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.

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

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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.

Key words: Unbalance incomplete design, family effect, intrablock information.

Zusammenfassung

In einem unvollständigen Kreuzungsplan bestehen Fehlermöglichkeiten bei der Schätzung der „Allgemeinen Kombinationseignung (AKE). Beispielsweise kann ein Mutterbaum von nur geringer genetischer Qualität eine gute Nachkommenschaft hervorbringen, wenn er mit einem guten Vaterbaum gekreuzt wird. Zur Problemlösung wird eine mathematische Auswertungsmethode dargestellt.

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 to 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 perforrnance 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.

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

Male Parent	Female Parent								
	R	S	T	U	V	W	X	Y	Z
	-------height in arbitrary units----------								
A	4	--	16	20	25	--	--	--	--
B	--	15	19	--	31	35	--	--	--
C	--	--	26	--	34	--	45	--	--
D	--	--	--	35	41	46	49	54	--
E	--	--	--	--	44	50	56	60	65
F	--	--	--	--	--	54	61	66	69
G	34	41	--	--	--	--	64	70	76
H	41	--	49	--	--	--	--	75	--
I	46	49	--	60	--	--	--	--	85

---

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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.

First mentioned male parent	Second mentioned male parent									Sum for first mentioned male parent
	A	B	C	D	E	F	G	H	I	
	--------Ave. diff. of ht. in arbitrary units-------									
A	0	-4.5	-9.5	-15.5	-19	--	-30	-35	-41	-154.5
B	4.5	0	-5	-10.5	-14	-19	-26	-30	-34	-134.0
C	9.5	5	0	-5.5	-10.5	-16	-19	-23	--	-59.5
D	15.5	10.5	5.5	0	5	-10.7	-15.5	-21	-25	-45.7
E	19	14	10.5	5	0	-4.8	-9.7	-15	-20	-0.9
F	--	19	16	10.7	4.8	0	-4.7	-9	-16	20.7
G	30	26	19	15.5	9.7	4.7	0	-6	-9.7	89.2
H	35	30	23	21	15	9	6	0	-5	134.0
I	41	34	--	25	20	16	9.7	5	0	150.7

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 first. If we want to compare male parents A and B in *Table 1*, we should pay attention only to four full-sib families: AxT, AxV, BxT and BxV. On the other hand, families which the female parent has mated 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 4.5 units 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 — 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 Feff + 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 Feff + 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 such 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 Wright (1960) obtained 53 control-pollinated 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 Wright (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 H is excellent in disease resistance and we want to know how good is the general combining ability in height growth for that par-

