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ORIGINAL PAPER

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General and specific combining ability from partial diallels of radiata pine: implications for utility of SCA in breeding and deployment populations

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Abstract Variances for general combining ability (GCA) and specific combining ability (SCA) and the relationship between mid-parental GCA and SCA effects were estimated for tree diameter (DBH) from a series of 20 sets of 6×6 half-diallel mating experiments in radiata pine, planted at ten sites across Australia. Significant SCA variance for DBH was almost equal to GCA variance for the combined analysis of all ten sites. The importance of SCA variance varied among sites, from non-significant to SCA variance accounting for all genetic variation among full-sib families. Significant SCA × site interaction was detected among the ten sites. A significant and positive correlation between mid-parental breeding values and best linear unbiased predictions of the SCA effects was observed. About a quarter of extra genetic gain is achievable through use of SCA variance if selection is based on the best breeding values. To fully exploit genetic gain from SCA variance in a deployment population, positive assortative matings are required for the best parents. It is estimated that the additional deployment gain of 46.0% for ten sites combined, or 52.9% for four sites combined that had significant GCA as well as SCA effects, were achievable relative to gain from GCA only, if all SCA variance within this breeding population was exploited. For a breeding population, selection for breeding values may be sufficient due to positive correlations between breeding values and SCA values. For a deployment population to capture more SCA genetic gain, it is preferable to make more pair-wise mating for parents with higher breeding values.

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Introduction

The presence of additive genetic variance in populations of forest trees is supported by the majority of genetic studies (Zobel and Talbert 1984; van Buijtenen 1988). However, evidence for non-additive (dominance and epistasis) genetic variance in tree species appears to be less certain and more varied (Kriebel et al. 1972; Foster and Bridgwater 1986; Boyle 1987; Yeh and Heaman 1987; Dieters et al. 1995; Yanchuk 1996; Paul et al. 1997; Kleinhentz et al. 1998). The importance of non-additive genetic variance relative to additive genetic variance also changes with tree age. For example, in loblolly pine (*Pinus taeda*), non-additive variance was found to increase at early ages and then decline in late ages (Byram and Lowe 1986; Balocchi et al. 1993). On the other hand, a trend of increasing dominance genetic variance was observed in Sitka spruce (*Picea sitchensis*) (Samuel 1991) and black spruce (*Picea mariana*) (Boyle 1987) as trees grew. Stonecypher et al. (1996) reported non-additive genetic variance was only about one-half of the additive genetic variance for height in a series of 65 sets of six-parent, disconnected half-diallels in Douglas fir (*Pseudotsuga menziesii*).

Since additive genetic effects were usually found to be abundant and more important than non-additive genetic variance for previously unselected material in crops (Sprague and Tatum 1942) and in the first few generations of selected material in tree species (Namkoong et al. 1988, p. 57), most conifer breeding programs worldwide used additive genetic effects only by simple recurrent selection for general combining ability (GCA). They were typified by nucleus breeding strategies (Cotterill et al.1988), multiple-population strategies (Burdon and Namkoong 1983; Barnes 1986) and more recently, by rolling-front breeding strategies (Borralho and Dutkowski 1998). Several breeding programs adopted subline breeding strategies (Lowe and van Buijtenen 1986; Hodge et al. 1989; White et al. 1992; McKeand and Bridgwater 1993). While the main purpose of subline breeding is to manage or control relatedness among members of deployment

populations, the sublines also provide the opportunity to exploit non-additive genetic effects in breeding and deployment populations.

The relative importance of additive to non-additive genetic variance plays a vital role in practical tree breeding: choice of breeding and deployment population strategies, prediction of response to selection and evaluation of breeding systems. Within Australian populations of radiata pine (*Pinus radiata*), additive genetic parameters for growth traits and form traits (stem straightness, branching, forking) have been intensively investigated (Cotterill and Zed 1980; Dean et al. 1983; Matheson and Raymond 1984; Cotterill and Dean 1990; Matheson et al. 1994). However, there is limited information on non-additive variance and the ratio of non-additive to additive variances. Volker and Cameron (1988) reported that non-additive effects were not as important as additive variance at age 12.5 years in a design II trial in eastern Australia. Matheson et al. (1994) reported that non-additive variance exists only for the first 6 years in radiata pine for diameter. But both studies suffered from representing only a very small sample of parent trees. Estimates of non-additive genetic variance from radiata pine populations in New Zealand were mixed. Wilcox et al. (1975) analysed a 4×4 design II mating of radiata pine in New Zealand, and the estimated mean squares in their analysis of variance indicated that dominance variance was higher than additive variance for height, diameter and volume at age 5. Carson (1986) analysed data collected at 4.5 years from 18 5×5 disconnected, half-diallel matings established across two sites in New Zealand and reported that levels of dominance variance almost equal to the additive variance for diameter and volume at one site but were less important for growth traits at the other site. Later on, King and Johnson (1998) reported SCA variance declined relative to GCA variance for the same experiment. In addition, Dean (1990) estimated that additive genetic control was predominant in older *P. radiata* from a series of five sets of six parent, half-diallel matings between age 3 and 13 in two New Zealand trials, and Carson (1991) reported that the relative importance of SCA variance (e.g. $\sigma^2_{SCA}/2*\sigma^2_{GCA}+\sigma^2_{SCA}$) was between 6% and 98% among 11 sites in an experiment using five sets of 5×5 half diallels.

