigma_G^2 + \sigma_S^2 + 2\sigma_g^2 + \sigma_s^2 \qquad (z \neq z')$$

$$\mathrm{Cov}(Y_{(ik)\,(jl)z}, Y_{(ik)\,(jl')z'}) = 2\sigma_G^2 + \sigma_S^2 + \sigma_g^2 \qquad (l \neq l')$$

$$\mathrm{Cov}(Y_{(ik)\,(jl)z}, Y_{(ik')\,(jl')z'}) = 2\sigma_G^2 + \sigma_S^2 \qquad (k \neq k', l \neq l')$$

$$\mathrm{Cov}(Y_{(ik)\,(jl)z}, Y_{(ik)\,(j'l')z'}) = \sigma_G^2 + \sigma_g^2 \qquad (j \neq j')$$

$$\mathrm{Cov}(Y_{(ik)\,(jl)z}, Y_{(ik')\,(j'l')z'}) = \sigma_G^2 \qquad (j \neq j', k \neq k').$$

It becomes quite obvious that for an interpretation of these covariances the concept of relationship needs to be redefined or broadened. For example, the second and fourth covariance both refer, in the strict genetic sense, to covariances between halfsibs, and yet these covariances as expressed by their right hand sides may be quite different. The problem it seems is to give some genetic interpretation to σ_G^2 and σ_S^2 by introducing what might be called a coefficient of association which is based on some degree of similarity of gene pools for different populations. One definitely needs some structure among the populations (KEMPTHORNE, 1972) and a "simple" way to describe this structure. This problem is presently under investigation.

For each individual hybrid population $P_i \times P_j$ one can use the methods presented by STUBER and COCKERHAM (1966) to characterize the gene effects and genetic variability. Again, an extension of their methods to the situation considered in this paper does not seem to be straight forward and is still under study.

6. Modifications of the mating design

Here we shall make some general remarks about some modifications of the mating design proposed in this paper. Hopefully, this will convey the general idea of what can be done and might be done in addition to what has been presented. Details need to be worked out and will be reported at another time.

1. For several reasons one may wish to include the crosses $P_i \times P_i$ ($i = 1, 2, \ldots, m$), i.e. the usual diallel crosses of Typ II, each consisting of n(n—1)/2 individual crosses. A suitable model for the overall analysis can be obtained by modifying the one used by HARVEY (1960) for analyzing data from purebreds and crossbreds. One important aspect of such an analysis would be to test for heterosis. A simpler ad hoc method would be to consider for each i and j the three crosses $P_i \times P_i$, $P_j \times P_j$, $P_i \times P_j$, and by using a one-way classification analysis compare $(\bar{y}_{(i\,\cdot)\,(i\,\cdot)\,.} + \bar{y}_{(j\,\cdot)\,(j\,\cdot)\,.})/2 - \bar{y}_{(i\,\cdot)\,(j\,\cdot)\,.}$, where the $\bar{y}$'s are the cross means.

2. The analysis presented in Section 4 assumed that the mating design was embedded in a completely randomized environmental design. Another environmental design that could have been used is the randomized complete block design. The analysis would be similar to that used by GRIFFING (1956) in connection with diallel experiments. Basically, as far as the inference about the crosses and their components is concerned, this will not be different from the analysis presented here. But obviously the block size for this kind of experiment will be quite large and hence may not be feasible. An incomplete block design may be the answer to this problem. This needs to be investigated.

3. A partial answer to the problem just mentioned is to use an incomplete mating design, which basically may be one of the following two types: (i) the simple incomplete design, or (ii) the doubly incomplete design.

The simple incomplete design consists of m(m—1)/2 crosses $P_i \times P_j$ but of only a sample of crosses $I_{ik} \times I_{jl}$ for every (i, j). The doubly incomplete design consists of a sample of all population crosses $P_i \times P_j$ and, for those crosses sampled, of a sample of crosses $I_{ik} \times I_{jl}$. The methods of construction follow familiar principles:

For (i): The same principles can be used here that are used for the ordinary partial diallel cross Type I. For every population cross a correspondence is set up between the I_{ik} and the treatments and the I_{jl} and the blocks of a PBIB design such that if treatment k occurs in block l then $I_{ik} \times I_{jl}$ is made. Since $k, l = 1, 2, \ldots, n$ regular PBIB's with n treatments and n blocks will be used (Hinkelmann, 1966).

