GENERAL AND SPECIFIC COMBINING ABILITY IN FAMILIES OF PINUS RADIATA IN NEW SOUTH WALES, AUSTRALIA

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ABSTRACT

Diameter at 1.3 m and total height were assessed at $11^1/_2$ years from planting in a control-pollinated progeny test of *Pinus radiata* D. Don in New South Wales, Australia. The material represented an 18-female × 4-male North Carolina II mating design, with eight crosses missing. The stem diameter and height of each tree were combined in a measure of conic volume.

General combining ability (GCA) and specific combining ability (SCA) variances were estimated as measures of additive genetic and dominance variances respectively. Ratios of estimated GCA to SCA for the traits diameter and volume were low (0.4 to 0.5), while that for height was high (3.0). Individual heritability estimates were low (0.07 to 0.09) and imprecise for diameter and volume, but that for height was moderate (0.24). Additive genetic correlations between pairs of growth traits were positive, and relatively high.

The over-all agreement in rank between observed means of crosses and values from parental GCAs was such that actual crosses between the few highest-GCA females and males also included a high proportion of the top-ranked families. These results support a "general combiner" strategy of mating parents on the basis of GCA, in control-pollinated seed orchards, over the operationally more expensive alternative of reproducing tested crosses.

Keywords: general combining ability; specific combining ability; factorial cross; selection; *Pinus radiata*.

INTRODUCTION

Most breeding programmes for *Pinus radiata* in Australia and New Zealand in the past have relied on open-pollinated seed orchards, containing clones selected for general combining ability (GCA), to bring improved genotypes into routine production. This approach, which is designed to exploit additive genetic variance only, has had practical disadvantages in many cases, such as fluctuating seed yields in orchards from year to year (Pederick & Brown 1976) and possible losses of potential genetic gain through both selfing and pollen contamination from outside (Griffin 1982; I. G. Johnson, unpubl. data).

In recent years there has been an upsurge in interest in more closely controlled systems for producing improved genotypes, including clonal seed orchards in which pollen application is artificially controlled. Control-pollinated seed orchards are gaining favour in New Zealand particularly, where they are expected to produce seed more rapidly, and of better genetic quality, than conventional orchards (Carson 1986). Relatively small amounts of expensive seedlings produced this way can be "bulked up" for plantation use by mass vegetative propagation.

In order to decide how to select clones to be crossed in control-pollinated orchards, to optimise genetic gains, knowledge is required of the relative importance of additive and non-additive (putatively dominance) genetic variance in the traits under selection. A portion of the non-additive variance (reflected in specific combining ability, or SCA) can be exploited by reproducing proven full-sib families in the orchard and vegetatively multiplying the seedlings (Cotterill *et al.* 1987). However, this approach may be efficient in terms of gain and workload only if SCA effects are important relative to GCA effects. If GCA effects are more important, crossing among the best general combiner clones would be a more efficient strategy for producing improved seed (Carson 1986).

Estimates of the relative levels of additive and non-additive genetic variance, as the relative importance of GCA *versus* SCA, are scarce for *P. radiata.* Estimates have been published for *P. radiata, P. pinaster* Aiton, and *P. elliottii* Engelm. in South Africa (Cotterill *et al.* 1987) and *P. radiata* in New Zealand (Wilcox *et al.* 1975; Carson 1986). Wilcox *et al.* reported significant SCA effects for vigour in 5-year-old trees of 16 crosses, indicating that the performance of some individual crosses would be poorly correlated with the mean performance of the parents. Carson (1986) found SCA to be relatively unimportant compared with GCA for several growth and form traits in 150 full-sib families, assessed at 8 years over two sites in New Zealand, and advocated crossing superior GCA parents in control-pollinated orchards. Cotterill *et al.* (1987) found GCA variance levels to be the same as or greater than SCA variance levels in 53 full-sib families of *P. radiata* in South Africa, assessed at 8 years of age.

In this paper estimates are presented of GCA and SCA genetic variances, and the relative magnitudes of SCA and GCA effects for growth traits of 64 crosses in *P. radiata* in southern New South Wales, Australia, assessed at 11 years from planting. Implications of these results for strategies to produce genetically superior seed in control-pollinated seed orchards are then discussed.