Compared with all these estimates in radiata pine, the Australian-wide diallel mating design experiment provides by far the largest population to estimate the relative levels of additive and non-additive variance. In addition, breeders are not only interested in the relative importance of non-additive to additive genetic variance, and the age pattern of the ratio, but also the distribution of additive values relative to non-additive values. If additive genetic values were positively correlated with non-additive values, then selection for additive value would facilitate the use of non-additive genetic variance. Even if there is no correlation between additive and non-additive genetic values, the tree breeder may still be able to capture some non-additive genetic variance in the deployment population (Yanchuk 1996). However, if there were negative correlations between additive and non-additive values, the breeder may face a challenge in deploying additive genetic variance.

This paper examines four issues relating to non-additive genetic variance in this Australia-wide radiata pine experiment: (1) importance of SCA variance relative to GCA variance in a large, radiata pine breeding population (114 parents); (2) interaction patterns between SCA and sites (i.e. whether SCA performs similarly across sites); (3) relationship between SCA and GCA estimates; and (4) size of extra genetic gain which can be derived from SCA variance in deployment and possible deployment strategies using SCA variance.

Materials and methods

From 1976 to 1986, 21 sets of 6×6 half-diallels were created from 120 selected parents by then-five organizations within Australia [CSIRO Division of Forest Research, Canberra (ACT), NSW Forestry Commission (NSW), CSIRO Division of Forest Research, Mount Gambier (SA), Forests Commission, Victoria (VIC) and Western Australian Forests Department (WA)]. Among 120 parents, nine were from New Zealand selections and 111 were selections made between the 1950s and 1970s from unimproved Australian plantations. All diallel sets were incomplete with missing crosses (between 1 and 12 crosses were missing, depending on set and planting site). Progenies of this Australian-wide diallel experiment were planted in 1986 and 1987. In 1986, seedlings of 100 families from seven sets of half-diallel were raised in a Cowwarr nursery in Victoria with four blocks of 30 seeds each. These seedlings were planted in four sites within four regions (Fig. 1): PT5455 (Mount Gambier region, SA), VRC52 (Traralgon region, VIC), BIL133 (Billapaloola region, NSW) and RAD199 (Myrtleford region, VIC). In 1987, seedlings were raised in a Mount Gambier nursery for 216 families from 16 half-diallel sets. The 16 sets include 13 new sets and three sets the same as for 1986. One set from Western Australia (WA 3) was not planted because fewer than half the crosses were made. The seedlings were planted in the following six sites in five regions: PT5459 (Mount Gambier), VRC60 (Traralgon), BIL149 (Billapaloola), RAD211 (Myrtleford),

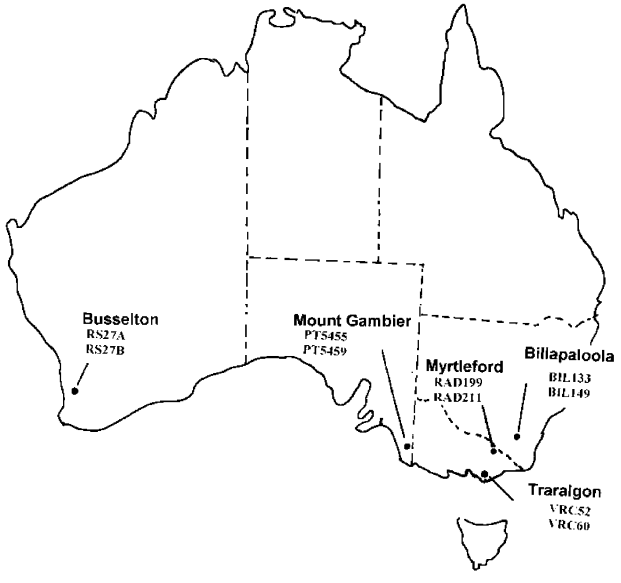

Fig. 1 Locations of ten testing sites for Australia-wide radiata pine diallel mating progenies

RS27A and RS27B (Busselton region, WA). The number of families planted within each set varied in the 1987 plantings. A row and column design within each complete block was implemented with four tree-row plots.

Assessment of trees on ten sites was carried out in the summer season 1997–1998 (11.5- and 10.5-year-olds from planting for 1986 and 1987 sites, respectively). The following seven traits were measured:

1. Diameter (DBH)—diameter over bark at breast height (1.3 m above ground) to the nearest millimetre (diameter tape).
2. Stem straightness (STEM)—a six-point subjective index of stem straightness, with 1 = most crooked and twisted trees in the trial (about 5% of trees), and 6 = most straight and vertical trees in the trial (about 5% of trees).
3. Branch angle (BRA)—a six-point subjective index of branch angle, with 1 = steepest branches for the site, and 6 = flattest branches for the site.
4. Branch size (BRS)—a six-point subjective index of branch size, with 1 = thickest branch for the site, and 6 = thinnest branch size for the site.
5. Fork (FORK)—number of forks on the main bole counted for each tree (0 = no fork, 1, . . . n=1, . . . n forks); fork was not measured for site Bill149 due to high mortality.
6. Ramicorn (RAM)—number of ramicorns is counted for each tree.
7. Cluster number (CLUST)—cluster refers the number of branch whorls between 1 m and 6 m of the main bole and is counted for each tree.

A preliminary analysis using SAS MACRO programs (Wu and Matheson 2000, 2001) indicated SCA effects were significant for DBH and RAM. However, only DBH was analysed in great detail for the importance of SCA because SCA variance for RAM was significant at only two sites, and RAM score had a non-normal distribution.

