GENERAL AND SPECIFIC COMBINING ABILITY IN EIGHT SELECTED CLONES OF RADIATA PINE

M. D. WILCOX, C. J. A. SHELBOURNE and A. FIRTH
Forest Research Institute, New Zealand Forest Service, Rotorua

(Received for publication 28 February 1975)

ABSTRACT

Eight selected seed orchard clones of radiata pine (**Pinus radiata** D. Don) were mated together in a factorial mating design, with four clones as female and four as male parents. The progeny were planted at Kaingaroa Forest and measured 5 years after planting.

Vigour, stem straightness, branching quality, and resistance to a needle cast disease associated with **Naemacyclus minor** all showed highly significant general combining ability effects. Only height, diameter, and volume showed important specific combining ability effects.

The cross between clones 96 and 55 was the best of the 16 crosses tested. Its exceptional vigour resulted from high specific combining ability together with the good general combining ability of both its parents. This full-sib family also exhibited good stem straightness and excellent branching characterstics, and suffered little from needle cast.

INTRODUCTION

Both open- and control-pollinated progeny tests are used in the *Pinus radiata* breeding programme of the New Zealand Forest Service. The main purpose of such tests is to identify parent trees for use in clonal seed orchards which consistently produce above-average progeny when crossed with other trees. Parents with high average breeding values show good *general combining ability* (GCA). Use can also be made of control pollinated progeny tests to identify individual crosses which perform better than expected from the general combining abilities of the two parents. Such crosses possess good *specific combining ability* (SCA).

North Carolina Design II is a two-factor mating design enabling the variation among full-sib families to be partitioned into GCA and SCA effects. The two factors are sets of unrelated male and female parents. Examples of the use of this design in plant breeding are described in Bingham *et al.,* 1969; Hanover and Barnes, 1962; Kraus, 1973; Singh *et al.,* 1974; Weir and Zobel, 1972.

The experiment described here is a 4 × 4 balanced North Carolina Design II progeny test, the parents representing eight of the 42 select clones of a series in present North Island seed orchards. Our objective was to assess the relative importance of GCA and SCA, for a number of characters, in progeny of this particular group of parents.

N.Z. J. For. Sci. 5 (2): 219-25 (1975).

MATERIALS AND METHODS

History of the Parents

The eight trees used as parents in this study were selected in the early 1950s from unimproved plantations (Table 1). The trees were picked after intensive searching for near-perfect specimens with straight stems, small-diameter multinodal branching, and stem diameters considerably greater than those of close neighbours.

TABLE 1—Particulars of parent trees

Clone	Origin	Selected by
7	Shelterbelt, 88 Valley, Nelson (1885)	G. R. Fenton (1950)
19	Compt. 1184, Kaingaroa Forest (1926)	G. R. Fenton (1950)
55	Atiamuri, N.Z. Forest Products Ltd. (1927)	J. E. Henry (1953)
89	Compt. 1186, Kaingaroa Forest (1926)	A. J. Carruthers (1954)
96	Compt. 37, Kaingaroa Forest (1928)	A. J. Carruthers (1954)
97	Compt. 1188, Kaingaroa Forest (1927)	A. J. Carruthers (1954)
99	Compt. 1206, Kaingaroa Forest (1927)	A. J. Carruthers (1954)
121	Compt. 1183, Kaingaroa Forest (1926)	R. Collins (1956)

Description of Experiment

Controlled pollinations were made on grafts of the parents in 1960-63, and seed was sown in unreplicated nursery plots at Rotorua in December 1966. Seedling progeny of the 16 crosses were raised as 1/1 stock which were topped to a uniform and convenient height before planting.

The field layout was a randomised complete blocks design, with four single tree plots per cross per replication, and with 16 replications.

The experiment was established in 1968 at 2.7 × 2.7 m spacing in Compartment 1350, Kaingaroa Forest. The soil here consists of pumice overlain by about 30 cm of basaltic scoria (Tarawera Ash). Average annual rainfall for this site from 1969-73 was 1900 mm, and the altitude is approximately 400 m.

Measurements

Three trees per full-sib family per replication were chosen at random for measurement. Individual trees were assessed for the following characters in December 1973, 5 years from planting:

Height; in dm.

Diameter; at 1.4 m, in mm.

Stem straightness; scored on a scale of 1-9, 1 being very crooked and 9 being completely straight.

Branch quality; scored on a scale of 1-9, 1 being coarse uninodal branching with ramicorns prevalent, and 9 being small diameter, horizontal, multinodal branching.

