

- RIEMENSCHNEIDER, D. E., W. E. BERGUSON, D. I. DICKMANN, R. B. HALL, J. G. ISEBRANDS, C. A. MOHN, G. R. STANOSZ and G. A. TUSKAN (2001): Poplar breeding and testing strategies in the north-central U.S.: demonstration of potential yield and consideration of future research needs. *For. Chron.* **77**: 245–253.
- ROBISON, D. J. and K. F. RAFFA (1996): Importance of cutting diameter and method of production on early growth of hybrid poplar. *Tree Plant. Not.* **47**: 76–80.
- SAS INSTITUTE, Inc. (2004): SAS/STAT® 9.1 User's Guide. Cary, NC.
- SCARASCIA-MUGNOZZA, G. E., R. CEULEMANS, P. E. HEILMAN, J. G. ISEBRANDS, R. F. STETTLER and T. M. HINCKLEY (1997): Production physiology and morphology of *Populus* species and their hybrids grown under short rotation. II. Biomass components and harvest index of hybrid and parental species clones. *Can. J. For. Res.* **27**: 285–294.
- SCHROEDER, W. R. and D. S. WALKER (1991): Effect of cutting position on rooting and shoot growth of two poplar clones. *New For.* **4**: 281–289.
- SHIPMAN, R. D. (1974): Gibberellin affects rooting of hybrid poplar clone NE-277. *Tree Plant. Not.* **25**: 19–21.
- SMITH, N. G. and P. F. WAREING (1974): The distribution of latent root primordia in stems of *Populus x robusta*, and factors affecting the emergence of preformed roots from cuttings. *Forestry* **45**: 197–209.
- SMITH, N. G. and P. F. WAREING (1972): Rooting of hardwood cuttings in relation to bud dormancy and the auxin content of the excised stems. *New Phytol.* **71**: 63–80.
- TSCHAPLINSKI, T. J. and T. J. BLAKE (1989): Correlation between early root production, carbohydrate metabolism, and subsequent biomass production in hybrid poplar. *Can. J. Bot.* **67**: 2168–2174.
- VOLK, T. J., B. BALLARD, D. J. ROBISON and L. P. ABRAHAMSON (2004): Effect of cutting storage conditions during planting operations on the survival and biomass production of four willow (*Salix* L.) clones. *New For.* **28**: 63–78.
- WILCOX, J. R. and R. E. FARMER, JR. (1968): Heritability and C effects in early root growth of eastern cottonwood cuttings. *Heredity* **23**: 239–245.
- WILCOX, J. R. and R. E. FARMER, JR. (1967): Variation and inheritance of juvenile characters of eastern cottonwood. *Silvae Genet.* **16**: 162–165.
- YING, C. C. and W. T. BAGLEY (1977): Variation in rooting capability of *Populus deltoides*. *Silvae Genet.* **26**: 204–207.
- YING, C. C. and W. T. BAGLEY (1976): Genetic variation of eastern cottonwood in an eastern Nebraska provenance study. *Silvae Genet.* **25**: 67–73.
- ZALESNY, R. S., JR., R. B. HALL, E. O. BAUER and D. E. RIEMENSCHNEIDER (2005a): Soil temperature and precipitation affect the rooting ability of dormant hardwood cuttings of *Populus*. *Silvae Genet.* **54**: 47–58.
- ZALESNY, R. S., JR., D. E. RIEMENSCHNEIDER and R. B. HALL (2005b): Early rooting of dormant hardwood cuttings of *Populus*: analysis of quantitative genetics and genotype x environment interactions. *Can. J. For. Res.* **35**: 918–929.
- ZALESNY, R. S., JR., E. O. BAUER and D. E. RIEMENSCHNEIDER (2004): Use of belowground growing degree days to predict rooting of dormant hardwood cuttings of *Populus*. *Silvae Genet.* **53**: 154–160.
- ZALESNY, R. S., JR., R. B. HALL, E. O. BAUER and D. E. RIEMENSCHNEIDER (2003): Shoot position affects root initiation and growth of dormant unrooted cuttings of *Populus*. *Silvae Genet.* **52**: 273–279.

## Early Selection of Radiata Pine

### I. Trends over Time in Additive and Dominance Genetic Variances and Covariances of Growth Traits

Ensis, Joint Venture between CSIRO (Australia) and Scion (formerly Forest Research, New Zealand)

By C. A. DEAN<sup>1,\*</sup>, P. P. COTTERILL<sup>2</sup> and R. D. BURDON<sup>3</sup>

(Received 10<sup>th</sup> November 2005)

#### Abstract

Additive genetic, dominance genetic and phenotypic variances and corresponding correlations were estimated

<sup>1</sup>) Present Address: Weyerhaeuser, PO Box 9777, Federal Way, WA 98063-9777 (USA).

<sup>2</sup>) Present Address: PO Box 1525, Mount Gambier, SA 5290 (Australia).

<sup>3</sup>) Senior Scientist: Ensis, Private Bag 3020, Rotorua (New Zealand).

\*) Corresponding Author: christine.dean@weyerhaeuser.com

for growth data collected from disconnected half-diallel progeny trials involving 25 *Pinus radiata* D. DON parents and replicated across two sites in central North Island, New Zealand. Sectional area of stem was measured at three, seven, 10 and 13 years after planting at both sites, and height at three and 10 years at one site.

Sectional area at three years exhibited similar levels of estimated additive ( $\sigma_A^2$ ) and dominance ( $\sigma_D^2$ ) genetic variance. However, levels of  $\sigma_D^2$  remained approximately constant between three and 13 years while  $\sigma_A^2$  increased substantially. Thus, sectional-area growth changed from

being under equal additive and dominance genetic control at three years to almost complete additive genetic control from seven to 13 years. The greater increase in additive variance relative to phenotypic variance led to increases in individual heritability from 0.16 to 0.28 to 0.35 for sectional-area increments between 3–7, 7–10 and 10–13 years, respectively. Height growth exhibited negligible levels of  $\sigma_D^2$  for the three- and 10-year measurements.

The early sectional-area increment between 3–7 years showed an estimated additive genetic correlation of 0.87 with “mature” sectional area at 13 years. Subsequent sectional-area increments between 7–10 and 10–13 years showed estimates of additive genetic correlations of 0.99 with sectional area at 13 years. Dominance genetic correlations were much lower in magnitude, reflecting inconsistent dominance effects over time.

*Key words:* *Pinus radiata*, additive variation, dominance variation, juvenile-mature correlation, heritability.

## Introduction

Most tree breeding programs are based on a combination of selection for growth, form and/or wood traits of relatively juvenile trees, with the objective of indirectly improving productivity of mature trees at the end of the crop rotation. Reliable genetic information about potential selection criteria, particularly juvenile-mature correlations and changing heritabilities over time, are required to determine the most efficient method of early selection. BURDON (1989) has discussed other issues that are important for efficient early selection in forest species.

A few authors have addressed trends over time in genetic parameters (additive variance, dominance variance, juvenile-mature correlations) for *Pinus radiata* D. DON. However, given the importance of *P. radiata* in plantations in Chile, New Zealand and Australia, there is clearly scope for further documentation. WILCOX *et al.* (1975) studied a small factorial cross of *P. radiata* at age 5-years, which was reassessed at ages eight and 18-years (LOW, 1990). COTTERILL and DEAN (1988) and MATHESON *et al.* (2002) have estimated additive genetic variance, dominance variance and additive genetic correlations for growth between early ages and 16 and 13-years, respectively, for *P. radiata* in South Australia. The study of MATHESON *et al.* (2002) included a dimension of estimates across five different levels of inbreeding. MATHESON *et al.* (1994) studied juvenile-mature correlations based on annual sectional area of breast-height disks to 14 years of age. KING and BURDON (1991) studied trends in additive genetic parameters until 17 years in a large open-pollinated progeny trial of *P. radiata* in central North Island New Zealand. Since then, APIOLAZA *et al.* (2000) studied such trends in Chile to eight years of age. There are substantial differences across these few studies in sample size (numbers of parents and families involved), site environment (climate, soil, altitude, disease and insect problems) and silvicultural history (weed control, thinning).