Several linear models were fitted to examine the importance of SCA variance and SCA × site interaction. First, a multi-site interaction variance model was fitted. Since preliminary analysis for individual sites indicated unequal error variances among sites, two approaches were used to account for this heterogenous variance in fitting the multi-site interaction variance genetic model. The first approach was to log transform the raw data. Then the following linear model in matrix form was fitted to the transformed data:

$$\mathbf{Y} = \mathbf{X}\beta + \mathbf{Z}_{\mathrm{GCA}}\mathbf{u}_{\mathrm{GCA}} + \mathbf{Z}_{\mathrm{SCA}}\mathbf{v}_{\mathrm{SCA}} + \mathbf{Z}_{\mathrm{GCA*site}}\mathbf{u}_{\mathrm{GCA*site}} + \mathbf{Z}_{\mathrm{SCA*site}}\mathbf{v}_{\mathrm{SCA*site}} + \mathbf{e} \quad (1)$$

with

$$\mathbf{u}_{\mathrm{GCA}} \sim (\mathbf{0},\mathbf{G}_{\mathrm{GCA}}), \mathbf{v}_{\mathrm{SCA}} \sim (\mathbf{0},\mathbf{G}_{\mathrm{SCA}}), \mathbf{u}_{\mathrm{GCA*site}} \sim (\mathbf{0},\mathbf{G}_{\mathrm{GCA*site}}), \mathbf{v}_{\mathrm{SCA*site}} \sim (\mathbf{0},\mathbf{G}_{\mathrm{SCA*site}}), \text{ and } \mathbf{e} \sim (\mathbf{0},\mathbf{R}) \quad (2)$$

where

$$\mathbf{Y} = \begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \vdots \end{bmatrix}, \quad (3)$$

X, and Z_{GCA}, . . . are the incidence matrices corresponding to each component, β is a vector of fixed effect of site and replicates within sites, $\mathbf{u}_{\mathrm{GCA}}$ and $\mathbf{v}_{\mathrm{SCA}}$ are vectors of GCA effects and SCA effects across m sites,

$$\mathbf{u}_{\mathrm{GCA*site}} = \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \vdots \\ \mathbf{u}_m \end{bmatrix} \text{ and } \mathbf{v}_{\mathrm{SCA*site}} = \begin{bmatrix} \mathbf{v}_1 \\ \mathbf{v}_2 \\ \vdots \\ \mathbf{v}_m \end{bmatrix} \quad (4)$$

are vectors of GCA × site and SCA × site interaction effects, respectively,

$$\mathbf{e} = \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \vdots \end{bmatrix} \quad (5)$$

$$\mathbf{G}_{\mathrm{GCA}} = \sigma^2_{\mathrm{GCA}} * I_a, \mathbf{G}_{\mathrm{SCA}} = \sigma^2_{\mathrm{SCA}} * I_b, \mathbf{G}_{\mathrm{GCA*site}} = \sigma^2_{\mathrm{SCA*site}} * I_{am}, \mathbf{G}_{\mathrm{SCA*site}} = \sigma^2_{\mathrm{SCA*site}} * I_{bm}, \quad (6)$$

and

$$\mathbf{R} = \begin{bmatrix} \sigma^2_e & & \\ & \sigma^2_e & \\ & & \ddots \end{bmatrix}. \quad (7)$$

In the second approach, a heterogenous variance model to account for heterogenous error variances among sites was fitted. The model is the same as above but with a different structure for the error variance matrix:

$$\mathbf{R} = \sum\nolimits_{\oplus}\mathbf{R}_i \text{ with } \mathbf{R}_i = \begin{bmatrix} \sigma^2_{e_i} & & \\ & \sigma^2_{e_i} & \\ & & \ddots \end{bmatrix}. \quad (8)$$

REML methodology was used for the model fitting. The significance of the variance component was determined by (1) the ratio of the component relative to its standard error or (2) likelihood ratio test (LRT). If the variance component was more than two standard errors from zero, then the variance component was considered significant. If the variance component was less than one standard error from zero, then the variance component was considered non-significant. To test variance components between one or two standard errors from zero, LRT was applied with the model fitted with and without the component. The log likelihoods were compared as LRT 2(log L_{p+g}–log L_p) where log L_{p+g} is the log likelihood with the variance component and p+g degrees of freedom and Log L_p is the log likelihood without the variance component with p degrees of freedom. This LRT was distributed as a χ^2_q with q degrees of freedom.

To estimate the genetic correlation between sites for SCA, a covariance model was fitted with

$$\mathbf{G}_{\mathrm{SCA*site}} = \begin{bmatrix} \sigma^2_{\mathrm{SCA}_1} * I_{b_1} & \sigma_{\mathrm{SCA}_{12}} * I_{b_{12}} & \cdots \\ \sigma_{\mathrm{SCA}_{21}} * I_{b_{21}} & \sigma^2_{\mathrm{SCA}_2} * I_{b_2} & \cdots \\ \cdots & \cdots & \cdots \end{bmatrix}$$

and $\mathbf{R} = \sum\nolimits_{\oplus}\mathbf{R}_{\mathrm{i}}$ (9)

$\sigma^2{}_{\mathrm{SCA1}}$ is SCA variance in site 1 and σ_{SCA12} is SCA covariance between sites 1 and 2, and b_1, b_2, and b_{12} are SCA effects at site 1, site 2, and common SCA effects across two sites, respectively. The ASREML program was used for the variance and covariance modelling (Gilmour et al. 2000).

