AGE-AGE CORRELATIONS AND EARLY SELECTION FOR END-OF-ROTATION WOOD DENSITY IN RADIATA PINE

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ABSTRACT

In this study, age-age correlation for wood density and its component traits (earlywood density, latewood density and latewood ratio) were investigated in 30-year-old trees of 50 open-pollinated families of *Pinus radiata* D. Don. From each of the tree, 5-mm pith-to-bark breast-height increment core was taken for X-ray densitometry analysis. Apart from ring density (RD) alone, earlywood density, latewood density and latewood ratio were also included in selection index to evaluate their effect on relative efficiency of early selection for end-of-rotation wood density. Heritability estimates of RD and its component traits increased with age. Latewood ratio was found least heritable trait compared to other traits considered in this study. Estimates of individual-tree heritability of RD increased from 0.57, at core age 2 years, to 0.81 at core age 10 years. Estimated genetic correlation of RD, at core age 3 years, with RD at harvest age was 0.86, and it increased to 0.96 at the age 10 years. Using RD, relative efficiency of family and individual selection was 82 and 76 %, respectively, when early selection was carried out at core age of 5 years. Index selection, using information on the components of RD, gave slightly higher relative efficiency compared to using RD alone.

Key words: ring density, heritability, early selection, genetic correlation, index selection, *Pinus radiata*.

INTRODUCTION

Selection at an early age, with the goal of improving a trait expressed at harvest-age, can be called as early or indirect selection. Early selection for various economical traits is used to minimise the generation interval. In general, there is no perfect relationship between performance at early assessments and performance at harvest age. There is generally an obvious trade-off between the reliability of selection as trees get older and shortening of the generation time that early selection can allow. For radiata pine in New Zealand, trees are normally selected for various growth and form traits at around seven to 10 years after planting with the hope of improving total productivity over a 25 to 35 year plantation rotation.

Early selection can be employed for 'forwards' selection for achieving cumulative additive genetic gains over successive generations and also for 'backwards' selection for seed orchards (BURDON 1989). Numerous efforts have been made to evaluate the relative efficiency of early selection (LAMBETH 1980, KANG 1985, COTTERILL & DEAN 1988, MAGNUSSEN 1988, BURDON 1989). All of these studies have mainly focussed on growth traits. Wood density is probably the most important indicator of wood quality because of its important role in determining wood strength, pulp yield and several other wood properties. Understanding the genetics of wood density is complicated by the composite nature of this trait. There are some other studies where genetic variation of wood density was evaluated to explore the feasibility for early selection for this trait (NICHOLLS 1967, LOO *et al.* 1984, VARGAS-HERNANDEZ & ADAMS 1992, GREAVES *et al.* 1997, HYLEN 1999).

Average ring density (RD) measured at early age can be used as selection criteria to improve average RD at harvest-age. GWAZE *et al.* (2002) reported that early selection for wood density in loblolly pine would be possible at age 5 years. There are no published estimates of efficiency of early indirect selection for improving average growth ring density at harvest-age in *Pinus radiata*. A particular value of ring wood density can result from various combinations of its component traits. Thus, knowledge of genetic control of these component traits would help in understanding the genetics of overall wood density. Most commonly used components of ring density (RD) are earlywood density, latewood density and latewood ratio. Index selection including multiple early traits could improve the efficiency of early selection (FOSTER 1986, COTTERILL & DEAN 1988, BURDON 1989). Vargas-Hernandez and

Adams 1992 showed that, in Douglas-fir, the efficiency of early selection for wood density was improved by including ring density components in an selection index.

The present study was conducted with two main objectives: first, to describe age trends in variance components and heritabilites, and age-age correlations for wood density and its component traits; second, to evaluate relative efficiency of index selection using ring density components for early selection for end-of-rotation wood density.

