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## Changes in the Genetic Control of Growth of *Radiata* pine to 16 Years and Efficiencies of early Selection

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### Summary

Additive genetic and phenotypic variances and covariances were estimated for height and basal area at about 2½, 4½, 6½, 10½ and 16 years after planting in an open-pollinated progeny trial of *Pinus radiata* in South Australia. At about 11 years the trial was thinned to 45% original stocking. Heritability and additive variance of annual height increments were high between 2½ and 6½ years after planting but declined sharply from 6½ years (following stand closure) to thinning. Heritability and additive variance of basal area increments increased steadily with time, particularly following thinning at 11 years. The phenotypic variance of growth increments increased with time despite the fact the actual rate of height growth diminished.

Indirect selection of individual trees on either height increments to 6½ years (when trees were 10 m tall) or a restricted index combining height and basal area increments to 6½ years may be expected to produce over 60% more gain per year in volume at 16 years, compared with later direct selection on volume 16 itself. Indirect selection on traits measured at 10½ years produced less gain per

year because of the extended generation interval. For early traits having high heritabilities indirect individual selection proved more efficient than indirect family selection.

*Key words:* Heritability, juvenile-mature correlations, early selection, indices.

### Zusammenfassung

Anhand einer Prüfung frei abgeblühter Nachkommen-schaften von *Pinus radiata* in Südastralien wurden additiv genetische und phänotypische Varianzen und Kovarianzen für Höhe und Grundfläche des Stammfußes etwa 2½, 4½, 6½, 10½ und 16 Jahre nach dem Auspflanzen geschätzt. Im Alter von etwa 11 Jahren wurde der Versuch bis auf 45% seiner Ursprungsdichte durchforstet. Die Heritabilität und die additive Varianz des jährlichen Höhenzuwachses waren in der Zeit zwischen 2½ und 6½ Jahren nach dem Auspflanzen hoch, nahmen aber nach 6½ Jahren (nach Bestandesschluß) bis zur Durchforstung schnell ab. Die Heritabilität und die additive Varianz der Zuwächse im Bereich der Grundfläche des Stammfußes stieg mit der Zeit beständig an, besonders nach der Durchforstung im Alter von 11 Jahren. Die phänotypische Varianz der Höhenzuwächse erhöhte sich mit der Zeit, trotz der Tatsache, daß sich die aktuelle Höhenzuwachsrate verringerte.

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Bei einer indirekten Selektion auf Einzelbäume aufgrund der Höhenzuwächse bis zum Alter 6<sup>1</sup>/<sub>2</sub> (als die Bäume 10 m hoch waren) oder mit Hilfe eines eingeschränkten Index, der Höhen- und Grundflächenzuwächse bis zum Alter 6<sup>1</sup>/<sub>2</sub> kombiniert, wird ein um mehr als 60% höherer Gewinn im Volumen im Alter 16 erwartet, als bei einer späteren direkten Selektion auf das Volumen im Alter 16. Eine indirekte Selektion auf die im Alter 10<sup>1</sup>/<sub>2</sub> gemessenen Merkmale ergab aufgrund der ausgedehnten Generationsintervalle weniger Gewinn pro Jahr. Für Frühstestmerkmale mit hohen Heritabilitäten zeigte sich indirekte Einzelauslese als effizienter als indirekte Familienauslese.

### Introduction

The genetic improvement of forest trees is based largely on selection and mating of relatively young trees showing superior performance during early phases of growth. This early selection is used to minimise the generation interval. However, the aspiration of breeders is invariably to improve lifetime productivity of plantations over a number of thinnings and final clearfelling. In the case of radiata pine (*Pinus radiata* D. DON) in South Australia superior trees are normally selected for growth and other attributes at around five to 12 years after planting with the hope of improving total productivity over a 30 to 40 year plantation rotation. The success of early indirect selection will depend on the heritabilities of the early and mature traits and, of course, on the genetic associations between these traits.

The tree breeding literature contains reports of efficiencies of early indirect selection. However, many of these studies are based on phenotypic (rather than genetic) associations between early and mature traits and the efficiency calculations must therefore be interpreted with caution (e.g. WAKELEY, 1971, for *P. elliotii*, *P. taeda*, *P. palustris* and *P. echinata*; SQUILLACE and GANSEL, 1974, for *P. elliotii*; STEINHOFF, 1974, for *P. ponderosa* and *P. monticola*; LAMBETH *et al.*, 1983, for *P. taeda*). NAMKOONG *et al.* (1972), NAMKOONG and CONKLE (1976), FRANKLIN (1979) and LAMBETH *et al.* (1983) studied family variances and covariances for *P. ponderosa*, *P. taeda* and Douglas-fir (*Pseudotsuga menziesii*) over extended periods of time. FRANKLIN (1979) also examined genetic parameters of early and mature traits of *P. elliotii* but did not attempt to calculate efficiencies of early indirect selection for mature performance. LAMBETH (1980) reanalysed data from many of these earlier studies in an effort to develop guidelines for early selection. His main conclusion was that selection of individual trees at around six to eight years after planting should be reasonably efficient, depending on the length of the plantation rotation. However, there are no published estimates of efficiencies of early indirect selection for *P. radiata*.

The aim of this study is to examine trends in additive genetic variances, heritabilities and genetic associations among growth traits of *P. radiata* to 16 years after planting at one site near Mount Gambier, South Australia. The genetic parameters estimated are used to determine efficiencies of early selection of both individual trees and families.

### Materials and Methods

#### Site, Silviculture and Measurements

Mount Gambier (lat. 37°45'S., long. 140°47'E., elevation 65 m a.s.l.) has a mediterranean-type climate with an average annual rainfall of 710 mm. The experimental site is on a deep, moderately fertile, sandy soil. Previous vegetation consisted of improved grazing pasture.

The progeny trial (identified locally as trial 5031) involved open-pollinated offspring of 28 female parents which were selected for superior growth and form in genetically unimproved plantations (COTTERILL and ZED, 1980). The open-pollinated seed was collected in 1968 from the then uncultured Tallaganda clonal orchard (New South Wales) established in 1957. Seedlings were raised in a nursery near Mount Gambier with each family grown in one unreplicated nursery plot.

Eight-month old, open-rooted seedlings were lifted from the nursery and planted in June 1969 at a spacing of 2.1 × 2.1 m. Strong competition occurred from unchecked growth of pasture grasses (particularly *Phalaris tuberosa*) until the canopies of the trees began to close about five years after planting. The field layout of the progeny trial involved six-tree row plots of each family replicated across 12 randomised complete blocks: giving 2016 trees planted (72 trees per family). A total of 1969 trees survived to thinning which occurred between February and June 1980.

At thinning (commencing February 1980) the first tree in each six-tree plot was removed as an outrow. Of the remaining trees in each plot, the two individuals having the smallest diameter and poorest form were also felled. Strong winds occurred after this initial thinning and further trees had to be removed in June 1980 because of broken tops or severe leaning. On a few occasions the wind damage necessitated removal of entire plots but mostly two or three trees remained per plot leaving a total of 894 trees in the entire experiment (between 26 and 36 trees per family).