MATERIALS AND METHODS

Test Site and Design

The progeny test (local number Q14/1.11) used for the study was established by the Forestry Commission of New South Wales in August 1971, in Wee Jasper State Forest, Tumut Forestry District, in the southern highlands of New South Wales. Site details are listed below:

Altitude:	960 m
Rainfall:	1400 mm per year
Geology:	Metabasic parent material with some serpentinite; some metamorphic influence.

The test seedlings were raised as bare-rooted stock in Bondo Nursery, Tumut Forestry District, between September 1970 and August 1971. There was no replication of the seedlots in the nursery. The planting espacement in the test was 3.0 m between rows and 2.5 m within rows (1333 trees/ha). No fertiliser was used on the site. Low pruning, to about 2.5 m, was carried out at 8 years of age.

The test as a whole consists basically of a North Carolina Design II (NC-II, or four-tester) layout, with a total of 144 full-sib families. Additional full-sib families including parents from A.C.T., Victoria, and New Zealand were also planted in the test, to make up a total of 30 blocks, each with 140 trees in single-tree plots.

Families Studied for Genetic Parameters

A subset of 64 full-sib families was selected from the over-all progeny test for study, consisting of the largest and most balanced group of crosses available from the North Carolina II design. This subset comprised 64 families present over 72 possible cells (18 female parents × 4 male parents unrelated to the females).

The male parents are first-generation selections from New South Wales, while the female parents are first-generation selections from New South Wales (16 parents), Victoria (one parent), and New Zealand (one parent). These parents were selected in plantations, primarily for superior growth rate, stem straightness, and fine (hence multinodal) branching. Apical dominance and freedom from forks were other important selection criteria. The selection intensity was very high in all places, for example, about 1 : 60 000 in New South Wales. The four male parents were chosen mainly because of easy availability of pollen from these clones.

Each of the 64 families studied was originally planted in from 17 to 30 blocks of the test (between 17 and 30 trees per family). Severe mortality was caused by frost in some blocks soon after planting. There was also some minor snow damage in the trial when the trees were 10 years old. At the time of the assessment, the number of trees considered measurable (*see* below) in the 64 families studied averaged 65%, ranging from 37% to 90% in individual families. In one block, over 50% of the trees of these families were not assessable, and the block was dropped from consideration. The early mortality was random, and did not favour some of the 64 families over others by giving them more space to grow freely from competition – trees in families which ranked well for volume (*see* later discussion) had a similar number of nearest neighbours to those of poor-volume families at the time of assessment.

Assessments

In January 1983, 11½ years after planting, diameter at 1.3 m above ground and total height were measured in the 64 families in the subset of the progeny test chosen for analysis. All surviving trees were measured, except those severely suppressed or severely damaged by wind or snow. A conic volume index was calculated for each measured tree, using the formula:

$$\text{Conic Volume} = \pi\ (\text{diameter}/2)^2 \times (\text{height}/3).$$

Analyses of Data

Estimation of variance components

Each of the three growth trait data sets for the 64 families was analysed using the SAS General Linear Models (GLM) procedure (SAS Institute 1985), owing to the large number of missing cells in the design, and the missing plots. Because the design was single-tree plots with several replications per family, the analysis followed the model

$Y_{ijk} = \mu + f_i + m_j + fm_{ij} + r_k + e_{ijk}$

Y_{ijk} corresponds to individual tree values for families in blocks.

μ is the overall test mean for a trait

f_i is the effect of the ith female parent

m_j is the effect of the jth male parent

fm_{ij} is the female × male parent interaction

r_k is the effect of the kth replicate (block)

e_{ijk} is the experimental error, including interactions between families and blocks (k).

Expectations of mean squares for the analysis of the data are given in Appendix 1.

Least-squares means were calculated for diameter, total height, and conic volume of female and male parents, and each of the 64 specific crosses.

Estimates of variances due to female parents (σ^2_f), male parents (σ^2_m), female × male parent interactions (σ^2_{fm}), and experimental error (σ^2_e), for each of the traits diameter, total height, and volume were calculated from the Type III sums of squares estimated by the GLM Procedure, since the data were unbalanced.

Assuming all parents to be unrelated, and epistatic variance (due to interactions of gene effects between two or more genetic loci) to be negligible, $4\hat{\sigma}^2_f$ may be used as an estimate of additive variance. This value may, however, over-estimate the true level of additive variance if variance due to common-environmental (e.g., maternal) effects (σ^2_c) is appreciable (Cotterill *et al.* 1987). Variance due to common-environmental effects could not be estimated in this study, and was assumed to be zero.