MATERIALS AND METHODS

The trial and assessment

A progeny trial of 600 open-pollinated (OP) families of plus-trees of *Pinus radiata* D. Don was established in 1969 on a site in the central North Island of New Zealand (SHELBOURNE & LOW 1980). The initial selection of plus-trees was carried out in 1,780 acres of radiata pine stand, giving a selection intensity of approximately one tree to every three acres. Open-pollinated families of plus-trees were assumed to be closely approximating half-sib families (Personal communication with Dr C. J. A. SHELBOURNE). The trial was established as 5 replications of 10-tree row plots of each OP family. The parents were ranked on the basis of their 10-year-old progeny performance for various growth and form traits, and the top 50 selections were deployed in seed orchards (SHELBOURNE & LOW 1980). The trial was thinned at different stages, leaving 3 to 4 trees per plot. In 1999, when the progenies were 30 years old, a study was undertaken to investigate the wood quality traits of top-selected parents. For X-ray densitometry (POLGE 1965, COWN & CLEMENT 1983) analysis, one 5-mm pith-to-bark breast-height increment core was taken from 8–9 tress of each of the top 50 families. Depending upon the availability, the number of trees sampled from each replication varied for different families.

X-ray densitometry of each core revealed within-and-between rings wood density changes across 28 annual growth rings, numbered from pith-to-bark. The first and last annual rings from each sample were discarded and for each of the remaining rings, minimum, maximum, average RD and the ring width were obtained. The width and average densities for earlywood density and latewood density, and latewood ratio were obtained for each ring by using the average of the minimum and maximum density in the ring as the criterion to separate earlywood from latewood (GREEN & WORRALL 1964, NICHOLLS *et al.* 1980, VARGAS-HERNANDEZ & ADAMS 1992). Weighted average across the core was obtained for RD, earlywood density and latewood density, by weighting each individual ring value by its respective width. The averages obtained for each core age represents the value that would have been obtained if increment core samples had been taken at that age (in terms of number of rings from the pith represented). The averages obtained by including all growth rings represented the overall trait value at the harvest age (30 years in this study). Latewood ratio across the core was obtained as the sum of the latewood width of individual rings divided by the length of the core sample.

Statistical analysis

As multi-tree row plots were used in the trial design, the model for statistical analysis would include replicate, family, plot, and residual factors. Preliminary analysis revealed that replicate and plot effects were insignificant. Thus, the following simple model was used for single trait analysis:

$$Y_{ij} = \mu + f_i + e_{ij} \qquad [1]$$

where Y_{ij} is the phenotypic value for the j^{th} individual in the i^{th} family for a given trait; μ is the general mean; f_i is the random effect of i^{th} family; e_{ij} is the random error effect. Using age-20 year data from this same experiment, COWN *et al.* (1992) had used similar model for estimating inheritance of wood density. Estimate of narrow-sense heritability ($\hat{h}^2$) and family-mean haritability ($\hat{h}_f^2$) for each trait were obtained as:

$$\hat{h}^2 = 4\hat{\sigma}_f^2/(\hat{\sigma}_f^2 + \hat{\sigma}_e^2) \qquad [2]$$

$$\hat{h}_f^2 = \hat{\sigma}_f^2/(\hat{\sigma}_f^2 + \hat{\sigma}_e^2/n) \qquad [3]$$

where $\hat{\sigma}_f^2$ and σ_e^2 are the estimated among-family and within-family variance, respectively; n is the number of half-sib offspring per family. Approximate standard error (SE) of heritability estimate was calculated following FALCONER & MACKAY (1996, page 180). Estimates of covariance components between all pairs of traits were obtained using expected cross-products (Table 1). Table 1 shows that estimates of $\boldsymbol{E}$ and $\boldsymbol{\Psi}$ are $\boldsymbol{MS_E}$ and $(\boldsymbol{MS_B} - \boldsymbol{MS_E})/n$, respectively. SAS PROC GLM (SAS INSTITUTE INC. 1989) was used to obtain sums-of-squares and cross-products matrices. Assuming half-sib families, estimate of $\boldsymbol{\Psi}$ is equivalent to $\frac{1}{4}\hat{\boldsymbol{G}}$, where $\hat{\boldsymbol{G}}$ is the estimate of genetic variance-covariance matrix. Estimates of genetic correlations were obtained using appropriate variance and covarian-

Table 1. Form of multivariate analysis of variance (MANOVA). SS = Sums-of-squares, CP = cross-products, MS = Mean sums-of-squares, E(MS & CP) = Expected values of MS and CP.