Tree height was measured in December 1971 (2<sup>1</sup>/<sub>2</sub> years after planting), diameter (over-bark at 1.3 m above ground) was measured in December 1973 (4<sup>1</sup>/<sub>2</sub> years), and height and diameter (over-bark at 1.3 m) in December 1975 (6<sup>1</sup>/<sub>2</sub> years), November 1979 (10<sup>1</sup>/<sub>2</sub> years; prior to thinning), and May 1985 (16 years; at the time of a second thinning). The diameters measured at 1.3 m were converted to cross-sectional areas of stem (over-bark) and hereafter referred to as basal areas. (Basal area was preferred to diameter for studying trends in size and variance of trees over time). Annual increments of height and basal area growth were calculated for the intervals between each measurement. Diameter (under-bark) at 1.5 m and 7.5 m were also measured in May 1985 and, together with height, used to calculate stem volume at 16 years according to volume models for *P. radiata* in South Australia (LEWIS and MCINTYRE, 1963).

#### Data Analyses

Analyses of variance were carried out using the following model — (1)

$$Y_{jkl} = \mu + a_j + b_k + ab_{jk} + e_{jkl} \quad (1)$$

where  $Y_{jkl}$  represents an individual tree observation,  $\mu$  the overall mean,  $a_j$  the effect of the  $j$ th open-pollinated family,  $b_k$  the effect of the  $k$ th randomised block,  $ab_{jk}$  the family × block interaction, and  $e_{jkl}$  the within-plot error. The analyses were based on both (a) data for all 1969 trees surviving to thinning at 11 years (called the unthinned population), and (b) data for only the 894 trees retained after thinning and measured at 16 years (the thinned population).

Components of variance due to families ( $\sigma_f$ ), family × block interactions ( $\sigma_{fb}^2$ ) and within-plot error ( $\sigma_w^2$ ) were calculated according to expectations of mean squares given

in Table 1. The open-pollinated offspring were assumed half-sib and additive genetic variance (denoted  $\sigma_a^2$ ) for each trait was calculated as  $4\sigma_f^2$ . Isozyme analyses suggest there was over 90% outcrossing in the Tallaganda orchard (MORAN *et al.*, 1980) and the assumption of half-sib progeny especially after thinning, seems reasonable. Phenotypic variance ( $\sigma_p^2$ ) was calculated as the sum of  $\sigma_a^2$ ,  $\sigma_{fb}^2$  plus  $\sigma_w^2$  (i.e. denominator of Equation 2). Heritabilities were calculated on an individual tree ( $h_i^2$ ) and family ( $h_f^2$ ) basis in the manner detailed in COTTERILL and ZED (1980) and elsewhere — (2) and (3)

$$h_i^2 = \frac{\sigma_a^2}{\sigma_p^2} = \frac{4\sigma_f^2}{(\sigma_f^2 + \sigma_{fb}^2 + \sigma_w^2)} \quad (2)$$

$$h_f^2 = \frac{\sigma_f^2}{(\text{mean squares for families}/k_5)} = \frac{\sigma_f^2}{(\sigma_f^2 + \sigma_{fb}^2 k_2/k_5 + \sigma_w^2/k_5)} \quad (3)$$

where the k coefficients are taken from Table 1. Standard errors of  $h_i^2$  were determined according to SWIGER *et al.* (1964). Additive genetic correlations ( $r_a$ ) were calculated from the analyses of variance and covariance of individual tree data. Standard errors of  $r_a$  were estimated according to TALLIS (1959). Phenotypic correlations ( $r_p$ ) were calculated on an individual tree basis.

In preliminary analyses individual tree data were converted to plot means and additive genetic correlations recalculated from analysis of covariance of this reduced data. The  $r_a$ 's estimated from plot mean analysis were almost identical to the  $r_a$ 's estimated from individual tree analysis and, therefore, only the latter values have been presented. The purpose of the plot mean analysis was to check the associations between early traits as measured for all trees in the unthinned population and mature traits measured in the truncated population after thinning.

#### Selection Indices

Selection indices were used to combine early traits (measured at 10½ years or sooner) and volume at 16 years; with a BINET restriction (BINET, 1965; COTTERILL and JACKSON, 1981) on the latter "mature" trait. The BINET restriction is intended to maximise indirect genetic response in traits which are of economic value but for some reason (usually time or cost) are not actually measured. In this case the BINET restriction is used to maximise indirect response in volume at 16 years which is included in the index but, in the interest of minimising generation interval, is not meas-

Table 1. — Expectations of mean squares for analyses of variance.

Source	d.f.	Expected mean squares <sup>a</sup>
Block	11	$\sigma_w^2 + k_1 \sigma_{fb}^2 + k_4 \sigma_b^2$
Family	27	$\sigma_w^2 + k_2 \sigma_{fb}^2 + k_5 \sigma_f^2$
Family x block	297 <sup>b</sup> /288 <sup>c</sup>	$\sigma_w^2 + k_3 \sigma_{fb}^2$
Within-plot error	1633 <sup>b</sup> /567 <sup>c</sup>	$\sigma_w^2$

<sup>a</sup> The variance component  $\sigma_b^2$  is due to blocks,  $\sigma_f^2$  families,  $\sigma_{fb}^2$  family x block interactions, and  $\sigma_w^2$  within-plot error. The coefficients of variance components relevant to estimating heritability were estimated according to the direct approach of HARVEY (1960) as  $k_2 = 5.879$ ,  $k_3 = 5.858$  and  $k_5 = 70.312$  for unthinned data and  $k_2 = 2.819$ ,  $k_3 = 2.772$  and  $k_5 = 31.853$  for thinned data.

<sup>b</sup> Degrees of freedom for unthinned data.

<sup>c</sup> d.f. for thinned data.

ured. The economic weightings placed on volume at 16 years in this study were 100 times greater (per unit phenotypic standard deviation) than weightings placed on early traits.

The application of the BINET restriction requires knowledge of additive genetic and phenotypic variances and covariances (correlations) between all traits in the index including the mature trait (or traits) on which the restriction is applied (COTTERILL and JACKSON, 1981). If the restriction were used in practice to select indirectly on early traits *a priori* estimates would of course be required of the likely correlations between early and mature traits and the heritability of the mature trait. Such estimates will become increasingly available from the literature over the next few years (at least for *P. radiata*). It is worth stressing that the fundamental appeal of the BINET restriction in this instance is to attempt to create (using genetic and economic information) a rational and objective breeding goal; namely maximising gain in mature economic performance. In the case of unrestricted indices combining early traits the selection goal is merely to maximise gain in early performance which, in itself, is of trivial commercial value.

