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CONTROL-POLLINATED SEED ORCHARDS OF BEST GENERAL COMBINERS — A NEW STRATEGY FOR RADIATA PINE IMPROVEMENT

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ABSTRACT

Results from a diallel test of improved *Pinus radiata* planted on two Central North Island sites indicate that general combining (GCA) effects are more important than specific combining ability (SCA) effects for tree growth rate, stem form, and resistance to *Dothistroma pini*. These results support current use of well-isolated open-pollinated clonal seed orchards of the best general combiners for the production of improved radiata pine seed. Mass controlled pollination and vegetative multiplication will soon allow large-scale production of crosses. Given the moderate levels of SCA and the finite number of crosses that can be tested, maximum gains seem attainable by selecting for parental GCA.

Parental GCA estimates have previously been obtained from trials of open-pollinated progenies. In future, control-pollinated polycross progenies will be used for GCA ranking of parents. Greater genetic gains should result from large-scale production of the best general combiners, rather than selection and multiplication of best full-sib families.

KEYWORDS

General and specific combining ability, controlled pollination, polycross, diallel, selection.

INTRODUCTION

Genetic improvement of radiata pine in New Zealand is accomplished through recurrent selection and progeny testing of superior trees. Candidate trees have been phenotypically selected and tested for their general combining ability (GCA) for several economically important traits. Tested clones have been established in clonal seed orchards to supply up to 5000 kg/year of open-pollinated radiata pine seed for forest plantings.

Mass controlled pollination and the multiplication of seedlings by vegetative propagation may soon make conventional clonal seed orchards obsolete. The new control-pollinated seed orchards will offer more rapid production of improved seed and complete control of pollen pedigree, and will allow parental selection intensities to be higher than is possible with conventional orchards. In addition, a range of special-purpose radiata 'breeds' can be produced either to meet specific site requirements (e.g. frost resistance), or to capture large genetic gains in specific log or wood quality traits (e.g. high-density wood).

Breeding for improved GCA, utilising additive genetic variance, is the basic approach used in most forest tree improvement programmes. Both additive and non-additive genetic variance can only be fully utilised through clonal selection and afforestation. Only a small proportion of the potential gains from non-additive genetic variance can be captured in seedling trees by reproducing tested full-sib crosses (despite the attention that this has received in the literature). This portion of non-additive variance is termed specific combining ability (SCA). With large specific combining ability effects control-pollinated seed orchards could be used to reproduce tested crosses yielding greater genetic gains than can be obtained from progeny of conventional orchards. Alternatively, control-pollinated seed orchards can be set up to make crosses among the best general combiners, relying only on GCA.

The choice of option has important implications for both testing and production of control-pollinated seed. In the testing phase, tests should be efficient in either screening large numbers of full-sib crosses, or screening for parental GCA performance. Similarly, crossing in the control-pollinated orchards may follow any mating design, but a polycross design using a pollen mix of the best general combiners may be the most practical.

The radiata pine improvement programme at the Forest Research Institute is well-placed to follow either the tested-cross or general-combiner selection options. Progeny testing of parents for GCA has been routinely done using open-pollinated progeny tests. In addition, advanced-generation breeding populations exist in the form of nested diallel, or factorial progeny trials which can provide information on specific crosses, as well as some GCA information on parents.

Wilcox *et al.* (1975) reported evidence for strong SCA effects for vigour in radiata pine at age 5 years from results of a 4 x 4-parent factorial experiment. The demonstration of severe inbreeding depression for growth rate of selfed progenies provided supporting evidence for the existence of non-additive variance controlling this trait (Wilcox, 1983b). However, Burdon (unpub. results), in an analysis of a breeding trial involving four male testers and 23 female parents of an improved radiata pine population (North Carolina Design model II), found that SCA effects for growth rate were smaller than GCA effects (particularly as the trees got older) and SCA effects for tree-form and disease-resistance traits were relatively unimportant.

This paper reports the results of a diallel analysis and compares the importance of SCA and GCA. The implications for tree breeders choosing between alternatives of reproducing tested crosses or crossing general combiners in control-pollinated orchards are discussed.

MATERIALS AND METHODS

A set of 18 modified disconnected half-diallels of second-generation improved *P. radiata* seedlings was planted at each of two central North Island locations (Kawerau and Kaingaroa Forests) in 1980 (Wilcox, 1983a). Ninety-one parents were crossed to produce 150 full-sib families; parents were each represented in one to five half-sib families, with an effective average of 3.3 crosses per parent. Trees were planted to a single-tree plot, 'sets-in-replications' design, with 46 field replications at Kawerau and 50 replications at the Kaingaroa Forest site. Trees were assessed in late 1984 for a number of traits, including

- Tree height (m).
- Diameter at height 1.4 m (cm).
- Stem straightness — using a nine-point subjective rating, where:
  1 = crooked
  9 = very straight
- Malformation — using a nine-point subjective rating, where:
  1 = multiple forking of the leading stem
  9 = no leader malformation
- *Dothistroma pini* resistance (assessed at Kaingaroa Forest only) — infection assessed in 5% classes of '% cross infected'.
- Tree volume (dm^3) — derived from measurements of tree height and diameter using an equation developed for predicting growth of radiata pine in Central North Island forests (Mensuration table M12).