Source	Degrees of freedom	SS and CP	MS and CP	E (MS & CP)
Among families	$f-1$	S_B	MS_B	$E + n\Psi$
Within families	$f(n-1)$	S_E	MS_E	E

ce components. Approximate standard errors (SE) of estimated genetic correlations were calculated following FALCONER & MACKAY (1996, page 316).

Predicted genetic gain

The ratio of genetic gain in the target trait expected from indirect selection based on an early age, relative to the gain expected when the selection is made directly on the target trait, was called the relative efficiency (RE) of indirect or early selection. Average RD, obtained by weighting each individual ring value by its width, at the harvest-age was assumed as the target trait to improve. The genetic gain in the target trait by direct selection can be calculated as (FALCONER & MACKAY 1996, page 189):

$$\Delta_G = ih^2\sigma_p \qquad [4]$$

The correlated response in the target trait (y) from indirect selection will be:

$$\Delta_{g*} = ih_x h_y r_g \sigma_{p(y)} \qquad [5]$$

The ratio of genetic gain obtained from Eq. 5 to that obtained from Eq. 4, expressed in percentage, was calculated for various selection ages. Relative efficiency (%) was calculated for both 'forwards' (individuals) as well as 'backwards' (parental) selections. When selection criteria contained more than one trait (called index selection), the correlated response (in the unit of measurement) in the target trait was calculated following WHITE & HODGE (1989, page 244–245). The estimated relative efficiency of index selection was calculated as the ratio of genetic gain obtained from index selection to that obtained from Eq. 4. Selection intensity (i) was assumed to be 1 in all calculations.

RESULTS AND DISCUSSION

Age trends in trait means

Overall means for RD, earlywood density, latewood density and latewood ratio are shown in Figure 1. In general, overall means for all traits increased slowly with increasing core age. RD increased from 326 kg·m^{-3} at core age 2 years to 349 kg·m^{-3} at core age 10 years. Similarly, earlywood density increased from 302 kg·m^{-3} at core age 2 years to 321 kg·m^{-3} at core age 10 years. At harvest-age, population mean for RD and earlywood density was 380 and 336 kg·m^{-3}, respectively. Latewood ratio decreased from 0.18 at core age 2 years to 0.15 at core age 4, and then leveled off to 0.18 at age 10. At harvest-age, latewood ratio was found to be 0.25. Latewood density increased from 441 kg·m^{-3} at core age 2 years to 476 kg·m^{-3} at core age 10 years, and reached to 518 kg·m^{-3} at harvest-age. Age trends of ring density and its components, observed in this study, were similar to those observed by COWN & BALL (2001) in 10 full-sib families of radiata pine. NICHOLLS & BROWN (1971) also reported increasing trend in RD and its components with age in radiata pine.

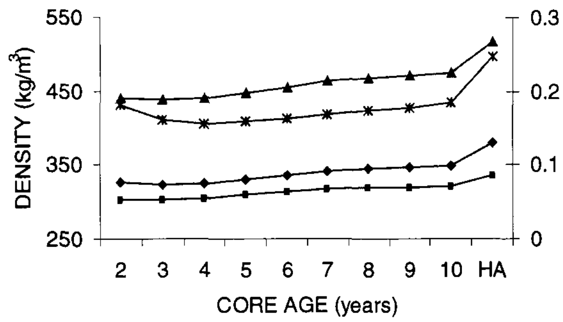

Figure 1. Age associated changes in population mean. (◆ Ring density, ▲ Latewood density, * Latewood ratio (LP), ■ Earlywood density, HA : harvest age).