#### Efficiency of Early Indirect Selection

The efficiency (Q) of indirect selection on a trait 1 (say height at 2½ years) to achieve maximum gain in trait 2 (volume at 16 years), compared with direct selection on trait 2 itself, can be determined on a per generation basis as — (4)

$$Q_{\text{gen}} = \frac{\text{gain in trait 2 under indirect selection on trait 1}}{\text{gain in trait 2 under direct selection on trait 2}} = (i_1 h_1 h_2 r_a \sigma_{p2}) / (i_2 h_2^2 \sigma_{p2}) \quad (4)$$

The  $i_1$  and  $i_2$  represent the standardised selection differentials for indirect and direct selection, respectively;  $r_a$  represents the additive genetic correlation between traits 1 and 2;  $h_1$  and  $h_2$  the square root of the heritabilities of the traits; and  $\sigma_{p2}$  the phenotypic standard deviation of trait 2. The parameters on the right hand side of Equation 4 may be calculated on an individual or family basis depending on whether selection is for individual trees or families. If  $i_1 = i_2$ , Equation 4 reduces to — (5)

$$Q_{\text{gen}} = (r_a h_1/h_2) \times 100\% \quad (5)$$

where  $Q_{\text{gen}}$  is expressed as a percentage.

The validity of the assumption  $i_1 = i_2$  used in deriving Equation 5 is open to debate (LAMBETH, 1980). In practice the death and silvicultural thinning of trees over time would tend to reduce the intensity  $i_2$  of direct selection on mature traits. Therefore  $i_2$  may often be less than  $i_1$  and Equation 5 would tend to underestimate the efficiency of early selection.

The efficiency of indirect selection can also be determined on a per year basis (LAMBETH, 1980) as — (6)

$$Q_{\text{year}} = (r_a h_1 l_2/h_2 l_1) \times 100\% \quad (6)$$

where  $l_1$  and  $l_2$  are the generation intervals (in years) of indirect and direct selection. The generation intervals actually used in this study are  $l_1 = 13, 15$  or  $19$  years for indirect selection on early growth traits measured at  $4\frac{1}{2}, 6\frac{1}{2}$  or  $10\frac{1}{2}$  years, respectively, and  $l_2 = 25$  years for direct selection on volume at 16 years. These intervals are calculated by subtracting or adding years (depending on the

age at selection) to the time-table of operations given in COTTELL (1986; Appendix 2) for breeding *P. radiata*.

### Results and Discussion

Table 2 lists overall means of growth traits calculated using data for all trees surviving to thinning (unthinned population) and trees retained after thinning at 11 years (thinned population). It is evident from the overall means that rapid growth occurred in the measurement periods between 2½ or 4½ years and 6½ years with annual increments (referred to as  $\Delta HT_{2\frac{1}{2}-6\frac{1}{2}}$  and  $\Delta BA_{4\frac{1}{2}-6\frac{1}{2}}$ ) of 2.1 m year<sup>-1</sup> for height and 45 cm<sup>2</sup> year<sup>-1</sup> for basal area in the unthinned population (Table 2). Basal area growth declined markedly to 29 cm<sup>2</sup> year<sup>-1</sup> between 6½ and 10½ years, presumably due to stand closure and increasing competition. However, any increase in competition in the stand did not greatly reduce height growth which averaged 1.9 m year<sup>-1</sup> between 6½ and 10½ years.

The thinning of trees at 11 years was not highly selective for growth and did not have a dramatic effect on the population means. For instance, the mean basal area at 10½ years was only moderately larger in the thinned population (304 cm<sup>2</sup>; Table 2) compared with the unthinned population (282 cm<sup>2</sup>). The mean heights of the two populations at 10½ years were almost identical (17.6 m c.f. 17.1 m; Table 2).

There was a marked increase in basal area growth after thinning with  $\Delta BA_{10\frac{1}{2}-16}$  averaging 43 cm<sup>2</sup> year<sup>-1</sup>. However, height growth failed to respond to thinning with  $\Delta HT_{10\frac{1}{2}-16}$  averaging a relatively low 1.2 m year<sup>-1</sup>. At 16 years after planting the trees had reached 24.3 m mean height, 539 cm<sup>2</sup> mean basal area (over-bark at 1.3 m) and 508 dm<sup>3</sup> mean volume (under-bark).

#### Parameter Estimates for Height Traits

(1) *Variances and Heritabilities*: Comparison of variance components in Table 3 for the thinned and unthinned populations illustrate the consequences of thinning *per se* in simply truncating the data. These effects are distinct from the consequences of thinning in altering stand structure and thereby influencing subsequent patterns of growth and variability over time.

Table 2. — Overall means ( $\pm$  standard deviations) of growth traits for the unthinned and thinned populations of trees.

Growth trait <sup>a</sup>	Unthinned population	Thinned population
<b>Age 2½ and 4½ years</b>		
Height 2½ (m)	1.6±0.28	1.6±0.26
Basal area 4½ (cm <sup>2</sup> )	74±24.2	76±21.6
<b>Age 6½ years</b>		
Height 6½ (m)	9.8±1.0	10.1±0.8
Basal area 6½ (cm <sup>2</sup> )	168±48.5	175±42.2
$\Delta HT_{2\frac{1}{2}-6\frac{1}{2}}$ (m year <sup>-1</sup> )	2.1±0.20	2.1±0.17
$\Delta BA_{4\frac{1}{2}-6\frac{1}{2}}$ (cm <sup>2</sup> year <sup>-1</sup> )	45±13.6	48±12.0
<b>Age 10½ years</b>		
Height 10½ (m)	17.1±1.7	17.6±1.3
Basal area 10½ (cm <sup>2</sup> )	282±101	304±88.5
$\Delta HT_{6\frac{1}{2}-10\frac{1}{2}}$ (m year <sup>-1</sup> )	1.9±0.28	1.9±0.23
$\Delta BA_{6\frac{1}{2}-10\frac{1}{2}}$ (cm <sup>2</sup> year <sup>-1</sup> )	29±15.1	33±13.7
<b>Age 16 years</b>		
Height 16 (m)		24.3±2.5
Basal area 16 (cm <sup>2</sup> )		539±197
Volume 16 (dm <sup>3</sup> )		508±228
$\Delta HT_{10\frac{1}{2}-16}$ (m year <sup>-1</sup> )		1.2±0.31
$\Delta BA_{10\frac{1}{2}-16}$ (cm <sup>2</sup> year <sup>-1</sup> )		43±22.6

<sup>a</sup>) Height 2½ refers to height at 2½ years after planting, basal area 4½ refers to basal area at 4½ years, and so on.

$\Delta HT_{2\frac{1}{2}-6\frac{1}{2}}$  refers to the annual increment of height growth between 2½ and 6½ years,  $\Delta BA_{4\frac{1}{2}-6\frac{1}{2}}$  refers to the annual increment of basal area between 4½ and 6½ years, and so on.

Table 3. — Individual heritabilities ( $h_i^2 \pm$  standard errors), additive genetic variances ( $\sigma_a^2$ ) and phenotypic variances ( $\sigma_p^2$ ) for height traits in the unthinned and thinned populations.

