Conclusions

(1) The hypothesis of the genetic superiority of "plus" trees over "ordinary" trees being due to more outbreeding in the former than in the latter is further supported. (2) Family as well as mass selection out of the "plus" trees is more advantageous than similar selection out of the "ordinary" trees for specified selection differentials. (3) Establishment of seed orchards of "plus" trees and control pollination among phenotypically superior trees in the second generation is indicated as a possible step to increase genetic gain.

Acknowledgements

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References


Estimating parent effects in full-sib progeny tests following use of an irregular mating design

By F. H. Kong

(Received March 1 August 1978)

Summary

In an irregular mating design, a particular female might produce good progeny because it was mated with good males rather than because of her own genetic quality. To overcome that difficulty, direct comparisons are made among families sharing pairs of parents. The general combining ability of a parent then is the average difference between that parent and all parents in the test.

Zusammenfassung

In einem unvollständigen Kreuzungsplan bestehen Fehl-

merkmale bei der Schätzung der allgemeinen Kombi-

nationseignung (AKE). Beispielsweise kann ein Lucifer-

baum von nur geringer genetischer Qualität eine große

Nachkommenschaft hervorbringen, wenn er mit einem gut-


Introduction

Full-sib progeny tests can provide information on specific combining ability as well as general combining ability. Data on general combining ability are obtained by calculating the effects due to female parents and male parents. Differences among family means due to the particular combination between male and female parents rather than to general male or female effects are considered to constitute specific combining ability. Effects due to female or male parents are calculated easily for a diallel experiment in which every female is crossed with every other tree in all possible combinations. They are also easily calculated for experiments following NC State Design II, where each female is crossed with the same three or four males. In either case the effect due to a particular female (or male) parent is calculated by considering the average performance of the offspring of that female (or male) parent in all combinations because every female was crossed with the same set of males.

Either by design or by accident, it is not always true that each female is crossed with the same set of males. Usually each female is crossed with a different set of males, or a given set of males might be crossed with one set of females and another set of males crossed with another set of females. In that case, a particular female might produce good progeny because it was mated with good males rather than because of its own genetic quality. If so, it could be regarded as having high general combining ability even though it was really below average genetically.

The present method was devised to overcome that difficulty. Briefly, the method involves a series of comparisons among families sharing pairs of parents.

The following table gives the results of analysis of variance. The value of 175 is the average height of all the control pollinated seedlings. The other heights are differences from this average. The data were analyzed using analysis of variance and Duncan's new multiple range test. The results are presented in Table 1.

Table 1. Height of control pollinated offspring resulting from crossing male parents A through I with female parents R through Z.

<table>
<thead>
<tr>
<th>Male</th>
<th>Parent</th>
<th>Female Parent</th>
<th>Height in arbitrary units</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>4</td>
<td>16</td>
<td>25</td>
</tr>
<tr>
<td>B</td>
<td>25</td>
<td>19</td>
<td>31</td>
</tr>
<tr>
<td>C</td>
<td>26</td>
<td>34</td>
<td>45</td>
</tr>
<tr>
<td>D</td>
<td>35</td>
<td>41</td>
<td>49</td>
</tr>
<tr>
<td>E</td>
<td>44</td>
<td>56</td>
<td>60</td>
</tr>
<tr>
<td>F</td>
<td>54</td>
<td>61</td>
<td>66</td>
</tr>
<tr>
<td>G</td>
<td>34</td>
<td>41</td>
<td>56</td>
</tr>
<tr>
<td>H</td>
<td>41</td>
<td>49</td>
<td>55</td>
</tr>
<tr>
<td>I</td>
<td>46</td>
<td>49</td>
<td>60</td>
</tr>
</tbody>
</table>

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Table 2. — Average differences in male effects, calculated from the data in Table 1 by considering families having common male and female parents. The family means for the second-mentioned male parent were subtracted from the family means for the first-mentioned male parent.