Age trends in variance components and heritabilities

Age trends in additive (A), environmental (E), phenotypic (P) variance components for ring density and its component traits are shown in Figure 2. Variance components in Figure 2 were expressed in terms of coefficients of variation (CV) to avoid confounding scale effects (e.g. VARGAS-HERNANDEZ & ADAMS

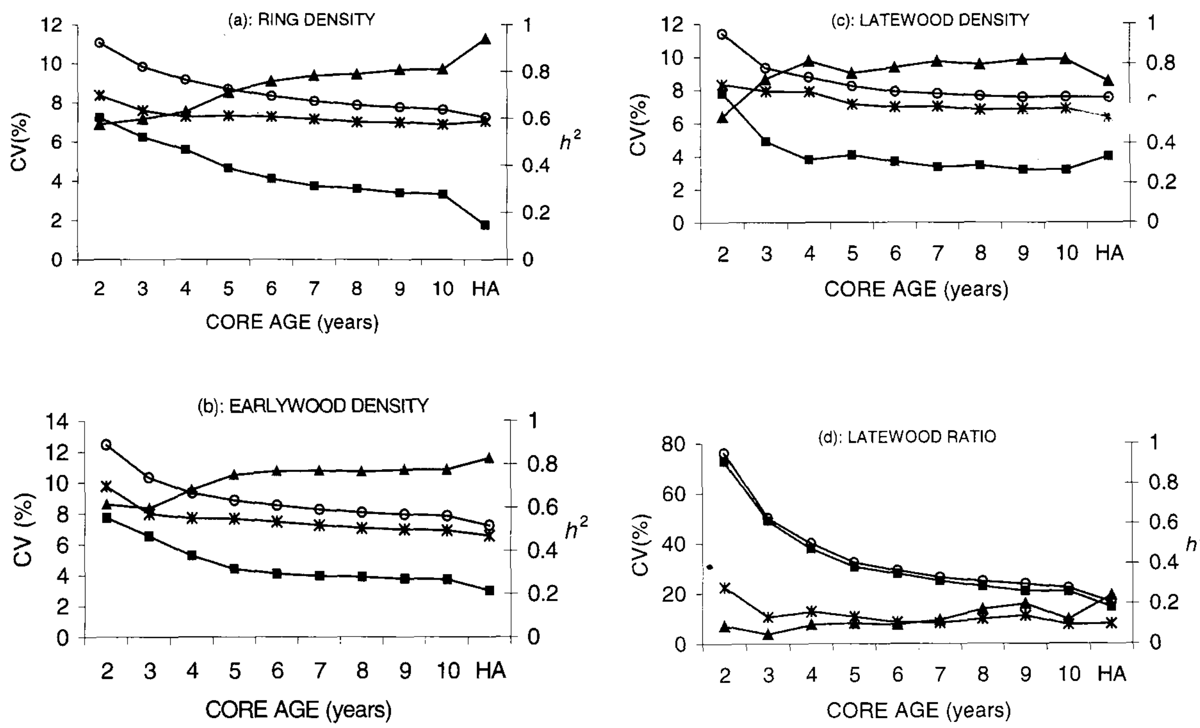

Figure 2. Age trends in variance components. (■ Environment, * Additive, o Phenotypic, ▲ Heritability (h^2), HA: harvest age).

1992). Individual-tree heritability estimates are also shown in Figure 2. In general, the CV for all the variance components for overall ring density, early wood density, latewood density is low compared with the CV for latewood ratio. These trends in variance components are similar to those found in Douglas-fir (VARGAS-HERNANDEZ & ADAMS 1992) and Norway spruce (HYLEN 1999). A decreasing trend in the magnitude of the environmental CV, and consequently in the phenotypic CV, was observed for all traits with the increasing core age. However, for latewood density, the decline in the environmental and phenotypic CV was very minor after the core age of 4-years.