Height trait	Unthinned population			Thinned population		
	$h_i^2 \pm$ s.e.	$\sigma_a^2$	$\sigma_p^2$	$h_i^2 \pm$ s.e.	$\sigma_a^2$	$\sigma_p^2$
$\Delta HT_{2\frac{1}{2}-6\frac{1}{2}}$	0.33±.11	0.0130 <sup>a</sup>	0.0395 <sup>b</sup>	0.44±.17	0.0117 <sup>a</sup>	0.0265 <sup>b</sup>
$\Delta HT_{6\frac{1}{2}-10\frac{1}{2}}$	0.13±.05	0.0092	0.0731	0.09±.07	0.0038	0.0416
$\Delta HT_{10\frac{1}{2}-16}$				0.13±.08	0.0116	0.0924
Height 2½	0.16±.06	0.0120	0.0767	0.20±.10	0.0128	0.0627
Height 6½	0.29±.09	0.2450	0.8563	0.36±.15	0.2018	0.5648
Height 10½	0.30±.10	0.7562	2.5411	0.32±.14	0.4371	1.3664
Height 16				0.19±.10	1.0584	5.6450

<sup>a</sup>)  $\sigma_a^2 = 4\sigma_f^2$ , where  $\sigma_f^2$  is the variance due to families.

<sup>b</sup>)  $\sigma_p^2 = \sigma_f^2 + \sigma_{fb}^2 + \sigma_w^2$ , where  $\sigma_{fb}^2$  and  $\sigma_w^2$  are variances due to family  $\times$  block interactions and within-plot error.

It is apparent from comparing the thinned and unthinned populations that the truncation of data consistently led to a decline in phenotypic variances ( $\sigma_p^2$ ) of height traits measured prior to thinning (i.e. the 2½, 6½ and 10½ year traits; Table 3). The reduction in phenotypic variance was, as might be expected, more marked for 10½ year traits measured closer to the time of thinning. The truncation of data also had the effect of reducing additive genetic variances ( $\sigma_a^2$ ) of all height traits except the earliest height 2½ (Table 3). In general the reduction in  $\sigma_p^2$  was greater than the reduction in  $\sigma_a^2$  and individual heritabilities tended to be higher in the thinned (or truncated) population (with the exception of  $\Delta HT_{6\frac{1}{2}-10\frac{1}{2}}$ ). The individual heritabilities of  $\Delta HT_{2\frac{1}{2}-6\frac{1}{2}}$  and height 6½ were increased fairly markedly by the truncation from high values of  $h_i^2 = 0.33$  and 0.29, respectively, to even higher values of  $h_i^2 = 0.44$  and 0.36 (Table 3). However, differences between the two populations in heritabilities of other height traits were relatively small.

The thinning carried out in the present trial was, as previously mentioned, not highly selective for growth with many trees removed for poor form, wind damage or as out-rows. MATHESON and RAYMOND (1984a) also found that non-selective truncation of data had little influence on heritabilities of growth of *P. radiata*. However, these authors report large increases in heritability when data were truncated on the computer in a strictly selective manner removing the smallest trees in each plot regardless of other considerations. This sort of highly selective thinning on one trait is perhaps rarely likely to occur in practice.

Subsequent discussion of genetic parameters will focus on trends over time rather than the effects of truncating data. Emphasis is placed on changes in variance components in the thinned population since this group of trees are continuous from planting to the final measurement at 16 years. However, attention will be drawn to discrepancies between the two populations.

The magnitude of additive variance for annual height increments declined between the 2½—6½ year and 6½—10½ year periods of measurement (Table 3). As a consequence of the decline in  $\sigma_a^2$  there was an abrupt decrease in heritability in the thinned population from  $h_i^2 = 0.44$  for  $\Delta HT_{2\frac{1}{2}-6\frac{1}{2}}$  to  $h_i^2 = 0.09$  for  $\Delta HT_{6\frac{1}{2}-10\frac{1}{2}}$ . The same trend occurred in the unthinned population although the decline in  $\sigma_a^2$  was not as great. This change in expression of additive variance coincides approximately with stand closure and increasing competition in the stand prior to thinning. The level of  $\sigma_a^2$  increased for height growth fol-

lowing thinning but  $\sigma_p^2$  was also high and, therefore, heritability remained relatively low ( $h^2_i = 0.13$  for  $\Delta HT10\frac{1}{2}$ —16; Table 3).

The cumulative effects of additive variances and heritabilities of height increments were reflected, to some extent, in changes in the heritabilities of absolute height over time. For instance, the strong expression of additive variance of height increment between 2½ and 6½ years led to a substantial increase in  $\sigma_a^2$  (and heritability) for absolute height at 6½ years compared with height 2½ (in both the thinned and unthinned populations; Table 3). Between 6½ and 10½ years the heritabilities of absolute height remained fairly stable as both  $\sigma_a^2$  and  $\sigma_p^2$  increased evenly with the increasing size of trees. There was a decrease in heritability of height 16 because, following thinning,  $\sigma_p^2$  increased far more than  $\sigma_a^2$ . Other published estimates of heritability of height of *P. radiata* (COTTERILL and ZED, 1980; DEAN *et al.*, 1983; MATHESON and RAYMOND, 1984b) each examine absolute height measured at relatively uniform ages (mainly between six and 11 years after planting) and provide little evidence to either confirm or deny the trends reported here.

NAMKOONG and CONKLE (1976) and FRANKLIN (1979) also observed fairly abrupt changes in additive genetic variance of absolute height of *P. ponderosa* and *Pseudotsuga menziesii* at around the time of stand closure. FRANKLIN (1979) actually used changes in additive genetic variance and heritability of absolute height to attempt to define "genetic phases" of stand development. However, it seems from the results reported in Table 3 that changes in genetic variance of growth increments (rather than absolute measurements) may provide a more sensitive guide to changing phases of stand development.

In the present study there appeared to be a juvenile phase of stand development characterised by rapid growth increments as trees strived to attain dominant positions in the canopy. During this juvenile phase trees were able to express their full genetic potential for height growth and levels of additive variance and heritability were high. A more mature phase of stand development was reached following the closure of crowns when trees probably became increasingly locked into dominant, co-dominant or suppressed positions in the canopy. Although the average growth in height was still reasonably rapid during the period between stand closure and thinning the increased competition seemed to diminish additive genetic control over height increments, as characterised by diminishing levels of  $\sigma_a^2$  and  $h^2_i$ . (It will be seen later that increasing competition had the opposite effect on basal area increments and led to large increases in  $\sigma_a^2$ ). Perhaps the most important change in variance components of height increments were the substantial (almost twofold) increases in  $\sigma_p^2$  from one period of measurement to the next (i.e. from 2½—6½ to 6½—10½ to 10½—16 years). These increases in  $\sigma_p^2$  are despite the fact that the rate of height growth was steadily diminishing from one period to the next. The inflation of phenotypic variance of height increments over time may be due to competition allowing taller trees to continue growing taller while shorter trees become increasingly suppressed (even after thinning).

