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Genetic correlations among juvenile wood quality and growth traits and implications for selection strategy in *Pinus radiata* D. Don

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Abstract

• Juvenile wood quality in *Pinus radiata* is affected by factors such as low density, stiffness, and high microfibril angle, spiral grain, and shrinkage. Adverse genetic correlations between growth and wood quality traits remain as one of the main constraints in radiata pine advanced generation selection breeding program.

• Juvenile wood property data for this study were available from two progeny tests aged 7 and 6 y. We estimated the genetic correlations between stiffness, density, microfibril angle, spiral grain, shrinkage in the juvenile core and DBH growth in radiata pine, and) to evaluated various selection scenarios to deal with multiple objective traits.

• Negative genetic correlations were found for modulus of elasticity (MoE) and density with microfibril angle, spiral grain, shrinkage, and DBH. We observed low to moderate unfavourable genetic correlations between all wood quality traits and DBH growth.

• These low to moderate genetic correlations suggest that there may be some genotypes which have high DBH growth performance while also having high wood stiffness and density, and that the adverse correlation between DBH and MoE may not entirely prohibit the improvement of both traits. Results indicate that, in the short term, the optimal strategy is index selection using economic weights for breeding objective traits (MAI and stiffness) in radiata pine.

• In the long-term, simultaneously purging of the adverse genetic correlation and optimizing index selection may be the best selection strategy in multiple-trait selection breeding programs with adverse genetic correlations.

Résumé – Corrélations génétiques entre la qualité du bois juvénile et les caractéristiques de croissance et implications pour la stratégie de sélection de *Pinus radiata* D. Don.

• La qualité du bois juvénile chez *Pinus radiata* est affectée par des facteurs tels que la faible densité, la rigidité, et un angle de microfibrille grand, la fibre torse, et les fentes de retrait. Les mauvaises corrélations génétiques entre la croissance et les caractéristiques de la qualité du bois restent l'une des principaux obstacles à un programme poussé d'amélioration de *Pinus radiata*.

Les données sur les propriétés du bois juvénile pour cette étude étaient disponibles à partir de deux tests de descendance âgés de 7 ans et 6 ans. Nous avons estimé les corrélations génétiques entre la rigidité, la densité, l'angle des microfibrilles, la fibre torse, les fentes de retrait dans le cœur juvénile et la croissance en diamètre à hauteur de poitrine (DBH) de *Pinus radiata*, et pour évaluer différents scénarios de sélection pour faire face à de multiples caractéristiques objectives.

• Des corrélations génétiques négatives ont été trouvées pour le module d'élasticité (MoE) et la densité avec l'angle des microfibrilles, la fibre torse, les fentes de retrait, et la croissance en diamètre à hauteur de poitrine (DBH). Nous avons observé des corrélations génétiques défavorablement faibles à modérées entre toutes les caractéristiques de la qualité du bois et la croissance en diamètre à hauteur de poitrine (DBH).

• Ces corrélations génétiques faibles à modérées suggèrent que peut être certains génotypes, ont une croissance importante en diamètre à hauteur de poitrine (DBH) tout en ayant une rigidité et une densité du bois élevée, et que les corrélations défavorables entre DBH et MoE peuvent ne pas

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interdire entièrement l'amélioration de ces deux caractéristiques. Les résultats indiquent que, dans le court terme, la stratégie optimale est l'index de sélection en utilisant le poids économique pour un objectif d'amélioration des caractéristiques (AMI et rigidité) chez *Pinus radiata*.

- À long terme, à la fois la purge de la corrélation génétique défavorable et l'optimisation de l'index de sélection peut être la meilleure stratégie de sélection multicaractère dans les programmes sélection améliorés ayant des corrélations génétiques défavorables.

1. INTRODUCTION

Australia has an advanced breeding program for *Pinus radiata* D. Don which has over the last 50 y significantly improved many characteristics of this widely planted fast growing conifer (Cotterill and Dean, 1990; Matheson et al., 1986; Wu et al., 2008a). Early tree improvement programs for *P. radiata* in Australia have concentrated most of their effort on improving growth and form traits, and realized gains in volume after the first generation of breeding were about 30% over unimproved seedlots (Matheson et al., 1986; Wright and Eldridge, 1985; Wu and Matheson, 2002). Considerable genetic variation and high heritabilities in both juvenile wood (also called corewood), (Burdon et al., 2004) and mature wood quality traits of *P. radiata* have been reported in Australia. For example, density, stiffness, microfibril angle, spiral grain, shrinkage and juvenile-mature wood transition have been reported to be under moderate to high genetic control (Baltunis et al., 2007; Dungey et al., 2006; Gapare et al., 2006; 2007; 2008; Li and Wu, 2005). Similarly, high heritabilities for wood quality traits were observed in New Zealand *P. radiata* populations (Jayawickrama, 2001; Kumar, 2004; Kumar et al., 2002).

As radiata pine breeding advances to third generation selections in Australia, there is an increasing need to include wood quality traits in the breeding program. This is due to the increased proportion of juvenile wood in harvested logs which is causing a variety of problems for wood utilization owing to lower stiffness (modulus of elasticity (MoE)), or strength (modulus of rupture (MOR)) (Cown, 1992; Cown and van Wyk, 2004). Besides lower wood stiffness and strength, dimensional instability is also a problem in juvenile wood, in which microfibril angle (MfA) is greater and spiral grain more pronounced, and a significant amount of compression wood is present. The low-stiffness wood zone becomes a strategic research topic for improving radiata pine wood quality in order to achieve shorter rotations with high stiffness wood.