Statistical analysis

Assessment data were analysed using programs "DIALL" (Schaffer and Usanis, 1969) and "GSCA" (Snyder, 1975) as well as both "GENSTAT" and "SAS" procedures on a VAX 780 computer. "DIALL" was used to estimate variance components for GCA and SCA for each diallel, and "GSCA" was used to estimate parental breeding value and SCA effects for each cross. Diallel effects and overall tests of statistical significance were calculated using "PROC GLM" of "SAS" in an analysis for each location including terms for replications (reps), diallels, reps x diallels, crosses in diallels and error. Heritability estimates for individual trees were calculated from estiamtes of variance components from "DIALL" and from "SAS PROC VARCOMP".

The relative importance of SCA for each trait was calculated from the pooled variance component estimates from "DIALL" as:

Relative importance of SCA (%)

$$= \frac{\text{SCA variance}}{2\,(\text{GCA variance}) + \text{SCA variance}} \times 100$$

(Baker, 1978)

This statistic measures the average relative contribution of SCA effects to a cross, relative to the contribution of GCA effects from the parent clones.

Genetic gains over the mean for the breeding population were predicted both for selection of parents and of full-sib families for volume, tree form, and *dothistroma* resistance. Gains were predicted for a range of selection intensities using the formula:

Genetic gain = $G = i\,h^2\,\sigma_p$ (Falconer, 1981)
where i = selection intensity (Becker, 1975)
h^2 = heritability
σ_p = standard deviation of phenotypic variance

For selection of tested crosses:

$h^2 = h^2_{hs}$ where h^2_{hs} = heritability of half-sib family means

and $\sigma_p = \sigma_{p_{hs}}$ = standard deviation of the phenotypic variance of a parent's breeding value.

For selection of parents on GCA:

$h^2 = h^2_{FS}$ where h^2_{FS} = heritability of full-sib family means

and $\sigma_p = \sigma_{p_{FS}}$ = standard deviation of the phenotypic variance of a full-sib family mean.

In order to provide a valid comparison of the alternative selection options, gains were predicted for selections from a breeding population of 300 parents which were either:

(a) tested in a polycross (for GCA information) or
(b) crosses mated in a partial factorial comprising three sets of 100 parents, each represented in four crosses (for tested cross information).

The main comparison assumed a fixed test size (of 30,000 plants tested) for both options, and a requirement that three parents or three unrelated crosses be selected under either option. Gains were also predicted for the 'tested cross' option for a test five times as large (150,000 plants tested) involving 3000 crosses.

RESULTS

Growth at Kawerau was faster than at Kaingaroa Forest. Average tree heights differed by 2 m, and tree volumes were on average 46 dm^3 at Kawerau, versus 19 dm^3 at Kaingaroa Forest (Table 1, columns 1 and 4). Average

Table 1. Population means, estimates of narrow-sense heritability and estimates of relative importance of SCA: from age 4 results of a *Pinus radiata* diallel at two central North Island sites.

	Kawerau			Kaingaroa Forest		
Trait	Population means	Heritability[1]	Rel. importance of SCA[2]	Population means	Heritability[1]	Rel. importance of SCA[2]
Height (m)	7.5	0.24	11	5.5	0.20	7
Diameter (cm)	13.7	0.09	47	9.5	0.11	17
Volume (dm^3)	46	0.10	42	19	0.13	14
Straightness (1-9)	5.6	0.14	23	6.0	0.17	13
Malformation (1-9)	7.4	0.07	14	7.2	0.09	28
D. pini infection (%	-	-	-	11.7	0.37	6

[1] Narrow-sense heritability = h^2 = $\frac{4\sigma^2_{gca}}{\sigma^2_{gca} + \sigma^2_{sca} + \sigma^2_{e}}$

where σ^2_{gca} = variance component for general combining ability within diallels.

σ^2_{sca} = variance component for specific combining ability within diallels.

σ^2_{e} = variance component estimate for error (individuals within families).

[2] Relative importance of SCA (%)

$$= \frac{\sigma^2_{sca}}{2\sigma^2_{gca} + \sigma^2_{sca}} \times 100$$

tree form (i.e. straightness and malformation) was similar at the two sites. At Kaingaroa, the average 12% crown infection by dothistroma was sufficient to discriminate among crosses for resistance to this disease, although it was below the level considered to contribute to serious growth loss. Cross means differed significantly ($P>0.001$) from one another for all traits at each site according to the F-test from an ANOVA combined over diallels.