Thinning the stand at 11 years opened the canopy and allowed better expression of additive genetic potential (higher  $\sigma_a^2$ ) for subsequent height growth. However, the phenotypic variance of post-thinning height increments also increased and heritability remained low. It is interest-

Table 4. — Additive genetic ( $r_a \pm$  standard errors) and phenotypic ( $r_p$ ) correlations between height increments or absolute measurements of height in the thinned population.

Height trait	$\Delta HT$ 2½-6½	$\Delta HT$ 6½-10½	$\Delta HT$ 10½-16
$\Delta HT$ 2½-6½		.81±.23 <sup>a</sup>	.41±.26
$\Delta HT$ 6½-10½	.16 <sup>b</sup>		.44±.37
$\Delta HT$ 10½-16	.37	.18	

  

	Height 2½	Height 6½	Height 10½	Height 16
Height 2½		.26±.26 <sup>a</sup>	.24±.27	-.12±.31
Height 6½	.54 <sup>b</sup>		.98±.03	.79±.12
Height 10½	.34	.74		.84±.09
Height 16	.34	.65	.76	

<sup>a</sup>) Additive genetic correlations above the diagonal.

<sup>b</sup>) Phenotypic correlations below the diagonal.

ing to speculate whether very early thinning of the stand (before the initial closure of crowns) may have extended the juvenile phase of highly inherited height increment growth. This sort of early thinning silviculture is common in *P. radiata* in New Zealand and could prove a useful tool for prolonging the effectiveness of height increment as an early selection criterion. This would be contrary to FRANKLIN's (1979) proposal to grow progeny trials at close spacings in the hope of inflating  $\sigma_a^2$  by intense early competition.

(2) *Correlations*: The additive genetic association between the two periods of height increment measured prior to thinning proved highly positive. In the case of the thinned population the genetic correlation between  $\Delta HT2\frac{1}{2}$ —6½ and  $\Delta HT6\frac{1}{2}$ —10½ was  $r_a = 0.81 \pm 0.23$  (Table 4). Although results are not presented, the corresponding correlation between  $\Delta HT2\frac{1}{2}$ —6½ and  $\Delta HT6\frac{1}{2}$ —10½ estimated for the unthinned population was even higher at  $r_a = 0.90 \pm 0.06$ . However, the genetic associations between pre-thinning height increments and the post-thinning  $\Delta HT10\frac{1}{2}$ —16 increment were weaker ( $r_a = 0.41$  and  $0.44$ ; thinned population Table 4). Phenotypic correlations between height increments were also positive but always lower in magnitude than corresponding genetic correlations. The lower magnitude of phenotypic correlations compared with genetic correlations has implications in interpreting results of some previous studies of efficiency of early indirect selection which are based only on phenotypic associations between early and mature traits.

Genetic correlations between absolute heights showed a steady decline as pairs of measurements became more distant in time. Height 2½ was poorly positively correlated with height 6½ ( $r_a = 0.26$ ) and height 10½ ( $r_a = 0.24$ ), but

Table 5. — Individual heritabilities ( $h^2_i \pm$  standard errors), additive genetic variances ( $\sigma_a^2$ ) and phenotypic variances ( $\sigma_p^2$ ) for basal area traits in the unthinned and thinned populations.

Basal area trait	Unthinned population			Thinned population		
	$h^2_i$ s.e.	$\sigma_a^2$	$\sigma_p^2$	$h^2_i$ s.e.	$\sigma_a^2$	$\sigma_p^2$
$\Delta BA$ 4½-6½	0.10±0.05	19.26 <sup>a</sup>	185.79 <sup>b</sup>	0.13±0.08	18.52 <sup>a</sup>	139.46 <sup>b</sup>
$\Delta BA$ 6½-10½	0.21±0.07	47.04	228.08	0.30±0.13	55.48	184.25
$\Delta BA$ 10½-16				0.44±0.16	238.84	543.26
Basal area 4½	0.07±0.04	43.88	588.58	0.08±0.07	34.81	453.75
Basal area 6½	0.08±0.04	196.3	2350.9	0.10±0.07	166.2	1717.5
Basal area 10½	0.15±0.06	1567	10137	0.21±0.11	1571	7615
Basal area 16				0.37±0.15	14731	40018

<sup>a</sup>)  $\sigma_a^2 = 4 \sigma_f^2$ , where  $\sigma_f^2$  is the variance due to families.

<sup>b</sup>)  $\sigma_p^2 = \sigma_f^2 + \sigma_{fb}^2 + \sigma_w^2$ , where  $\sigma_{fb}^2$  and  $\sigma_w^2$  are variances due to family × block interactions and within-plot error.

negatively correlated with height 16 ( $r_a = -0.12$ ; Table 4). Negative correlations between very early juvenile height and post-thinning height were also observed by NAMKOONG and CONKLE (1976), FRANKLIN (1979) and LAMBETH (1980) for a range of species. It seems likely that this switch in sign (positive to negative) of juvenile-mature correlations is due to a steady diminishing over time of the effects of pre-planting factors such as nursery environment and seed weight. Analysis of the unthinned population again revealed somewhat higher genetic correlations than those reported in Table 4 for absolute heights measured to 10½ years (e.g.  $r_a = 0.45 \pm 0.19$  between height 2½ and 6½;  $r_a = 0.31 \pm 0.22$  between height 2½ and 10½; and  $r_a = 0.99 \pm 0.01$  between height 6½ and 10½ in the unthinned population).

#### Parameter Estimates for Basal Area Traits

(1) *Variances and Heritabilities*: It is evident from comparison of the unthinned and thinned populations that the truncation of data consistently led to a reduction in  $\sigma_p^2$  for basal area traits measured to 10½ years (Table 5). Likewise, the truncation often led to a reduction in  $\sigma_a^2$  (except for  $\Delta BA_{6\frac{1}{2}-10\frac{1}{2}}$  and basal area 10½), but any decline in  $\sigma_a^2$  was always less than the corresponding decline in  $\sigma_p^2$ . Heritability, therefore, was consistently greater in the thinned population.

As far as changes in variance of basal area increments over time are concerned the most important trend was a large and consistent increase in  $\sigma_a^2$  in both the unthinned and thinned populations. Phenotypic variance also increased in both populations from one period of measurement to the next but not as much as  $\sigma_a^2$ . Heritability therefore increased from  $h^2_i = 0.13$  for  $\Delta BA_{4\frac{1}{2}-6\frac{1}{2}}$  to  $h^2_i = 0.30$  for  $\Delta BA_{6\frac{1}{2}-10\frac{1}{2}}$  to  $h^2_i = 0.44$  for  $\Delta BA_{10\frac{1}{2}-16}$  (thinned population; Table 5). The same sort of trend was evident for additive variances and heritabilities of absolute measurements of basal area. The increase in  $\sigma_p^2$  from one period of measurement to the next was of about the same proportion for basal area increments as previously observed for height increments (Table 3 c.f. Table 5). However, the increase in  $\sigma_a^2$  for basal area increments is clearly contrary to the decline in  $\sigma_a^2$  observed for height increments between about the time of stand closure and thinning. LAMBETH *et al.* (1983) also reported similarly large increases in  $\sigma_a^2$  of conical volume of *P. taeda* over consecutive thinnings, but generally found only marginal increases in  $\sigma_a^2$  of corresponding height measurements.