The CV of additive genetic variance followed very similar trend for different traits. In general, the additive CV followed a decreasing trend up to the age of 4 or 5 years and then remained almost same up to age 10 years (Figure 2). In general, the CV for all traits decreased with age, but there was a larger decline in the environmental CV than in the additive variance CV. VARGAS-HERNANDEZ & ADAMS (1992) observed similar trends for latewood density and latewood ratio in Douglas-fir. Similar trend in additive and environmental variance has been reported for growth traits in conifers (LAMBETH *et al.* 1983, FOSTER 1986, COTTERILL & DEAN 1988, KING & BURDON 1991).

The strong decrease in the environmental CV resulted in steady increase, with age, in individual-tree heritability estimates of ring density and its component traits. The within-site individual-tree heritability estimate of ring density compare favourably to those reported by BURDON & LOW (1992). Heritability estimates obtained from a single site will be biased upwards if family x site interaction is not taken into account. BURDON & LOW (1992) reported minimal family x site interaction for wood density in New Zealand. For all traits except latewood ratio, the increase in heritability estimate was minimal after the core age of 6-years (Figure 2). Heritability estimates for ring density, earlywood density and latewood density were very similar across various core ages. Other studies in Douglas-fir (VARGAS-HERNANDEZ & ADAMS 1992) and Eucalyptus (GREAVES *et al.* 1997) reported lower heritability of component traits compared to ring density itself. It was suspected by GREAVES *et al.* (1997) that incorrect placement of earlywood-latewood boundary within a ring increases the residual variance of each, thus reducing the apparent heritability relative to the whole ring heritability. On the other hand, HYLEN (1999) reported higher estimated heritability of latewood density compared to overall ring density.

Similar to other studies in Douglas-fir (VARGAS-HERNANDEZ & ADAMS 1992), Norway spruce (HYLEN 1999), Eucalyptus (GREAVES *et al.* 1997) and radiata pine (NICHOLLS *et al.* 1980), latewood ratio was found to be the least heritable trait among various ring density components considered in this study (Figure 2). This indicates that latewood proportion is more affected by the environment variation. The drop in heritability of latewood ratio, when individual growth ring was added to the core, was observed for ring 10. This might be caused by a large environmental variation for this ring, masking the genetic influence. Standard errors of heritability estimates for ring density, earlywood density and latewood density were very similar and varied between 0.18–0.21, while for latewood ratio it varied between 0.11–0.14. As the number of offspring per family varied between 8–9, estimated family-mean repeatability (h_f^2) was slightly lower than individual-tree heritability (h^2). For example, h_f^2 for RD was 0.64 and 0.68 at core ages 5 and 10 years respectively (details not shown), while h^2 was 0.71 and 0.81 respectively (Figure 2(a)).

Age-age correlations

Estimated genetic correlations of all traits at early ages, with their respective values at harvest age are shown in Figure 3. For all traits except latewood ratio, there was high (>0.80) estimated genetic correlation between early ages and harvest age. Estimated genetic correlations dropped slightly from core age 2-years to 4-years and then a steady increase was observed. Similar drops were observed for some of these traits, especially latewood ratio, in other studies (VARGAS-HERNANDEZ & ADAMS 1992; HYLEN 1999). Approximate standard errors of estimated genetic correlations varied between 0.01 – 0.06 for RD, earlywood density and latewood density, and between 0.01–0.38 for latewood ratio. Age-age correlations, at the family-mean level, were also calculated (Figure 4). Family-mean correlations for latewood ratio were lowest in comparison to other traits. In general, the magnitude of family-mean phenotypic correlations was somewhat lower than the genetic correlations. KING & BURDON (1991) reported similar results for stem diameter and wood density traits in radiata pine. One possible explanation for this could be that both genetic and environmental components are involved in family-means, and likely possibility of poor or adverse environmental correlations between various core ages.