Appendix I. —

```
C
C   CARD DECK SET-UP :
C
C   (A)   JCL - 3 CARDS.
C
C   (B)   COMMENTS FOR THE PROGRAM.  PRECEDED BY LETTER 'C' IN COL 1 OF
C         EACH CARD.
C
C   (C)   PROGRAM - SUBDIVIDED INTO SUBROUTINES.
C
C   (D)   JCL - 2 CARDS.
C
C   (E)   DATA INPUT :
C         1ST CARD - COL 1 - 3, IROW
C                    COL 4 - 6, ICOL
C         2ND CARD AND ON : DATA IN PRE-DETERMINED FORMAT
C
C   (F)   TERMINATION CARD - 2 CARDS.
C
C   NOTE :
C
C   (1)   CODE OF 0.0 IN INPUT DATA CORRESPONDS TO NO DATA RATHER THAN
C         ZERO-READINGS.
C
C   (2)   CODE OF -999.0 IN (I,J)TH POSITION OF OUTPUT MEANS ROWS I AND J
C         HAVE NO NON-ZERO PAIRED ELEMENTS IN SAME COLUMN.
C
C   (3)   THE INPUT DATA WERE TRANSPOSED TO PERFORM COLUMN OPERATION
C         UNDER THE SAME SCHEME.  RESULTS WERE TRANSPOSED FIRST BEFORE
C         OUTPUT.
C
C   (4)   OPERATIONS FOR SIMULTANEOUS EQUATIONS ARE DESCRIBED IN
C         SUBROUTINE SIMEQU.
C
C   (5)   IT IS NECESSARY TO CHANGE ALL FORMAT CARDS TO SUIT SPACING FOR
C         INPUTS AND OUTPUTS OF DIFFERENT DIMENSIONS EXCEPT THOSE FOR
C         HEADING OUTPUTS.
C
C*****************************************************************
C
C   NOTE ON DIMENSION FORMAT :
C
C      THE ARRAYS USED IN THIS PROGRAM ARE BASED ON MANIPULATION WITHIN
C   A REGION OF 100K.  LARGER WORKING AREAS ARE POSSIBLE THROUGH DECLARATION
C   OF REGION = N * K,  WHERE N IS USUALLY TAKEN TO BE 128, 192, 200, 256,
C   300, UP TO 560.  ALL ARRAYS CAN THUS BE EXPANDED ACCORDING TO THE
C   RATIO OF N : 100 AS FOLLOWS :
C
C               N        MAX. R X C
C              ---       ----------
C
C              100          1600


C              128          1948
C              192          3072
C              200          3200
C              256          3896
C              300          4800
C              400          6400
C              500          8000
C              560          8960
C
C*****************************************************************
```

```
C
C   SIMULTANEOUS EQUATIONS WERE SET UP AS FOLLOWS :
C
C   (1)   SCAN OUTPUT MATRIX AT ROW(I) FOR -999.0.
C
C   (2) IF NO -999.0, GO TO (1) FOR NEXT ROW.
C
C   (3)   IF -999.0 IS ENCOUNTED, COUNT ITS APPERANCE IN ROW(I), SAY
C         KNT.  THEN COMPUTE A = COLUMN KOUNT - KNT.
C
C   (4)   SET 1ST VARIABLE IN 1ST EQUATION TO A*X(I), WHERE I IS ROW(I)
C         WITH -999.0.
C
C   (5)   SET X(J), J = 2,...., N TO CORRESPOND TO COLUMN COUNT WITH
C         -999.0, COEFFCIENT = 1.
C
C   (6)   SET 1ST EQUATION AS :
C
C            A*X(I) + X(J) + ... + X(N) = ROWSUM(I)
C
C   (7)   SET CORRESPONDING EQUATIONS AS :
C
C         X(I) + A*X(J) + X(J+1) ... + X(N) = ROWSUM(J)
C         AND CONTINUES TO GET N UNKNOWNS WITH N EQUATIONS.
C
C   (8)   PERFORM GAUSSIAN ELIMINATION TO SOLVE FOR X(I), I = 1,...., N.
C
```

```
      REAL MATRIX(40,40),OUTPUT(40,41),TEMP(40,40),VARBLE(40)
      INTEGER STATUS(40)
      COMMON MATRIX,OUTPUT,IROW,ICOL,ICOLL
      READ (5,10) IROW,ICOL
   10 FORMAT (2I3)
      READ (5,11) ((MATRIX(I,J),J=1,ICOL),I=1,IROW)
   11 FORMAT (13F2.0)
      WRITE (6,13)
   13 FORMAT ('1',120('*')/'0','INPUT DATA'/)
      WRITE (6,15) ((MATRIX(I,J),J=1,ICOL),I=1,IROW)
   15 FORMAT (' ',13F7.1)
      WRITE (6,17)
   17 FORMAT ('1',120('*')/'0AVERAGE DIFFERENCE BETWEEN ROWS WHICH HAVE
     * COMMON COLUMNS')
      CALL ROWDIF
      CALL ROWSUM(0)
      CALL SEPRAT(0,VARBLE,STATUS)
      CALL SIMEQU(0,VARBLE,STATUS)
      DO 900 I=1,IROW
      DO 900 J=1,ICOL
      TEMP(J,I)=MATRIX(I,J)
  900 CONTINUE
      DO 910 I=1,ICOL
      DO 910 J=1,IROW
      MATRIX(I,J)=TEMP(I,J)
  910 CONTINUE
      WRITE (6,19)
   19 FORMAT ('1',120('*')/'0AVERAGE DIFFERENCE BETWEEN COLUMNS WITH
     *COMMON ROWS')
      IROW=ICOL
      CALL ROWDIF
      CALL ROWSUM(1)
      CALL SEPRAT(1,VARBLE,STATUS)
      CALL SIMEQU(1,VARBLE,STATUS)
      STOP
      END
```

```
C   ROW SUMMATION OF DIFFERENCES OF ELEMENTS IN DIFFERENT ROWS.
C
C   CODE :
C       MATRIX - STORAGE AREA FOR INPUT
C       OUTPUT - STORAGE AREA FOR OUTPUT
C       ISUM - SUMMATION OF ROW DIFFERENCES