One explanation for the increase in  $\sigma_a^2$  of basal area growth over time is the effect of competition tending to in-

Table 6. — Additive genetic ( $r_a \pm$  standard errors) and phenotypic ( $r_p$ ) correlations between basal area increments or absolute measurements of basal area in the thinned population.

Basal area trait	$\Delta BA$ 4½-6½	$\Delta BA$ 6½-10½	$\Delta BA$ 10½-16
	$\Delta BA$ 4½-6½		.93±.06 <sup>a</sup>
$\Delta BA$ 6½-10½	.76 <sup>b</sup>		.95±.04
$\Delta BA$ 10½-16	.55	.74	

  

Basal area trait	Basal area 4½	Basal area 6½	Basal area 10½	Basal area 16
	Basal area 4½		.78±.17 <sup>a</sup>	.29±.35
Basal area 6½	.89 <sup>b</sup>		.87±.09	.73±.17
Basal area 10½	.71	.90		.96±.03
Basal area 16	.54	.72	.88	

a) Additive genetic correlations above the diagonal.

b) Phenotypic correlations below the diagonal.

flate the variance between families as larger families become increasingly dominant and smaller families increasingly suppressed (CORRELL and ANDERSON, 1983). The average growth in basal area of the stand was definitely influenced by competition prior to thinning. However, the particularly large increase in  $\sigma_a^2$  following thinning may have been due, at least in part, to trees greatly improving their rate of growth in girth and thereby allowing better expression of genetic potential for basal area increment.

(2) *Correlations*: Genetic correlations between  $\Delta BA_{4\frac{1}{2}-6\frac{1}{2}}$ ,  $\Delta BA_{6\frac{1}{2}-10\frac{1}{2}}$  and  $\Delta BA_{10\frac{1}{2}-16}$  in the thinned population were consistently highly positive ( $r_a \geq 0.89$ ) with low standard errors (Table 6). Although results are not presented, the corresponding genetic correlations to 10½ years in the unthinned population were even higher than those for the thinned population (as was the case for height traits).

Genetic correlations between absolute basal areas were generally lower in magnitude than those between basal area increments, and declined to a far greater extent as pairs of measurements became increasingly distant in time. For instance, basal area 4½ was reasonably strongly correlated with basal area 6½ ( $r_a = 0.78$ ), poorly correlated with basal area 10½ ( $r_a = 0.29$ ), and very poorly genetically correlated with post-thinning basal area 16 ( $r_a = 0.10$ ; Table 6). Absolute basal areas measured at 6½, 10½ and 16 years were all reasonably strongly genetically correlated ( $r_a \geq 0.73$ ) with relatively low standard errors.

Phenotypic correlations between basal area increments were consistently positive but much smaller in magnitude than corresponding genetic correlations. However, phenotypic correlations among absolute basal area measurements were generally larger than corresponding genetic correlations.

#### Early Selection of Individual Trees

Table 7 lists heritabilities, together with genetic and phenotypic associations between early growth traits (measured up to 10½ years after planting) and volume 16. Also given are the corresponding efficiencies of indirect selection of best individual trees or best families for each of the early traits. The parameters presented in Table 7 are for the thinned population only and discussion concentrates on this population which is continuous from planting to 16 years. However, comparison is sometimes made with efficiencies of early selection estimated for the unthinned population. Note that volume 16, rather than height 16 or basal area 16, has been used as the mature trait to measure efficiency of indirect selection because improving volume production is presently the major objective of breeding *P. radiata*.

Indirect selection on the earliest traits, height 2½ and basal area 4½, proved very inefficient. Selection on height 2½ would actually be expected to cause a decline in volume at 16 years due to the negative genetic correlation  $r_a = -0.18$  observed between height 2½ and volume 16 (Table 7). Indirect selection of individual trees on basal area 4½ would be expected to produce no more than 12% of the response in volume 16 achieved by direct selection, even where efficiency is calculated on a per year basis to take account of the shorter generation interval under indirect selection (i.e.  $Q_{year} = 12\%$  for basal area 4½; Table 7).

The poor reliability of height 2½ as a criterion for early selection in the present study may be due, at least in part, to slow growth of trees over the first two years after planting. The trees had reached a mean height of only 1.6 m at 2½ years (see overall means, Table 2), but then grew at a

Table 7. — Individual heritabilities ( $h^2_i$ ), additive genetic correlations ( $r_a \pm$  standard error) and phenotypic correlations ( $r_p$ ) between early growth traits and volume at 16 years in the thinned population, and resulting efficiencies per generation ( $Q_{gen}$ ) and per year ( $Q_{year}$ ) of early indirect selection of individual trees for volume 16. Also given are corresponding heritabilities ( $h^2_f$ ) and efficiencies per generation calculated on a family basis.

Early trait		Individual tree basis					Family basis	
		$h^2_i$	$r_a \pm$ s.e.	$r_p$	$Q_{gen}^a$ (%)	$Q_{year}^a$ (%)	$h^2_f$	$Q_{gen}^b$ (%)
Height	2½	.20	-.18±.27	.33			.55	
Basal area	4½	.08	.13±.35	.49	6	12	.34	9
Height	6½	.36	.81±.10	.66	80	133	.71	78
Basal area	6½	.10	.75±.17	.68	39	65	.41	55
ΔHT	2½-6½	.44	.89±.07	.63	97	162	.77	90
ΔBA	4½-6½	.13	.98±.07	.73	58	97	.49	79
Index	6½ <sup>c</sup>	.43	.91±.06	.71	98	164	.76	91
Height	10½	.32	.87±.07	.72	81	106	.67	82
Basal area	10½	.21	.97±.03	.86	73	96	.63	88
ΔHT	6½-10½	.09	.89±.18	.43	44	58	.36	61
ΔBA	6½-10½	.30	.99±.02	.88	89	117	.72	96
Index	10½ <sup>d</sup>	.46	.95±.04	.81	106	139	.79	97

- a) The efficiencies of early individual selection were calculated with  $h^2_i = 0.37 \pm .15$  for volume 16.  
 b) Efficiency of early family selection calculated with  $h^2_f = 0.76$  for volume 16.  
 c) Index 6½ combines ΔHT2½-6½ and ΔBA4½-6½ with a BINET restriction on volume 16.  
 d) Index 10½ combines ΔHT2½-6½, ΔBA4½-6½, ΔHT6½-10½ and ΔBA6½-10½ with a BINET restriction on volume 16.

rapid 2.1 m year<sup>-1</sup> over the subsequent period from 2½ to 6½ years. If competition from grasses and weeds had been controlled by regular herbicide application during the first two years (which is now routine practice in newly established *P. radiata* plantations in South Australia) the immediate post-planting growth of trees would have been far more rapid, and height 2½ may have been a more reliable guide to later performance. NAMBIAR and ZED (1980) report a mean height of 1.8 m at only 17 months for *P. radiata* grown under weed-free conditions on a comparable site.