Selection for a single trait (such as growth) not only changes the genetic variance of the trait directly selected, but also changes the genetic variances of correlated traits and covariances between correlated traits (Bulmer, 1971). It is therefore important to study the genetic correlations of wood quality traits with traits included in the radiata pine breeding program such as growth and stem form. As an initial step in incorporating these wood quality traits into the breeding program, we have studied the genetic control in the juvenile core of radiata pine for stiffness, density, microfibril angle, (Baltunis et al., 2007), spiral grain (Gapare et al., 2007), shrinkage (Gapare et al., 2008), and dynamic MoE derived from acoustic time-of-flight measurements (Matheson et al., 2008). As might be expected for most wood quality traits

(Zobel and van Buijtenen, 1989), there was evidence of significant genetic control in these traits. For example, heritability for density, MfA and MoE measured using SilviScan® (Evans and Ilic, 2001) and MoE measured acoustically were moderately high (0.70, 0.50, 0.54, and 0.53, respectively) (Baltunis et al., 2007; Matheson et al., 2008). Spiral grain and longitudinal shrinkage were moderately heritable (0.45 and 0.20, respectively) (Gapare et al., 2007; 2008).

Since most of these wood quality traits are related, a change in any of these traits is likely to have either a favourable or unfavourable effect on other traits. For example, MfA is one of the major factors that controls MoE (a major breeding objective for radiata pine breeding in Australia, see Ivković et al., 2006a) and is also a predictor of tendency to warp (Myszewski et al., 2004). A reduction in MfA and increase in MoE in the first growth rings should improve the structural and shrinkage properties of wood because lower MfA and spiral grain in the first growth rings will limit volumetric shrinkage and therefore, the drying distortion of sawn timber (e.g., Lindström et al., 2005). Ivković et al. (2008) used path analysis to examine how much component wood quality traits such as density, MfA, spiral grain and ring width could account for wood stiffness, strength and shrinkage. Their major finding was that the preferred method for predicting juvenile tree MoE was using standing tree acoustic MoE and whole core density. For the purpose of selection and breeding, it is generally desirable to include only a few traits in a selection index (e.g., Cotterill and Dean, 1990).

Genetic correlations estimate the degree of relationship between two traits owing to genetic causes. There are two biological explanations for such correlations. One is pleiotropy, where the two traits are affected by the same set of genes. Another mechanism for genetic correlation, although transient, is gametic phase linkage disequilibrium (LD), which may occur when individuals from two populations with different gene frequencies intermate, as a side effect of recent directional selection or by biased or limited sampling (e.g., Hannrup et al., 2000; Sánchez et al., 2008). In breeding programs, genetic correlations are used for predicting how selection for one or several traits will affect correlated traits in the next generation. The genetic correlations between growth rate and wood quality traits have major implications for developing selection and breeding strategies.

The specific objectives of the present study were two-fold: (i) to estimate the genetic correlations between stiffness, density, microfibril angle, spiral grain, shrinkage in the juvenile core and DBH growth in radiata pine, and (ii) to evaluate various selection scenarios to deal with multiple objective traits, particularly where adverse genetic correlations between stiffness and growth traits in radiata pine exist.

Table I. Site details of *Pinus radiata* progeny tests sampled for wood quality traits study.

Details	Flynn	Kromelite
Test number	BR9611	BR9705
Date planted	6/1996	7/1997
Cambial age at time of sampling	7	6
Spacing	3.6 m × 2.5 m	2.74 m × 2.5 m
Latitude	38° 14' S	37° 50' S
Longitude	146° 45' E	140° 55' E
Elevation (m)	166	55
Annual rainfall (mm)	760	900
Soil type	Sandy loam	Sandy clay-loam
Site type	2nd pine rotation	2nd pine rotation
Number of families	250	110
Number of blocks	4	3

2. MATERIALS AND METHODS

2.1. Data source

The study was based on two progeny trials: BR9611, located at Flynn (latitude 38° 14' S; longitude 146° 45' E), Victoria and managed by Hancock Victorian Plantations, and BR9705, located at Kromelite (latitude 37° 50' S; longitude 140° 55' E), South Australia and managed by Green Triangle Forest Products. Both sites were initially prepared by ploughing followed by mounding, and soil drainage was considered good. Site details are presented in Table I. There was a fertilizer application (NPK) at Flynn at a rate of 347 kg ha⁻¹ in 2000, followed by another aerial fertiliser application in 2003 at a rate of 329 kg ha⁻¹. Trial maintenance at Kromelite included herbicide application in the first two years of growth aimed at complete weed control. Unlike at Flynn, there was no fertiliser application.

Flynn was planted in June, 1996 with 250 families, consisting of 88 polycross families, 157 full-sib families, and 5 controls, planted in a 10 × 25 row-column experimental design (see Williams et al., 2002) with 5 blocks and four-tree row plots. Kromelite was planted in July, 1997 with 110 families, consisting of 70 polycross families, 40 full-sib families with no controls, planted in a 10 × 11 row-column design with 5 blocks and four-tree row plots. These trials contained a total of 344 different families from both full-sib and half-sib families from polymix crosses derived from Southern Tree Breeding Association (STBA) breeding population. There were 41 parents and only 16 full-sib families common to both sites. Stem discs and increment cores were collected from the two trials and juvenile wood traits at ages 6 and 7 y were measured including DBH. The total numbers of trees sampled per family were different for each site and so were the number of trees per trait. Generally, wood quality traits (e.g., stiffness, density, MfA) with higher levels of additive genetic control do not require large sample sizes to detect significant genetic variation. In addition, sample preparation and measurements for such traits are time consuming and expensive.

SilviScan predicted modulus of elasticity (MoE_{SS}), density (DEN) and microfibril angle (MfA)

For the assessment of SilviScan predicted modulus of elasticity (MoE_{SS}), density (DEN) and microfibril angle (MFA), twelve millimetre bark-to-bark increment cores were collected at breast height (1.3 m). 980 trees were sampled at Flynn and 660 trees were sampled at Kromelite and assessed by SilviScan® (Evans and Ilic, 2001).

Dynamic modulus of elasticity (MoE_{IML})

Acoustic measurements were recorded from standing trees at both sites. In total, measurements were available from 2 454 trees at Flynn and 1 284 trees at Kromelite. The IML electronic hammer (instrumenta mechanik labor GmbH) was used to measure the time of flight. The standing tree time-of-flight technique provides an acoustic wave velocity for the stem. Dynamic modulus of elasticity (MoE_{IML}) was estimated using velocity and green density values derived from DEN (Rolf Booker, unpublished data). When MoE is measured in this way it is known as dynamic MoE in contrast to static MoE which is measured by bending. The dynamic and static measured MoE values are highly related in green and dry wood (Booker and Sorensson, 1999; Ilic, 2001).