The literature contains other reference to additive genetic parameters of *P. radiata* estimated over fairly narrow bands of younger ages (JOHNSON, 1990; JAYA-

WICKRAMA, 2001; KING *et al.*, 1998). These studies provide important insights into the overall genetic control of economic traits, but make limited contribution to optimising early selection.

This paper presents estimates of additive and dominance genetic variances and correlations for growth traits of *P. radiata* between three and 13 years after planting on two sites in central North Island, New Zealand. The work is from post-graduate studies completed by the senior author in 1988 (DEAN, 1990). Part II of these articles on early selection examines strategies to optimize the efficiency of early selection.

## Materials and Methods

### *Diallel Matings*

The genetic material comprised full-sib *P. radiata* families that came from five disconnected half-diallel matings of five parents each. With 10 crosses (no selfs) per half-diallel, a total of 25 parents and 50 full-sib families were involved. The 25 parents are known as the “850” series selected for superior growth and form phenotype in genetically unimproved plantations in New Zealand, mainly in central North Island. The “850”s constitute part of New Zealand’s first-generation *P. radiata* breeding population (SHELBOURNE *et al.*, 1986) and are evidently derived from two genetically similar mainland Californian populations of *P. radiata* (MORAN and BELL, 1987; BURDON, 1992).

### *Site, Silviculture and Field Design*

The two progeny trials (hereafter referred to as Trials 327 and 905) are located in Compartments 327 (latitude 38°28’S, longitude 176°31’E, altitude 530 m) and 905 (latitude 38°38’S, longitude 176°21’E, altitude 560 m), Kaingaroa Forest, central North Island. These two trials belong in a series reported by CARSON (1991) who addressed a different set of variables. The soil type at both sites is Kaingaroa silty sand, derived from pumice showers (VUCETICH *et al.*, 1960). Mean annual rainfall is around 1500 mm. Trial 905 was on a colder site than Trial 327, that was more prone to frost and needle blight (*Dothistroma* blight) caused by *Dothistroma pini* HULBARY.

Seed from the half-diallel crosses was sown in four randomised complete blocks in February 1974 in a nursery at Rotorua. In June 1975, seedlings were planted at both field sites at 5 × 5 m spacing. At the same time, seedlings from commercial nurseries were interplanted (as “fillers”) between the half-diallel seedlings to reduce weed competition and give a final planting espacement of 5 × 2.5 m (800 stems ha<sup>-1</sup>). The “fillers” were removed by thinning, well before crown closure, at five years after planting, to leave 400 half-diallel seedlings ha<sup>-1</sup>.

The field layout at each site involved six randomised complete blocks with five-tree non-contiguous plots, giving 30 progeny per full-sib family per site. Each half-diallel was planted as a separate set in a complete sets-in-replicates design (cf. SCHUTZ and COCKERHAM, 1966). All 50 families were represented at each site. Trees (except for serious malforms and runts) were pruned to

1.6 m in August 1980, 4 m in October 1983, and to 6 m in March 1994.

### Measurements

At both sites diameter of stems was measured over-bark at half-stem height in June 1978 (three years after planting) and over-bark at 1.4m in June 1982 (seven years), March 1985 (about 10 years) and March 1988 (about 13 years). These diameter measurements were converted to cross-sectional areas of stem and hereafter are referred to as “sectional areas” (abbreviated SA3, SA7, SA10 and SA13 for sectional area at the respective ages). Sectional area has a higher coefficient of variation, which matches more closely variation in stem volume. As such, sectional area was preferred to stem diameter for studying trends in size and variance of trees over time; subject to its data properties proving acceptable.

Mean annual increments of sectional-area growth were calculated for the intervals between each measurement. The sectional-area increment between three and seven years is denoted  $\Delta SA_{3-7}$ , between seven and 10 years,  $\Delta SA_{7-10}$ , and between 10 and 13 years,  $\Delta SA_{10-13}$ . Tree height was measured at three and 10 years in Trial 327 only and a periodic annual increment ( $\Delta HT_{3-10}$ ) was calculated. The year-7 height was measured using poles and 10-year height using a Suunto clinometer.

### Data Analyses

Analyses of the half-diallel matings were carried out using the DAG program (Diallel Analysis by GENSTAT) and procedures outlined by DEAN and CORRELL (1988). Each of the five half-diallels was analysed separately and then sums of squares and cross-products, and degrees of freedom, were summed across the individual diallels. Observed mean squares were determined by dividing these pooled sums of squares by their respective degrees of freedom (DEAN and CORRELL, 1988).

Table 1. – Expectations of mean squares relevant to estimation of genetic parameters from analyses of the half-diallel mating design.

Source of variation	d.f.	Expectations of mean squares <sup>A</sup>
Family	$[p(p-1)/2]-1$	$\sigma_e^2 + k_1 \sigma_{fb}^2 + k_6 \sigma_f^2$
gca	$p-1$	$\sigma_e^2 + k_2 \sigma_{fb}^2 + k_7 \sigma_{sca}^2 + k_9 (p-2) \sigma_{gca}^2$
sca	$p(p-3)/2$	$\sigma_e^2 + k_3 \sigma_{fb}^2 + k_8 \sigma_{sca}^2$
Family × site	$(s-1)p(p-1)/2$	$\sigma_e^2 + k_4 \sigma_{fb}^2 + k_9 \sigma_{fs}^2$
Family × block	$(b-1)p(p-1)/2$	$\sigma_e^2 + k_5 \sigma_{fb}^2$
Residual	$N-bp(p-1)/2$	$\sigma_e^2$

<sup>A</sup> There are  $p = 5$  parents in each half-diallel,  $b = 6$  blocks,  $s = 2$  sites,  $N = 496, 461, 412, 413$  and  $421$  trees analyzed for the combined data, and  $N = 225, 205, 182, 177$  and  $178$  trees for Trial 327. The variance component  $\sigma_f^2$  is due to families,  $\sigma_{gca}^2$  general combining ability,  $\sigma_{sca}^2$  specific combining ability,  $\sigma_{fb}^2$  family × block interaction,  $\sigma_{fs}^2$  family × site interaction and  $\sigma_e^2$  the residual error. Coefficients of variance components relevant to estimating genetic parameters are, for across site analyses:  $k_4 = 4.07$ ,  $k_9 = 28.93$  and  $k_6 = 142.19$ ; and for Trial 327:  $k_4 = 3.61$  and  $k_9 = 111.30$ .

Equating the expectations of mean squares (Table 1) with these pooled mean square values provided estimates of variance due to full-sib families ( $\sigma_f^2$ ), general combining ability ( $\sigma_{gca}^2$ ), specific combining ability ( $\sigma_{sca}^2$ ), full-sib family × block interaction ( $\sigma_{fb}^2$ ), full-sib family × site interaction ( $\sigma_{fs}^2$ ) and residual error ( $\sigma_e^2$ ). Coefficients of the variance components (“k coefficients”; Table 1) were computed using the synthesis procedure of HARTLEY (1967). Preliminary analyses were made to ensure that average genotypic value for growth traits was reasonably consistent across the five diallels analysed, and to confirm that there was no necessity for data transformation.

Significant ( $P < 0.01$ ) effects were found for families, gca and sca, while those of the interaction, family × block and family × site, were not significant ( $P > 0.05$ ). Analyses of sectional-area traits reported here are for data combined across both sites, as variances over time were similar at both sites and the family × site interaction was not significant. Analyses of height traits were completed for Trial 327 only.