Narrow-sense heritability (h^2), broad-sense heritability (H^2), half-sib family heritability (or repeatability of half-sib family effect, h^2_{hf}), full-sib family heritability (h^2_{ff}) were computed across ten sites as

$$h^2 = \frac{4 * \sigma^2_{\mathrm{GCA}}}{2 * \sigma^2_{\mathrm{GCA}} + \sigma^2_{\mathrm{SCA}} + 2 * \sigma^2_{\mathrm{GCA*site}} + \sigma^2_{\mathrm{SCA*site}} + \sigma^2_e} \quad (10)$$

$$H^2 = \frac{4 * \left(\sigma^2_{\mathrm{GCA}} + \sigma^2_{\mathrm{SCA}}\right)}{2 * \sigma^2_{\mathrm{GCA}} + \sigma^2_{\mathrm{SCA}} + 2 * \sigma^2_{\mathrm{GCA*site}} + \sigma^2_{\mathrm{SCA*site}} + \sigma^2_e} \quad (11)$$

$$h^2_{\mathrm{hf}} = \frac{\sigma^2_{\mathrm{GCA}}}{\sigma^2_{\mathrm{GCA}} + \sigma^2_{\mathrm{SCA}}/(C-1) + \sigma^2_{\mathrm{GCA*site}}/S + \sigma^2_{\mathrm{SCA*site}}/(C-1) * S + \sigma^2_e/(C-1) * S * N} \quad (12)$$

$$h^2_{ff} = \frac{2 * \sigma^2_{GCA} + \sigma^2_{SCA}}{2 * \sigma^2_{GCA} + \sigma^2_{SCA} + 2 * \sigma^2_{GCA*site}/S + \sigma^2_{SCA*site}/S + \sigma^2_e/S * N} \quad (13)$$

where C-1 is the harmonic mean of number of crosses for each parent (C is equal to the number of parents if there are no missing crosses for a half-diallel mating structure), S is the number of sites, N is the harmonic mean of individuals within sites for each cross. Heritabilities for individual sites were also estimated.

Non-additive genetic correlation among-sites was estimated as

$$\gamma_{SCA} = \frac{\sigma_{SCA12}}{\sigma_{SCA1} * \sigma_{SCA2}}. \quad (14)$$

Standard errors were estimated for heritabilities, non-additive genetic correlations according to Taylor's expansion (Namkoong 1979).

The importance of SCA variance was measured by two parameters: the ratio of SCA variance to GCA variance and the ratio of SCA variance to $2*\sigma^2_{GCA}+\sigma^2_{SCA}$. The second ratio was used because the total variance ($2*\sigma^2_{GCA}+\sigma^2_{SCA}$) estimates total genetic variance among progenies of all crosses from inbred pure lines (Baker 1978), and this ratio determines the relative importance of GCA and SCA in determining progeny performance. The terms 'dominance variance' and 'SCA variance' were often used interchangeably in the literature although SCA variance includes a portion of epistatic variance (Matzinger and Kempthorne 1956).

The relationships between GCA and SCA values were examined by plotting mid-parental breeding values of mating pairs and their corresponding estimates of SCA. Best linear unbiased predictions (BLUP) for GCA and SCA effect were estimated using the REML program ASREML (Gilmour et al. 2000).

Genetic gain for utilising SCA variance was estimated by two methods: (1) actual estimates from the predicted breeding value in the experiment and (2) theoretical estimates from estimated genetic parameters. In the actual estimate for the experiment, breeding values for each parent and BLUP of SCA were estimated for all pair-crosses in the diallel crosses. To examine how much extra gain from SCA variance can be achieved relative to selection based on breeding values of the same parents only, 5% of the best pair-crosses (based on mid-parental breeding value) in the experiment were selected to compute genetic gain from breeding values and from BLUP estimates of SCA values. The extra genetic gain from SCA was examined for three types of deployment strategies: (1) a single deployment population for all ten sites, (2) a single deployment population for the four sites having both significant GCA and SCA effects (PT5459, RAD211, RS27A, and RS27B) and (3) four deployment populations for the four sites having both significant GCA and SCA variance (utilising SCA × site interaction).

In the second method, genetic gain from SCA variance was estimated by the difference between gains of half-sib and full-sib family selections. Since not all pair-wise matings among parents were made in the experiment, this method is equivalent to computing theoretical gains from SCA variance assuming each parent was mated with all other parents. The gain was computed by the equation Gain $= i * \sigma_{ph} * h^2$ where i is the selection intensity (same selection intensity of 5% was applied for all strategies), σ_{ph} is the phenotypic deviation for half- or full-sib family selection and h^2 is the heritability for half- or full-sib selections.

Results and discussion

Importance of SCA variance and estimates of narrow- and broad-sense heritability

Analyses of ten sites combined indicated that GCA, SCA, GCA × site and SCA × site variances were all significant for DBH, whether using log-transformed data or using a heterogeneous error variance model (Table 1). The SCA variance was almost equal to GCA variance for DBH (95% for non-transformed data), and the proportion of SCA variance relative to total genetic variance in the progenies was about 32%.

Both narrow- and broad-sense heritability for DBH were low across ten sites (0.036 and 0.070, respectively, for non-transformed data). However, half- and full-sib family heritabilities (repeatabilities) were moderately high (0.513 and 0.596, respectively, for non-transformed data).