Spiral grain

For the assessment of spiral grain, samples were collected from 628 trees at Flynn and 316 trees at Kromelite. Spiral grain angle was measured using a pivoting digital protractor. Spiral grain angle, in degrees ±0.1°, was measured on the tangential surface of the latewood of each ring segment, as the deviation of grain angle from perpendicular to the plane of reference. The mean grain angle in each ring can be considered a measure of average grain angle deviation from the vertical axis of the cambial cylinder in each year of growth (e.g., Hansen and Roulund, 1998).

Shrinkage

For shrinkage measurements, data were available from 466 trees at Flynn and 308 trees at Kromelite. The procedures for determining shrinkages for the samples were similar to those used by Kingston and Risdon (1961). Radial, tangential and longitudinal dimensions were measured using a digital displacement gauge with readings graduated to 0.001 mm. One measurement was taken in the middle of the sample and subsequently adjusted for distortion and or bow.

2.2. Data analysis

A multivariate pooled-site analysis was used in this study to estimate variance components in order to estimate genetic correlations among the wood quality traits and growth. A multivariate mixed model REML analysis using the program ASREML (Gilmour et al., 2005) was used for the multivariate pooled-site analysis:

$$\mathbf{y}_j = \mathbf{X}_j \mathbf{b}_j + \mathbf{Z}_{a_j} \mathbf{a}_j + \mathbf{Z}_{f_j} \mathbf{f}_j + \mathbf{Z}_{p_j} \mathbf{p}_j + \varepsilon_j \quad (1)$$

where \mathbf{y}_j is the vector of individual tree observations denoted (j) by trait, \mathbf{b}_j is the vector of fixed effects (trait mean, tests and blocks within tests) and \mathbf{X}_j is the known incidence matrix relating the individual tree observations in \mathbf{y}_j to the fixed effects in \mathbf{b}_j where

$$\mathbf{X}_j \mathbf{b}_j = \begin{bmatrix} \mathbf{X}_{\text{MOE}} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \mathbf{X}_{\text{IML}} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{X}_{\text{DEN}} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{X}_{\text{MFA}} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{X}_{\text{SG}} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathbf{X}_{\text{LSH}} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{X}_{\text{DBH}} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{\text{MOE}} \\ \mathbf{b}_{\text{IML}} \\ \mathbf{b}_{\text{DEN}} \\ \mathbf{b}_{\text{MFA}} \\ \mathbf{b}_{\text{SG}} \\ \mathbf{b}_{\text{LSH}} \\ \mathbf{b}_{\text{DBH}} \end{bmatrix},$$

\mathbf{a}_j is a vector of random genetic effects of individual genotypes $\sim \text{MVN}(\mathbf{0}, \mathbf{G} \otimes \mathbf{A})$ where

$$\mathbf{G} = \begin{pmatrix} \sigma_{\text{AMOE}}^2 & \sigma_{\text{AMOE}^{\text{AIML}}} & \sigma_{\text{AMOE}^{\text{ADEN}}} & \sigma_{\text{AMOE}^{\text{AMFA}}} & \sigma_{\text{AMOE}^{\text{ASG}}} & \sigma_{\text{AMOE}^{\text{ALSH}}} & \sigma_{\text{AMOE}^{\text{ADBH}}} \\ \sigma_{\text{AMOE}^{\text{AIML}}} & \sigma_{\text{AIML}}^2 & \sigma_{\text{AIML}^{\text{ADEN}}} & \sigma_{\text{AIML}^{\text{AMFA}}} & \sigma_{\text{AIML}^{\text{ASG}}} & \sigma_{\text{AIML}^{\text{ALSH}}} & \sigma_{\text{AIML}^{\text{ADBH}}} \\ \sigma_{\text{AMOE}^{\text{ADEN}}} & \sigma_{\text{AIML}^{\text{ADEN}}} & \sigma_{\text{ADEN}}^2 & \sigma_{\text{ADEN}^{\text{AMFA}}} & \sigma_{\text{ADEN}^{\text{ASG}}} & \sigma_{\text{ADEN}^{\text{ALSH}}} & \sigma_{\text{ADEN}^{\text{ADBH}}} \\ \sigma_{\text{AMOE}^{\text{AMFA}}} & \sigma_{\text{AIML}^{\text{AMFA}}} & \sigma_{\text{AIML}^{\text{AMFA}}} & \sigma_{\text{AMFA}}^2 & \sigma_{\text{AMFA}^{\text{ASG}}} & \sigma_{\text{AMFA}^{\text{ALSH}}} & \sigma_{\text{AMFA}^{\text{ADBH}}} \\ \sigma_{\text{AMOE}^{\text{ASG}}} & \sigma_{\text{ASG}^{\text{AMFA}}} & \sigma_{\text{ASG}^{\text{ADEN}}} & \sigma_{\text{ASG}^{\text{AMFA}}} & \sigma_{\text{ASG}}^2 & \sigma_{\text{ASG}^{\text{ALSH}}} & \sigma_{\text{ASG}^{\text{ADBH}}} \\ \sigma_{\text{AMOE}^{\text{ALSH}}} & \sigma_{\text{AMOE}^{\text{AIML}}} & \sigma_{\text{AMOE}^{\text{ADEN}}} & \sigma_{\text{AMOE}^{\text{AMFA}}} & \sigma_{\text{ASG}^{\text{ALSH}}} & \sigma_{\text{ALSH}}^2 & \sigma_{\text{ALSH}^{\text{ADBH}}} \\ \sigma_{\text{AMOE}^{\text{ADBH}}} & \sigma_{\text{AIML}^{\text{ADBH}}} & \sigma_{\text{ADEN}^{\text{ADBH}}} & \sigma_{\text{AMFA}^{\text{ADBH}}} & \sigma_{\text{ASG}^{\text{ADBH}}} & \sigma_{\text{ALSH}^{\text{ADBH}}} & \sigma_{\text{ADBH}}^2 \end{pmatrix}$$