### Genetic Parameters

Under the assumptions of unrelated parents, negligible epistasis and negligible maternal effects, additive ( $\sigma_A^2$ ) and dominance ( $\sigma_D^2$ ) genetic variances can be related to gca and sca effects as follows – (1) and (2)

$$\sigma_A^2 = 4\sigma_{gca}^2 \quad (1)$$

$$\sigma_D^2 = 4\sigma_{sca}^2 \quad (2)$$

(see details in COTTERILL *et al.*, 1987; for example). Individual heritabilities ( $h^2$ ) were estimated according to the following relationship between additive and phenotypic ( $\sigma_P^2$ ) variance – (3)

$$h^2 = \sigma_A^2 / \sigma_P^2 \quad (3)$$

In the case of sectional-area data combined across sites the phenotypic variance was estimated as – (4)

$$\sigma_P^2 = 2\sigma_{gca}^2 + \sigma_{sca}^2 + \sigma_{fb}^2 + \sigma_{fs}^2 + \sigma_e^2 \quad (4)$$

The family × site component ( $\sigma_{fs}^2$ ) was omitted from  $\sigma_P^2$  used to estimate heritability for height traits because the heights were recorded at one site only. Negative estimates of variance components were set to zero in estimating  $\sigma_P^2$ . Standard errors of heritability estimates were approximated according to JENSEN and BARR (1971).

Additive genetic correlations ( $r_A$ ) and dominance genetic correlations ( $r_D$ ) were estimated from the mean squares and mean cross-products of individual-tree data (COTTERILL *et al.*, 1987). Approximate estimates of the standard errors of the genetic correlations were obtained following BECKER (1985). Phenotypic correlations ( $r_P$ ) were calculated on an individual-tree basis.

### Combining Abilities

In each half-diallel, the “observed” genetic value ( $gv_{ij}$ ) for the full-sib family produced by mating the  $i^{\text{th}}$  female and the  $j^{\text{th}}$  male parent was estimated as the difference between the least-squares mean ( $\hat{A}_{ij}$ ) of the particular

family and the overall mean of all trees across both progeny trials ( $\bar{A}_{..}$ ) – (5)

$$gv_{ij} = \bar{A}_{ij} - \bar{A}_{..} \quad (5)$$

These least-squares means take account of inequalities in progeny per family across both blocks and sites (COTTERILL *et al.*, 1983).

The general combining ability ( $gca_i$ ) of the  $i^{\text{th}}$  parent was estimated as the average of the observed genetic means ( $gv_{ij}$ ) of the full-sib families produced by mating the  $i^{\text{th}}$  parent (as either a female or male) with the four other parents in each half-diallel – (6)

$$gca_i = 1/4 \sum_j gv_{ij} \quad (6)$$

where  $1 \leq i \leq 5$ ;  $1 \leq j \leq 5$ ;  $i \neq j$ . “Predicted” genetic values ( $\hat{gv}_{ij}$ ) were determined for each full-sib family as the sum of the female and male parents general combining abilities (or the sum of “breeding values” of the parents) – (7)

$$\hat{gv}_{ij} = gca_i + gca_j \quad (7)$$

Specific combining ability ( $sca_{ij}$ ) of the  $i^{\text{th}}$  female mated to the  $j^{\text{th}}$  male parent was calculated as the difference between the observed and predicted genetic values for the particular cross – (8)

$$sca_{ij} = gv_{ij} - \hat{gv}_{ij} \quad (8)$$

## Results and Discussion<sup>1</sup>

### Growth Trends

Figure 1 shows trends in sectional-area increment and variance components from analyses of combined data across both sites. Sectional-area growth was least during the first measurement period between three and seven years after planting with  $\Delta SA_{3-7} = 67 \text{ cm}^2 \text{ year}^{-1}$ , and peaked during the subsequent measurement period between seven and 10 years with  $\Delta SA_{7-10} = 112 \text{ cm}^2 \text{ year}^{-1}$  (Figure 1). This near-doubling in sectional-area increment from the 3–7 year to the 7–10 year periods was due, at least in part, to the 50% thinning of both progeny trials at five years. During the 10–13 year period when competition between trees increased, sectional area growth declined to  $\Delta SA_{10-13} = 88 \text{ cm}^2 \text{ year}^{-1}$ .

In analyses not reported here, we found similar trends in growth over time when each site was considered separately. Although sectional-area increment peaked at 7–10 years, in both sites, the absolute rate of growth was slower in Trial 905 because the site was harsher and there was some loss of foliage following early frost damage and persistent *Dothistroma* blight. By 13 years the trees in Trial 327 had reached a mean sectional area  $SA_{13} = 953 \text{ cm}^2$  which was around 20% greater than the mean sectional area  $SA_{13} = 811 \text{ cm}^2$  in Trial 905.

The maximum sectional-area increment observed in the present study ( $\Delta SA_{7-10} = 112 \text{ cm}^2 \text{ year}^{-1}$ ) was over twice the maximum increment of  $48 \text{ cm}^2 \text{ year}^{-1}$  reported by COTTERILL and DEAN (1988) in an open-pollinated

<sup>1</sup>) For convenience of presentation, estimates of genetic parameters are often expressed as if they were actual parameter values.

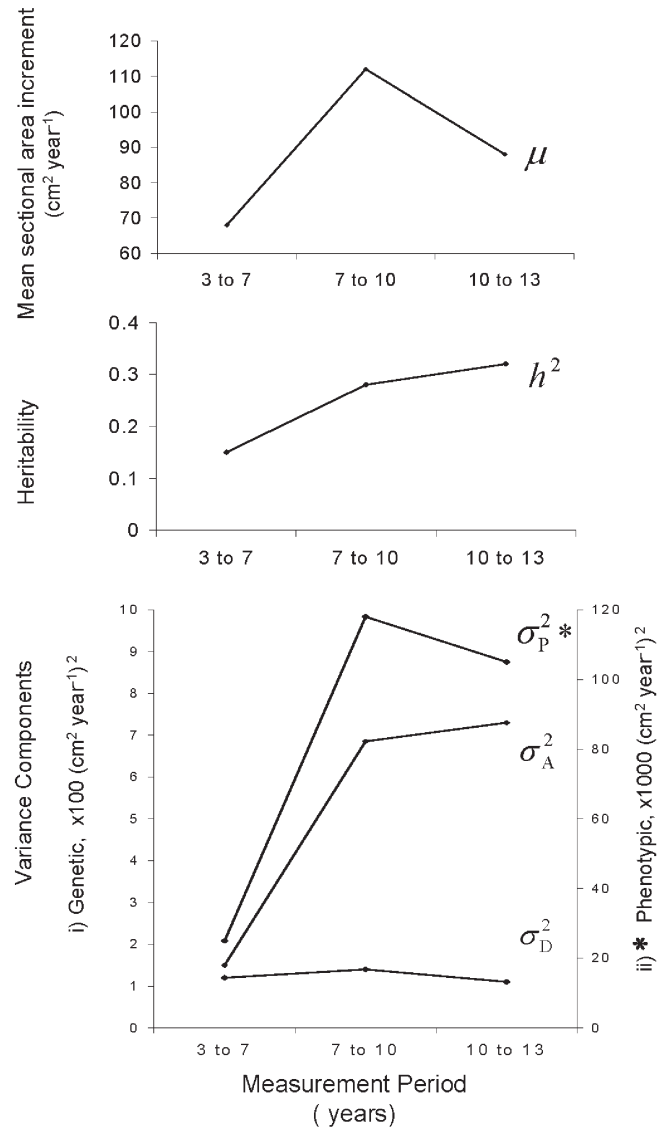


Figure 1. – Overall means ( $\mu$ ), estimated additive ( $\sigma_A^2$ ) and dominance genetic variances ( $\sigma_D^2$ ), phenotypic variances ( $\sigma_P^2$ ) and heritabilities ( $h^2$ ) over time for sectional-area increments measured across both progeny trials (Trials 327 and 905).

trial of *P. radiata* in South Australia. The South Australian trial, however, was planted at a high stocking rate of  $2265 \text{ stems ha}^{-1}$  and only thinned to 1260 stems at 10 years. The New Zealand trials reported here were planted at  $1600 \text{ stems}$  and thinned to 800 stems before five years. Differences in thinning regime, weed control, insect attack, disease levels, and other “environmental” factors can, of course, be very important in comparing findings across studies.