For (ii): This is a combination of partial diallel crosses of Type I and II. At the population level the methods for constructing a partial diallel cross Type II can be used. A correspondence is set up between the populations and the treatments of a PBIB design with blocks of size two. If treatments i and j occur together in a block then $P_i \times P_j$ will be present (Hinkelmann and Kempthorne, 1963). At the individual level the same principles will be applied as in (i) for every $P_i \times P_j$ sampled.

Summary

A two-level diallel mating design has been defined. A model for the observations from this design has been given together with an appropriate analysis that yields information about various types of combining abilities. The problem of a genetic interpretation of combining ability variances has been discussed. Finally some modifications of the mating design have been mentioned.

Key words: Diallel, mating design, inter-population crosses, combining abilities, incomplete mating design.

Zusammenfassung

Ein zweistufiger dialleler Kreuzungsplan wird definiert. Ein Modell für die Beobachtungen nach diesem Plan wird vorgeschlagen mit der dazugehörigen Auswertung. Hieraus erhält man Information über verschiedene Arten von Kombinationseignungen. Das Problem der genetischen Interpretation der Kombinationseignungsvarianzen wird kurz diskutiert. Schließlich werden noch einige Modifikationen des Kreuzungsplanes erwähnt.

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Genetischer Abstand zwischen Populationen

I. Zur Konzeption der genetischen Abstandsmessung

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(Eingegangen im Januar 1974)

Das Ziel der vorliegenden Ausführungen besteht darin, aus der Diskussion einiger in der Praxis häufiger zur Anwendung gelangter genetischer Abstandsmaße Kriterien herzuleiten, die geeignet sind, eine klare Konzeption des Begriffes ‘genetischer Abstand zwischen Populationen’ zu formulieren. Hieraus werden sich auf natürliche Weise mehrere konkrete Vorschläge für die genetische Abstandsmessung ergeben.

Diskussion einiger gebräuchlicher genetischer Abstandsmaße

Ein Vergleich zweier Populationen auf genetischer Grundlage wird im allgemeinen an zwei verschiedenen Stufen interessieren, an der Stufe des Genotyps oder des Gens. Die unmittelbarste Art und Weise, einen solchen Vergleich anzustellen besteht wohl darin zu klären, bis zu welchem Grade die Genotyp- bzw. Genhäufigkeiten, d. h. also die genetischen Strukturen bzw. die genetischen Kompositionen beider Populationen miteinander identifiziert werden können. Andererseits leitet sich die genetische Struktur einer Population aufgrund spezieller Paarungsverhältnisse im Zusammenhang mit Selektion, Drift etc. von ihrer genetischen Komposition ab, so daß also der genetischen Komposition die elementarere Bedeutung zukommt. Es ist daher sinnvoll, den als Grad der Abweichung von der Identität aufgefaßten Abstand zwischen zwei Populationen auf die Genhäufigkeiten zu beziehen und jede Population durch ihre genetische Komposition darzustellen. Die Messung eines Abstandes zwischen Populationen (bzw. deren genetischen Kompositionen) geschieht in der Mathematik mit Hilfe einer Metrik, die definiert ist auf der Menge aller miteinander zu vergleichenden Populationen. Ein ‘genetisches Abstandsmaß’ sollte möglichst alle Eigenschaften einer solchen Metrik besitzen, d. h. es sollte 1) nur nichtnegative reelle Werte annehmen, 2) symmetrisch sein, d. h. Population A sollte zu Population B den gleichen Abstand wie Population B zu Population A haben, 3) den Wert 0 nur genau dann annehmen, wenn die beiden verglichenen Populationen identisch sind, 4) der Dreiecksungleichung genügen, damit die Abstände einer Population zu zwei anderen miteinander verglichen werden können. Diese Forderungen bringen offensichtlich zum Ausdruck, was man sich intuitiv unter einem ‘Abstand’ vorstellt.

Denkt man sich die Allel-Wahrscheinlichkeiten an den zu betrachtenden Loci in Vektorform angeordnet, so erhält man auf natürliche Weise eine Repräsentation der einzelnen Populationen als Punkte (Ortsvektoren) in einem