Narrow-sense heritability estimates ranged from 0.07 for malformation at Kawerau, to 0.37 for resistance to dothistroma at Kaingaroa Forest (Table 1, columns 2 and 5).

Values for the relative importance of SCA ranged from 6% for dothistroma resistance to 47% for diameter growth at Kawerau (Table 1, columns 3 and 6); these data show that SCA is important for diameter (and therefore volume) growth, but is only moderately important for stem form and malformation, and has negligible effect on height and resistance to dothistroma.

Genetic gains from a control-pollinated seed orchard were predicted for the alternative strategies of (1) reproducing the best tested full-sib crosses and (2) pair-mating based on selection for GCA of parent clones (Table 2). Gains are expressed as percentages of population means. They were calculated as if selection was applied to single traits.

Selection of the best three parents per set based on their breeding values (Table 2, column 1) would yield substantial genetic gains for most traits. Gains in tree volume would be greater than 18% at both sites, and gains in tree-form traits would be sufficient to markedly decrease plantation management costs and increase log quality. Predicted relative gains in dothistroma resistance were very high, and easily justify the creation of a special resistant breed for high-hazard sites.

Selection of the best single cross from each of the three sets of 200 tested (and unrelated) crosses would yield less genetic gains than an equivalent selection of parents for GCA for all traits except volume/tree at Kawerau (Table 2, column 2). If as many as 3000 unrelated crosses were tested in order to select three crosses for multiplication in a control-pollinated orchard (Table 2, column 3), genetic gains would be roughly similar to those for selection of three of 300 parents.

DISCUSSION

This study supports current strategies for improving radiata pine in New Zealand (Shelbourne *et al*, in prep.). Though heritabilities are fairly low, necessitating progeny testing, substantial proportions of additive genetic variance for most traits make selection and breeding for improved GCA a good strategy for making genetic gains in the breeding population.

Seed from existing clonal seed orchards is showing moderate genetic gains in tree growth rate, stem form, health and wood quality. Controlled pollination of the very best parents for GCA will give larger gains, owing to the complete control of pollen pedigree and higher selection intensities than can be used in conventional orchards, and

Table 2. Predicted percentage gains for radiata pine progenies of best tested crosses compared with gains for progenies of polycrosses among best parents for GCA — using estimates from a diallel test at two sites.

Trait	Site[1]	Predicted percentage genetic gains[2] for selection of: Parents[3] (3/300)	Crosses[4] (3/600)	Crosses[5] (3/3000)
Volume (dm^3)	KA	18	19	23
Volume (dm^3)	KF	29	24	29
Straightness (1-9)	KA	25	23	27
Straightness (1-9)	KF	26	22	27
Malformation (1-9)	KA	18	16	19
Malformation (1-9)	KF	24	22	27
D. pini resistance		116	92	113

[1] KA = Kawerau, KF = Kaingaroa Forest.

[2] Gains are expressed as percentages of means for cross progenies and breeding values for parents.

For selection of parents: $G = 2i\, h^2_{hs}\, \sigma p_{hs}$

For selection of crosses: $G = i\, h^2_{FS}\, \sigma p_{FS}$ (Falconer, 1981)

where: i = selection intensity = 2.508 for 3 of 300 parents
= 2.746 for 3 of 600 crosses
= 3.367 for 3 of 3000 crosses (Becker, 1975)

h^2_{hs} = heritability of a parental breeding value

σp_{hs} = standard deviation of variance of parental breeding values

h^2_{FS} = heritability of a full-sib family mean

σp_{FS} = standard deviation of variance of full-sib family means

[3] Selection of parents based on a polycross test for GCA, (with numerous pollen parents) for 300 polycross families (one polycross = one parent), 50 replications of each.

[4] Crosses based on a partial factorial design comprising three sets of 100 parents each, each parent crossed with four others in the set for a total of 200 crosses per set, 600 crosses overall, 25 replications of each (i.e. total test size equivalent to that for the polycross test).

[5] As for 4, except total number of crosses now 3000 (i.e. total test size five times that for the polycross test).

the ability to produce breeds targeted to specific site or trait requirements.

Estimates of the relative importance of SCA versus GCA confirm the trends noted by Burdon (unpub. results), in that GCA effects are always greater than SCA effects. Although SCA effects were important for volume growth at Kawerau, they still contributed less to growth than did the GCA effects. Wilcox *et al.* (1975) concluded that large SCA effects for growth rate were important enough to justify their exploitation either through the use of vegetative propagation of clones or through seed of specific crosses produced from two-clone orchards (control-pollinated orchards were not then seen as an economic option). Results from the diallel test do not support this conclusion. The predicted gain comparisons in Table 2 illustrate the advantages of selection of parents of GCA information over selection of the best single crosses. These two options would be typical of those available in many tree improvement programmes in which GCA information is routinely obtained on all parents in the breeding population, and tested-cross information is available from progeny tests containing the advanced-generation breeding population.