and \mathbf{A} = the additive relationship matrix, \mathbf{Z}_{aj} is the known incidence matrix relating observations in \mathbf{y}_j to the genetic effects in \mathbf{a}_j , $\sigma_{A_j}^2$ is the estimated additive genetic variance, σ_{AxAy} is the estimated genetic covariance between additive effects of the two traits, \mathbf{f}_j is a vector of random effects of full-sib families $\sim \text{MVN}(\mathbf{0}, \mathbf{S} \otimes \mathbf{I}_s)$ where

$$\mathbf{S} = \begin{pmatrix} \sigma_{f_{\text{MOE}}}^2 & \sigma_{f_{\text{MOE}}^{\text{IML}}} & \sigma_{f_{\text{MOE}}^{\text{DEN}}} & \sigma_{f_{\text{MOE}}^{\text{MFA}}} & \sigma_{f_{\text{MOE}}^{\text{SG}}} & \sigma_{f_{\text{MOE}}^{\text{LSH}}} & \sigma_{f_{\text{MOE}}^{\text{DBH}}} \\ \sigma_{f_{\text{MOE}}^{\text{IML}}} & \sigma_{\text{IML}}^2 & \sigma_{\text{IML}^{\text{DEN}}} & \sigma_{\text{IML}^{\text{MFA}}} & \sigma_{\text{IML}^{\text{SG}}} & \sigma_{\text{IML}^{\text{LSH}}} & \sigma_{\text{IML}^{\text{DBH}}} \\ \sigma_{f_{\text{MOE}}^{\text{DEN}}} & \sigma_{\text{IML}^{\text{DEN}}} & \sigma_{\text{DEN}}^2 & \sigma_{\text{DEN}^{\text{MFA}}} & \sigma_{\text{DEN}^{\text{SG}}} & \sigma_{\text{DEN}^{\text{LSH}}} & \sigma_{\text{DEN}^{\text{DBH}}} \\ \sigma_{f_{\text{MOE}}^{\text{MFA}}} & \sigma_{\text{IML}^{\text{MFA}}} & \sigma_{\text{IML}^{\text{MFA}}} & \sigma_{\text{MFA}}^2 & \sigma_{\text{MFA}^{\text{SG}}} & \sigma_{\text{MFA}^{\text{LSH}}} & \sigma_{\text{MFA}^{\text{DBH}}} \\ \sigma_{f_{\text{MOE}}^{\text{SG}}} & \sigma_{\text{ISG}^{\text{MFA}}} & \sigma_{\text{ESG}^{\text{DEN}}} & \sigma_{\text{ISG}^{\text{MFA}}} & \sigma_{\text{SG}}^2 & \sigma_{\text{ISG}^{\text{LSH}}} & \sigma_{\text{ISG}^{\text{DBH}}} \\ \sigma_{f_{\text{MOE}}^{\text{LSH}}} & \sigma_{\text{IML}^{\text{LSH}}} & \sigma_{\text{IML}^{\text{LSH}}} & \sigma_{\text{ISG}^{\text{LSH}}} & \sigma_{\text{ISG}^{\text{LSH}}} & \sigma_{\text{LSH}}^2 & \sigma_{\text{LSH}^{\text{DBH}}} \\ \sigma_{f_{\text{MOE}}^{\text{DBH}}} & \sigma_{\text{IML}^{\text{DBH}}} & \sigma_{\text{DEN}^{\text{DBH}}} & \sigma_{\text{IMFA}^{\text{DBH}}} & \sigma_{\text{ISG}^{\text{DBH}}} & \sigma_{\text{LSH}^{\text{DBH}}} & \sigma_{\text{DBH}}^2 \end{pmatrix}$$

and \mathbf{I}_s is an identity matrix equal to the number of full-sib families, \mathbf{Z}_{f_j} is the incidence matrix relating the observations in \mathbf{y}_j to the effects in \mathbf{f}_j , $\sigma_{f_j}^2$ is the estimated variance attributed to full-sib families (specific combining ability), and $\sigma_{f_{xy}}$ is the estimated covariance between full-sib family effects of two traits, \mathbf{p}_j is a vector of random effects of plot within block and test $\sim \text{MVN}(\mathbf{0}, \mathbf{I}_{p_j} \sigma_{p_j}^2)$ where \mathbf{I}_{p_j} is an identity matrix equal to the number of plots, $\sigma_{p_j}^2$ is the estimated variance associated with plots within block and test, ε_j is a random vector of residual terms $\sim \text{MVN}(\mathbf{0}, \mathbf{R} \otimes \mathbf{I})$ where