<table>
<thead>
<tr>
<th>First mentioned male parent</th>
<th>Second mentioned male parent</th>
<th>Sum for first mentioned male parent</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>0.00</td>
<td>-4.5</td>
<td>-9.5</td>
</tr>
<tr>
<td>B</td>
<td>4.5</td>
<td>0</td>
</tr>
<tr>
<td>C</td>
<td>9.5</td>
<td>5</td>
</tr>
<tr>
<td>D</td>
<td>15.5</td>
<td>10.5</td>
</tr>
<tr>
<td>E</td>
<td>18.0</td>
<td>14.0</td>
</tr>
<tr>
<td>F</td>
<td>30.0</td>
<td>26.0</td>
</tr>
<tr>
<td>G</td>
<td>35.0</td>
<td>30.0</td>
</tr>
<tr>
<td>H</td>
<td>41.0</td>
<td>34.0</td>
</tr>
</tbody>
</table>

Details of the Method

The first step is to compile a table similar to Table 1 showing the performance of each full-sib family. Note that Table 1 is so organized as to show quickly which families share the same male parent or share the same female parent.

The next step is to calculate differences among families sharing female parents and having the same pair of male parents. Let us consider the families sharing female parents A and B in Table 1, we shall pay attention only to four full-sib families: AxT, AxV, BxT and BxV. On the other hand, families which the female parent has married only once, either to A or B but never to both, should be excluded. Those families excluded from comparison between A and B are AxR, AxU, BxS and BxW. By the same token, family ExV should be excluded if male parents E and F are compared.

The families having male parent A (families AxT and AxV) have mean heights of 16 and 25, or a mean height for the two families of (16 + 25)/2 = 20.5. The families having male parent B (families BxT and BxV) have mean heights of 19 and 31, or a mean height for the two families of (19 + 31)/2 = 25. The difference between the offspring of A having a mean height of 20.5 and the offspring of B having a mean height of 25 is 20.5 — 25 = —4.5, which value is entered in Table 2 as the difference between first-mentioned male parent A and second-mentioned male parent B. That difference of —4.5 is one way of saying that male parent A has a 4.5 unit less genetic quality than male parent B, where the possible effect of female parent has been nullified.

Let us pursue this example, and compare male parents A and C. Both have been mated with female parents T and V to produce families AxT, AxV, CxT and CxV, with means of 16, 25, 26 and 34 respectively. The average height of the offspring of male parent A is (16 + 25)/2 = 20.5 and the average height of the offspring of male parent C is (26 + 34)/2 = 30. Therefore, the average A — C difference is 20.5 — 30.0 = —9.5, which is the value entered in Table 2 as the difference between first-mentioned male parent A and second-mentioned male parent C.

In a similar manner, all other comparisons between families having male parent A and other male parents were made. No comparison between the offspring of A and F could be made because no females which had been crossed with A had also been crossed with F. The sum for male parent A as the first-mentioned male parent is —154.5 (Table 2). In the same way, male parent F is compared with all the other male parents, and is found to produce a sum of 20.7 for all F vs others comparisons.

Let us denote the effect of parent A in a family as Aeff, and the effect of parent B in a family as Beff. The first line in Table 2 can be considered as:

(Aeff — Aeff) + (Aeff — Beff) + (Aeff — Ceff) + (Aeff — Deff) + (Aeff — Eeff) + (Aeff — Feff) + (Aeff — Geff) + (Aeff — Heff) + (Aeff — Ieff) = —154.5

The sum of (Aeff + Beff + … + Ieff) = 0 deviation from the population mean, so the above statement can be reduced to

8 Aeff — 0 + Feff = 8 Aeff + Feff = —154.5

Similarly, the sixth line in Table 2 can be reduced to 8 Beff + Aeff = 20.7. Now there are two equations for estimating the Aeff and Feff even though the direct comparisons between A and F are missing. These can be considered to be simultaneous equations and solved accordingly in the following manner:

8 Aeff + Feff = —154.5
8 Beff + Aeff = 20.7
Aeff = —19.95, Feff = 5.09

In similar manner, two simultaneous equations can be formed to solve for Ceff and Ieff, since there are no direct comparisons between C and I.