### Additive Genetic Variance and Heritability

**1. Increment Traits:** The large increase in sectional-area growth between the 3–7 and 7–10 year periods was associated with an almost seven-fold increase in additive genetic variance ( $\sigma_A^2$ ; Figure 1). The phenotypic variance ( $\sigma_P^2$ ) of sectional-area increment also increased with increasing rate of growth between 3–7 and 7–10 years, but not to the same extent as  $\sigma_A^2$ . Consequently, there was an increase in individual heritability of sec-

tional-area increment from  $h^2 = 0.16$  for  $\Delta SA_{3-7}$  to  $h^2 = 0.28$  for  $\Delta SA_{7-10}$  (Figure 1).

As the rate of sectional-area growth slowed in the 10–13 year period there was some plateauing in the level of  $\sigma_A^2$ . However, the slower growth rate was associated with a decline in phenotypic variance which led to a corresponding increase in individual heritability to a high  $h^2 = 0.35$  for  $\Delta SA_{10-13}$  (Figure 1). In analyses not reported here, these trends in  $h^2$ ,  $\sigma_A^2$  and  $\sigma_P^2$  over time were found to be consistent across both sites. The standard errors of all heritability estimates were high.

In the South Australian study by COTTERILL and DEAN (1988), estimated heritability of sectional-area increment increased steadily from  $h^2 = 0.13$  for  $4\frac{1}{2}$ – $6\frac{1}{2}$  years to  $h^2 = 0.30$  for  $6\frac{1}{2}$ – $10\frac{1}{2}$  years to  $h^2 = 0.44$  for  $10\frac{1}{2}$ – $16$  years. These values are similar to the  $h^2 = 0.16$ ,  $0.28$  and  $0.35$  reported for roughly corresponding measurement periods in the present study. Despite major differences in stocking rate, and hence patterns of diameter growth, between the South Australian and New Zealand studies, the trend of increasing heritability of sectional-area increment of *P. radiata* over time is remarkably consistent.

The height increment measured between three and 10 years in Trial 327 showed a moderate to high individual heritability of  $h^2 = 0.36$  (Table 2) again with a large standard error. COTTERILL and DEAN (1988) estimated a similarly high heritability of  $h^2 = 0.44$  for early height increment between  $2\frac{1}{2}$  and  $6\frac{1}{2}$  years, but the heritability declined dramatically to  $h^2 = 0.09$  between  $6\frac{1}{2}$  and  $10\frac{1}{2}$  years, and remained low. COTTERILL and DEAN (1988) attributed this fall in heritability of height increment to the early canopy closure of the closely spaced stand. MATHESON *et al.* (2002) also observed that trends in additive variance and heritability seemed to be closely related to stand development in South Australian progeny trials. In the present study we are not able to determine trends in heritability of height increment from the limited height data recorded.

**2. Absolute Growth Traits:** The cumulative effects of increasing heritabilities of sectional-area increments over time are reflected in corresponding increases in heritability of absolute measurements (Figure 2). The individual heritability of absolute sectional area increased from a low  $h^2 = 0.06$  for SA3 to  $h^2 = 0.16$  for SA7 and high values of  $h^2 = 0.26$  for SA10 and  $h^2 = 0.35$  for SA13. It is apparent from Figure 2 that this increasing heritability of absolute sectional area is due to proportionally greater increases in  $\sigma_A^2$  over time than  $\sigma_P^2$ . Of course, there is no decline in  $\sigma_P^2$  for absolute sectional area (as was observed for the increments) because of the continuing increase in absolute size of trees. The standard errors of these heritability estimates are high suggesting these values should be interpreted with caution; however, the general trend is apparent.

KING *et al.* (1998) analysed data from disconnected-diallel crosses of the “875” series *P. radiata* parents planted in North Island New Zealand and also found that the estimated individual heritability of diameter increased over time; from  $h^2 = 0.09$  at four years to  $0.28$  at age-7. The trend was more marked in the case of

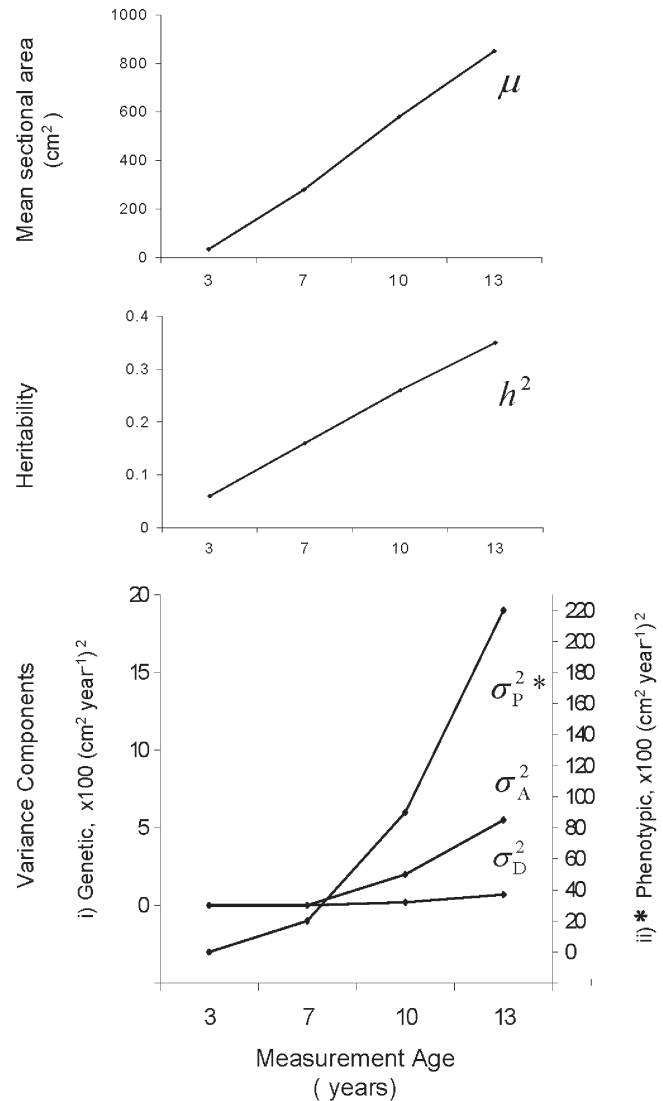


Figure 2. – Overall means ( $\mu$ ), estimated additive ( $\sigma_A^2$ ) and dominance genetic variances ( $\sigma_D^2$ ), phenotypic variances ( $\sigma_P^2$ ) and heritabilities ( $h^2$ ) over time for absolute measurements of sectional area across both progeny trials (Trials 327 and 905).

height with  $h^2 = 0.07$  at age-2,  $0.24$  at age-4 and  $0.25$  at age-7. KING and BURDON (1991) observed the opposite trend in heritability of stem diameter in an open-pollinated progeny trial of “268”-series *P. radiata* parents in North Island New Zealand. In this case, estimated individual heritability declined from  $h^2 = 0.34$  at age-5, to  $0.28$  at age-10; stabilising at  $h^2 = 0.25$  at 17 years from planting. KING and BURDON (1991) noted that diameter growth of *P. radiata* is sensitive to needle cast, and the trial studied by these authors was quite heavily affected by needle cast *Cyclaneusma minus* (BUTIN) DICOSMO, PEREDO & MINTER.

#### Dominance Genetic Variance

**1. Increment Traits:** The estimated additive genetic variance  $\sigma_A^2$  was similar to the estimated dominance genetic variance  $\sigma_D^2$  for  $\Delta SA_{3-7}$  (Figure 1). Dominance variance for sectional-area increment increased relatively little between the 3–7 and 7–10 year periods, compared to the corresponding increase in  $\sigma_A^2$ . Hence, for

both  $\Delta SA7-10$  and  $\Delta SA10-13$  the level of  $\sigma_A^2$  was around seven times larger than  $\sigma_D^2$ . This trend of relatively diminishing dominance genetic control and increasing additive control over time was evident in analyses conducted for each site separately, as well as in the combined analysis reported here. It is important to note that it is not possible to differentiate between maternal effects and dominance genetic variance in the half-diallel design. Certainly, if maternal effects are present, they would be expected to decline in importance over time and their influence may be contributing to the decreasing relative level of dominance variance in *Figure 1*. (However, in this study there should have been minimal confounding with nursery effects because the nursery design was replicated; see Materials and Methods).