C       KNT - COUNT OF NON-ZERO PAIRED ELEMENTS IN SAME COLUMN,
C             DIFFERENT ROWS
C       SUM - SUMMATION OF OUTPUT ROWWISE
C       IROW - NUMBER OF ROWS IN INPUT
C       ICOL - NUMBER OF COLUMNS IN INPUT
C       NO999 - STORAGE AREA FOR ROWS WITH NO -999.0
C       KNTNO - COUNT OF ROWS FOR NO999
C       HAS999 - STORAGE AREA FOR ROWS WITH -999.0
C       KNTHAS - COUNT OF ROWS FOR HAS999
C       SIMUL - STORAGE AREA FOR COEFFICIENTS OF SIMULTANEOUS EQUATIONS
C       SIMROW - ROW COUNT FOR SIMUL
C       SIMCOL - COLUMN COUNT FOR SIMUL
C       ICOEFF - STORAGE ARRAY FOR VARIABLE COEFFICIENTS UNDER CURRENT
C                OPERATION
C       STATUS - INDICATION FOR ROWS IN SIMUL FOR OPERATION :
C            0 - REQUIRES OPERATION
C            1 - OPERATION COMPLETED
C            2 - REQUIRES NO OPERATION
C       VARBLE - STORAGE ARRAY FOR VARIABLES
C
C


C*****************************************************************
C
C
C   SUBROUTINE ROWDIF AND ROWSUM OPERATIONS :
C
C       LET I = ROW UNDER OPERATION
C           J = NEXT ROW UNDER OPERATION
C           K = COLUMN UNDER OPERATION
C
C   (1)   SET I=1, J=1, K=0, ISUM=0, KNT=0
C
C   (2)   K=K+1
C         IF K > ICOL, GO TO 6
C
C   (3)   IF EITHER OR BOTH MATRIX(I,J) OR MATRIX(J,I)=0, GO TO 2
C
C   (4)   DIFF=MATRIX(I,K)-MATRIX(J,K)
C         KNT=KNT+1
C
C   (5)   ISUM=ISUM+DIFF, GO TO 2
C
C   (6)   IF KNT=0, ISUM=-999
C         OUTPUT(I,J)=ISUM
C         OUTPUT(J,I)=-ISUM
C         K=0, ISUM=0, KNT=0,
C         J=J+1
C         IF J > IROW, GO TO 8
C
C   (7)   GO TO 2
C
C   (8)   I=I+1,
C         IF I <= IROW, GO TO 2
C
C   (9)   SUMMATION OF I-TH ROW (I=1,IROW) IN OUTPUT MATRIX AND PUT SUM
C         IN OUTPUT(I,ICOL+1)
C
C*****************************************************************
C
C   SUBROUTINE SEPRAT OPERATIONS :
C
C      AFTER CARRYING OUT THE ROW DIFFERENCE AND SUMMATION OPERATIONS,
C   THE OUTPUT IS SORTED INTO TWO MATRICES :
C
C   NO999 - CONSISTS OF ROWS WITH NO -999.0 UNDER SUITABLE HEADING.
C
C   HAS999 - CONSISTS OF ROWS HAVING -999.0 UNDER SUITABLE HEADING.
C
C*****************************************************************
C
```

```
      SUBROUTINE SIMEQU(IFLG,VARBLE,STATUS)
      REAL MATRIX(40,40),OUTPUT(40,41),SIMUL(20,21),VARBLE(40)
      INTEGER STATUS(40),SIMROW,SIMCOL,ICOEFF(20)
      COMMON MATRIX,OUTPUT,IROW,ICOL,ICOLL

      DO 600 I=1,IROW
      KNTCOE=0
      IF (STATUS(I).EQ.1.OR.STATUS(I).EQ.2) GO TO 600
      KNTCOE=KNTCOE+1
      ICOEFF(KNTCOE)=I
      VARCNT=0.0
      DO 610 J=1,ICOL
      IF (OUTPUT(I,J).NE.-999.0) GO TO 611
      KNTCOE=KNTCOE+1
      ICOEFF(KNTCOE)=J
      GO TO 610
  611 VARCNT=VARCNT+1.0
  610 CONTINUE
      SIMROW=KNTCOE
      SIMCOL=KNTCOE+1
      DO 620 K=1,SIMROW
      DO 630 L=1,SIMROW
      SIMUL(K,L)=1.0
  630 CONTINUE
      SIMUL(K,K)=VARCNT
  620 CONTINUE
      DO 640 J=1,SIMROW
      JJ=ICOEFF(J)
      STATUS(JJ)=1
      SIMUL(J,SIMCOL)=OUTPUT(JJ,ICOLL)
  640 CONTINUE
      MULTPY=SIMROW-1
      DO 650 J=1,MULTPY
      JJ=J+1
      DO 660 K=JJ,SIMROW
      PIVOT=SIMUL(J,J)/SIMUL(K,J)
      DO 660 L=J,SIMCOL
      SIMUL(K,L)=SIMUL(K,L)*PIVOT
  660 CONTINUE
      DO 670 K=JJ,SIMROW
      DO 670 L=J,SIMCOL
      SIMUL(K,L)=SIMUL(J,L)-SIMUL(K,L)
  670 CONTINUE
  650 CONTINUE
      DO 680 J=1,SIMROW
      JJ=SIMROW+1-J
      IF (J.EQ.1) GO TO 685
      JK=JJ+1
      SUM=0.0
      DO 690 K=JK,SIMROW
      SUM=SUM+SIMUL(JJ,K)
  690 CONTINUE
      SIMUL(JJ,SIMCOL)=SIMUL(JJ,SIMCOL)-SUM
  685 SIMUL(JJ,SIMCOL)=SIMUL(JJ,SIMCOL)/SIMUL(JJ,JJ)
      JROW=ICOEFF(JJ)
      VARBLE(JROW)=SIMUL(JJ,SIMCOL)
      DO 695 KK=1,JJ
      SIMUL(KK,JJ)=SIMUL(JJ,SIMCOL)*SIMUL(KK,JJ)
  695 CONTINUE
  680 CONTINUE


  600 CONTINUE
      IF (IFLG.EQ.1) GO TO 697
      WRITE (6,556)
  556 FORMAT ('1',120('*')/'0VALUES OF VARIABLES : ')
      DO 920 I=1,IROW
      WRITE (6,557) (I,VARBLE(I))
  557 FORMAT ('0X(',I2,') = ',F8.3)
  920 CONTINUE
      RETURN
  697 WRITE (6,556)
      DO 930 I=1,IROW
      WRITE (6,558) (I,VARBLE(I))
  558 FORMAT ('0Y(',I2,') = ',F8.3)
  930 CONTINUE
      RETURN
      END
```