$$\mathbf{R} = \begin{pmatrix} \sigma_{\text{EMOE}}^2 & \sigma_{\text{EMOE}^{\text{EIML}}} & \sigma_{\text{EMOE}^{\text{EDEN}}} & \sigma_{\text{EMOE}^{\text{EMFA}}} & \sigma_{\text{EMOE}^{\text{ESG}}} & \sigma_{\text{EMOE}^{\text{ELSH}}} & \sigma_{\text{EMOE}^{\text{EDBH}}} \\ \sigma_{\text{EMOE}^{\text{EIML}}} & \sigma_{\text{EIML}}^2 & \sigma_{\text{EIML}^{\text{EDEN}}} & \sigma_{\text{EIML}^{\text{EMFA}}} & \sigma_{\text{EIML}^{\text{ESG}}} & \sigma_{\text{EIML}^{\text{ELSH}}} & \sigma_{\text{EIML}^{\text{EDBH}}} \\ \sigma_{\text{EMOE}^{\text{EDEN}}} & \sigma_{\text{EIML}^{\text{EDEN}}} & \sigma_{\text{EDEN}}^2 & \sigma_{\text{EDEN}^{\text{EMFA}}} & \sigma_{\text{EDEN}^{\text{ESG}}} & \sigma_{\text{EDEN}^{\text{ELSH}}} & \sigma_{\text{EDEN}^{\text{EDBH}}} \\ \sigma_{\text{EMOE}^{\text{EMFA}}} & \sigma_{\text{EIML}^{\text{EMFA}}} & \sigma_{\text{EIML}^{\text{EMFA}}} & \sigma_{\text{EMFA}}^2 & \sigma_{\text{EMFA}^{\text{ESG}}} & \sigma_{\text{EMFA}^{\text{ELSH}}} & \sigma_{\text{EMFA}^{\text{EDBH}}} \\ \sigma_{\text{EMOE}^{\text{ESG}}} & \sigma_{\text{ESG}^{\text{EMFA}}} & \sigma_{\text{ESG}^{\text{EDEN}}} & \sigma_{\text{ESG}^{\text{EMFA}}} & \sigma_{\text{ESG}}^2 & \sigma_{\text{ESG}^{\text{ELSH}}} & \sigma_{\text{ESG}^{\text{EDBH}}} \\ \sigma_{\text{EMOE}^{\text{ELSH}}} & \sigma_{\text{EMOE}^{\text{EIML}}} & \sigma_{\text{EMOE}^{\text{EDEN}}} & \sigma_{\text{EMOE}^{\text{EMFA}}} & \sigma_{\text{ESG}^{\text{ELSH}}} & \sigma_{\text{ELSH}}^2 & \sigma_{\text{ELSH}^{\text{EDBH}}} \\ \sigma_{\text{EMOE}^{\text{EDBH}}} & \sigma_{\text{EIML}^{\text{EDBH}}} & \sigma_{\text{EDEN}^{\text{EDBH}}} & \sigma_{\text{EIMFA}^{\text{EDBH}}} & \sigma_{\text{ESG}^{\text{EDBH}}} & \sigma_{\text{ELSH}^{\text{EDBH}}} & \sigma_{\text{EDBH}}^2 \end{pmatrix}$$

\mathbf{I} is the identity matrix with order equal to the number of observations, $\mathbf{0}$ is the null matrix, and $\sigma_{E_j}^2$ is the estimated residual variance for each trait and similarly, $\sigma_{E_{xy}}$ is the estimated residual covariance between two traits. Both residual and genetic variances were assumed homogenous across sites (i.e. a single estimate of additive variance and residual variance for each trait).

Variances are not independent of the scale and the mean of the respective traits (Sokal and Rohlf, 1995). Therefore, to compare the genetic variances of the different traits, a parameter measuring the genetic coefficient of variation was calculated as:

$$CV_{A_j} = \frac{100\% \times \sigma_{A_j}}{\bar{x}} \quad (2)$$

CV_{A_j} = coefficient of additive genetic variation

σ_{A_j} = square root of the additive genetic variance for the trait

\bar{x} = population mean for the trait.

The CV_{A_j} expresses the genetic variance relative to the mean of the trait of interest and gives a standardized measure of the genetic variance relative to the mean of the trait. The higher the coefficient of additive genetic variation for a trait, the higher is its relative variation.

The genetic correlation r_G between two traits was estimated within the ASREML software as:

$$r_G = \frac{\sigma_{AxAy}}{\sqrt{(\sigma_{Ax}^2 \sigma_{Ay}^2)}} \quad (3)$$

where:

σ_{AxAy} = additive genetic covariance component between traits x and y ;

σ_{Ax}^2 = additive genetic variance component for trait x ;

σ_{Ay}^2 = additive genetic variance component for trait y .

Standard errors for each of the correlations were calculated using a truncated Taylor series in ASREML (Gilmour et al., 2005).

The optimal selection strategy was defined by the optimal breeding objective response in terms of profitability. Responses in breeding objective traits mean annual increment (MAI_{OBJ}) and stiffness (MoE_{OBJ}) at rotation age were evaluated through index selection based on two juvenile traits (MoE_{SS} and DBH). Economic weights for the breeding objective traits for an integrated company were estimated to be \$977 per one GPa increase of rotation-aged stiffness and \$416 per one $\text{m}^3 \text{y}^{-1} \text{h}^{-1}$ of MAI at rotation age (Ivković et al, 2006a). Three different selection scenarios were considered:

- (A) index selection using MoE_{SS} and DBH as selection traits and maximising profitability;
- (B) restricted index selection keeping juvenile wood MoE_{SS} constant;
- (C) restricted index selection where selection is restricted to genotypes with positive breeding values for both MoE_{SS} and DBH .

We also created another more general index using genetic parameters for radiata pine obtained from the literature review by Wu et al., (2008b), and the following scenarios based in part on Kumar (2004) and Kumar et al. (2006):

- (D) Index selection using average variance-covariance parameters from literature (Wu et al., 2008b) for selection and objective traits;
- (E) Economic weight on MoE_{OBJ} (MoE as the objective trait) was increased by 50%;
- (F) Heritability of selection traits DEN and MoE_{SS} was reduced 50%;
- (G) Genetic and phenotypic correlations between objective traits MAI_{OBJ} and MOE_{OBJ} and the selection traits DEN and MoE_{SS} were reduced by 50%;
- (H) Heritability of selection traits DEN and MoE_{SS} was reduced 50% and correlations of the objective traits (MAI_{OBJ} and MOE_{OBJ}) with the selection traits (DEN and MoE_{SS}) were reduced by 50%.

Table II. Mean and percent coefficient of additive genetic variation (CV_A) of various wood quality traits of *Pinus radiata*.

