WOOD PROPERTIES AND STEM DIAMETER OF *PINUS RADIATA* IN NEW ZEALAND: GENETIC PARAMETER ESTIMATES OF CLONAL AND SEEDLING MATERIAL*

S. KUMAR†, R. D. BURDON, and G. T. STOVOLD
Scion**, Private Bag 3020, Rotorua, New Zealand.

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ABSTRACT

Two genetic trials were sampled in order to study variation and inheritance of wood properties and diameter at breast height in *Pinus radiata* D. Don. The study involved: (1) Five female testers with 56 pollen parents, c. five individuals per full-sib family, at ages 8 and 13 years; and (2) 33 pair-crosses (from 33 parents) × 10 clones/cross × six ramets/clone, at age 8–9 years. Sampling was at one site for each trial. Wood properties studied, directly or indirectly, were density, acoustic velocity, longitudinal shrinkage, collapse on drying, and resin pockets (as resin bleeding).

Coefficients of variation for density, velocity. and diameter at breast height were 7%, 11%, and 13%, respectively (rounded to nearest whole number). Estimated broad-sense heritabilities (H^2) around age 8 were ≈ 0.6 for all wood properties except resin bleeding, but narrow-sense (h^2) estimates were much lower for all traits except density. For diameter at breast height estimated h^2 and H^2 were ≈ 0.25 and ≈ 0.3 respectively. Diameter at breast height showed generally adverse genetic correlations with wood properties. Notable genetic correlations between wood properties involved density and collapse (r_g –0.3 to –0.6). Even allowing for indirect measures of traits, and generally adverse genetic correlations with diameter at breast height, the prospects for genetic improvement of the wood properties are encouraging.

Keywords: genetic parameters; wood properties; heritability; growth variables; stiffness; internal checking; *Pinus radiata*.

INTRODUCTION

The increasing proportion of corewood from fast-grown, early-harvested plantations, combined with the past emphasis on growth and form traits in the Radiata Pine Tree Improvement Programme, have serious effects on the quality of *Pinus radiata*

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† Corresponding author: Satish.Kumar@scionresearch.com

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timber. However, New Zealand breeders working with *P. radiata* have been proactive in trying to improve wood quality. A High Density breed was formulated in 1991, and an updated breeding strategy, including the formation of Structural Timber, and Appearance - Clear-cuttings breeds, has been put in place (Jayawickrama & Carson 2000).

While the inheritance of wood density in *P. radiata* is generally well understood (e.g., Burdon & Low 1992; Kumar 2004), it has become clear that other wood properties are economically important, especially in young crops. Microfibril angle and compression wood can be additional influences on stiffness and longitudinal shrinkage, and can strongly influence stability. Collapse on drying, and incidence of resin pockets, can also be important. Preliminary studies on small numbers of families / clones have shown moderate-to-high heritabilities of wood stiffness in *P. radiata* (e.g., Shelbourne 1997; Matheson *et al*. 1997; Kumar *et al*. 2002; Kumar 2004). There are two main reasons for further work on genetic parameters of wood properties of *P. radiata*. Firstly, estimates of genetic parameters, including genetic correlations with density and growth rate, are needed for properties other than density, based on broader genetic sampling. Secondly, genetic expression of different economic traits often varies with the environment, such that genetic parameter estimation should be conducted on different sites.

The purpose of this paper was to report results from a number of research projects that were recently undertaken to investigate: (i) the variances and heritabilities of wood properties, including wood density, stiffness, longitudinal shrinkage, internal checking, and external resin bleeding; (ii) genetic correlations among wood properties, and between diameter and wood properties. Parameter estimates obtained from a seedling progeny trial were also compared with those obtained from a clonal test.