**2. Absolute Growth Traits:** In the case of SA3 the estimates of  $\sigma_A^2$  and  $\sigma_D^2$  were nearly equal (*Figure 2*). However, the trend of increasing additive genetic control of sectional-area increments was reflected in absolute measurements made at seven years and later. The relative levels of  $\sigma_A^2$  increased to around six-fold compared with  $\sigma_D^2$  for SA13 (*Figure 2*). In the case of absolute height traits  $\sigma_D^2$  was low or zero at both three and 10 years in Trial 327 (*Table 2*).

*Table 2.* – Overall means ( $\mu \pm$  standard deviation), estimated additive ( $\sigma_A^2$ ) and dominance ( $\sigma_D^2$ ) genetic variances, phenotypic variances ( $\sigma_P^2$ ) and heritabilities ( $h^2 \pm$  standard error) for height traits measured in Trial 327. Also presented are estimated genetic ( $r_A \pm$  standard error) and phenotypic ( $r_P$ ) correlations between height traits and sectional area at 13 years.

Parameter	Height Trait		
	HT3 (m)	HT10 (m)	$\Delta HT3-10$ (m year <sup>-1</sup> )
$\mu \pm$ s.d.	2.6 $\pm$ 0.04	14.8 $\pm$ 0.70	1.8 $\pm$ 0.01
$\sigma_A^2$	0.49	4.58	0.01
$\sigma_D^2$	0.20	0.00	0.00
$\sigma_P^2$	1.96	12.72	0.02
$h^2$	0.26 $\pm$ 0.21	0.36 $\pm$ 0.29	0.36 $\pm$ 0.28
Correlations with SA13			
$r_A$	0.72 $\pm$ 0.29	0.65 $\pm$ 0.25	0.47 $\pm$ 0.31
$r_P$	0.55	0.60	0.44

The results presented here are part of only a few published estimates of trends over time in dominance genetic control of *P. radiata*. In a Design II cross WILCOX *et al.* (1975) found very strong apparent  $\sigma_{sca}^2$  for stem diameter at five years of age, but this had disappeared by 18 years in favour of strong  $\sigma_{gea}^2$  which matched resistance to needle cast (LOW, 1990). KING *et al.* (1998) found a marked decline in  $\sigma_D^2$  relative to  $\sigma_A^2$  for height and diameter growth until seven years after planting in the “875s” half-diallel trial in New Zealand. For example, variance due to sca ( $\sigma_{sca}^2$ ) was 130% of  $\sigma_{gea}^2$  for stem height at two years, and under 10% at age-7. KING *et al.* (1998) also noted the possibility of confounding of dominance genetic effects and maternal effects or even nursery effects. MATHESON *et al.* (2002) have reported additive and dominance variances over time for *P. radiata* with different levels of inbreeding (although sample

sizes were perhaps marginal for estimating  $\sigma_A^2$  and  $\sigma_D^2$  within populations). DIETERS *et al.* (1995) found that in full-sib progeny tests of *P. elliotii* the level of  $\sigma_A^2$  approximately doubled relative to  $\sigma_D^2$  for volume between five and 14 years after planting.

There are other estimates of  $\sigma_D^2$  of *P. radiata* in the literature, but all are for traits measured at only one point in time. CARSON (1986) presented ratios of  $\sigma_A^2$  and  $\sigma_D^2$  for height and diameter of *P. radiata* measured at 4<sup>1</sup>/<sub>2</sub> years in another series of half-diallel progeny trials established across two sites in North Island, New Zealand. In that study the estimate of  $\sigma_A^2$  was four times greater than the estimated  $\sigma_D^2$  for height, but the relative levels of  $\sigma_D^2$  for diameter varied greatly between sites. COTTERILL *et al.* (1987) reported higher estimated levels of  $\sigma_A^2$  than  $\sigma_D^2$  for diameter, and in particular height, measured at eight years in a factorial mating trial of *P. radiata* in South Africa. VOLKER and CAMERON (1988) estimated almost four-fold greater  $\sigma_A^2$  than  $\sigma_D^2$  for sectional area measured at 12<sup>1</sup>/<sub>2</sub> years in a Design II trial in eastern Australia. JOHNSON (1990) presents an opposing result for a Design II trial of *P. radiata* in New South Wales, Australia, with levels of estimated  $\sigma_A^2$  around half  $\sigma_D^2$  for diameter and volume at 12 years. However,  $\sigma_A^2$  was three-fold higher than  $\sigma_D^2$  for height.

The current study provides further evidence that there may be little benefit in attempting to exploit dominance variance in breeding to improve mature productivity of *P. radiata*. CARSON (1986) and COTTERILL *et al.* (1987) showed that even where levels of  $\sigma_A^2$  and  $\sigma_D^2$  are approximately equal, it is possible to design efficient breeding programs that are based essentially on additive genetic models and aim at exploiting a maximum amount of the  $\sigma_A^2$  available. The present study supports the previous literature in suggesting that levels of  $\sigma_D^2$  may be comparable to levels of  $\sigma_A^2$  in juvenile *P. radiata* but this non-additive variation has minimal influence on later productivity. Not only do relative levels of  $\sigma_A^2$  for growth increase with age but, as shown in the next section, there are strong additive and weak dominance genetic associations between early and later growth.

#### Additive Genetic and Phenotypic Correlations

Additive genetic and phenotypic correlations from analyses of combined sectional-area data across sites are presented in *Table 3*.

**1. Increment Traits:** The early sectional-area increment  $\Delta SA3-7$  had strong additive genetic correlations with both  $\Delta SA7-10$  and  $\Delta SA10-13$  ( $r_A = 0.84$  and  $0.81$  respectively; *Table 3*), while the post-thinning increments,  $\Delta SA7-10$  and  $\Delta SA10-13$  were even more strongly correlated ( $r_A = 0.96$ ). Juvenile-mature additive genetic correlations between early increment traits and the final measurement of sectional area at 13 years increased from a high value of  $r_A = 0.87$  for  $\Delta SA3-7$  to even higher values of almost unity ( $r_A = 0.99$ ) for  $\Delta SA7-10$  and  $\Delta SA10-13$ . COTTERILL and DEAN (1988) reported similarly large correlations of  $r_A = 0.98$  to  $0.99$  between volume at 16 years and sectional-area increments measured at 4<sup>1</sup>/<sub>2</sub>–6<sup>1</sup>/<sub>2</sub> or 6<sup>1</sup>/<sub>2</sub>–10<sup>1</sup>/<sub>2</sub> years. Standard errors of

Table 3. – Estimates of additive genetic ( $r_A \pm$  standard error) and phenotypic ( $r_P$ ) correlations between increments or absolute measurements of sectional area measured across both progeny trials (Trials 327 and 905). Additive genetic correlations are above diagonals, phenotypic correlations below diagonals.

Sectional-area trait	$\Delta SA_{3-7}$	$\Delta SA_{7-10}$	$\Delta SA_{10-13}$	SA13
$\Delta SA_{3-7}$		$0.84 \pm 0.37$	$0.81 \pm 0.31$	$0.87 \pm 0.27$
$\Delta SA_{7-10}$	0.54		$0.96 \pm 0.25$	$0.99 \pm 0.19$
$\Delta SA_{10-13}$	0.53	0.63		$0.99 \pm 0.20$
SA13	0.78	0.86	0.88	
	SA3	SA7	SA10	SA13
SA3		$0.75 \pm 0.26$	$0.71 \pm 0.29$	$0.72 \pm 0.23$
SA7	0.70		$0.94 \pm 0.20$	$0.90 \pm 0.27$
SA10	0.54	0.85		$0.99 \pm 0.18$
SA13	0.49	0.78	0.94	

additive genetic correlations are large in this study relative to the magnitude of the coefficients (Table 3).