Trait	<i>N</i>	Mean	$CV_A(\%)$
MoE _{SS} (GPa)	1 602	6.56	17.3
MoE _{IML} (GPa)	2 548	4.72	14.4
DEN (kg m ⁻³)	2 771	349.2	4.8
MfA (degrees)	1 602	29.6	8.8
SG (degrees)	932	4.16	21.9
LSH (%)	757	1.33	21.0
DBH (cm)	6 083	15.9	53.2

The index coefficients for all scenario – *s* were calculated according to Schneeberger et al., (1992) for selection traits:

$$\mathbf{b} = \mathbf{G}_{SS}^{-1} \mathbf{G}_{SO} \mathbf{w} \quad (4)$$

where:

\mathbf{b} is a vector of index weights for the predicted breeding values for the selection criteria in the index, \mathbf{G}_{SS}^{-1} is the inverse of the genetic variance-covariance matrix of the selection criteria in the index (DBH and MoE_{SS}) from current study), assumed to be known without error, \mathbf{G}_{SO} is the genetic covariance matrix between the selection criteria in the index and the breeding objective traits (using genetic parameters reported by Wu et al., 2008b), and \mathbf{w} is the vector of economic weights for the breeding objective traits (Ivković et al., 2006a). Restriction of response in MoE_{SS} while maximising index response was achieved using the “generalized reduced gradient” nonlinear optimization (Fylstra et al., 1998) implemented in the Microsoft Excel Solver[®].

3. RESULTS AND DISCUSSION

3.1. Trait means and genetic variation

The overall mean values and percent coefficient of additive genetic variation for wood quality and growth traits are presented in Table II. Mean values for MoE_{SS} and MoE_{IML} in the juvenile core of radiata pine were 6.56 GPa and 4.72 GPa, respectively. The difference between the two estimates may be due to the nature of the methods used for the measurements. MoE_{SS} is an estimate of clearwood MoE and is area-weighted, while MoE_{IML} is not necessarily measured over clearwood. Similar values were reported for area-weighted MoE_{ST} (rings 3–5) in radiata pine in New Zealand (Kumar et al., 2006). Mean density was 349 kg m⁻³ and was within the average density reported for radiata pine in other studies (Dungey et al., 2006; Wu et al., 2006). Similarly, MfA values were similar to those reported by Dungey et al. (2006) and Wu et al. (2006) in other radiata pine studies and other species at same age, such as loblolly pine (Megraw et al., 1998; Myszewski et al., 2004). Mean values for spiral grain (SG), longitudinal shrinkage (LSH) and DBH were in the range expected for juvenile wood in radiata pine and other conifers. For example, Cown et al., (1991) reported mean spiral grain angle of 4.7° in the first 10 rings from the pith in radiata pine trees grown in New Zealand.

Moderate to high levels of heritability were reported for component wood quality traits in the juvenile core of radiata

Table III. Estimates of genetic correlations among various wood quality traits in *Pinus radiata* at two test sites in Australia (heritability estimates along diagonal in italics).

	MoE _{SS}	MoE _{IML}	DEN	MfA	SG	LSH	DBH
MoE _{SS}	<i>0.55</i> (0.07)	0.96	0.47	-0.92	-0.56	-0.36	-0.34
MoE _{IML}		<i>0.48</i> (0.08)	0.41	-0.94	-0.55	-0.36	-0.26
DEN			<i>0.69</i> (0.06)	-0.14	-0.33	-0.02	-0.55
MfA				<i>0.53</i> (0.08)	0.40	0.45	0.11
SG					<i>0.42</i> (0.09)	-0.01	0.37
LSH						<i>0.24</i> (0.08)	0.19
DBH							<i>0.14</i> (0.05)

Note: Values in parentheses are approximate standard errors

pine (Tab. III) (see Baltunis et al., 2007; Gapare et al., 2007; 2008; Matheson et al., 2008). This suggested that there is an opportunity to improve juvenile wood quality traits as an integral part of the radiata pine breeding program in Australia. The level of genetic control of a trait and its interrelationships with other economically important traits determine the feasibility of incorporating traits in the breeding program (e.g. Kumar, 2004; Wu et al., 2008b).

Both MoE_{SS} and MoE_{IML} had more genetic variation than density; that is, they had almost 3 times the coefficient of additive genetic variation (CV_A) for density (Tab. II). Kumar et al., (2002) also found higher CV_A for MoE than for density in radiata pine. Similar estimates of CV_A have been reported for MoE in Douglas-fir (Johnson et al., 2006). The greater genetic variation in MoE relative to density may be a consequence of MoE being a composite trait related not only to wood density, but also to other variables such as MfA, and perhaps knots in the case of MoE_{IML}. Higher genetic variation of MoE (14.4% and 17.3%) relative to density (4.4%) with a similar heritability may indicate (1) density only contributes partially to MoE as indicated in other studies (Cave and Walker, 1994; Walker and Butterfield, 1996), and (2) direct selection based on MoE would be more effective than selection based on wood density. As might be expected, CV_A for other traits matched expectation (Wu et al., 2008b), i.e., more genetic variation in DBH growth compared to wood quality traits such as longitudinal shrinkage or spiral grain (Tab. II).

3.2. Genetic correlations and correlated response

Table III shows genetic correlations among the wood quality traits and DBH growth. The genetic correlations between MoE_{SS} and density, and MoE_{IML} and density were 0.47 ± 0.08 and 0.41 ± 0.08 , respectively. Other work on radiata pine reported the genetic correlation between density and MoE ranging from 0.44 to 0.64 (Baltunis et al., 2007; Kumar, 2004; Wu

et al., 2008a). As expected, the genetic correlation between MoE_{SS} and MoE_{IML} was close to unity (0.96 ± 0.02), suggesting that the measurements could be interchangeable as selection traits. Dynamic MoE, measured using ultrasound devices has been proven to strongly correlate with static bending MoE of the same clearwood samples (e.g., Booker and Sorensson, 1999). Tools such as IML hammer are therefore useful to assess acoustic stiffness on standing trees. For breeding purposes, acoustic measurements of stiffness (MoE_{IML}) may be more effective than measurements of component traits such as density and MfA as shown in this and other studies (Dungey et al., 2006; Kumar, 2004; Kumar et al., 2006; Matheson et al., 2008). In addition, MoE was recommended as one of the major breeding objective traits for radiata pine in Australia (Ivković et al., 2006a). It may be more economical to measure standing trees using acoustic tools and density derived from increment cores (e.g., Matheson et al., 2008) than assessment of MoE_{SS} .