Such simultaneous equations are not needed for male parents B, D, E, G, and H, for which there were direct comparisons with all other parents. In some cases it is possible to calculate the male parent effects directly from Table 2 by means of a single equation for each male parent. For example, 9 Beff = —134.0 and Beff = —14.9; 9 Deff = —45.7 and Deff = —5.1.

Calculation of Female Effects

The above discussion described the method of calculating effects due to male parent. Exactly the same technique may be used to calculate the effect of female parent. Calculation of the male and female effects can proceed separately.

Practical Example

In a study of breeding blister rust resistant western white pine, Bingham, Squillace and Weight (1960) obtained 53 control-polliinated progenies from eighteen different parents. Because six parents were used as both male and female parents, there were 11 female and 13 male parents presented in their Table 2.

A computer program was written to solve above example. The program, the reproduction of their Table 2 and the solution are listed in the Appendix. With a few substitutions on the dimension and format cards, the reader can obtain estimates of parent effect from an irregular mating experiment.

Discussion

Although a simple simulated example was used here for illustration, the proposed method will work on a larger full-sib progeny test experiment in a very irregular manner. The computer program listed in the Appendix can handle up to 8960 crosses (missing crosses included). For a 5-tester breeding program, 1792 mother trees can be evaluated. The computer program has been checked against hand computation using data from Table 1, and found to be functional with data from Bingham, Squillace and Weight (1960).

The proposed method is specially suitable to study a few parents which have direct comparison with all other parents, because the solution does not involve solving simultaneous equations. In contrast to the least square solution which requires calculation for all parent effects, this one gives the user liberty to calculate parent effect one by one. For example, assuming that male parent B is excellent in disease resistance and we wish to know how good is the general combining ability in height growth for that par-
Appendix I.

CADDY SETUP

(1)讀入程式，並以信件C1於一欄
(2)解析程式，並於另一欄
(3)JCL = 2 CARDS.
(4)DATA REM: 1
(5)END CARD AND 2 DATA 0
(6) TERMINATION CARD = 2 CARDS.

NOTE

(1) DATA REM: 1 IN INPUT DATA CORRESPONDS TO NO DATA RATHER THAN
(2) DATA REM: 1 STOP.
(3) DATA REM: 3 INSIDE PROCESS REMARKS IS USED TO IDENTIFY COLUMN.
(4) DATA REM: 1 IN OUTPUT DATA CORRESPONDS TO BETA COLUMN.
(5) DATA REM: 1 IN OUTPUT DATA REMARKS IS USED TO IDENTIFY COLUMN.
(6) OPERATIONS FOR SIMULTANEOUS EQUATIONS ARE DESCRIBED IN
(7) MANUFACTORING SIMPLI.

NOTE ON DIMENSION FORMAT

A REPORT CARD IN THIS PROGRAM ARE BASED ON MANIPULATION WITHIN
(1) 100 CARDS, 3 DATA PER CARD (600 TEN-LETTER DATA ITEMS)
(2) EACH CARD IS FREQUENTLY COUNTED FROM THE TOP,
(3) EACH CARD HAS A COLUMN WITH A COLUMN.

SIMULTANEOUS EQUATIONS WERE SET UP AS FOLLOWS 1
(1) SCAN OUTPUT MATRIX AT POINT1 FOR #ROW.
(2) IF NO WHITES OR 10 TO 11 FOR NEXT ROW.
(3) IF WHITES IS ENCOUNTERED, COUNT IN COLUMN, SET
(4) IF WHITES IS ENCOUNTERED, COUNT IN COLUMN
(5) IF WHITES IS ENCOUNTERED, COUNT IN COLUMN
(6) IF WHITES IS ENCOUNTERED, COUNT IN COLUMN
(7) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(8) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(9) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(10) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(11) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(12) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(13) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(14) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(15) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(16) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(17) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(18) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(19) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
(20) OPERATIONS FOR SIMULTANEOUS EQUATIONS AS
ticular one, we need only complete the 9th row of Table 2 and we can see immediately parent H has a general combining ability of 134/9 = 14.89. If the problem were solved by the least square method and by hand calculation, it would be much more laborious.