Phenotypic correlations in the present study followed the same general trends as additive genetic correlations but the phenotypic correlations were markedly lower. This finding of lower phenotypic correlations is again consistent with the results of COTTERILL and DEAN (1988). Some previous studies of early selection in *Pinus* spp. have been based on phenotypic correlations and (because phenotypic associations seem to be weaker) the conclusions may be conservative. For example, WAKELEY (1971) and STEINHOFF (1974) concluded, on the basis of phenotypic correlations, that growth traits measured before around 20 years do not provide a reliable guide to mature performance of *P. elliottii* or *P. taeda*. Other research (LAMBETH *et al.*, 1983; FOSTER, 1986; COTTERILL and DEAN, 1988; KING and BURDON, 1991; MATHESON *et al.*, 2002; and this present study) based on genetic correlations has indicated a more promising result for selection at less than 10 years after planting in *P. radiata* and other *Pinus* spp.

Changing heritabilities over time will also impact on the efficiency of early selection and affect the optimum age for selection. The importance of the relative heritability of the early and later traits is considered in detail in Part II of this series on early selection, and also by KING and BURDON (1991), MATHESON *et al.* (2002) and DUNGEY (2004). Related but not truly parallel studies in other species have largely involved *P. taeda* (e.g. GWAZE *et al.*, 2000; 2002).

2. *Absolute Growth Traits:* Additive genetic correlations between absolute sectional-area measurements decreased as time elapsed between particular pairs of measurements. For example, the additive genetic correlations between SA13 and earlier measurements decreased from  $r_A = 0.99$  for SA10 to  $r_A = 0.90$  for SA7 to  $r_A = 0.72$  for SA3 (Table 3). However, the additive genetic correlation of  $r_A = 0.72$  between SA3 and SA13 is still quite high as far as using SA3 as an early selection criterion is concerned. Phenotypic correlations followed the

same trends as genetic correlations but again were lower in magnitude.

The absolute height measurements HT3 and HT10 had genetic correlations of  $r_A = 0.72$  and  $0.65$  respectively, with SA13 in Trial 327 (Table 2). This finding supports a pattern observed by BURDON *et al.* (1992) whereby trends in diameter growth track earlier trends in height growth.

COTTERILL and DEAN (1988) reported a negative  $r_A$  between volume at 16 years (VOL16) and height at around two years, but strong positive correlations between VOL16 and height at around six ( $r_A = 0.81$ ) or 10 years ( $r_A = 0.87$ ). MATHESON *et al.* (1994), using annual sectional area of breast-height disks of *P. radiata* in Australia, observed  $r_A$  values close to zero between ages of less than four years with age-14, but after four years the correlations with age-14 proved far higher. In the “268” open-pollinated progeny trial of *P. radiata* in New Zealand, KING and BURDON (1991) observed strong positive  $r_A$  of  $0.64$  and  $0.93$  for stem diameter at ages five and 10, respectively, with diameter at 17 years. In another study MATHESON *et al.* (2002) reported additive correlations of over  $0.7$  between sectional area measured at 13 years and early ages of five years or more for *P. radiata* in South Australia. This study of MATHESON *et al.* (2002) involved populations having different levels of inbreeding and higher inbreeding tended to produce higher juvenile-mature correlations. However, BURDON *et al.* (1992) observed some inflated age-age genetic correlations where inbreeding and/or basic maladaptation were involved. Moreover, KUMAR (2004) found essentially zero correlation between selfed and outcross growth rate in *P. radiata*.

#### Dominance Genetic Correlations

Estimates of dominance genetic correlations were far weaker than corresponding estimates of additive genetic correlations and also had quite high standard errors. Dominance correlations between the early increment  $\Delta SA_{3-7}$  and later increments decreased from  $r_D = 0.76$  for  $\Delta SA_{7-10}$  to  $r_D = 0.53$  for  $\Delta SA_{10-13}$  (Table 4). The dominance correlation between post-thinning increments  $\Delta SA_{7-10}$  and  $\Delta SA_{10-13}$  was even lower at  $r_D = 0.47$ . The juvenile-mature dominance genetic correlations between increment traits and sectional area at 13 years were consistently low with values between  $r_D = 0.39$  and  $0.45$ . Although results are not presented in Table 4, the  $r_D$  among absolute sectional-area traits were similar to correlations among increments. The dominance correlations involving the height traits were zero or near-zero.

Table 4. – Estimates of dominance genetic correlations ( $r_D$ ) between sectional-area increments and sectional area at 13 years measured across both progeny trials (Trials 327 and 905).

Sectional-area trait	$\Delta SA_{7-10}$	$\Delta SA_{10-13}$	SA13
$\Delta SA_{3-7}$	$0.76 \pm 0.27$	$0.53 \pm 0.28$	$0.45 \pm 0.26$
$\Delta SA_{7-10}$		$0.47 \pm 0.24$	$0.39 \pm 0.21$
$\Delta SA_{10-13}$			$0.41 \pm 0.20$

There appear to be no other published estimates of dominance genetic correlations for *P. radiata*. The most important implication of the estimates of  $r_D$  reported in this study is that dominance effects do not appear to be especially consistent and diminish over time. It seems that specific combining abilities observed for crosses among particular parents at one point in time may be different when measured at another time. This finding is discussed further in the next section.

### Combining Abilities

1. *General Combining Abilities*: Figure 3 presents gca's for sectional-area increments of the parents involved in one of the five half-diallels studied (Half-Diallel 5); and is used to illustrate the previously described trends over time in additive genetic variance and genetic correlations. One obvious feature of Figure 3 is that gca values for sectional-area increment become more widely dispersed, over time, particularly between the 3–7 and 7–10 year measurement periods. For example, the difference between the best and worst parents nearly doubles from 10.15  $\text{cm}^2\text{year}^{-1}$  for  $\Delta\text{SA}3-7$  to

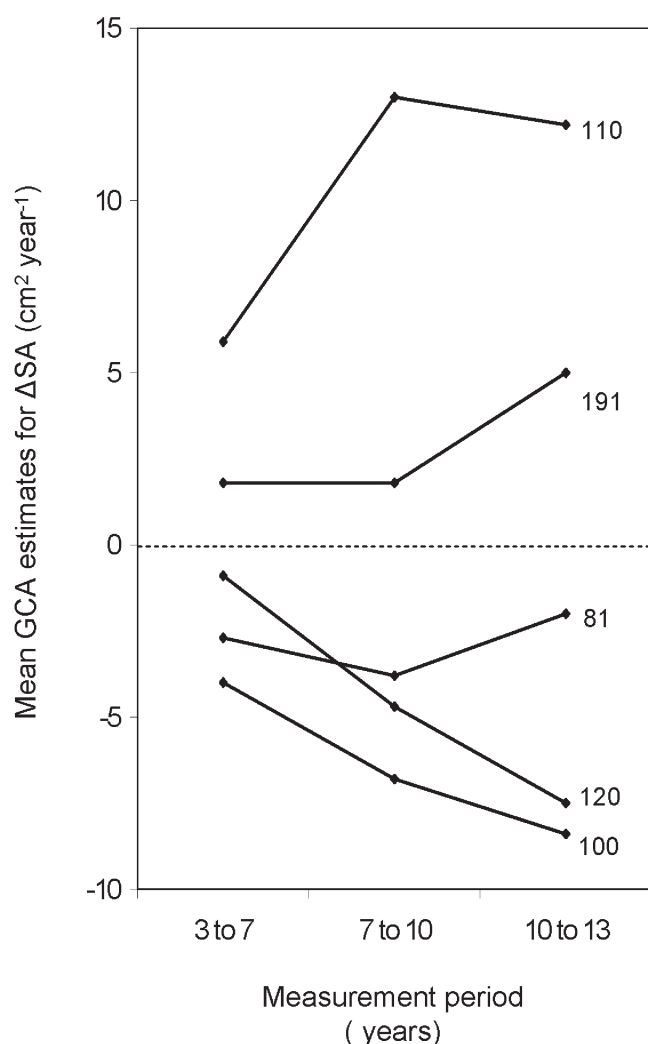


Figure 3. – General combining abilities of parents involved in Half-Diallel 5 for sectional-area increment traits measured across both progeny trials (Trials 327 and 905). The parents are identified as 81, 100, 110, 120 and 191.