The genetic correlation between MoE_{SS} and MfA was highly negative (-0.93 ± 0.02). A similar negative genetic correlation was observed between MoE_{IML} and MfA (-0.94 ± 0.02). Previous work on radiata pine by Lindstrom et al. (2005) and Dungey et al. (2006) reported such negative genetic correlations between MoE and MfA. A highly positive or negative genetic correlation implies that the same genes may be responsible for the two traits (pleiotropy) (e.g., Baltunis et al., 2007) and that selection for increased MoE would lead to reduced MfA in the juvenile core of radiata pine (e.g., Dungey et al., 2006; Kumar et al., 2004). This result is encouraging as it is relatively expensive to measure MfA because of the tedious nature of the methods available including time in measurement or sample preparation, and the indirect X-ray diffraction method, which requires a more expensive technology. Spiral grain and longitudinal shrinkage were all negatively correlated to MoE_{SS} , MoE_{IML} , and density (Tab. III). Again, this suggests that selection for increased MoE would lead to reduced spiral grain and longitudinal shrinkage. Consequently, a reduction in the pith-to-bark gradient for MfA and MoE would reduce shrinkage and drying distortion of timber (e.g., Lindström et al., 2005).

We observed adverse genetic correlations between all wood quality traits and DBH growth (Tab. III). The genetic correlations between MoE_{SS} , MoE_{IML} , DEN and DBH growth were -0.34 ± 0.12 , -0.26 ± 0.13 , and -0.55 ± 0.10 , respectively. Notably, most of the correlations between wood quality traits and DBH were estimated with large standard errors, even though large sample sizes were used in this study (Tab. II). Genetic correlations are functions of the magnitude of the correlation, the heritabilities and sample size. In this case, where no strong genetic correlations were found and heritabilities were low (e.g., heritability for LSH was 0.13 ± 0.08), a much larger sample size would have been required to give more precise estimates of genetic correlations for LSH and SG (e.g., Gapare et al., 2008; Klein et al., 1973).

Several other studies have reported adverse genetic correlations between wood density or stiffness and growth in radiata pine (Baltunis et al., 2007; Burdon and Low, 1992; Cotterill and Dean, 1990; Dean et al., 1983; Jayawickrama, 2001; Kumar, 2004; Li and Wu, 2005; Zobel and van Buijtenen,

1989). Wu et al. (2008b) reviewed estimates of genetic parameters including genetic correlations between density and growth in radiata pine and reported an average estimate of genetic correlation of -0.48 . Work on other conifers such as *Pinus teada*, *P. sylvetris* and *Picea abies* has consistently found negative genetic correlations ($r_A \sim -0.4$) between density and DBH (Costa E Silva et al., 1998; Hannrup et al., 2000; Lee, 1997; Rozenberg and Cahalan, 1998). These low to moderate genetic correlations reflect that there may be some genotypes with high DBH growth performance, high wood stiffness and density, and that the adverse correlation between DBH and MoE_{IML} may not entirely prohibit the improvement of both traits.

3.3. Selection strategy for coping with adverse genetic correlations

Index selection with optimal economic breeding objectives drives profitability for multiple-trait breeding programs (Ivković et al., 2006a). Selection index used in this study was based on juvenile selection traits (i.e., DBH and MoE_{SS}), and the measure of efficiency of index selection was profitability and not the genetic responses of individual traits. Therefore, genetic responses for individual traits could be favourable or unfavourable under such selection scenarios. Selection scenario A was the most optimal with profitability of Aus\$2409 / ha⁻¹ y⁻¹ (53.1% gain), based on juvenile genetic parameters from this study. However, there was a -3.7% and -5.3% decrease in juvenile wood DEN and MoE_{SS} , respectively (Tab. IV). The small reduction in MoE_{SS} is counterbalanced by the larger increase in DBH growth. The responses in other juvenile wood properties were also unfavourable while for growth rate the genetic response was positive (6.8%) (Tab. IV).

When MoE_{SS} was held constant by applying the restricted selection index (scenario B), there was a slight decrease in the genetic response in DBH compared to scenario A. Although this decrease was small, there were favourable responses in other wood properties. For example, MoE_{SS} increased relative to scenario A, whereas, MfA decreased (Tab. IV). By using index selection only within the genotypes with positive breeding values for both MoE_{SS} and DBH (scenario C), there was an 11% increase in genetic response in MoE_{SS} compared to scenario A (Tab. IV).

However, there was a reduction in the production system profitability for alternative scenarios (B and C) compared with index selection scenario A. For example, if the response in juvenile MoE_{SS} was restricted to 0 (no further increase from current levels), the index value expressed as per hectare net present value (NPV) profit of an integrated radiata pine production system decreased from Aus\$2409 to Aus\$2282 at 10% selection intensity (Tab. IV). Similarly, if the selections were made only from the genotypes with positive breeding values for both growth and MoE_{SS} , profitability decreased from Aus\$2409 to Aus\$1498. From purely biological responses, selection scenario B and C would be preferred since scenario C improves both MoE_{SS} and growth rate, while scenario B

Table IV. Predicted genetic responses at 10% selection intensity (percentage in parentheses) in juvenile growth and wood quality traits and net present value profitability (breeding objective response) for index selection using genetic parameters determined in this study. Three different scenarios were considered: (A) index selection using modulus of elasticity (MoE_{SS}) and diameter (DBH) as selection traits and maximising profitability; (B) restricted index selection keeping juvenile wood MoE_{SS} constant; (C) restricted index selection among the genotypes with positive breeding values for both MoE_{SS} and DBH.