Additive variance may also be estimated as $4\hat{\sigma}^2_m$, but this was not used. (In fact, the differences between males were non-significant in all traits from the GLM analysis, and $\hat{\sigma}^2_m$ was negative for diameter and volume.)

The female × male variance component σ^2_{fm}, assuming no complications from common-environmental effects, represents SCA variance, and $4\hat{\sigma}^2_{fm}$ provides an estimate of dominance genetic variance (assuming no epistasis), which was used in this study.

Estimates of individual heritability

Individual heritability was estimated (using seed parents only), for all three traits, as:

$h_f^2 = 4\sigma^2_f/\sigma^2_p$, where σ^2_p was calculated as $\sigma^2_f + \sigma^2_{fm} + \sigma^2_e$ for diameter and conic volume, and as $\sigma^2_f + \sigma^2_m + \sigma^2_{fm} + \sigma^2_e$ for height.

Estimates of genetic and phenotypic correlations

Genetic correlations for the paired traits diameter/height, diameter/volume, and height/volume were calculated using only maternal estimates of additive genetic variances and between-trait covariances, derived from the SAS GLM Procedure (SAS Institute 1985), and the MANOVA option under this procedure. Phenotypic correlations for the same paired traits were calculated using the SAS CORR Procedure (SAS Institute 1985) for all individual observations.

Estimates of combining abilities

The general combining ability effect ($GCA_{i.}$) of the ith female parent for each trait was estimated as the least-squares mean ($\bar{x}_{i.}$) of the half-sib offspring of the particular parent, minus the mean of the least-squares means of the female parents (equal to that of the male parents) for the particular trait ($\bar{x}_{i..ls}$):

$$GCA_{i.} = \bar{x}_{i.} - \bar{x}_{i..ls}$$

The GCA of each male parent (the jth) was estimated in a similar way. Least-squares means were used because of the incompleteness (non-orthogonality) of the matings, leading to differences between arithmetic and least-squares means. The variance of the GCA's of the female parents is equal to σ^2_f and the variance of the GCA's of the male parents is equal to σ^2_m.

The observed effect (gv_{ij}) for conic volume of the full-sib family produced by mating the ith female parent to the jth male parent (or Observed Genetic Value, following the terminology of Cotterill *et al.* 1987), was calculated as the least-squares mean of the particular full-sib family minus the mean of the least-squares means of the female parents, for conic volume:

$$gv_{ij} = \bar{x}_{ij} - \bar{x}_{i..ls}$$

The predicted effect ($\hat{gv}_{ij}$), determined for each full-sib family (or Predicted Genetic Value, following the terminology of Cotterill *et al.* 1987), was calculated as the sum of the female and male GCA's for each cross.

The Specific Combining Ability of the cross between the ith female parent and the jth male parent (SCA_{ij}) was calculated as the Observed Genetic Value minus the Predicted Genetic Value for the particular cross. The variance of the SCA's is equal to σ^2_{fm} (Cotterill *et al.* 1987).

RESULTS AND DISCUSSION

The over-all means and phenotypic standard deviations for the traits diameter, total height, and conic volume of the 64 families analysed are shown in Table 1.

TABLE 1–Test means and phenotypic standard deviations for three growth traits of all assessed trees of the 64 crosses studied in *Pinus radiata* Progeny Test Q14/1.11

Trait	No. trees	Test mean	Phenotypic SD
Diameter (cm)	1177	19.2	4.7
Total height (m)	1177	14.7	2.2
Conic volume (dm^3)	1177	156.5	81.7

Mean squares from the analysis of variance are shown in Table 2. The effect of female parents was highly significant for height ($p = 0.0001$), but statistically non-significant for diameter ($p = 0.09$) and for conic volume ($p = 0.07$). The effect of males was non-significant ($p > 0.10$) for all the traits. The female × male interaction was highly significant for diameter and conic volume ($p = 0.001$ and 0.006 respectively), but non-significant for height ($p = 0.06$).