Appendix II. —

```
      SUBROUTINF ROWSUM(IFLG)
      REAL MATRIX(40,40),OUTPUT(40,41),TEMP(41,40)
      COMMON MATRIX,OUTPUT,IROW,ICOL,ICOLL
      DO 300 I=1,IROW
      SUM=0.0
      DO 310 J=1,ICOL
      IF (OUTPUT(I,J).EQ.-999.0) GO TO 310
      SUM=SUM+OUTPUT(I,J)
  310 CONTINUE
      OUTPUT(I,IROW+1)=SUM
  300 CONTINUE
      ICOLL=IROW+1
      IF (IFLG.EQ.1) GO TO 320
      WRITE (6,500) (I,I=1,IROW)
  500 FORMAT ('0',3X,11(5X,I2),1X,'ROWSUM'/)
      WRITE (6,501) (I,(OUTPUT(I,J),J=1,ICOLL),I=1,IROW)
  501 FORMAT (' ',I2,')',12F7.1)
      RETURN
  320 WRITE (6,511) (I,I=1,IROW)
  511 FORMAT ('0',7X,13(5X,I2))
      DO 330 I=1,IROW
      DO 330 J=1,ICOLL
      TEMP(J,I)=OUTPUT(I,J)
  330 CONTINUE
      DO 340 I=1,ICOLL
      IF (I.EQ.ICOLL) GO TO 345
      WRITE (6,512) (I,(TEMP(I,J),J=1,IROW))
  512 FORMAT (' ',4X,I2,')',13F7.1)
      GO TO 340
  345 WRITE (6,513) (TEMP(I,J),J=1,IROW)
  513 FORMAT (' ','COLSUM)',13F7.1)
  340 CONTINUE
      RETURN
      END
```

```
      SUBROUTINE ROWDIF
      REAL MATRIX(40,40),OUTPUT(40,41),ISUM
      COMMON MATRIX,OUTPUT,IROW,ICOL,ICOLL
      DO 100 I=1,IROW


      DO 110 J=I,IROW
      ISUM=0.0
      KNT=0
      DO 120 K=1,ICOL
      IF (MATRIX(I,K).EQ.0.OR.MATRIX(J,K).EQ.0) GO TO 120
      ISUM=ISUM+(MATRIX(I,K)-MATRIX(J,K))
      KNT=KNT+1
  120 CONTINUE
      IF (KNT.EQ.0) GO TO 200
      OUTPUT(I,J)=ISUM/FLOAT(KNT)
      IF (I.EQ.J) GO TO 110
      OUTPUT(J,I)=-OUTPUT(I,J)
      GO TO 110
  200 OUTPUT(I,J)=-999
      OUTPUT(J,I)=-999
  110 CONTINUE
  100 CONTINUE
      RETURN
      END
```

```
********************************************************************************
INPUT DATA
    8.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0   18.0    0.0   14.0    0.0    0.0
    7.0    0.0    0.0    0.0    0.0    5.0    0.0    0.0    4.0    0.0    3.0    0.0    0.0
    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0   25.0    0.0   24.0    0.0    0.0
   18.0   16.0    7.0   37.0   16.0   40.0   30.0    0.0    0.0    5.0   16.0    0.0   24.0
    5.0    0.0    6.0    0.0    0.0    0.0   40.0   25.0    0.0    0.0    6.0    0.0    4.0
    0.0    0.0    0.0   34.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    1.0    0.0
   35.0    0.0    0.0   36.0    0.0    0.0    0.0    0.0   22.0    6.0   17.0    0.0    0.0
    0.0    0.0   12.0   23.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0
    0.0    8.0    0.0    0.0   12.0    6.0    0.0    0.0    0.0    0.0   17.0    0.0    0.0
    9.0    0.0    0.0    0.0    0.0    5.0    0.0    0.0   21.0    0.0    0.0    8.0    0.0
    0.0    0.0   15.0   49.0   43.0   46.0   34.0   36.0   35.0   24.0   21.0   23.0   11.0
********************************************************************************
AVERAGE DIFFERENCE BETWEEN ROWS WHICH HAVE  COMMON COLUMNS
         1      2      3      4      5      6      7      8      9     10     11 ROWSUM