MATERIALS AND METHODS

Genetic Material

Experiment 1: Female-tester trial

A female-tester trial was established in 1993 at three sites (Esk and Kaingaroa Compartment 1286 in the North Island, New Zealand, and Warrengong in NSW, Australia) using a single-tree-plot, sets-in-replicates design. The purpose of this trial was to obtain breeding-value estimates of promising untested parents, and to confirm breeding value prediction for parents that have already been tested. The testers used in this trial were middle- to high-ranked females in the "875" series (*see* Jayawickrama *et al*. 1997 for details of different selection series). For this exploratory study, only the Esk site (Hawke's Bay) was considered. In addition to various form traits, diameter at breast height and external resin bleeding were measured, at age 8, on all surviving trees. In addition to diameter at breast height

and form traits, a subset of replicates (10 out of 30) was also measured for basic density and acoustic velocity using FAKOPP (Anonymous 2000).

At age 13 from planting, a subset of 56 (out of 189) pollen-parent families, representing a wide range of variation for both growth and form traits, was assessed for diameter at breast height and wood properties. Fifteen replicates (individual trees) of each the 56 pollen-parent families were assessed for diameter at breast height, basic density, and acoustic velocity (using TreeTap™). The replicates assessed for basic density and acoustic velocity at age 8 and age 13 were not all the same. On average, there were five offspring per pollen-parent family that were common to both assessments (ages 8 and 13) of density and acoustic velocity. Although only 10–15 replicates were sampled for wood properties, at least four out of the five female testers were represented in the offspring sampled within each pollen-parent family for wood properties at ages 8 and 13.

Experiment 2: Control-pollinated clonal test

A group of 33 full-sib families, involving 33 parents (representing average-to-high diameter at breast height performance) of various selection series: "850" (three parents), "268" (17 parents), "875" (five parents), and "880" (eight parents) (*see* Jayawickrama *et al.* 1997 for details of different selection series) were used for establishing a clonal test. On average, each parent was involved in two crosses, but this number varied from one to five. Fourteen out of 33 parents in this experiment were also used as pollen parents in the Female-tester trial, which provided a reasonable level of genetic connection between the two experiments. Ten clones from each of the 33 full-sib families were chosen for trial establishment in July 1997 at two sites, namely Tarawera and Woodhill in the North Island of New Zealand. Both Tarawera and Woodhill were ex-forest sites, but their soil types were scoria-ash and coastal sand respectively. A sets-in-replicates design (Schutz & Cockerham 1966) with single-tree plots was used, with one ramet per clone planted in each of six replicates at each site. At age 8–9 years from planting, all surviving and unsuppressed ramets of each clone were assessed for diameter at breast height and form traits, but the wood properties (basic density, acoustic velocity (using TreeTap™), internal checking, and external resin bleeding) were measured on only three replicates (which had high survival, and better growth) of each clone. Data from only one site (Tarawera) were available for this paper.

Assessment techniques for wood properties

Average basic density: For assessment of basic density, a 5-mm bark-to-bark core was collected at breast height, but only one pith-to-bark radius, with the least compression wood, was used for measuring density by the water-displacement method (Smith 1954).

Acoustic velocity: Details for assessing standing-tree acoustic velocity using FAKOPP are reported elsewhere (Anonymous 2000; Kumar *et al.* 2002). FAKOPP was the first standing-tree tool evaluated by the Radiata Pine Breeding Company, but for various practical and operational reasons the Radiata Pine Breeding Company later chose TreeTap^{TM} (Anonymous 2008) as a preferred tool for assessing standing-tree stiffness. Unpublished studies showed that TreeTap^{TM} and FAKOPP measurements are highly correlated. For any standing-tree tool, the zone of wood being measured is limited in extent to a shallow strip of outerwood between the transducers.

Longitudinal shrinkage: A mathematical model developed using data from various unpublished studies was used to predict longitudinal shrinkage from density and modulus of elasticity measurements. Modulus of elasticity was not measured as such, but assuming a constant green density of 1000 kg/m^3, the standing-tree velocity^2 would provide a reasonable approximation of modulus of elasticity of green timber (Huang *et al.* 2003). Thus, density and velocity^2 obtained from this study were used as independent variables in the model for predicting longitudinal shrinkage. The mathematical model that was used in our study predicts the "maximum" longitudinal shrinkage for a given set of density and acoustic velocity^2 values.