Needle retention; scored on a scale of 1-6, 1 being severe needle cast, and 6 being normal healthy foliage. The needle cast was associated with infection by the fungus *Naemacyclus minor* Butin.

Volume, a measure of stem volume (V) in dm^3 was calculated from height (h) and DBH (d) from

$$V = 0.2618\ (d/100)^2\ h$$

This assumes that the stems are conical.

Analysis

Tests of significance for GCA and SCA effects: Analyses of variance on individual tree measurements were made assuming the following model:

$$Y_{ijkm} = \mu + (gca_i + gca_j) + sca_{ij} + r_k + e_{ijkm} \quad - - - - - \quad (1)$$

where Y_{ijkm} = value of the mth tree in the kth replication of the cross between the ith female and jth male

μ = the general mean

gca_i = the general combining ability effect of the ith female

gca_j = the general combining ability effect of the jth male

sca_{ij} = the specific combining ability of the cross between the ith female and jth male

r_k = the effect of the kth replication

e_{ijkm} = the random error.

GCA and SCA effects were regarded as fixed, and the hypotheses that all GCA effects were equal, and all SCA effects were equal, were tested using F-tests.

Estimation of means and combining ability effects

1. Means were estimated as follows:

General mean: $\hat{\mu} = \bar{Y}_{..}$, the arithmetic mean of all 768 trees.

GCA or half-sib family means: $\hat{\mu}_i = \bar{Y}_{i.}$, the arithmetic mean of the 192 trees in the ith maternal half-sib family

$\hat{\mu}_j = \bar{Y}_{.j}$, the arithmetic mean of the 192 trees in the jth paternal half-sib family.

Cross or full-sib family means: $\hat{\mu}_{ij} = \bar{Y}_{ij}$, the arithmetic mean of the 48 trees in the cross between the ith female and jth male.

2. Effects were estimated as follows:

GCA effects: $\widehat{gca}_i = \bar{Y}_{i.} - \bar{Y}_{..}$

$\widehat{gca}_j = \bar{Y}_{.j} - \bar{Y}_{..}$

SCA effects: $\widehat{sca}_{ij} = \bar{Y}_{ij} - \bar{Y}_{i.} - \bar{Y}_{.j} + \bar{Y}_{..}$

Restrictions implied in these definitions are:

$\Sigma_i\, gca_i = \Sigma_j gca_j = 0$

$\Sigma_i\, sca_{ij} = 0$ for males

$\Sigma_j\, sca_{ij} = 0$ for all females

The mean performance of a cross can be expressed in terms of combining ability effects as

$$\hat{\mu}_{ij} = \hat{\mu} + \widehat{gca}_i + \widehat{gca}_j + \widehat{sca}_{ij} \quad - - - - - - - - - - \quad (2)$$

RESULTS

The F-tests in Table 2 show that significant differences in GCA for all characters occurred among the parents. GCA effects for straightness and branch quality were considerably weaker than for vigour traits. This could reflect the intensive phenotypic selection of the parent trees for tree form.

Vigour traits showed highly significant SCA effects, indicating that the performance of individual crosses would in some cases be poorly correlated with the mean performance of the parents.

Means and combining ability effects are shown in Tables 3 and 4.

TABLE 2—Analysis of variance of general and specific combining ability

Source	df	Mean squares Volume	Height	Diam.	Straightness	Branch quality	Needle retention
GCA	6	2348.4	1135.5	6240.5	10.42	23.08	44.40
SCA	9	792.8	273.0	2227.8	1.95	5.02	0.26
REPS	15	159.3	59.8	601.4	4.37	1.38	3.14
ERROR	737	126.5	60.2	388.1	2.76	3.76	0.71
F-tests							
GCA		18.56**	18.83**	16.08**	3.78**	6.14**	19.49**
SCA		6.27**	4.53**	5.74**	0.71n.s.	1.34n.s.	0.37n.s.

** significant at the 1% level
n.s. not significant

General Combining Ability

Of the females, clone 96 clearly produced the most vigorous and best-branched progeny. They were also reasonably straight and had good needle retention. Clone 97 was notable for the poor needle retention of its progeny.