 1)    0.0    8.7   -8.5   -6.0    5.5 -999.0  -11.3 -999.0   -3.0   -2.0  -12.0  -28.7
 2)   -8.7    0.0  -21.0  -19.7   -0.5 -999.0  -20.0 -999.0   -7.5   -6.3  -30.0 -113.7
 3)    8.5   21.0    0.0    8.0   18.0 -999.0    5.0 -999.0    7.0    4.0   -3.5   68.0
 4)    6.0   19.7   -8.0    0.0    6.8    3.0   -4.5    4.5   11.3   22.0   -8.5   52.2
 5)   -5.5    0.5  -18.0   -6.8    0.0 -999.0  -20.5   -6.0  -11.0   -4.0   -7.6  -78.9
 6) -999.0 -999.0 -999.0   -3.0 -999.0    0.0   -2.0   11.0 -999.0   -7.0  -18.5  -19.5
 7)   11.3   20.0   -5.0    4.5   20.5    2.0    0.0   13.0    0.0   13.5  -12.0   67.8
 8) -999.0 -999.0 -999.0   -4.5    6.0  -11.0  -13.0    0.0 -999.0 -999.0  -14.5  -37.0
 9)    3.0    7.5   -7.0  -11.3   11.0 -999.0    0.0 -999.0    0.0    1.0  -25.0  -20.8
10)    2.0    6.3   -4.0  -22.0    4.0    7.0  -13.5 -999.0   -1.0    0.0  -23.3  -44.5
11)   12.0   30.0    3.5    8.5    7.6   18.5   12.0   14.5   25.0   23.3    0.0  154.9
********************************************************************************
OUTPUT OF ROWS WITH -999.0
         1      2      3      4      5      6      7      8      9     10     11 ROWSUM
 1)    0.0    8.7   -8.5   -6.0    5.5 -999.0  -11.3 -999.0   -3.0   -2.0  -12.0  -28.7
 2)   -8.7    0.0  -21.0  -19.7   -0.5 -999.0  -20.0 -999.0   -7.5   -6.3  -30.0 -113.7
 3)    8.5   21.0    0.0    8.0   18.0 -999.0    5.0 -999.0    7.0    4.0   -3.5   68.0
 5)   -5.5    0.5  -18.0   -6.8    0.0 -999.0  -20.5   -6.0  -11.0   -4.0   -7.6  -78.9
 6) -999.0 -999.0 -999.0   -3.0 -999.0    0.0   -2.0   11.0 -999.0   -7.0  -18.5  -19.5
 8) -999.0 -999.0 -999.0   -4.5    6.0  -11.0  -13.0    0.0 -999.0 -999.0  -14.5  -37.0
 9)    3.0    7.5   -7.0  -11.3   11.0 -999.0    0.0 -999.0    0.0    1.0  -25.0  -20.8
10)    2.0    6.3   -4.0  -22.0    4.0    7.0  -13.5 -999.0   -1.0    0.0  -23.3  -44.5
********************************************************************************
OUTPUT OF ROWS WITH NO -999.0
         1      2      3      4      5      6      7      8      9     10     11 ROWSUM
 4)    6.0   19.7   -8.0    0.0    6.8    3.0   -4.5    4.5   11.3   22.0   -8.5   52.2
 7)   11.3   20.0   -5.0    4.5   20.5    2.0    0.0   13.0    0.0   13.5  -12.0   67.8
11)   12.0   30.0    3.5    8.5    7.6   18.5   12.0   14.5   25.0   23.3    0.0  154.9
********************************************************************************
VALUES OF VARIABLES :
X( 1) =   -2.212
X( 2) =  -10.058
X( 3) =    6.712
X( 4) =    4.747
X( 5) =   -6.485
X( 6) =   -1.356
X( 7) =    6.167
X( 8) =   -2.794
X( 9) =   -1.481
X(10) =   -3.476
X(11) =   14.085
```

```
      SUBROUTINE SEPRAT(IFLG,VARBLE,STATUS)
      REAL MATRIX(40,40),OUTPUT(40,41),HAS999(20,41),NO999(20,41),
     *TEMP(41,20),VARBLE(40)
      INTEGER INO(40),IHAS(40),STATUS(40)
      COMMON MATRIX,OUTPUT,IROW,ICOL,ICOLL
      KNTNO=0
      KNTHAS=0


      DO 400 I=1,IROW