Internal checking: Collapse, which is considered a surrogate trait for internal checking, was measured using 12-mm bark-to-bark breast-height increment cores after a drying schedule prescribed by D.McConchie, J.Turner, R.McKinley, G.Young, & C.Treloar (unpubl. data). After drying, each core was assessed for severity of collapse. Both qualitative and quantitative assessments have been used in different studies. In Experiment 1, each core was visually assessed, and a score (0 = none, 1 = low, 2 = moderate, 3 = severe) was assigned to each core. For quantitative assessment in Experiment 2, each growth ring in the sapwood was assessed for actual collapse using callipers. Our pilot results have shown that estimated genetic correlations between qualitative and quantitative assessments were high (≈ 0.8; s.e. ≈ 0.10).

External resin bleeding: Standing trees were assessed for resin bleeding using a visual score (0 = none, 1 = low, 2 = moderate, 3 = severe).

Assessment criteria for different traits are summarised in Table 1.

Data Analysis

Experiment 1: Female-tester trial

For each trait, the following general mixed linear model proved appropriate:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{f} + \mathbf{e} \quad [1]$$

where **y** is a vector of observations on a trait, **b** is a vector of fixed effects (i.e., mean and replicates), **a** is a vector of random additive genetic effects of individual

TABLE 1–Assessment criteria for various traits.

Trait	Units	Description
Dbh	cm	Diameter at breast height
DEN	kg/m^3	Basic density measured using 5-mm pith-to-bark breast height cores
VEL	km/sec	Acoustic velocity measured on standing trees using FAKOPP or TreeTapTM
Collapse	0 to 3 scale	Measured on 12-mm pith-to-bark breast height cores in Experiment 1. 0 = none, to 3 = severe
Collapse	Tangential (%)	Measured on 12-mm breast height cores in Experiment 2.
ERB	0 to 3 scale	Measured on standing trees. 0 = no external resin bleeding, to 3 = severe external resin bleeding
LS	%	Longitudinal shrinkage obtained from a function of DEN and VEL

genotypes, **f** is a vector of random specific full-sib family effects (specific combining ability effects), and **e** is a vector of random residual values. Sets effects were very minor and largely non-significant, and thus were not fitted in the model. **X**, $\mathbf{Z}_1$, and $\mathbf{Z}_2$ are known incidence matrices relating the observations in **y** to effects in **b**, **a**, and **f**, respectively. The variances associated with the random effects **a**, **f**, and **e** were σ^2_a ($\approx \sigma^2_A$), σ^2_f ($\approx \sigma^2_{SCA}$), and σ^2_e respectively. σ^2_A and σ^2_{SCA} ($\approx 0.25\sigma^2_D$) are the variances due to additive genetic effects, and specific combining ability (SCA) of the pair-crosses. σ^2_e represents the remaining non-additive genetic variance and environmental variance. Epistasis variance was assumed to be zero because the material was not suitable for estimating such effects. Multivariate analyses were also conducted, using Model 1, to estimate genetic correlations between different traits. Residual effects were assumed correlated, and were fitted using a residual variance-covariance matrix. ASReml software (Gilmour *et al*. 1997) was used for implementing Equation [1].

Estimates of narrow-sense (h^2) and broad-sense (H^2) heritability, and genetic correlations (r_g) were obtained from:

$$h^2 = \sigma^2_a / (\sigma^2_a + \sigma^2_{SCA} + \sigma^2_e) \quad [2]$$

$$H^2 = (\sigma^2_a + 4\sigma^2_{SCA}) / (\sigma^2_a + \sigma^2_{SCA} + \sigma^2_e) \quad [3]$$

$$r_g = \sigma_{cov} / \sqrt{(\sigma^2_{a1} \times \sigma^2_{a2})} \quad [4]$$

In Equation 4, the additive genetic covariance between a pair of traits is denoted by σ_{cov}, and σ^2_{a1} and σ^2_{a2} denote additive genetic variances of two traits.