There was a marked improvement from 2½ or 4½ year growth traits to 6½ year traits in additive genetic correlations with volume 16 and efficiencies of early selection. This is perhaps not surprising in view of the fact that the trees grew from an average 1.6 m in height at 2½ years to around 10 m at 6½ years (Table 2). In general, the efficiencies of early indirect selection at 6½ years were much greater for selection on height traits compared with basal area traits, and greater for indirect selection on increments compared with absolute measurements. The height increment ΔHT2½-6½ and a restricted index (referred to as index 6½) combining ΔHT2½-6½ and ΔBA4½-6½ appeared to be particularly reliable traits for early selection having both high heritabilities and strong genetic correlations with volume 16 ( $r_a = 0.89 \pm 0.07$  and  $0.91 \pm 0.06$ ; Table 7). Indirect selection of individual trees on ΔHT2½-6½ should yield 97% of the response per generation and 162% of the response per year in volume 16 expected from direct selection (i.e.  $Q_{gen} = 97\%$  and  $Q_{year} = 162\%$ ; Table 7). Corresponding efficiencies for the index 6½ were  $Q_{gen} = 98\%$  and  $Q_{year} = 164\%$ . The basal area increment ΔBA4½-6½ had a very strong genetic correlation of  $r_a = 0.98 \pm 0.07$  with volume 16. However, the low heritability of ΔBA4½-6½ reduced the response per year expected in volume 16 from indirect selection to marginally

less than that expected from direct selection (i.e.  $Q_{year} = 97\%$  for ΔBA4½-6½; Table 7).

It is interesting to note that the much higher heritability of ΔHT2½-6½ compared with ΔBA4½-6½ caused the former trait to receive overwhelming emphasis in the index 6½. This readily apparent from the equation actually computed for solving index 6½—(7)

$$\text{Index } 6\frac{1}{2} = 34.5 P_1 + 0.1 P_2 \quad (7)$$

where  $P_1$  and  $P_2$  represent the phenotypic values of individual trees for ΔHT2½-6½ and ΔBA4½-6½, respectively. Indeed index 6½ and ΔHT2½-6½ are essentially the same trait having almost identical heritabilities, correlations and efficiencies (Table 7). In circumstances such as this where one early trait is much more highly heritable than other traits and is strongly correlated with mature performance there may be little practical benefit from using restricted indices. It may be equally efficient and more simple to base indirect selection on the highly heritable trait itself.

Absolute measurements of height and basal area at 6½ years proved to be less strongly genetically correlated with volume 16 than was the case for corresponding increments to 6½ years. However, the high heritability of height 6½ made it a reasonably efficient trait for early selection with  $Q_{year} = 133\%$  (Table 7). On the other hand, basal area 6½ had both a low heritability and a relatively low correlation with volume 16 ( $r_a = 0.75 \pm 0.17$ ). Consequently indirect selection on basal area 6½ proved only 65% as efficient per year as later direct selection. This is an important finding because absolute basal area (or closely associated traits such as absolute diameter and conical volume) measured at around five to 12 years are presently the main criteria for improving growth of *P. radiata* in Australia (e.g. COTTERILL and ZED, 1980; DEAN *et al.*, 1983). It appears that selection on height increments or even absolute height at around six years may be much more efficient in improving mature volume production.

At 10½ years there was an improvement in the reliability of basal area traits as indirect selection criteria (e.g.  $Q_{gen} = 89\%$  for ΔBA6½-10½) and a dramatic decline in the reliability of height increments ( $Q_{gen} = 44\%$  for ΔHT6½-10½). The index 10½, which combines all height and basal area increments measured to 10½ years, had the highest efficiency of 106% per generation. This efficiency of greater than 100% per generation under indirect selection on index 10½, compared with direct selection on volume 16, is due to the higher heritability of the index ( $h^2_i = 0.46$  for index 10½ c.f.  $h^2_i = 0.37$  for volume 16) and a strong juvenile-mature genetic correlation. The index 10½ is interesting because it produced considerably greater efficiency per generation than any one of its four component traits (i.e. ΔHT2½-6½, ΔBA4½-6½, ΔHT6½-10½ or ΔBA6½-10½) and demonstrates a worthwhile gain advantage for the BINET restriction.

Despite the high efficiency per generation of index 10½, the longer generation interval associated with indirect selection at 10½ years reduced the efficiency per year for this index to well below the efficiencies per year for earlier traits such as ΔHT2½-6½ and index 6½. In this sense indirect selection at around six years, or when trees reach around 10 m height, may be an optimum for maximising response in volume 16 of *P. radiata* in South Australia. It seems more meaningful to define optimums for early selec-

tion in terms of the average size of trees (optimum stage of growth) as distinct from the concept of optimum age used by LAMBETH (1980) and others. This is because at any given age a stand on a good site may be at a very different stage of growth and development than a stand on a poor site. (Likewise for comparing optimums for early selection across fast and slower growing species).

When efficiencies were determined using genetic parameters of early traits in the unthinned population (including additive genetic correlations with volume 16 calculated on a plot mean basis) the values of  $Q_{gen}$  and  $Q_{year}$  were generally lower than those reported in Table 7. This is because the heritabilities of early traits were generally lower in the unthinned compared with the thinned population (see Tables 3 and 5). However, the optimum for early selection seemed to remain at about the time when trees reached 10 m height (or 6½ years). For instance, in analyses not reported, the efficiencies per year in the unthinned population were estimated as  $Q_{year} = 140\%$  for  $\Delta HT_{2\frac{1}{2}} - 6\frac{1}{2}$ , 141% for index 6½ and 120% for index 10½.

Under circumstances where selected trees are cloned in breeding arboreta to facilitate controlled crossing it may be possible to select *P. radiata* at 6½ years and again at around 9½ years (i.e. two-stage selection) without greatly extending the generation interval beyond that required for selection at 6½ years only. The stage 1 of selection at 6½ years would involve choosing say twice the number of trees actually required for future breeding (see theory developed in COTTERILL and JAMES, 1981), and cloning these selected ortets in breeding arboreta. The breeding arboreta usually require around three years to reach sexual maturity. Hence, at around 9½ years (immediately prior to the beginning of controlled-crossing), the ortets selected at stage 1 would be remeasured and the new information on growth used to finally choose (stage 2) the best half of the ortets for crossing. This stage 2 of selection may be on a restricted index combining growth increments from around one or two to 6½ years and 6½ to 9½ years. The increasing cost of measuring height of taller trees, and the apparently poor heritability of later height increments of *P. radiata*, may persuade many tree breeders to measure only basal area increments from 6½ to 9½ years.