Of the males, clone 55 stood out as the best parent. Its progeny were the most vigorous, the straightest, and had the best branch quality and needle retention of the four paternal half-sib families. The high GCA of clone 55 has also been demonstrated in several open-pollinated progeny tests. Clone 121 showed very low GCA for needle retention. It seems that, regardless of what other tree it is crossed with, this clone produces offspring with poor needle retention. The apparently strong additive mode of inheritance of this character (which is assumed to reflect resistance or tolerance to infection by *Naemacyclus minor*) suggests that breeding for resistance would be straightforward.

Specific Combining Ability

Strong positive SCA for vigour was shown by the crosses 96 × 55, 97 × 19, and 89 × 121. The cross 96 × 55 was noteworthy for its great vigour, especially in diameter growth (Table 3). Using the combining ability model, Equation (2), given earlier, the mean volume of 96 × 55 progeny can be partitioned as

$$43.6 = 30.5 + 3.4 + 5.5 + 4.2$$

This is the only cross in which GCA and SCA effects were all positive for vigour traits. Of the total effect (13.1 dm^3) of this cross, 68% of the superiority over the mean was due to the combined GCA effects of the parents, and 32% was due to the SCA effect. Its mean volume of 43.6 dm^3 was 43% better than the mean of all 16 crosses, whereas clone 96, the best general combiner for volume, had a GCA only 18% better than the overall mean.

TABLE 3—Full-sib family, half-sib family and general means

(1) Volume (dm^3)

Female \ Male	7	19	55	121	Mean
89	27.3	23.3	24.2	32.6	26.8
96	36.4	28.0	43.6	36.0	36.0
97	30.0	29.9	32.4	25.7	29.5
99	27.5	25.0	35.7	30.7	29.7
Mean	30.3	26.6	34.0	31.2	30.5

(2) Height (dm)

Female \ Male	7	19	55	121	Mean
89	69.5	67.5	71.6	73.1	70.4
96	75.1	70.3	78.8	71.8	74.0
97	72.5	72.1	77.1	68.9	72.6
99	69.8	68.2	78.7	69.2	71.5
Mean	71.7	69.5	76.6	70.7	72.1

(3) Diameter (mm)

Female \ Male	7	19	55	121	Mean
89	118	113	109	127	117
96	133	121	143	136	133
97	125	124	125	116	122
99	119	115	128	127	122
Mean	124	118	126	126	123

(4) Straightness (1 - 9)

Female \ Male	7	19	55	121	Mean
89	4.71	4.75	5.42	4.69	4.89
96	4.94	5.17	5.21	4.21	4.88
97	4.92	4.83	5.17	4.60	4.88
99	4.90	4.94	5.60	4.83	5.07
Mean	4.86	4.92	5.35	4.58	4.93

(5) Branch quality (1 - 9)

Female \ Male	7	19	55	121	Mean
89	4.13	3.67	5.27	4.52	4.40
96	4.90	5.15	5.33	4.56	4.98
97	4.29	4.29	4.54	4.13	4.31
99	3.96	4.08	5.02	4.10	4.29
Mean	4.32	4.30	5.04	4.33	4.50

(6) Needle retention (1 - 6)

Female \ Male	7	19	55	121	Mean
89	2.48	2.58	2.73	1.94	2.43
96	2.54	2.42	2.54	1.81	2.33
97	2.08	2.15	2.40	1.54	2.04
99	2.56	2.63	2.60	1.88	2.42
Mean	2.42	2.44	2.57	1.79	2.30

TABLE 4—General and specific combining effects*

(1) Volume (dm^3)

Female \ Male	7	19	55	121	GCA
89	0.7	0.4	-6.1	5.0	-3.7
96	0.6	-4.0	4.2	-0.8	5.5
97	0.7	4.4	-0.6	-4.5	-1.0
99	-2.0	-0.7	2.5	0.3	-0.8
GCA	-0.2	-4.0	3.4	0.7	

(2) Height (dm)

Female \ Male	7	19	55	121	GCA
89	-0.5	-0.3	-3.2	4.0	-1.7
96	1.5	-1.0	0.4	-0.8	1.9
97	0.3	2.0	0.0	-2.3	0.5
99	-1.2	-0.7	2.8	-0.9	-0.7
GCA	-0.4	-2.6	4.4	-1.4	

(3) Diameter (mm)

Female \ Male	7	19	55	121	GCA
89	1.0	1.5	-10.1	7.7	-7.0
96	-0.3	-6.4	7.0	-0.3	9.8
97	2.3	7.0	-0.2	-9.0	-1.5
99	-3.0	-2.0	3.4	1.7	-1.3
GCA	0.1	-5.6	2.6	2.9	