Experiment 2: Control-pollinated clonal test

The model used for analyses of data from this experiment is an extension of Model 1. For each trait at each site, the following general mixed linear model was used:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{f} + \mathbf{Z}_3\mathbf{c} + \mathbf{e} \quad [5]$$

where **y** is a vector of observations on a trait, **b** is a vector of fixed effects (i.e., site mean and replicates), **a** is a vector of random additive genetic effects of individual genotypes, **f** is a vector of random specific full-sib family effects, **c** is a vector of random specific effects of clones within full-sib families, and **e** is a vector of random residual effects. Sets effects were minor and largely non-significant, and thus excluded from Model 5. $\mathbf{X}$, $\mathbf{Z}_1$, $\mathbf{Z}_2$, and $\mathbf{Z}_3$ are known incidence matrices relating the observations in **y** to effects in **b**, **a**, **f**, and **c**, respectively. Observations on different ramets of a clone were treated as repeated measurements on a single genotype. The variances associated with the random effects **a**, **f**, **c**, and **e** were σ^2_a ($\approx \sigma^2_A$), σ^2_f ($\approx \sigma^2_{SCA}$), σ^2_c ($\approx \sigma^2_{C(FS)} - 2\sigma^2_{GCA}$), and σ^2_e respectively. σ^2_A ($\approx 4\sigma^2_{GCA}$) , σ^2_{SCA} ($\approx 0.25\sigma^2_D$), $\sigma^2_{C(FS)}$($\approx 0.5\sigma^2_A + 0.75\sigma^2_D$), and σ^2_D are the variances due to additive effects, general combining ability (GCA) of parents, specific combining ability (SCA) of the pair-crosses, differences between clones within full-sib families, and dominance effects, respectively. Estimates of a portion of epistatic variances (only high-order interactions among loci) were also obtained ($= \sigma^2_c - 3\sigma^2_f$) even though this was incidental to the experiment. C-effects (these are persistent epigenetic effects which typically exaggerate the differences among ramets within a clone, and/or the differences among clones beyond what would be expected from their purely genetic differences) introduced by cloning (Libby & Jund 1962), were not estimable from this experiment, and were therefore assumed to be negligible or absent. A similar model was previously used by Costa e Silva *et al.* (2004) and Kumar (2006) for analyses of clones-within-families data. Estimated h^2 and H^2 were obtained as the ratios of additive variance (σ^2_a) to phenotypic variance, and of total genetic variance ($= \sigma^2_a + \sigma^2_f + \sigma^2_c$) to phenotypic variance, respectively. Phenotypic variance is the sum of variances of all random effects in model [5].

Multivariate analyses were also conducted to obtain within-site estimates of genetic correlations between various traits, using the simpler model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{e} \quad [6]$$

where **g** is a vector of random total genetic effects of individual clones. Note that Model [6] is a shorter version of the model in [5] where the random effects **a**, **f**, and **c** are combined as one random effect **g**. The variance associated with the random effect **g** was σ^2_g (which represents total genetic variance, and could also be obtained by summing the three components σ^2_a, σ^2_f, and σ^2_c). Owing to non-convergence problems with REML, Model 6 (instead of Model 5) was used for multivariate analyses. It is important to note that the resulting estimates of between-trait correlations would be interpreted as "genotypic" correlations instead of "additive genetic" correlations.

All models described above were implemented using ASREML software (Gilmour *et al.* 1997). Approximate standard errors of estimates of heritabilities and genetic

correlations were calculated using ASREML software, which uses the Delta method (*see* Lynch & Walsh 1998, p. 807) based on Taylor Series approximation, for estimating standard error of a given function of variance components.

RESULTS

Means, Variation, and Heritabilities

Phenotypic coefficients of variation and heritability estimates are shown for the two experiments in Tables 2 and 3 respectively. The coefficients of variation differed greatly according to variable, being least for density (c. 7%), slightly higher for velocity, and generally much higher for longitudinal shrinkage, collapse, and external resin bleeding.

At around age 8 all the actual wood properties showed high H^2 estimates (c. 0.6), resin bleeding somewhat lower, and diameter at breast height lower again overall,

TABLE 2–Trait means, coefficients of variation (CVs),and estimates of narrow-sense (h^2) and broad-sense (H^2) heritabilities in Experiment 1. Approximate standard errors are shown in parentheses.