      IFLAG=0
      STATUS(I)=2
      DO 410 J=1,ICOL
      IF (OUTPUT(I,J).EQ.-999.0) IFLAG=1
  410 CONTINUE
      IF (IFLAG.EQ.1) GO TO 430
      KNTNO=KNTNO+1
      INO(KNTNO)=I
      DO 420 J=1,ICOLL
      NO999(KNTNO,J)=OUTPUT(I,J)
  420 CONTINUE
      VARBLE(I)=OUTPUT(I,ICOLL)/FLOAT(IROW)
      GO TO 400
  430 KNTHAS=KNTHAS+1
      STATUS(I)=0
      IHAS(KNTHAS)=I
      DO 440 J=1,ICOLL
      HAS999(KNTHAS,J)=OUTPUT(I,J)
  440 CONTINUE
  400 CONTINUE
      IF (IFLG.EQ.1) GO TO 445
      IF (KNTHAS.EQ.0) GO TO 411
      WRITE (6,510)
  510 FORMAT ('1',120('*')/'0OUTPUT OF ROWS WITH -999.0')
      WRITE (6,501) (I,I=1,IROW)
  501 FORMAT ('0',3X,11(5X,I2),1X,'ROWSUM')
      WRITE (6,520) (IHAS(I),(HAS999(I,J),J=1,ICOLL),I=1,KNTHAS)
  520 FORMAT (' ',I2,')',12F7.1)
  411 IF (KNTNO.EQ.0) RETURN
      WRITE (6,530)
  530 FORMAT ('1',120('*')/'0OUTPUT OF ROWS WITH NO -999.0')
      WRITE (6,501) (I,I=1,IROW)
      WRITE (6,520) (INO(I),(NO999(I,J),J=1,ICOLL),I=1,KNTNO)
      RETURN
  445 IF (KNTHAS.EQ.0) GO TO 412
      DO 455 I=1,ICOLL
      DO 455 J=1,KNTHAS
      TEMP(I,J)=HAS999(J,I)
  455 CONTINUE
      WRITE (6,515) (IHAS(I),I=1,KNTHAS)
  515 FORMAT ('1',120('*')/'0OUTPUT OF COLUMNS WITH -999.0'/
     *'0',7X,13(5X,I2))
      DO 460 I=1,ICOLL
      IF (I.EQ.ICOLL) GO TO 465
      WRITE (6,525) (I,(TEMP(I,J),J=1,KNTHAS))
  525 FORMAT (' ',4X,I2,')',13F7.1)
      GO TO 460
  465 WRITE (6,526) (TEMP(I,J),J=1,KNTHAS)
  526 FORMAT (' ','COLSUM)',13F7.1)
  460 CONTINUE
  412 IF (KNTNO.EQ.0) RETURN
      DO 470 I=1,ICOLL
      DO 470 J=1,KNTNO
      TEMP(I,J)=NO999(J,I)
  470 CONTINUE
      WRITE (6,535) (INO(I),I=1,KNTNO)
  535 FORMAT ('1',120('*')/'0OUTPUT OF COLUMNS WITH NO -999.0'/
     *'0',7X,13(5X,I2))
      DO 480 I=1,ICOLL
      IF (I.EQ.ICOLL) GO TO 485
      WRITE (6,545) (I,(TEMP(I,J),J=1,KNTNO))
  545 FORMAT (' ',4X,I2,')',13F7.1)
      GO TO 480
  485 WRITE (6,546) (TEMP(I,J),J=1,KNTNO)
  546 FORMAT (' ','COLSUM)',13F7.1)
  480 CONTINUE
      RETURN
      END
```

```
********************************************************************************
AVERAGE DIFFERENCE BETWEEN COLUMNS WITH    COMMON ROWS
             1      2      3      4      5      6      7      8      9     10     11     12     13
     1)    0.0   -2.0   -5.0   10.0   -2.0    5.3   23.5   20.0    1.5  -21.0   -3.4   -1.0    2.5
     2)    2.0    0.0   -9.0   21.0    2.0   11.0   14.0 -999.0 -999.0  -11.0    4.5 -999.0    8.0
     3)    5.0    9.0    0.0   25.0   18.5   32.0   25.3   21.0   20.0    3.5    5.0    8.0    3.7
     4)  -10.0  -21.0  -25.0    0.0  -15.7    0.0  -11.0  -11.0  -14.0  -29.0  -20.3  -29.5  -25.5
     5)    2.0   -2.0  -18.5   15.7    0.0    7.0    2.5   -5.0   -8.0  -15.0   -2.5  -20.0  -12.0
     6)   -5.3  -11.0  -32.0    0.0   -7.0    0.0  -11.0   -8.0    1.3  -16.7   -3.6  -10.0  -25.5
     7)  -23.5  -14.0  -25.3   11.0   -2.5   11.0    0.0   -5.5    1.0  -17.5  -20.3  -11.0  -21.7