The importance of SCA variance relative to GCA variance varied among ten sites (Table 2). The ratio of SCA/GCA variance ranged from 20% to 1,035%. At PT5455, SCA variance contributed all the genetic variance (no GCA variance). The proportion of SCA variance relative to total genetic variance varied from 9% to 100%. Among ten sites, SCA variance was non-significant at four sites (BIL133, BIL149, RAD199 and VRC52, see Fig. 1). Thus, all sites from Busselton and Mount Gambier regions, and one site from Myrtleford (RAD211) and one from Traralgon (VRC60) have significant SCA effects. Within the six sites with significant SCA vari-

Table 1 Importance of specific combining ability (*SCA*) variance and genetic parameters in tree diameter (*DBH*) (mm) for the ten sites combined analysis of radiata pine in Australia-wide diallel mating experiment (before and after natural logarithm transformation)

Sources of variation	Before log transformation		After log transformation	
	Variance	Ratio[a]	Variance	Ratio
GCA[b]	9.956	3.06	0.258E-3	2.68
SCA	9.426	2.32	0.233E-3	1.96
GCA × site	27.390	6.75	1.092E-3	7.83
SCA × site	34.405	5.08	1.315E-3	5.69
Residual	991.980[c]	-	27.974E-3	-
SCA/GCA	95%	-	90%	-
SCA/(2×GCA+SCA)	32%	-	31%	-
Narrow-sense h^2	0.036±0.012	-	0.032±0.012	-
Broad-sense H^2	0.070±0.016	-	0.061±0.017	-
Half-sib family h_{hf}^2	0.513±0.096	-	0.463±0.107	-
Full-sib family h_{ff}^2	0.596±0.058	-	0.531±0.070	-

[a] Between variance component and its standard error
[b] General combining ability
[c] Residual for the original data analysis (before log transformation) with heterogeneous error variances is the mean residual for the ten sites

Table 2 Importance of SCA variance on DBH and estimates of h^2 and H^2 and standard errors (SE) for individual sites of the Australia-wide diallel mating experiment

Sources of variation	Sites									
	Bil133	Bil149	PT5455	PT5459	RAD199	RAD211	RS27A	RS27B	VRC52	VRC60
GCA	154.0	85.5	0.0 ns[a]	13.5	73.3	27.1	32.2	44.3	38.8	4.2 ns
SCA	30.8 ns	31.5 ns	86.2	24.5	43.9 ns	111.2	121.9	107.6	7.7 ns	42.9
Residual	1375.8	1155.6	595.5	424.2	1466.0	1177.7	1475.6	1202.2	549.1	920.8
SCA/GCA (%)	20	37	∞	182	60	410	379	243	20	1035
SCA/(2×GCA+SCA) (%)	9	16	100	48	23	67	65	55	9	84
h^2	0.359	0.252	0.000	0.113	0.177	0.081	0.077	0.127	0.244	0.017
SE	0.084	0.074	0.000	0.037	0.061	0.039	0.043	0.060	0.069	0.024
H^2	0.431	0.345	0.506	0.319	0.283	0.412	0.371	0.435	0.293	0.194
SE	0.107	0.095	0.112	0.096	0.075	0.083	0.087	0.101	0.084	0.068

[a] *ns* Not significant at 5% probability level from likelihood ratio test

ance, two sites (PT5455 and VRC60) had non-significant GCA variance. This means that four sites (PT5459, RAD211, RS27A and RS27B) had both GCA and SCA variances significant. Narrow-sense heritabilities varied from 0 to 0.359, and broad-sense heritability varied from 0.194 to 0.506. Broad-sense heritability was significant for all ten sites.

The significant SCA variance and the high ratio of SCA/GCA variance (95%) in this experiment at age 10.5 and 11.5 years was similar to the ratio observed by Wilcox (1975) for 5-year-old radiata pine and to the ratio estimated for maize yield (average ratio 94% based on 99 estimates, Hallauer and Miranda 1981), but is larger than the estimates in all other radiata pine studies (Carson 1986; Cotterill et al. 1987; Volker and Cameron 1988; Dean 1990; Carson 1991; Matheson et al. 1994; King and Johnson 1998). King and Johnson (1998) observed that SCA variance for height decreased with time, i.e. SCA variance declined from 130% of the GCA variance at age 2 to less than 10% at age 7. The similar trend was also observed for diameter with the ratio of 103% at age 4 to 24% at age 7. Such a trend of decline in SCA variance was also observed in other two radiata pine studies, between ages 3 and 13 in New Zealand (Dean 1990) and between ages 2 and 14 in Australia (Matheson et al. 1994). Analyses of the completed 4×23 design II across two sites from the Wilcox (1975) study showed that the ratio of non-additive to additive variance was only 1.1 and 0.5 at ages 5 or 6, and even lower at age 10 (Cotterill et al. 1987).