19.50  $\text{cm}^2\text{year}^{-1}$  for  $\Delta\text{SA}7-10$  and 20.08  $\text{cm}^2\text{year}^{-1}$  for  $\Delta\text{SA}10-13$ . This increasing spread of gca over time led to the increase in additive genetic variance  $\sigma_A^2$  reported previously (Figure 1). The widening of differences between parental gca's is almost certainly due in part to competition within the stand permitting large families to grow relatively larger, while small families grow more slowly. However, these trends in genetic parameters do not appear to be due entirely to competitive factors. Between three and 10 years there was a remarkably consistent trend of increasing  $\sigma_A^2$  in both the South Australian study of COTTERILL and DEAN (1988) and present New Zealand study. Yet, during this three-to-ten-year period the sectional-area increment was diminishing in the South Australian study, but increasing in the New Zealand study; probably due to earlier thinning. Between five and 10 years, the stocking rate (and maybe competition) differed by a factor of five between the two studies. These observations suggest that changes in genetic variances of sectional-area growth may be due partly to biological changes in expression of genetic differences over time, as well as being partly due to changes in stand competition.

Another feature of Figure 3 is the relatively minor changes in parent rankings for sectional-area increment over time. This consistency in parent rankings reflects the strong additive genetic correlations described previously between sectional-area traits measured at different ages (Table 3). The two parents ranking highest for  $\Delta\text{SA}3-7$  were also the highest ranking for  $\Delta\text{SA}7-10$  and  $\Delta\text{SA}10-13$  (Figure 3).

The changes in ranking in Diallel 5 involved Parents 81 and 120. Parent 81 tended to perform relatively constantly over time while Parent 120 deteriorated. However, there was no evidence in any of the half-diallels studied of parents having poor early sectional-area growth, subsequently becoming outstanding, or vice versa. This is interesting because any tendency of *P. radiata* to exhibit rank changes in growth rate over time would be expected to show up in trials such as these grown under low stocking rates.

2. *Specific Combining Ability*: Figure 4 plots the sca's for sectional-area increments of eight of the 10 full-sib families produced by crossing parents in Half-Diallel 5 (the other two families have been omitted to simplify the graph). As outlined in Materials and Methods, the predicted genetic value is the sum of parental gca's (Equation 7), while the sca represents the difference between observed and predicted values (Equation 8). It is apparent that there is not as much increase in the spread of sca's over time (i.e. differences between maximum and minimum sca's for each measurement period) as was the case for gca's (Figure 3). This trend is reflected in the reasonably low levels of  $\sigma_D^2$  reported previously for sectional-area increments over time (Figure 1).

Some families displayed very consistent sca's for sectional-area increments over time (e.g. families 110 x 191, 100 x 81 and 191 x 120; Figure 4). However, the sca values for other families were very inconsistent over the different measurement periods. For example, the cross between Parents 110 x 100 had a negative sca

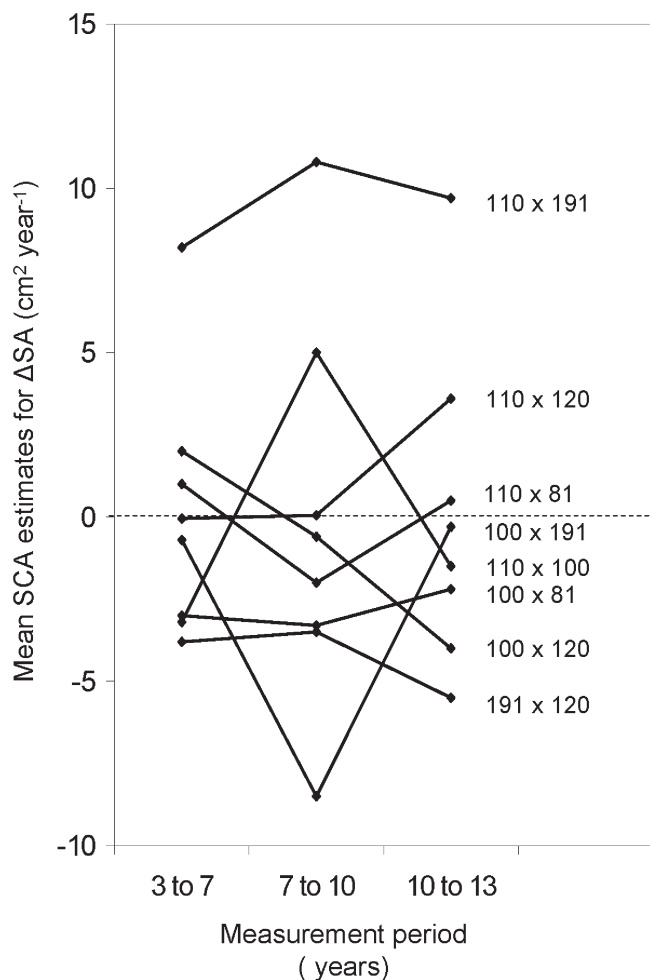


Figure 4. – Specific combining abilities of full-sib families in Diallel 5 for sectional-area increment traits measured across both progeny trials (Trials 327 and 905). The crosses are identified as 110 x 191, 110 x 120, 110 x 81, and so on.

of  $-2.79 \text{ cm}^2\text{year}^{-1}$  for  $\Delta\text{SA}_{3-7}$ , a positive *sca* of  $5.4 \text{ cm}^2\text{year}^{-1}$  for  $\Delta\text{SA}_{7-10}$ , and then fell to  $-1.43$  for  $\Delta\text{SA}_{10-13}$ . Family 100 x 191 also displayed large inconsistencies in *sca* with values of  $-0.61$ ,  $-8.63$  and  $-0.61 \text{ cm}^2\text{year}^{-1}$  for successive sectional-area increments (Figure 4). These changes in family rankings over time for *sca* are reflected in the low dominance genetic correlations reported previously (Table 4). There is clearly no guarantee in *P. radiata* breeding that families expressing high levels of *sca* for early sectional-area growth continue to express high, or even positive, *sca* as time passes. It seems that this study represents the first attempt to record *sca* effects over time in forestry and the findings clearly favour breeding strategies based on fully exploiting additive genetic effects.

## Conclusions

In this study  $\sigma_A^2$  and  $\sigma_D^2$  were approximately equal for sectional area of *P. radiata* at three years, but after this time the genetic control of sectional-area increment became predominantly additive. In the case of height there was little or no  $\sigma_D^2$  present for absolute measurements at three and 10 years, or for the corresponding

height increment. Furthermore, low dominance genetic correlations observed among sectional-area measurements reflect the fact that dominance (*sca*) effects are not as consistent as additive (*gca*) effects over time.

The increase in  $\sigma_A^2$  for sectional-area growth over time, particularly between the 3–7 and 7–10 year periods, was due to pronounced widening of differences among families. This widening of family differences may be due to biological changes in gene action as well as to the inevitable changes in stand competition.

Strong additive genetic correlations  $r_A$  were observed between early measurements of sectional area or height and the “mature” sectional area at 13 years. These high correlations will clearly favour early selection of *P. radiata*. However, the increasing heritability of sectional area over time tends to favour somewhat later selection.