TABLE 2–Mean squares for the GLM analysis of the NC-II design component of Progeny Test Q14/1.11, and error mean squares

Source of variation	d.f.	Diameter (cm)	Total height (m)	Conic volume (dm^3)
Female parent	17	62.200 ns	20.786***	20 638.514 ns
Male parent	3	9.145 ns	9.102 ns	1 000.748 ns
Female × male parent	43	37.693***	5.294 ns	11 627.945**
Error mean square		20.703	3.819	6 156.666

*** = $p<0.001$
** = $p<0.01$
ns = not significant at $\alpha=0.05$

GCA and SCA Variance

Estimates of additive genetic and dominance variance for the three growth traits are shown in Table 3. The additive genetic variance values, estimated by $4\sigma^2_f$, may over-estimate the true additive variances, since they were not adjusted for maternal effects. These estimates may also be inflated by exclusion of the estimate of GCA variance obtained from the male component (σ^2_m) from the calculation, for reasons explained earlier. The paternal estimate for height was positive, though small (0.06).

The estimated dominance variance ($4\hat{\sigma}^2_{fm}$) considerably exceeded the maternal estimates of additive variance for both diameter and volume (3.81 *versus* 1.61 and 1226 *versus* 592). Expressed another way, the ratio of additive to dominance variance was 0.42 for diameter and 0.48 for volume. The similarity of these ratios must reflect the large contribution of diameter to volume.

For height, the maternal (seed parent) estimate of additive variance was much larger than that of dominance variance, giving a ratio of 3.04.

TABLE 3–Additive genetic variance and dominance genetic variance estimates, estimated ratios of GCA/SCA variance, and individual heritabilities estimated from seed parents, for growth traits

Parameter estimate	Trait		
	Diameter (cm)	Total height (m)	Conic volume (dm^3)
Maternal estimate of additive genetic variance ($4\sigma^2_f$)	1.61	1.01	592
Paternal estimate of additive genetic variance ($4\sigma^2_m$)	Negative	0.06	Negative
Dominance genetic variance ($4\sigma^2_{fm}$)	3.81	0.33	1226
Additive/Dominance variance ratio (σ^2_f/σ^2_{fm})	0.42	3.04	0.48
Maternal estimate of individual h^2 (h^2_f)	0.07	0.24	0.09

No estimates of ratios of additive/dominance variances for *P. radiata* in Australia have so far been published. Ratios for diameter and volume in the present test are considerably lower than values obtained for this species in other studies, in South Africa and New Zealand, despite their being obtained from an appreciable sample of crosses (64), and at a fairly advanced age. Cotterill *et al.* (1987), in South Africa, recorded ratios for diameter of 1.5 and for volume of 0.9. Their paternally based estimates of ratios of additive/dominance variances for these traits were even higher than the maternally based ratios, by a factor of four. In a 23 female × 4 male North Carolina II design test in New Zealand, ratios of 3.6 and 2.0 (with female and male estimates of additive variance respectively) were obtained for diameter at 10 years (R. D. Burdon *et al.,* New Zealand FRI, unpubl. data).

Dean *et al.* (in press), in a study of five half-diallels of 10 crosses each of *P. radiata* at Kaingaroa Forest in New Zealand, found that the ratio of additive to dominance genetic variance for sectional area increased markedly between 3 and 13 years of age, from 1.0 to 6.0; the ratio at 10 years was 4.0. At age 10 years, dominance genetic variance for height was zero.

The low estimates of the ratio of additive to dominance variance for diameter and volume in this study compared with those from other studies may be due partly to the lack of replication of seedlots in the nursery. Effects of differential diameter growth of seedlings in different parts of the nursery would be confounded with full-sib family effects, tending to inflate SCA variance.

A measure of the relative importance of SCA for each trait over all families was calculated, based on a method developed by Baker (1978), which assesses the average contribution of SCA effects to a cross relative to the contribution of GCA effects from the parent clones, from the formula:

$$\text{Relative importance of SCA (\%)} = \frac{\text{SCA variance}}{2\ (\text{GCA variance}) + \text{SCA variance}} \times 100$$

Using this method in the present test, values of 54.1% for diameter, 14.1% for height, and 50.9% for volume were obtained. These values were of a similar order to those calculated by Carson (1986) for these traits from 18, 5 × 5, disconnected half-diallels at age 4½ years at one site in New Zealand (Kawerau): diameter 47%, height 11%, volume 42%. In a similar test at another New Zealand site (Kaingaroa) SCA was far less important for all traits, with the value for height still low relative to those for the other two traits (Carson 1986).