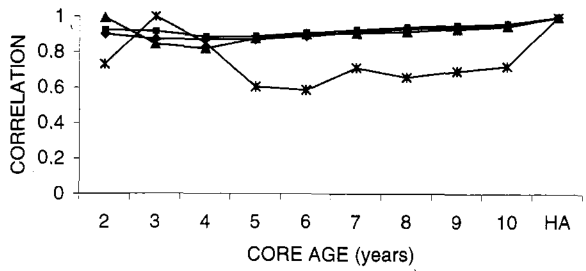

Figure 3. Genetic correlations for ring density and its component at different ages with their respective values at harvest age (HA). (◆ Ring density, ▲ Latewood density, * Latewood ratio, ■ Earlywood density).

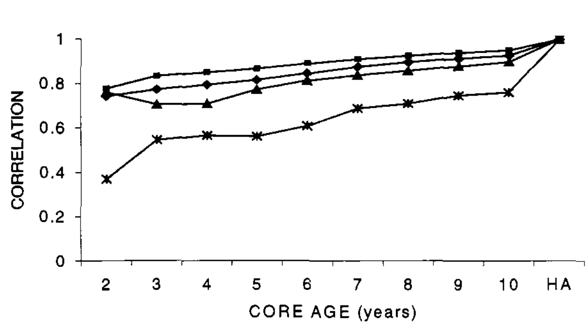

Figure 4. Family-mean correlations for ring density (RD) and its component at different ages with their respective values at harvest age (HA). (◆ Ring density, ▲ Latewood density, * Latewood ratio, ■ Earlywood density).

A comparison of Figure 3 and Figure 4 showed that as the age interval increases, genetic correlations declined more slowly than family-mean correlations. VARGAS-HERNANDEZ & ADAMS (1992) observed similar results for growth ring density and its component traits. Similar results were observed for genetic and phenotypic correlations for growth traits in radiata pine (COTTERILL & DEAN 1988) and loblolly pine (LAMBETH *et al.* 1983). The lower magnitude of phenotypic correlation compared with genetic correlation will underestimate potential gain from early indirect selection based only on phenotypic associations of early and mature traits (COTTERILL & DEAN 1988).

Efficiency of early selection

Assuming a harvest age of 30 years, the relative efficiency of early selection was calculated for family selection (Table 2). The relative efficiency of family selection at core age 3 years compared to selecting families at harvest age was 79 percent. As genetic and family-mean correlation between RD at core age 3 years and RD at harvest age were quite high (≈ 0.80), these results are not surprising. Such a high efficiency demonstrates that it is quite possible to carry out family selection for wood density at a core age of 3 years. Relative efficiency of family selection reached about 93 percent at core age of 10 years. The net increase of relative efficiency at age 10 years, over relative efficiency at core age 6 years, was about 8 percent.

The relative efficiency of using index (incorporating RD components) for early family selection was also evaluated (Table 2). Relative efficiencies were calculated for four scenarios: RD and earlywood density; RD and latewood density; RD and latewood ratio; RD,

Table 2. Relative efficiency (%) of early family selection for average ring density at harvest age (*HA*) when different selection criteria are used. *RD* = ring density, *ED* = earlywood density, *LD* = latewood density, *LP* = latewood ratio.

Selection age	Selection criteria				
	RD	*RD* and *ED*	*RD* and *LP*	*RD* and *LD*	*RD, ED, LD* & *LP*
3	79.1	79.8	81.4	85.0	85.2
4	80.2	81.4	81.7	85.1	87.2
5	82.3	83.1	84.5	87.5	90.7
6	85.2	85.9	88.1	90.0	94.1
7	88.3	89.2	89.9	91.3	94.5
8	90.1	90.6	91.3	92.2	94.4
9	91.7	92.1	92.9	93.6	95.7
10	93.0	93.5	94.1	94.7	96.1
HA	100	100	100	100	100

Table 3. Relative efficiency (%) of early individual selection for average ring density at harvest age (*HA*) when different selection criteria are used. *RD* = ring density, *ED* = earlywood density, *LD* = latewood density, *LP* = latewood ratio.