## Acknowledgements

We gratefully acknowledge the constructive reviews of this article by Drs. W. T. ADAMS, F. ISIK, C. A. RAYMOND, T. L. WHITE, R. R. WOOLASTON, and one anonymous reviewer. The progeny trials were established under the direction of C. J. A. SHELBORNE of Scion (formerly New Zealand Forest Research) and maintained by staff of the tree breeding section. Particular thanks are given to: S. CARSON, A. FIRTH and O. MOHRDIEK who directed the early field measurements; C. B. LOW for data preparation; and R. HAHUNGA, G. HOWELLS, B. ST. CLAIR, and N. WOODS who participated cheerfully in the later measurements. This article represents a portion of work by the senior author towards a Ph. D. degree in the Department of Botany at the University of Queensland.

## Literature Cited

- APIOLAZA, L. A., D. J. GARRICK and R. D. BURDON (2000): Optimising early selection using longitudinal data. *Silvae Genet.* **49**: 195–200.
- BECKER, W. A. (1985): Manual of procedures of quantitative genetics. Fourth edition. Washington State University Press, Washington.
- BURDON, R. D. (1989): Early selection in tree breeding: Principles for applying index selection and inferring input parameters. *Can. J. For. Res.* **19**: 499–504.
- BURDON, R. D. (1992): Genetic survey of *Pinus radiata*. 9: General discussion and implications for genetic management. *N. Z. J. For. Sci.* **22**: 274–298.
- BURDON, R. D., M. H. BANNISTER and C. B. LOW (1992): Genetic survey of *Pinus radiata*. 5: Between-trait and age-age correlations for growth rate, morphology, and disease resistance. *N. Z. J. For. Sci.* **22**: 211–227.
- CARSON, M. J. (1986): Control-pollinated seed orchards of best general combiners: A new strategy for radiata pine improvement. Pp. 144–149. Proc. Plant Breeding Symp. N.Z. Agronomy Society. Special publication No. 5. Lincoln, New Zealand.
- CARSON, S. D. (1991): Genotype x environment interaction and optimal number of progeny test sites for improving *Pinus radiata* in New Zealand. *N. Z. J. For. Sci.* **21**: 32–49.
- COTTERILL, P. P., R. L. CORRELL and R. BOARDMAN (1983): Methods of estimating the average performance of families across incomplete open-pollinated progeny tests. *Silvae Genet.* **32**: 28–32.

- COTTERILL, P. P. and C. A. DEAN (1988): Changes in genetic control of growth of radiata pine to 16 years and efficiencies of early selection. *Silvae Genet.* **37**: 138–146.
- COTTERILL, P. P., C. A. DEAN and G. VAN WYK (1987): Additive and dominance genetic effects in *Pinus pinaster*, *P. radiata* and *P. elliottii* and some implications for breeding strategy. *Silvae Genet.* **36**: 221–231.
- DEAN, C. A. (1990): Genetics of growth and wood density in radiata pine. Ph. D. Thesis, Department of Botany, University of Queensland, Australia.
- DEAN, C. A. and R. L. CORRELL (1988): Analysis of diallel matings with missing values. *Silvae Genet.* **37**: 187–193.
- DIETERS, M. J., T. L. WHITE and G. R. HODGE (1995): Genetic parameter estimates for volume from full-sib tests of slash pine. *Can. J. For. Res.* **23**: 1397–1408.
- DUNGEY, H. S. (2004): Early selection for *Pinus radiata* using a farm-field experimental design. *N. Z. J. For. Sci.* **34**: 121–138.
- FOSTER, G. S. (1986): Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. *For. Sci.* **32**: 944–958.
- GWAZE, D. P., F. E. BRIDGWATER, T. D. BYRAM, J. A. WOOLLIAMS and C. G. WILLIAMS (2000): Predicting age-age genetic correlations in tree-breeding programs: A case study of *Pinus taeda* L. *Theor. Appl. Genet.* **100**: 199–206.
- GWAZE, D. P., K. J. HARDING, R. C. PURNELL and F. E. BRIDGWATER (2002): Optimum selection age for wood density in loblolly pine. *Can. J. For. Res.* **31**: 1393–1399.
- HARTLEY, H. O. (1967): Expectations, variances and covariances of ANOVA mean squares by “synthesis”. *Biometrics.* **23**: 105–114.
- JAYAWICKRAMA, K. J. S. (2001): Genetic parameter estimates for radiata pine in New Zealand and New South Wales: A synthesis of results. *Silvae Genet.* **50**: 45–53.
- JENSEN, E. L. and G. R. BARR (1971): Standard errors of heritability estimates calculated from variance component analysis of a two-way classification. *J. Anim. Sci.* **32**: 1069–1077.
- JOHNSON, I. G. (1990): General and specific combining ability in families of *Pinus radiata* in New South Wales. *N. Z. J. For. Sci.* **20**: 3–15.
- KING, J. N. and R. D. BURDON (1991): Time trends in inheritance and projected efficiencies of early selection in a large 17-year-old progeny test of *Pinus radiata*. *Can. J. For. Res.* **21**: 1200–1207.
- KING, J. N., M. J. CARSON and G. R. JOHNSON (1998): Analysis of disconnected diallel mating designs. II. Results from a third generation progeny test of the New Zealand radiata pine improvement program. *Silvae Genet.* **47**: 80–87.
- KUMAR, S. (2004): Effect of selfing on various economic traits in *Pinus radiata* and some implications for breeding strategy. *For. Sci.* **50**: 571–578.
- LAMBETH, C. C., J. P. VAN BUIJTENEN, S. D. DUKE and R. B. MCCULLOUGH (1983): Early selection is effective in 20-year-old genetic tests of loblolly pine. *Silvae Genet.* **32**: 210–215.
- LOW, C. B. (1990): Interaction of *Cyclaneusma* needle cast with early selection. Pp. 113–115. Proc., FRI/NZFP Forests Ltd Clonal Forestry Workshop, Rotorua, New Zealand, FRI Bull. 160.
- MATHESON, A. C., D. J. SPENCER and D. MAGNUSSEN (1994): Optimum age for selection in *Pinus radiata* basal area under bark for age:age correlations. *Silvae Genet.* **43**: 352–357.
- MATHESON, A. C., H.-X. WU, D. J. SPENCER, C. A. RAYMOND and A. R. GRIFFIN (2002): Inbreeding in *Pinus radiata*. III. The effect of inbreeding on age-age correlation and early selection efficiency. *Silvae Genet.* **51**: 115–122.
- MORAN, G. F. and J. C. BELL (1987): The origin and genetic diversity of *Pinus radiata* in Australia. *Theor. Appl. Genet.* **73**: 616–622.
- SCHUTZ, W. M. and C. C. COCKERHAM (1966): The effect of field blocking on gain from selection. *Biometrics* **22**: 843–863.
- SHELBOURNE, C. J. A., R. D. BURDON, S. D. CARSON, A. FIRTH and T. G. VINCENT (1986): Development plan for radiata pine breeding. 142 pp. Ministry of Forestry, Forest Research Institute, Rotorua, New Zealand.
- STEINHOFF, R. J. (1974): Juvenile-mature correlations in ponderosa and western pines. Pp. 243–250. Proc., Joint IUFRO Meet. S.02.04.1-3, Stockholm.
- VOLKER, P. W. and J. N. CAMERON (1988): Non-additive genetic variance in *Pinus radiata* and implications for breeding strategy. Proc., 10<sup>th</sup> Meet., Research Working Group No. 1, Australian Forestry Council, Gympie, Australia.
- VUCETICH, C. G., M. L. LEAMY, M. A. POPPLEWELL, J. URE, C. R. TAYLOR, G. M. WILL, J. M. SUTTON and L. C. BLAKEMORE (1960): Soils, forestry and agriculture of the northern part of Kaingaroa Forest and the Galatea Basin. *N. Z. Soil Bureau* 18. 151 pp.
- WAKELEY, P. C. (1971): Relation of thirtieth year to earlier dimensions of southern pines. *For. Sci.* **17**: 200–209.
- WILCOX, M. D., C. J. A. SHELBORNE and A. FIRTH (1975): General and specific combining ability in eight clones of radiata pine. *N. Z. J. For. Sci.* **5**: 219–225.