The literature quoted above shows that the high ratio of SCA/GCA variance (95%) in this experiment seems inconsistent with estimates in other radiata pine studies. Such different patterns of SCA/GCA ratio were also observed in other pines. For example, in slash pine studies, Pswarayi (1993) and Dieters et al. (1995) observed a contrasting age pattern for the ratio of additive to non-additive genetic variance. Several factors may influence the precision and size of GCA and SCA estimates. Estimates of variance components are subject to large sampling errors, assumption of gene distribution [i.e. linkage-disequilibrium (LD)], existence of epistasis and environment effects. Hayman (1963), in discussing the number of parents required in diallel experiments, concluded that estimates of variance components could not be significant estimates of population parameters unless the number of parents exceeds ten. Populations may differ greatly in gene distribution, level of dominance and epistasis, as observed in maize (Hallauer and Miranda 1988, p. 116). Environmental and maternal effects may also contribute to the difference of SCA variance. King and Johnson (1998) attributed the declining trend of SCA/GCA ratio to extraneous effects such as nursery effect, seed size or other maternal effects for the initial high SCA variance, and these effects might disappear over time. On the other hand, one may attribute the declining trend of SCA variance to higher competition level within plots for families with large trees in the later age if SCA was positively related with GCA. Such competition may affect the true estimate of SCA/GCA ratio in the later ages, as we observed in a 13-year-old radiata pine inbreeding experiment in South Australia (Wu et al. 1998b).

The existence of significant dominance in radiata pine was unequivocally manifested from inbreeding depression at different ages (Wilcox 1983; Wu et al. 1998a, 1998b). It is a challenge to reconcile the ubiquitous existence of dominance from inbreeding experiments with the inconsistency of dominance and non-additive variance from cross-mating experiments. As indicated by Yanchuk (1996), the presence of inbreeding depression does not carry with it a direct indication of what the magnitude of non-additive genetic variance will be, in the form of SCA variance; it may be relatively few genes causing the obvious inbreeding depression, which may not contribute substantially to SCA variance in a large outcrossed population. But this argument needs to be further investigated since the number of genes affecting these traits and their distribution are unknown. The magnitude of the effect of loci involving dominance that cause inbreeding depression, and which also affect estimates of SCA variance, may be determined by the degree of dominance, gene frequencies of dominant and recessive alleles and the number of loci affecting the trait. With new knowledge of quantitative trait loci, we may be able to shed some light on the controversy.

With regard to the huge variation between estimates of dominance variance in maize and the use of non-additive genetic variance in that crop, Hallauer and Miranda (1988) indicated that non-additive gene effects seem to be small on average, but they may be important for one or a few unique combinations. This may also be true for tree breeding.

SCA × site interaction

Substantial SCA × site interaction was detected in this experiment for DBH, and the SCA × site variance was 3.65 times the SCA variance (Table 1). This high SCA effect × site interaction was also reflected in the low average SCA genetic correlation among the six sites with significant SCA effect (average r=0.08, Table 3). Examination of SCA correlations between regions and within regions revealed a high correlation (r=0.72) between two Mount Gambier sites, but relative low correlations between two Busselton sites (r=0.26). It was also observed that VRC60 in Victoria had extremely large interaction with the other five sites having significant SCA effects since SCA in VRC60 had zero or negative genetic correlations with the other five sites. RAD211, also in Victoria, showed large interactions with sites in Mount Gambier and in Busselton. Considering the non-significant SCA for BIL133 and BIL149, RAD199 and VRC52 and the large interactions between the other two Victorian sites and more western sites in Mount Gambier and Busselton, there seems to be some geographical pattern for SCA × site interactions. The relatively low interaction between Mount Gambier and Busselton sites may indicates that one deployment population for both Mountain Gambier and Busselton regions could increase genetic gain by using the common SCA variance.

It was observed that there was large GCA × site interaction in this experiment. However, SCA × site interaction was larger than GCA × site interaction, considering the size of interaction variance relative to genetic variance (2.76 for GCA × site and 3.65 for SCA × site). The major cause of GCA × site interaction was that the two Billapaloola sites behaved differently from other sites for GCA. However, the major cause of SCA × site interaction seems to be due to Victorian sites as described above. There were fewer interactions between SA and WA sites for SCA, but interactions were higher between these SA and WA sites and Victorian sites.

Significant SCA × site interaction means that development of different deployment populations would increase genetic gain for each region or site. However, the extra gains should be weighed against the extra costs of having different deployment populations.

Relationship between SCA and GCA values

There were positive relationships between mid-parental GCA and SCA predictions for four individual sites having significant GCA and SCA effects, for the four sites combined and for the all ten sites combined (Figs. 2, 3). The correlations were similar among the four sites (from r=0.477 to r=0.536). The GCA and SCA correlation for the four sites combined was 0.470, for the ten sites combined was 0.402. These positive correlations were all significant at the 1% probability level.

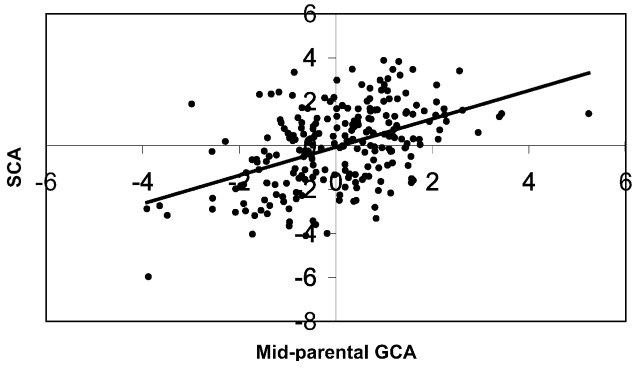

Fig. 2 Relationship between mid-parental general combining ability (GCA) and specific combining ability (SCA) prediction for four sites combined (PT5459, RAD211, RS27A and RS27B)