Selection age	Selection criteria				
	RD	*RD* and *ED*	*RD* and *LP*	*RD* and *LD*	*RD, ED, LD* & *LP*
3	69.3	70.7	73.6	79.7	80.7
4	71.3	71.6	75.4	81.9	82.1
5	75.6	75.8	80.6	83.7	84.6
6	79.8	80.1	85.5	87.5	89.9
7	83.5	84.1	87.4	89.8	91.5
8	85.4	86.1	88.4	90.4	91.6
9	87.5	88.2	90.4	92.5	93.5
10	88.8	89.6	91.7	93.6	94.3
HA	100	100	100	100	100

earlywood density, latewood density and latewood ratio. Relative efficiency of index selection using RD and earlywood density was almost identical to that obtained using RD alone. Index selection, using RD and latewood ratio, gave about 2 percent higher efficiency at early core ages, but only about 1 percent at later core ages. Selection by combining RD and latewood density increased the relative efficiency by about 5–6 percent at core age 3–6 years but only 2–3 percent at core age 7–10 years. Increase in relative efficiency by including latewood density, compared to earlywood density and latewood ratio, was because of its high heritability and high genetic correlation with the target trait. At core age 6 years, relative efficiency of index selection by combining all four traits was about 9 percent higher than that obtained from selection using RD alone, but the difference was only about 3 percent at core age of 10 years (Table 2). In general, the relative efficiency of index selection was higher only at early core ages, and these results are similar to those observed by VARGAS-HERNANDEZ & ADAMS (1992) in Douglas-fir.

Forwards (or individual) selection is an important component of advanced generation breeding programmes. Relative efficiencies of individual selection using RD and its components are shown in Table 3. It demonstrate that relative efficiency, using RD alone, varied from about 70 percent at core age 3 years to about 89 percent at core age 10 years. Results showed that forwards selection, with relative efficiency of 80 percent, could be carried out at a core age of 6 years. Similar to family selection, relative efficiency of individual selection increased when latewood density and latewood ratio were included in an index. At core age 6 years, relative efficiency of index selection by combining all four traits was about 10 percent higher than that obtained from selection using RD alone, but the difference was about 6 percent at core age of 10 years (Table 3).

The high estimated relative efficiency of multi-component selection was due to the high estimated heritabilities of component traits, and also the high genetic correlation with the target trait. However, when genetic correlation between a single selection trait (RD in our case) and target trait (average RD at harvest age) is high, very little additional increase in selection efficiency can be achieved when additional traits (like, RD components) are incorporated into the selection index (WHITE & HODGE 1991). In this study, index selection resulted in an increase of about 6–10 percent and 3–9 percent in selection efficiency, at various core ages, for individual and family selections, respectively. However, the cost of obtaining densitometric data will be higher than using a quicker and cheaper method (e.g. maximum moisture content method) of determining density. For a given budget, using a cheaper method will allow screening of more candidates, and thus allow higher selection intensity. Further study will be required to determine the cost-efficiency of using the latter approach.

Using RD alone, relative efficiency of family and individual selection was 79 and 69 %, respectively, when early selection was carried out at core age of 3 years. The age of a core, in this study, was defined in terms of number of rings represented from the pith. It should be noted, however, that the cores were sampled at breast-height, and thus trees itself would actually be about two year older than a given core age. In this study, only one 5-mm breast-height core was used for estimating density of each tree. It would be desirable to take two cores per tree, but COWN & MCCONCHIE (1983) suggested that one core could provide satisfactory estimate of wood density of whole tree. As the information from only one site was used, it could have some implications on the conclusions of this study. However, BURDON & LOW (1992) reported minimal family by site interaction for wood density in New Zealand, and thus the optimum selection age reported in this study would be generally applicable on various sites in New Zealand.

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