In future, the New Zealand radiata pine breeding programme is likely to rely on polycross tests at several sites to rank breeding population parents for GCA for selection of orchard clones, while full-sib mating designs will be used to create the new breeding population, (Burdon and Shelbourne, 1971). Advanced-generation selection will emphasise within-family selection in plantings of the best families. Information on SCA of tested crosses will, therefore, be limited relative to GCA information on parents.

Is it worthwhile to test a large number of crosses (over a representative number of site types) for the sole purpose of selecting the best for use in control-pollinated seed production? Genetic gains predicted for the best three single crosses of 3000 tested (column 3, Table 2) are similar to those obtained from selection of parents for GCA. These results clearly imply that resources expended on mass testing of crosses will yield marginal, if any, gains over the option of selecting on parental GCA.

CONCLUSION

Production of improved radiata pine seed through crossing among the best general combiners is both an efficient and an effective strategy for optimising genetic gains from control-pollinated seed orchards.

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SYMPOSIUM DISCUSSION

T.P. Palmer, Private Breeder, New Zealand

Were the plants used in your test cross from a selected population or from a wild population?

Carson

From trees improved after a generation of selection.

Palmer

Would you expect the situation to be different, with more specific combining ability effects, if you had been using an unimproved population?

Carson

No. All the tests we have so far indicate, if you're thinking of G.C.A. relative to S.C.A., that G.C.A. is more important for this species.

Palmer

Is this situation unusual?

Carson

The fact that there is only a small portion of non-additive variance that actually goes into selection of testing crosses is general, i.e. G.C.A. is always the main component of gain, which is why the S.C.A. would have to be quite large to tip the balance in favour of the tested cross option.

Dr H.S. Easton, Grasslands Division, DSIR

Most of the literature on open-pollinated perennial pasture grasses indicates that we have a similar situation with G.C.A. being more important than S.C.A.

Dr M.D. Wilcox, Forest Research Institute

The table which showed the combining ability variances in the trials for straightness and malformation of the trees showed the S.C.A. effect to be relatively small compared with the G.C.A. and yet the heritability itself is very low. What is the explanation of such a low heritability when additive variance relative to non-additive is quite high?

Carson

The two are not directly related. There is obviously environmental variance there which, if large, would reduce the heritability despite a high G.C.A. variance component. The narrow-sense heritabilities that I showed in the table, are probably lower than they would be on an older trial — we think trial results are more reliable at 8-10 years and heritabilities are higher for these traits at that age.

Dr R.D. Burdon, Forest Research Institute

The parents having been fairly intensively selected would tend to depress the apparent heritability for stem straightness.

Wilcox

Does that selection give a biased picture of the ratio of S.C.A. to G.C.A?

Carson

Maybe we should look at the heritability for straightness in the native population races.

Burdon

The native population experiments (paper 25) were not strictly comparable. Sometimes we did get appreciably higher heritabilities but the situation was complicated by the different experimental layout combined with the presence of a great deal of stem malformation in the base population.

Dr C.J.A. Shelbourne, Forest Research Institute

Have you any idea from your simulation of the gains from these options — selection of general combiners versus selection of specific crosses — how big the S.C.A. to G.C.A. ratio has got to get before there is a real advantage from the selection of specific crosses.

Carson

Yes, it has to be quite large. This is important with reference to the cloning option as well because we are talking about capturing non additive genetic variance, which has always been put forward as one of the big advantages of cloning. You have to assume quite a large amount of non additive variance, at least equivalent to the additive component before there is a significant gain from the clonal option, and certainly for the tested cross option there has to be a very large component of non additive variance effect.

Shelbourne

Greater than the G.C.A.?

Carson

In the tested cross option, I suspect so, and we do not seem to be getting that much S.C.A. for any of our traits.

Dr S.A. Menzies, Plant Diseases Division, DSIR

The heritability of disease resistance in *Dothistroma* is not high. Is there any indication of how many genes were involved in this resistance?

Carson

No, we do not know. There will be another paper on the subject of our breeding programme for *Dothostroma* resistance (Paper 66), we do not know what the genetic control is, although we haven't seen anything to suggest that its simply inherited.

Wilcox

We must remember the cost involved in all this. The cost of seed from controlled pollination is currently about $1000/kg compared to about $150/kg with conventional open-pollinated methods. To justify the extra expenses of controlled pollination we must be sure that there are substantial extra genetic gains.

Dr H.S. Easton, Grasslands Division, DSIR

How many viable seeds are there in a kilogram?

Carson

We get about 20 000-25 000 plantable seedlings per kg of seed so we can plant about 20 kg.