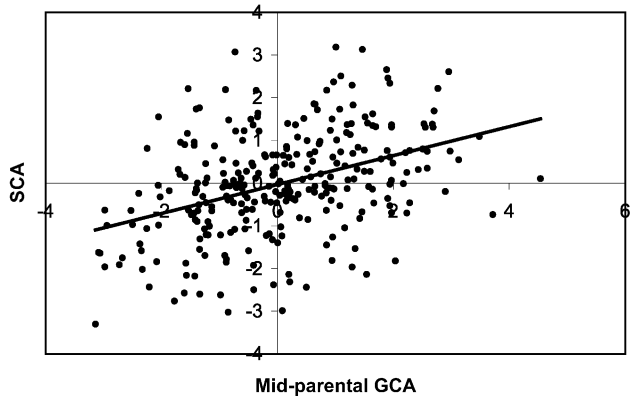

Fig. 3 Relationship between mid-parental GCA and SCA prediction for all ten sites combined

Table 3 Non-additive (SCA) genetic correlations (above-diagonal) and associated standard errors (below-diagonal) among six sites having significant SCA variances

	PT5455	PT5459	RAD211	RS27A	RS27B	VRC60
PT5455		0.72	–0.10	0.24	0.64	–0.74
PT5459	0.31		0.35	0.58	0.01	–0.20
RAD211	0.29	0.18		0.07	0.16	–0.21
RS27A	0.31	0.19	0.17		0.26	0.01
RS27B	0.27	0.24	0.19	0.20		–0.54
VRC60	0.39	0.27	0.22	0.25	0.28	

Table 4 Predicted genetic gain for DBH from utilization of non-additive (SCA) variance for three deployment strategies (selection for ten sites combined, selection for four sites combined having both GCA and SCA effect significant and selection for four sites individually) based on estimated variance components for a 5% selection intensity (i.e. assuming all parents were mated to each other)

	All sites	Four sites	PT5459	RAD211	RS27A	RS27B
Mating pair	290	232	211	211	208	165
Mean DBH	204	201	174	186	234	243
Half-sib family h^2	0.51	0.34	0.40	0.28	0.29	0.40
Full-sib family h^2	0.60	0.43	0.52	0.56	0.53	0.60
Half-sib phenotypic variance	19.41	33.47	33.59	95.18	112.53	112.10
Full-sib phenotypic variance	49.24	94.61	98.41	295.87	349.64	329.31
Half-sib gain	4.66	4.04	4.79	5.73	6.26	8.63
Full-sib gain	8.63	8.59	10.70	19.84	20.55	22.30
Half-sib gain	2.3%	2.0%	2.8%	3.1%	2.7%	3.6%
Full-sib gain	4.2%	4.3%	6.1%	10.7%	8.8%	9.2%
SCA total[a]	46.0%	52.9%	55.2%	71.1%	69.5%	61.3%

[a] SCA total=(full-sib gain−half-sib gain)/full-sib gain

This positive correlation between mid-parental GCA and SCA in radiata pine, perhaps the first time this has been observed in a tree species, contrasts with non-significant correlation observed in Douglas fir (Yanchuk 1996). However, positive correlation between yield of inbred lines and their crosses was usually true in maize (Hallauer and Miranda 1988, p. 282), although the correlation varied among experiments with the majority between 0.1 and 0.5 for yield and between 0.3 and 0.4 for plant height.

Determining genetic causes of such positive correlation is a substantial challenge. According to the theory of diallel mating, if genes are not independently distributed in the parents of the diallel mating, i.e. the presence or absence of an allele at a particular locus is statistically dependent on the presence or absence of an allele at any other locus (called linkage disequilibrium, LD), then a covariance between additive and dominance gene action would be introduced (Melchinger 1988). LD can be caused by genetic sampling effects (Nassar 1965), or by mixing of previously isolated and genetically different populations (i.e. from populations with different gene frequencies) (Barker 1979), or by selection (Bulmer 1971). Selection is well known to generate LD. The majority of plus trees used in this experiment were selected from plantations in Australia planted in the early twentieth century and a few were from New Zealand. The seed sources of these early radiata pine plantations are suspected to be from a relatively narrow genetic base (Fielding 1957; Moran and Bell 1987) and so there may have been a bottleneck effect. Such a bottleneck effect combined with intensive selection of plus trees for this experiment might be reasons for the positive correlation.

Regardless of genetic causes of such GCA and SCA correlation, the positive correlation renders an advantage in the practical use of SCA variance, i.e. selection of the best GCA will capture some portion of SCA variance.

Genetic gain and utilization of SCA variance in deployment and breeding populations

Theoretical gains were predicted using genetic parameters for ten sites combined, and for four sites having significant GCA and SCA effects, combined and individually. Table 4 shows that total genetic gain of 4.2% was achievable if selection was for full-sib families (using both GCA and SCA variance) for ten sites combined. Within this 4.2% gain, almost half (46.0%) was contributed by SCA variance. Total genetic gain of 4.3% was achievable by full-sib selection for the four sites (PT5459, RAD211, RS27A and RS27B) combined, and SCA contributed 52.9% towards the gain. Among the four individual sites, 6.1, 10.7, 8.8 and 9.2% total genetic gains were achievable for PT5459, RAD211, RS27A and RS27B, respectively, and SCA contributed for 52.2, 71.1, 69.5 and 61.3% to the gain, respectively.