The mean of the absolute GCA values for conic volume of female and male parents (22 values) in this trial was 12.2 dm^3, while the mean of the absolute SCA values (64 values) was 16.9 dm^3, further indicating that in this population of crosses SCA was more important than GCA.

Individual Heritabilities

"Maternal" estimates of individual heritability are shown in Table 3. Those estimates for diameter and conic volume were low (0.07 and 0.09 respectively), while that for height was moderate (0.24).

The maternal estimates of heritability in the present study were higher than those obtained for *P. radiata* in South Africa by Cotterill *et al.* (1987) for diameter and volume (both 0.03), and slightly lower than values calculated by Carson (1986) over two sites in New Zealand: 0.10 for diameter and 0.12 for volume. However, the estimates for diameter in the present test were considerably below others from Australian open-pollinated progeny tests between 4½ and 11 years old – for example, 0.18 (Cotterill & Zed 1980), 0.23 (Dean *et al.* 1983), 0.18 (Matheson & Raymond 1984). In four open-pollinated tests in New South Wales, assessed at ages of 10 to 13 years, individual heritability values for diameter ranged from 0.05 to 0.21 (I. G. Johnson, unpubl. data).

The agreement between published estimates of heritability for height in the present test (0.24) and Australian and New Zealand open-pollinated tests is much better – 0.29 (Cotterill & Zed 1980), 0.16 (Dean *et al.* 1983), 0.23 (Matheson & Raymond 1984), and 0.22 (Carson 1986) – while the figure of 0.15 obtained by Cotterill *et al.* (1987) was of the same order.

Genetic and Phenotypic Correlations

Additive genetic correlations (calculated using maternal estimates of additive variance and covariance) and phenotypic correlations are shown for the three pairs of traits in Table 4. As expected, these correlations were all positive and relatively high, with the phenotypic correlations tending to be slightly greater. Both types of correlation between diameter and volume were especially strong (0.97 and 0.96), as would be expected for these closely related growth traits. The weakest genetic correlation was that between diameter and height (0.60), although the corresponding phenotypic correlation was stronger (0.73).

TABLE 4–Genetic correlations, estimated from maternal components of additive genetic variance and covariance, and phenotypic correlations

Trait	Diameter	Total height	Conic volume
Diameter		0.60	0.96
Total height	0.73		0.77
Conic volume	0.97	0.76	

Note: Genetic correlations shown above the diagonal; phenotypic correlations shown below the diagonal.

The values of correlations in this test were very similar to, though slightly lower than, those obtained by Cotterill *et al.* (1987) in South Africa and those of Dean *et al.* (1983) for similar traits in Victoria. The fairly low genetic correlation of 0.60 for diameter/height falls in the lower end of the range of genetic correlations for these traits in open-pollinated tests in South Australia (Cotterill & Zed 1980), while the phenotypic correlation of 0.73 is in the upper end of the range of those in the South Australian tests.

General and Specific Combining Abilities

Since growth rate as a whole is best expressed by the conic volume index, results for volume only are discussed below. Values of GCA and SCA for this trait for all parents and crosses analysed are shown in Table 5. Female and male parents are listed in order of decreasing GCA in this Table. There was a wide range in the values of GCA for the female parents. Nine females showed a positive GCA – 20002, 20011, 20012, 20022, 20059, 20062, 20084, 20088 (from New South Wales) and 80086 (from New Zealand); 20011 and 80086 were particularly outstanding for GCA in this trait. The GCA values of the male parents tended to be similar to one another and near zero.

Females 20018 and 20087 from New South Wales performed very poorly for volume; 20087 was particularly poor (GCA of –43.16 dm^3). Female 30016, from Victoria, had a moderately poor GCA (–0.47 dm^3).