(4) Straightness (1 - 9)

Female \ Male	7	19	55	121	GCA
89	-0.11	-0.13	0.11	0.15	-0.04
96	0.13	0.30	-0.09	-0.32	-0.05
97	0.11	-0.04	-0.13	0.07	-0.05
99	-0.10	-0.12	0.11	0.11	0.14
GCA	-0.07	-0.01	0.42	-0.35	

(5) Branch quality (1 - 9)

Female \ Male	7	19	55	121	GCA
89	-0.09	-0.53	0.33	0.29	-0.10
96	0.10	0.37	-0.19	-0.25	0.48
97	0.16	0.18	-0.31	-0.01	-0.19
99	-0.15	-0.01	0.19	-0.02	-0.21
GCA	-0.18	-0.20	0.54	-0.17	

(6) Needle retention (1 - 6)

Female \ Male	7	19	55	121	GCA
89	-0.07	-0.01	0.03	0.02	0.13
96	0.09	0.07	-0.06	-0.01	0.03
97	-0.08	-0.03	0.09	0.01	-0.26
99	0.02	0.07	-0.09	-0.03	0.12
GCA	0.12	0.14	0.27	-0.51	

* SCA and GCA effects do not sum to zero in all cases because of rounding errors.

There were cases of negative SCA involving one of the best general combiners (e.g., diameter in 89 × 55, and also of positive SCA in crosses between below-average general combiners (e.g., height in 89 × 121). These examples illustrate the dangers of relying solely on single-pair matings (un-related full-sib families) for producing breeding populations for advanced generation selection. Unless GCA information is also available on each parent, some families and individuals could easily be wrongfully selected or rejected on the basis of the full-sib family mean alone.

DISCUSSION AND CONCLUSIONS

The validity of these results is somewhat weakened by the lack of replication of progenies in the nursery. There is therefore a possibility that observed differences among full sib families were inflated by nursery bed effects and that the SCA effects in particular were spurious to some degree.

Specific combining ability for vigour traits has been reported several times in trees (Hanover and Barnes, 1962; Kraus, 1973), but not before in *P. radiata.* Significant SCA effects provide evidence that non-additive gene action in the form of dominance and/or epistasis is contributing to the genetic variation among these young families of radiata pine.

The general combining ability effects shown by these eight parents appeared sufficiently strong to justify the multi-clone seed orchard approach to the genetic improvement of radiata pine. Maximum improvement in vigour, however, can only be obtained by exploiting the presently unused SCA. This can be done by vegetative propagation of vigorous individuals from the best crosses, and by mass production of the best crosses in 2-clone seed orchards.

From the genetic standpoint, the cross 96 × 55 appears ideal for the 2-clone orchard concept since it makes maximum use of GCA and at the same time gives considerable extra vigour from SCA. Mass production of this cross would achieve greater genetic improvement in volume per hectare than that obtainable from the existing first-generation multi-clone orchards. Investigations are in hand to determine whether the flowering biology of the two parents is sufficiently synchronous to permit free natural cross pollination. The self fertility, vigour of selfs, and importance of reciprocal effects (i.e., does 96 × 55 = 55 × 96?) are also under study. We do not, however, envisage 96 × 55 being used extensively alone because of the possible dangers from pests and diseases to such a genetically uniform variety, and the problems in producing enough seed.

REFERENCES

BINGHAM, R. T., OLSON, R. J., BECKER, W. A. and MARSDEN, M. A. 1969: Breeding blister rust resistant western white pine. V. Estimates of heritability, combining ability, and genetic advance based on tester matings. **Silvae Genet. 18 (1):** 28-38.

HANOVER, J. W. and BARNES, B. V. 1962: Heritability of height growth in year-old western white pine. **Forest Genet. Workshop Proc. Publ. 22:** 71-6.

KRAUS, J. F. 1973: Estimates of general and specific combining ability for height and rust resistance from single-crosses of slash pine. **Silvae Genet. 22 (4):** 121-4.

SINGH, F., SINGH, R. K. and SINGH, V. P. 1974: Combining ability studies in pearl millet (**Pennisetum typhoides** (Burm.) S. & H.). **Theor. Appl. Genet. 44 (3):** 106-10.

WEIR, R. J. and ZOBEL, B. J. 1972: Outstanding general combiners and their influence on breeding programmes. IUFRO Working Party on Progeny Testing, Proceedings, Macon, 26 October 1972: 127-44.