The contributions from SCA variance seem considerable in this experiment and suggest there is good reason to capture SCA in deployment populations. However, a positive correlation between GCA and SCA can facilitate the capture of partial SCA variances, i.e. selection of the best GCA will capture some SCA effects. It is also of interest to see how much SCA gain can be captured from selections based on estimated breeding values. Selection of the 5% of parents with the best GCA (11 parents from the total of 114 parents for all sites) should give us the corresponding SCA contribution. However, due to the disconnected nature of the diallel mating, most of these pair-matings among the 11 best-selected parents were not available. To overcome this problem, 5% of the best mating pairs with the best mid-parental breeding values (15 pairs from a total of 290 pairs) were selected to examine the extra contribution from SCA variance. These 15 mating pairs were found to involve 17 parents, but only 7 of these were among the best 11 parents for GCA. Consequently, the SCA contribution attributable to these 17 parents might be less relative to using the best 11 parents only. Nevertheless, some insights for gain contribution by SCA variance can be examined.

Selection of the best 15 mating pairs with the best mid-parental breeding values from the experiment population would produce 2.9% additive genetic gain when selection were made for the ten sites combined (Table 5). Based on estimated BLUP of SCA, selection of the same 5% of mating pairs will produce an additional 0.5% non-additive genetic gain from SCA variance. This translates that the total genetic gain was 3.4% with 14.0% of the gain contributed by SCA variance.

Table 5 Predicted genetic gain for DBH from utilization of non-additive (SCA) variance for three deployment strategies (selection for ten sites combined, selection for four sites combined having both GCA and SCA effect significant and selection for four sites individually) based on estimated breeding value and SCA effect for a 5% of parent-pairs having best breeding values (mid-parental BV) in the experiment

	All sites	Four sites	PT5459	RAD211	RS27A	RS27B
BV	5.97	5.55	7.03	8.76	10.29	11.85
BLUP SCA	0.97	1.48	2.82	7.12	6.8	5.24
Total gain	6.94	7.04	9.85	15.88	17.09	17.1
Gain from BV	2.9%	2.8%	4.0%	4.7%	4.4%	4.9%
Gain from SCA	0.5%	0.7%	1.6%	3.8%	2.9%	2.2%
Total gain	3.4%	3.5%	5.7%	8.5%	7.3%	7.0%
Gain from SCA total	14.0%	21.0%	28.6%	44.8%	39.8%	30.6%

Due to large SCA and site interactions, it is expected that selection for the four sites having significant GCA and SCA effects will produce more gains from non-additive genetic causes. When the four sites were combined, selection of the best 5% of mating-pairs based on mid-parental breeding values would produce 2.8% additive genetic gain (Table 5). However, based on estimated BLUP of SCA for the same four sites, selection of the same 5% of mating pairs will produce an additional 0.7% genetic gain from SCA. This is a total of 3.5% genetic gain with 21.0% of the gain contributed by SCA. This is higher than the 14% additional gain from SCA for ten sites combined.

More genetic gains were contributed by SCA if selection were for individual sites. For example, total genetic gains ranged from 5.7% for PT5459 to 8.5% for RAD211 based on the 5% of selection intensity. Among these genetic gains, SCA contributed between 28.6% and 44.8% to the total gain (Table 5). These contributions are higher than the 21% obtained above for the four sites combined.

In exploiting genetic gain from SCA, two issues arise: (1) whether breeders should exploit the SCA variance at all, and (2) how they should go about it. In this experiment, substantial SCA variance was observed. With such large SCA, there is incentive to exploit SCA variance, at least in a deployment population. The positive correlation between GCA and SCA facilitates the exploitation. As observed, the correlation between GCA and SCA was between 0.40 and 0.56. Hence, about 25% of SCA variance can be used if breeders select parents with only the best breeding values. The observation that SCA contributed from 28.6% to 44.8% to total genetic gain for four individual sites and for 15% and 21% for the ten and the four sites combined seems to confirm this correlation. However, to fully exploit SCA variance, special mating designs should be employed. As predicted from the gain equation, if all matings were made among the 114 parents in this study, the SCA contributed gain of 46.0% and 52.9% for the ten and the four sites combined relative to the total gain achievable by full-sib family selection. However, gain contributed from SCA by selection based on GCA only (using SCA and GCA correlation) was 14.0% and 21.0% only for the ten sites and the four sites. Hence, additional gain from deliberate selection of full-sib families from all mating-pairs would have contributed more gain beyond the gain achievable from the positive SCA and GCA correlation. In this radiata pine population, these extra gains were as 31% and 32% for ten sites and four sites combined.

Conclusions

1. Significant SCA variance was observed for DBH and number of ramicorns in the Australia-wide diallel experiment and SCA variance for DBH was almost equal to GCA variance when all ten sites were combined.
2. The importance of SCA variance for DBH varied among sites, from non-significant to SCA variance accounting for all the genetic variation among full-sib families.
3. There was significant SCA × site interaction for DBH, larger than GCA × site interaction. There was less SCA × site interaction among Mount Gambier (SA) and Busselton (WA) sites than between Mount Gambier and Victoria sites, or between Busselton and Victoria sites.
4. Significant and positive correlations between mid-parental breeding values and BLUP estimates of SCA effect for DBH were found.
5. About 25% more genetic gain than from GCA alone is achievable from SCA variance if selection is based on the best breeding values for DBH. To fully utilise genetic gain from SCA variance in a deployment population, positive assortative matings are required for the mating design.
6. For the breeding population, selection for breeding values may be sufficient due to positive correlation between breeding values and SCA values. For a deployment population to capture more SCA genetic gain, it is preferable to make more pair-wise mating for parents with higher breeding values.

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