     8)  -20.0 -999.0  -21.0   11.0    5.0    8.0    5.5    0.0   -3.0  -14.0  -18.0  -15.0  -24.0
     9)   -1.5 -999.0  -20.0   14.0    8.0   -1.3   -1.0    3.0    0.0  -13.5   -5.0  -12.5  -24.0
    10)   21.0   11.0   -3.5   29.0   15.0   16.7   17.5   14.0   13.5    0.0    8.5   -1.0    3.0
    11)    3.4   -4.5   -5.0   20.3    2.5    3.6   20.3   18.0    5.0   -8.5    0.0    2.0   -1.3
    12)    1.0 -999.0   -8.0   29.5   20.0   10.0   11.0   15.0   12.5    1.0   -2.0    0.0  -12.0
    13)   -2.5   -8.0   -3.7   25.5   12.0   25.5   21.7   24.0   24.0   -3.0    1.3   12.0    0.0
COLSUM)  -28.4  -42.5 -176.0  211.9   55.8  128.8  118.3   85.5   53.8 -144.7  -55.7  -78.0 -128.8
********************************************************************************
OUTPUT OF COLUMNS WITH -999.0
             2      8      9     12
     1)   -2.0   20.0    1.5   -1.0
     2)    0.0 -999.0 -999.0 -999.0
     3)    9.0   21.0   20.0    8.0
     4)  -21.0  -11.0  -14.0  -29.5

     5)   -2.0   -5.0   -8.0  -20.0
     6)  -11.0   -8.0    1.3  -10.0
     7)  -14.0   -5.5    1.0  -11.0
     8) -999.0    0.0   -3.0  -15.0
     9) -999.0    3.0    0.0  -12.5
    10)   11.0   14.0   13.5   -1.0
    11)   -4.5   18.0    5.0    2.0
    12) -999.0   15.0   12.5    0.0
    13)   -8.0   24.0   24.0   12.0
COLSUM)  -42.5   85.5   53.8  -78.0
********************************************************************************
OUTPUT OF COLUMNS WITH NO -999.0
             1      3      4      5      6      7     10     11     13
     1)    0.0   -5.0   10.0   -2.0    5.3   23.5  -21.0   -3.4    2.5
     2)    2.0   -9.0   21.0    2.0   11.0   14.0  -11.0    4.5    8.0
     3)    5.0    0.0   25.0   18.5   32.0   25.3    3.5    5.0    3.7
     4)  -10.0  -25.0    0.0  -15.7    0.0  -11.0  -29.0  -20.3  -25.5
     5)    2.0  -18.5   15.7    0.0    7.0    2.5  -15.0   -2.5  -12.0
     6)   -5.3  -32.0    0.0   -7.0    0.0  -11.0  -16.7   -3.6  -25.5
     7)  -23.5  -25.3   11.0   -2.5   11.0    0.0  -17.5  -20.3  -21.7
     8)  -20.0  -21.0   11.0    5.0    8.0    5.5  -14.0  -18.0  -24.0
     9)   -1.5  -20.0   14.0    8.0   -1.3   -1.0  -13.5   -5.0  -24.0
    10)   21.0   -3.5   29.0   15.0   16.7   17.5    0.0    8.5    3.0
    11)    3.4   -5.0   20.3    2.5    3.6   20.3   -8.5    0.0   -1.3
    12)    1.0   -8.0   29.5   20.0   10.0   11.0    1.0   -2.0  -12.0
    13)   -2.5   -3.7   25.5   12.0   25.5   21.7   -3.0    1.3    0.0
COLSUM)  -28.4 -176.0  211.9   55.8  128.8  118.3 -144.7  -55.7 -128.8
********************************************************************************
VALUES OF VARIABLES :
Y( 1) =   -2.187
Y( 2) =   -4.883
Y( 3) =  -13.538
Y( 4) =   16.301
Y( 5) =    4.295
Y( 6) =    9.905
Y( 7) =    9.103
Y( 8) =    9.339
Y( 9) =    5.821
Y(10) =  -11.128
Y(11) =   -4.288
Y(12) =   -8.828
Y(13) =   -9.910
```