TABLE 5–Specific combining abilities (SCAs) of crosses and general combining abilities (GCAs) of female and male parents, for conic volume

Female parent	Male parent				Female GCA
	20083	20055	20064	20058	
20011	-3.88	34.06	-4.58	-25.60	39.58
80086	-0.53		2.32	-1.79	24.13
20088	28.43		-2.89	-25.55	16.55
20012	-16.67	18.17	-12.21	10.71	14.77
20062	-1.28	-34.61		35.90	13.99
20084	36.94	-51.45	-17.84	32.34	8.27
20002		22.37	-18.21	-4.16	8.20
20022	12.68	-7.91	20.68	-25.44	5.85
20059	2.73	-11.70	15.92	-6.95	0.10
20080	7.62	4.06	-32.63	20.94	-2.45
30016	-18.80	-17.70		36.50	-4.66
20010	-36.16		37.20	-1.05	-7.46
20014	-34.12	26.99	-14.12	21.26	-8.11
20020	17.31	-23.74	-3.02	9.44	-10.21
20069	-8.81	27.53	-0.49	-18.32	-14.55
20086	2.81	8.53	2.71	-14.04	-17.08
20018	14.28		27.14	-41.42	-23.77
20087	-2.56	5.32		-2.77	-43.16
Male GCA	2.42	0.10	-0.68	-1.84	

GCA effects made a major contribution to the superiority of the volume of some crosses – for example, 20011 × 20064, 20011 × 20083, and 80086 × 20083. However, there was a larger number of superior crosses in which SCA effects were much more important than GCA effects, such as 20010 × 20064, 20062 × 20058, 20084 × 20058. These reflected the greater mean value of the absolute SCA's than of the absolute GCA's as discussed earlier.

Correlation of SCA with GCA Values

Levels of SCA for volume over all the 64 families analysed appear to be independent of levels of GCA. A very low linear correlation value ($r = -0.12$) was calculated between the predicted genetic values for these crosses (reflecting the total GCA effect) and their SCA's, for both of the traits diameter and conic volume.

These results agree closely with those of P. P. Cotterill, CSIRO Division of Forestry and Forest Products (pers. comm.), who found correlations of near zero (r = –0.07) between predicted genetic values and SCA for diameter in *P. pinaster* and *P. elliottii* in South Africa. In the present study, strong GCA's were evidently not consistently associated with either strong or weak SCA's.

Genetic Values

Rankings for predicted and observed genetic values (pair-cross effects) for conic volume of the best 20 crosses for predicted genetic value are shown in Table 6. Applying a strictly additive genetic model to this trait, the performance of each cross should equal the predicted genetic value, or sum of parental GCA's (Cotterill *et al.* 1987). The assumption of a strictly additive model for volume in this test was not supported, since the predicted and observed genetic values over the whole 64 crosses were frequently very different, and the over-all agreement in the ranks of these genetic values was not very close. The linear correlation between the observed and predicted genetic values for all crosses was weak (r = 0.65). These results reflect the relatively greater importance of SCA over GCA for volume in these crosses (54.1%), as discussed earlier, the low ratio of additive to dominance genetic variance, and the large values of SCA for many crosses.

The top-ranking crosses based on predicted genetic value (those with high parental GCA's) did, however, include a fairly high proportion which ranked well on observed

TABLE 6–Predicted and observed genetic values of the predicted best crosses for conic volume, and their rankings out of 64. Genetic values expressed as deviations from the mean of the least squares means for conic volume of the female (and male) parents (154.37 dm^3).

Family (cross)	Predicted genetic value (dm^3)	Rank	Observed genetic value (dm^3)	Rank
20011 × 20083	42.0	1	38.1	6
20011 × 20055	39.7	2	73.7	1
20011 × 20064	38.9	3	34.3	7
20011 × 20058	37.7	4	12.1	25
80086 × 20083	26.5	5	26.0	12
80086 × 20064	23.5	6	25.8	14
80086 × 20058	22.3	7	20.5	17
20088 × 20083	19.0	8	47.4	4
20012 × 20083	17.2	9	0.5	34
20062 × 20083	16.4	10	15.1	22
20088 × 20064	15.9	11	13.0	24
20012 × 20055	14.9	12	33.0	8
20088 × 20058	14.7	13	–10.8	21
20012 × 20064	14.1	14	1.9	32
20062 × 20055	14.1	15	–20.5	48
20012 × 20058	12.9	16	23.6	15
20062 × 20058	12.1	17	48.0	2
20084 × 20083	10.7	18	47.6	3
20084 × 20055	8.4	19	–43.1	61
20002 × 20055	8.3	20	30.7	9

genetic value. For example, the top 10 crosses for predicted value included four in the top-ranking 10 for observed value, while the expected best three crosses ranked in the top seven on observed value (*see* Table 6). Only one cross (20011 × 20058) in the predicted top five ranked poorly on observed genetic value (ranks 4 and 25, respectively) as the result of a large negative SCA of $-25.6\,\mathrm{dm}^3$.