Another advantage of using this method is the ease of comparison. Just by observing the 9th row of Table 2, one can see immediately that male parent H is inferior only to male parent I but is superior to all others. By conventional procedure, comparison cannot be made until all parent effects are calculated.

This procedure gives an approximate solution for irregular mating schemes. The better the regularity, the better is the approximation. If the procedure is applied to balanced data, results from this procedure are identical to the least square estimates. Usually the discrepancies are too small to be significant.

Literature Cited


Pinus patula Schiede and Deppe progeny tests in Rhodesia Genetic control of nursery traits

By R. D. BARNES and M. A. SCHWEPPE/NHAUSER

(Received May / August 1978)

Summary

A number of characteristics were assessed during the twelve-month nursery period of Pinus patula Schiede and Deppe seedlings raised for factorial (NCM II, 5 x 9) and reciprocal (diallel without selfs, 7 x 7) progeny tests. Both cotyledon number and length were under some general combining ability control with family heritabilities of 0.64 and 0.25 respectively and there was a high negative genetic correlation (~0.91) between them. Numbers of whorls and branches had family heritabilities of 0.55 and 0.45. Dominance effects were predominant in the genetic control of seedling height in the first six months of nursery life but general combining ability effects rose steadily and by 12 months dominance had disappeared and heritabilities were between 0.63 and 0.78; in addition, there was no correlation between seedling height at one and twelve months; this suggests that different genes control height at the beginning and end of the nursery phase. The seed weight-seedling height relationship was strongest at three months but had almost disappeared by twelve months. There is sufficient variation and genetic control of these nursery traits to indicate that investigation of correlations with mature field characteristics could prove useful.

Key words: Pinus patula Schiede and Deppe, progeny tests, diallel, factorial mating design, general combining ability, specific combining ability, maternal effects, reciprocal effects.

Zusammenfassung

In einer Baumschule in Rhodesien wurden bei einjährigen Sämlingen von Pinus patula Schiede et Deppe aus einem Kreuzungsdiallel (ohne Selbstungen) die Anzahl und Länge der Kotyledonen, die Anzahl der Quirlen und Äste sowie die Höhe ermittelt. Sowohl die Anzahl als auch die Länge der Kotyledonen zeigten eine gute allgemeine Kombinationsseignung mit Heritabilitäten (Familie) von 0.64 bzw. 0.25 und eine hohe negative Korrelation von ~0.91 zwi-

1) The paper is adapted from part of the senior author's Ph. D. thesis (1972).
2) Rhodesia Forestry Commission, Forest Research Centre, Salisbury, Rhodesia. (Commonwealth Forestry Institute, Oxford, England from October, 1977.)
3) Department of Agriculture, University of Rhodesia, Salisbury.

Introduction

A breeding programme for the genetic improvement of Pinus patula Schiede and Deppe in Rhodesia was started in 1958. Initially it was proposed that a polycross progeny test design would be used but in 1964 the plan was reviewed because it was felt that, particularly in the early stages of this programme, the progeny testing method used should not only identify the best general combiners, but should also yield information on population genetics. A revised plan was drawn up in which the polycross test was supplemented with factorial (NCM II) and reciprocal (diallel without selfs) mating designs. The review of progeny test methods, together with the adopted plan and the bases for analyses of variance, have been described by BURLEY, BURROWS, ARMITAGE and BARNES (1966). The controlled crosses for this test plan were completed in 1967 and the results of the nursery experiments are described here.

Materials

Nursery experiments were confined to the factorial and the reciprocal tests. In November 1967 seed was sown for the first part of the factorial test which consisted of 45 full-sib families with five tester clones used as pollen, on nine other clones as seed parents (see Figure 1). Seeds were soaked in water for 24 hours and those from the sinking fraction were sown singly in 8 cm (diameter) by 15.2 cm (depth) black polythene tubes which were filled with a uniform nursery soil mix. The experiment was laid out in a randomized complete block design with six replications of 30-seedling plots (10 x 3 tubes); the middle row of eight seedlings was the measured plot. Ungerminated or killed seedlings in the measured plot were replaced from the