In practice there would be no need to restrict measurement at 9½ years to only those ortets selected at stage 1. Trees not selected at stage 1, but showing rapid growth between 6½ and 9½ years, could easily be included in the controlled-crossing program as male (pollen) parents even though they were not represented in breeding arboreta.

The phenotypic correlations between volume 16 and growth traits at 6½ or 10½ years were consistently lower in magnitude than corresponding genetic correlations (Table 7). LAMBETH *et al.* (1983) observed the same for juvenile-mature correlations in *P. taeda*. As mentioned previously, this finding has implications in interpreting results of previous studies of early selection which are often based on phenotypic correlations only. After studying juvenile-mature phenotypic correlations for *P. elliottii*, *P. taeda*, *P. palustris* and *P. echinata*, WAKELEY (1971) recommended that indirect selection may be ineffective before about 20 years (when the mean heights of species ranged from 13 to 16 m). STEINHOFF (1974) reached similar conclusions after examining phenotypic correlations for *P. ponderosa* and *P. monticola*. However, evaluations of efficiency which take account of heritabilities and genetic associations between early and mature traits may favour much earlier indirect selection for these species.

LAMBETH (1980) used results from the literature (including the papers cited above) to attempt to develop a generalised regression model to predict juvenile-mature phenotypic correlations between height of trees measured at different ages across a range of species. As expected, the phenotypic correlations predicted from LAMBETH's model tend to be marginally lower than genetic correlations reported in the present study. Caution should be exercised in using the efficiencies per year of indirect selection tabulated in LAMBETH (1980) (and LAMBETH *et al.*, 1983) which are not only based directly (or indirectly) on phenotypic associations but also take no account of heritabilities. These efficiency calculations therefore ignore the large differences in inheritance which may occur between early and mature traits. Nevertheless, LAMBETH's (1980) general conclusion seem reasonable that early selection for growth may be most efficient between around six and eight years (depending on the plantation rotation or site quality), but certainly not before trees are at least 2 m tall.

It must be stressed that further studies are clearly required before optimum stages of growth can be reliably defined for early selection of *P. radiata*. The present study is conducted on one site only and it remains to be seen whether the trends reported in genetic parameters will be evident in *P. radiata* grown on other sites. It may also turn out that trends in genetic parameters are substantially altered by differing thinnings regimes.

Another limitation of the present study is that juvenile-mature correlations and other parameters are reported for traits measured to 16 years only (about half-rotation age). Where the breeding goal is to improve lifetime performance over full rotation (as distinct from performance to 16 years) the optimum stage for early selection may be sometime after trees reach 10 m height. However, the extremely long generation interval for direct selection after a 40 year rotation (i.e. the  $l_2$  in Equation 6) will act very strongly in favour of traits measured early. It is also worth noting that *P. radiata* in South Australia is producing commercially valuable saw logs at 16 years (around second thinning) and improving volume 16 may, in itself, represent a fairly sound economic breeding goal. It is certainly better than the current practice of selecting rather arbitrarily to improve early absolute diameter or volume.

#### Early Selection of Families

Table 7 lists the efficiencies of early indirect selection of families on a per generation basis, mainly for the purpose of comparison with corresponding efficiencies of indirect selection of individual trees. It is difficult to generalise about the efficiencies per year of family selection because in advanced-generation tree breeding family selection *per se* is more commonly used to cull clonal seed orchards (which has no influence on generation interval). Family information is sometimes utilised in combined indices to select individuals for future breeding (e.g. COTTERILL, 1986) but this option is not considered here. The efficiencies of family selection were determined by solving Equation 5 for family heritabilities  $h^2_f$  and the genetic correlations  $r_a$  given in Table 7. It is debatable whether the most appropriate correlations for determining  $Q_{gen}$  for family selection are the  $r_a$ 's in Table 7 or the correlations among family means for different traits (i.e. the "family mean correlation"; LAMBETH *et al.*, 1983). In any case both types of correlations were calculated in preliminary analyses and proved fairly similar with the family mean correlation usually slightly lower in magnitude.



Perhaps the most interesting feature of the efficiencies of indirect family selection is that they are consistently less than the efficiencies of indirect individual selection for those important early traits having the highest heritabilities. For instance, indirect family selection on  $\Delta HT2\frac{1}{2}-6\frac{1}{2}$ , index  $6\frac{1}{2}$  and index  $10\frac{1}{2}$  yielded efficiencies of 90, 91 and 97% per generation, respectively, while corresponding efficiencies for indirect individual selection were 97, 98 and 106% (Table 7). In other words, early selection applied on a family basis is not necessarily more appealing (relative to direct selection) than early selection applied on an individual tree basis. This finding does not imply that the absolute response in volume 16 achieved by indirect selection of best families would necessarily be less than the absolute response from indirect selection of best individuals; such would depend on relative intensities of selection. For instance, by solving the numerator of Equation 4 it can be shown that an indirect response of 239 dm<sup>3</sup> per generation is expected in volume 16 as a consequence of early family selection on  $\Delta HT2\frac{1}{2}-6\frac{1}{2}$  at an intensity of say one family in 10 (or  $i_1 = 1.54$  assuming finite population size; BECKER, 1984). However, the response in volume 16 declines to 87 dm<sup>3</sup> when the intensity of selection is reduced to one family in two ( $i_1 = 0.56$ ). The response expected in volume 16 as a consequence of individual selection on  $\Delta HT2\frac{1}{2}-6\frac{1}{2}$  at an intensity of one tree in 100 ( $i_1 = 2.51$ ) is 206 dm<sup>3</sup> (somewhat less than the gain under family selection at one in 10). These intensities of family and individual selection are representative of intensities commonly used in tree breeding.

In the case of early traits having substantially lower individual heritabilities than volume 16 the efficiencies of indirect family selection were greater than indirect individual selection. For instance, indirect family selection on the poorly inherited  $\Delta BA4\frac{1}{2}-6\frac{1}{2}$  ( $h^2_1 = 0.13$ ) yielded 79% efficiency per generation, while indirect individual selection yielded only 58% efficiency. The absolute responses expected in volume 16 from indirect family selection on  $\Delta BA4\frac{1}{2}-6\frac{1}{2}$  are 210 dm<sup>3</sup> for selection of one family in 10, and 76 dm<sup>3</sup> for selection of one family in two. The indirect response from individual selection on  $\Delta BA4\frac{1}{2}-6\frac{1}{2}$  at one tree in 100 is an intermediate 123 dm<sup>3</sup>.

In general, it is apparent that culling orchards on family (progeny test) performance for growth traits measured when offspring are around 10 m tall (such as  $\Delta HT2\frac{1}{2}-6\frac{1}{2}$  and index  $6\frac{1}{2}$ ) should yield around 90% of the response expected from much later (direct) culling on volume 16. There is considerable practical advantage in culling clonal orchards of *P. radiata* at around six years or before they begin producing commercial quantities of seed. However, the results of this study suggest that it would be unwise to cull orchards on progeny test performance at around 2½ or 4½ years.

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