Cotterill *et al.* (1987) reported a slightly closer agreement between predicted and observed genetic value rankings for diameter in a South African *P. pinaster* progeny test than was obtained for volume in this *P. radiata* test. The correlation between observed and predicted genetic values (0.67) in the *P. pinaster* test, however, was not much greater than in the present test. There was only one serious discrepancy between the ranks of the top five for predicted genetic value and their ranks for observed genetic value in the *P. pinaster* test.

Although genetic value results for diameter and height as separate traits are not discussed here, it is of interest that the top five crosses based on predicted genetic value for diameter did in fact include three which were also in the top five for the observed value, and there was only one serious discrepancy in ranks in this group, for the cross 20011 × 20058.

Practical Implications for Seed Production Operations

Parent clones for use in open-pollinated seed orchards are selected only on the basis of their high GCA, since gains from selection for SCA can be used only on the basis of direct knowledge of the performance of the pair-crosses. However, there are two main options open to seed orchard managers wishing to produce seed of high genetic quality from controlled pollinations in orchards, possibly followed up by the multiplication of the resulting seedlings by mass vegetative propagation. Carson (1986) referred to these options as the "tested cross" and "general combiner selection" options.

If SCA effects are very important in a breeding population, the tested cross option is likely to give substantial gains from control-pollinated orchards. Identification of the few very best crosses, however, would involve a heavy workload in crossing a large number of parent clones and testing many full-sib crosses.

General combiner selection is operationally simpler, in that large numbers of parents can be screened fairly quickly for GCA. Carson (1986) considered that this option is better for the New Zealand *P. radiata* breeding programme, under conditions where GCA effects for the major selection traits tend to be much greater than SCA effects. Calculations by Carson (1986) showed that selection of clones for control-pollinated orchards on the basis of parental GCA was likely to give gains at least as great as those from reproducing the best tested crosses.

Cotterill *et al.* (1987) also favoured general combiner selection over the tested cross option, and concluded that intermating best GCA parents with best GCA parents appears likely to produce outstanding families, even when dominance variance equals additive variance. The results of the present test lend some support to this contention. The four tested crosses between the three best GCA females and the best two GCA males for volume had rankings for predicted genetic value of 1, 2, 5, and 8. Three of these crosses also ranked very well for observed genetic value, with ranks between 1 and 6 (Tables 5 and 6). This was despite two of the crosses exhibiting high levels of SCA. However, the reliability of the predicted genetic values as a guide to superior crosses, such as would be sought for seed production, tended to fall in crosses between parents with high, but not outstanding, GCA. For example, the four tested crosses between females 20012 and 20062 and males 20083 and 20055 had predicted genetic value ranks between 9 and 15, but the observed values of three of the crosses were mediocre to poor (ranks 22 to 48), and two of the crosses had high SCA's.

These results indicate that even if SCA variance is large relative to GCA variance for volume in *P. radiata,* as was implied by this study, general combiner selection for seed orchard clones may still be effective, as long as only the few very best GCA parents are utilised.

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APPENDIX 1

EXPECTATIONS OF MEAN SQUARES FOR ESTIMATING GENETIC PARAMETERS FROM THE GLM ANALYSIS OF THE NC-II COMPONENT OF PROGENY TEST Q14/1.11

Source of variation	d.f.	Type III Expectations of mean squares
Replicate	28	$\sigma^2_e + 39.66\ \sigma^2_r$
Female	17	$\sigma^2_e + 17.52\ \sigma^2_{fm} + 61.56\ \sigma^2_f$
Male	3	$\sigma^2_e + 16.97\ \sigma^2_{fm} + 262.95\ \sigma^2_m$
Female × Male	43	$\sigma^2_e + 17.85\ \sigma^2_{fm}$
Error	1085	σ^2_e

There are 18 female parents, four male parents, and 29 replications. The variance component σ^2_f is due to females, σ^2_m is due to males, σ^2_{fm} is due to female × male interactions, σ^2_e is due to between-plot error and interactions between plots and replications.