Scenario	Predicted genetic response						
	DEN (kg m ⁻³)	DBH (mm)	MoE _{SS} (GPa)	MfA (deg)	SG (deg)	LSH (%)	Profitability (Aus\$ ha ⁻¹ y ⁻¹)
(A)	-13.0 (-3.7%)	10.7 (6.8%)	-0.25 (-5.3%)	0.56 (1.9%)	0.37 (9.4%)	0.06 (4.4%)	2409 (53.1%)
(B)	-10.37 (-2.9%)	10.44 (6.6%)	-0.04 (-0.5%)	-0.20 (-0.7%)	0.18 (4.5%)	0.05 (3.9%)	2282 (50.3%)
(C)	-3.51 (-1.0%)	7.02 (4.5%)	0.29 (6.0%)	-1.29 (-4.4%)	-0.16 (-4.1%)	0.02 (1.8%)	1498 (33.0%)

Table V. Predicted genetic responses at 10% selection intensity (percentage in parentheses) in juvenile growth and wood quality traits and net present value profitability (breeding objective response) for index selection based on the genetic parameters from the literature. Five different scenarios were considered: (D) base scenario using variance-covariance parameters from (Wu et al., 2008) for selection and objective traits; (E) economic weight on MoE_{OBJ} (MoE as the objective trait) was increased by 50%; (F) heritability of selection traits DEN and MoE_{SS} was reduced 50%; (G) genetic and phenotypic correlations between objective traits MAI_{OBJ} and MOE_{OBJ} and the selection traits DEN and MoE_{SS} were reduced by 50%; (H) heritability of selection traits DEN and MoE_{SS} was reduced 50% and correlations of the objective traits (MAI_{OBJ} and MOE_{OBJ}) with the selection traits (DEN and MoE_{SS}) were reduced by 50%.

Scenario	Predicted genetic response						
	DEN (kg m ⁻³)	DBH (mm)	MoE _{SS} (GPa)	MfA (deg)	SG (deg)	LSH (%)	Profitability (Aus\$ ha ⁻¹ y ⁻¹)
(D)	-13.63 (-3.8%)	3.53 (2.2%)	-0.35 (-5.0%)	-0.45 (-1.5%)	0.04 (1.0%)	0.02 (1.2%)	1500 (33.0%)
(E)	-5.58 (-1.6%)	2.18 (1.4%)	0.20 (2.9%)	-1.49 (-5.1%)	0.01 (2.6%)	-0.05 (-4.1%)	1387 (30.6%)
(F)	-5.09 (-1.4%)	2.71 (1.7%)	0.10 (1.4%)	-1.16 (-4.0%)	0.00 (0.0%)	0.03 (2.2%)	1293 (28.5%)
(G)	-6.07 (-1.7%)	3.28 (2.1%)	-0.07 (-1.0%)	-0.68 (-2.3%)	0.05 (1.2%)	-0.01 (-0.7%)	1197 (26.4%)
(H)	-2.57 (-0.7%)	2.83 (1.8%)	0.13 (1.9%)	-1.02 (-3.5%)	0.04 (1.0%)	-0.01 (-1.0%)	1160 (25.6%)

improves DBH and maintains MoE_{SS} at current levels. However, from the economic responses for enterprises, scenarios B and C were less advantageous than scenario A, even though in scenario A, juvenile wood quality traits showed unfavourable responses.

Under more general genetic parameters (scenarios D to H, Tab. V) estimated from literature review by Wu et al., (2008b) similar results were obtained. For example, even if genetic and phenotypic correlations between objective traits (MAI_{OBJ} and MOE_{OBJ}) and the selection traits (DEN and MoE_{SS}) were reduced by 50% (scenario G, Tab. V) there was a negative response in both DEN and MoE_{SS} (-1.7% and -2.3%, respectively). Under scenarios E, F and H MoE_{SS} had a positive response while DEN decreased. Generally, the genetic response in MoE_{SS} was less negative than in DEN, which was likely the consequence of the higher genetic correlation between MoE_{SS} and MoE_{OBJ} than DEN and MoE_{OBJ} ($r_g = 0.7$ vs. 0.5). When the economic weight on MoE_{OBJ} was increased 50% (scenario E, Tab. V) the response in MoE_{SS} was positive (2.9%), but the response in DEN was still slightly negative (-1.6%).

Generally, the index selection was more responsive to growth traits (DBH) as opposed to wood quality traits (MoE_{SS} and DEN) because DBH had more genetic variation. For example, DBH had almost 3-times the coefficient of additive genetic variation (CV_A) than MoE_{SS} (Tab. II). Moreover, as growth rate increases and rotation length decreases, there will be a higher proportion of juvenile wood with lower DEN and MoE than in the previous generations. The economic impact of reducing the quality and increasing the proportion of juvenile wood was not considered in current estimates of economic weights for radiata pine production system in Australia (Ivković et al., 2006b). We envisage that the economic weight on MoE may have to be increased relative to volume production in the next generation of selection, especially in the juvenile wood.

In general, as the mean of wood quality traits decreases, the economic value of wood quality increases relative to the economic value of volume production (Cown and van Wyk, 2004). Therefore, re-evaluation of economic weights may be necessary as the mean growth rate and the proportion of

juvenile wood increases, and the overall mean of wood density and stiffness decreases (Ivković et al., 2006b). A more detailed study is needed to quantify the relationship between the proportion of juvenile wood and its impact on the production system. In this way, it may be possible to avoid reaching a critical value at which a large proportion of boards are of unacceptable quality. This should be a concern for advanced generations of radiata pine (and other conifer) tree improvement programs.

In this paper, we only considered breeding strategies dealing with adverse genetic correlations for one generation. However, development of long-term breeding strategies require an understanding of both (1) how index selection affects genetic correlations, particularly for adverse ones such as between growth rate and juvenile wood quality traits, and (2) how improvement of biological traits affects the economic weights from one generation to the next. Selection of genotypes with positive breeding values for both traits (MoE and DBH) is not optimal using economic breeding objectives. However, more research is needed into the genetic basis of the negative genetic correlation, such as identifying possible major pleiotropic genes or close linkage. However, while linkage can be rapidly broken up by recombination, pleiotropic gene action will remain a constraint to selection for much longer (e.g., Conner, 2002). Insights from molecular genetics and association studies may enable breeders to purge the negative genetic correlation through repeated selections (King and Hansen, 1997; Sánchez et al., 2008). Simultaneously purging of the adverse genetic correlation and optimizing index selection would be the best selection strategy in multiple-trait selection breeding programs with adverse genetic correlations.

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