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

Bingham, R. T., Squillace, A. E., and Wright, J. W.: Breeding blister rust resistant western white pine. II. First results of progeny tests including preliminary estimates of heritability and rate of improvement. Silvae Genetica 9 (2): 33—41 (1960).

Pinus patula Schiede and Deppe progeny tests in Rhodesia Genetic control of nursery traits1)

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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 × 9) and reciprocal (diallel without selfs, 7 × 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 Quirle und Äste sowie die Höhe ermittelt. Sowohl die Anzahl als auch die Länge der Kotyledonen zeigten eine gute allgemeine Kombinationseignung mit Heritabilitäten (Familie) von 0,64 bzw. 0,25 und eine hohe negative Korrelation von — 0,91 zwischen beiden. Die Anzahl der Quirle und Äste wies Heritabilitäten von 0,55 bzw. 0,45 auf. In den ersten 6 Monaten herrschten bei der Höhe Dominanzeffekte vor, während sich danach die allgemeine Kombinationseignung bis zu Heritabilitäten zwischen 0,63 und 0,78 durchsetzte. Eine Korrelation zwischen der Sämlingshöhe im 1. und 12. Monat konnte nicht festgestellt werden. Daraus wird geschlossen, daß das Sämlingswachstum im ersten Jahr von verschiedenen Genen gesteuert wird. Die Korrelation Samengewicht — Sämlingshöhe war im 3. Monat am meisten ausgeprägt.

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 × 3 tubes); the middle row of eight seedlings was the measured plot. Ungerminated or killed seedlings in the measured plot were replaced from the

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1) The paper is adapted from part of the senior author's Ph. D. thesis (1973).

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.