Trait	Mean	CV (%)	h^2	H^2
Age 8				
Dbh (cm)	24.94	12	0.19 (0.06)	0.23 (0.08)
VEL (km/sec)	1.75	10	0.38 (0.13)	0.74 (0.22)
DEN (kg/m^3)	342	6	0.60 (0.13)	0.60 (0.13)
LS (%)	1.04	35	0.33 (0.13)	0.68 (0.23)
ERB (0–3 scale)	1.62	50	0.38 (0.08)	0.49 (0.09)
Age 13				
Dbh (cm)	38.01	14	0.24 (0.09)	0.38 (0.13)
VEL (km/sec)	2.93	12	0.37 (0.10)	0.43 (0.13)
DEN (kg/m^3)	354	7	0.32 (0.10)	0.49 (0.13)
LS (%)	0.20	49	0.29 (0.09)	0.38 (0.13)
Collapse (0–3 scale)	0.90	103	0.16 (0.08)	0.60 (0.12)

TABLE 3–Trait means (across clonal means), coefficients of variation (CV), and estimates of narrow-sense (h^2) and broad-sense (H^2) heritabilities in Experiment 2. Approximate standard errors are shown in parentheses. The CV values apply to clonal means.

Trait	Mean	CV(%)	h^2	H^2
Dbh (cm)	23.0	11	0.32 (0.10)	0.37 (0.04)
Velocity (km/sec)	2.59	9	0.35 (0.12)	0.56 (0.04)
DEN (kg/m^3)	328	6	0.58 (0.14)	0.63 (0.04)
LS (%)	0.26	39	0.27 (0.15)	0.51 (0.04)
Collapse (%)	8.3	36	0.21 (0.12)	0.35 (0.05)
ERB (0–3 scale)	0.79	74	0	0.27 (0.03)

but agreement between trials was generally close. Compared with the H^2 estimates, those for h^2 were similar for density and diameter but generally markedly lower for the other variables. The main exception to agreement between trials appeared to be much lower heritabilities for resin bleeding in Experiment 2. Estimated epistatic variance (expressed as a percentage of total phenotypic variance) was 5, 21, 5, 24, 14, and 11% for diameter at breast height, acoustic velocity, basic density, longitudinal shrinkage, collapse and resin bleeding, respectively (results not tabulated).

Compared with age-8 means, those for age 13 in the female-tester trial (Table 2) showed the expected increase in diameter and density, a considerable increase in velocity, and a major drop in longitudinal shrinkage. Coefficients of variation increased slightly with age. The age trends in estimated heritabilities were not statistically clear, and were mixed. For diameter, age-13 heritability estimates were slightly higher, especially for H^2. For the other variables, however, the estimates tended to drop, more so for H^2 than for h^2.

Genetic Correlations

Estimated genetic correlations are shown for the respective trials in Tables 4 and 5. Diameter at breast height was consistently involved in adverse correlations with the wood properties, although several of the individual estimates are very imprecise. Among the actual wood properties, almost complete correlation between longitudinal

TABLE 4–Estimates of genetic correlations between diameter at breast height and wood-quality traits (at breast height) in Experiment 1: Age 8 (above diagonal) and age 13 (below diagonal). Approximate standard errors are shown in parentheses. The values on the diagonals are the age-age genetic correlations.

	Dbh	VEL	DEN	LS	ERB
Dbh	0.96 (0.08)	–0.36 (0.20)	–0.29 (0.17)	0.33 (0.22)	0.54 (0.17)
VEL	–0.26 (0.21)	1.03 (0.13)	0.16 (0.19)	–0.93 (0.03)	–0.25 (0.22)
DEN	–0.47 (0.19)	0.38 (0.18)	0.97 (0.09)	0.17 (0.20)	0.12 (0.24)
LS	0.06 (0.24)	–0.93 (0.03)	–0.07 (0.22)	1.02 (0.16)	–0.18 (0.19)
Collapse	0.25 (0.31)	–0.02 (0.29)	–0.32 (0.27)	–0.12 (0.31)	–

TABLE 5–Estimates of genotypic correlations between diameter at breast height and wood-quality traits (at breast height) in Experiment 2. Approximate standard errors are shown in parentheses.

	VEL	DEN	LS	ERB	Collapse
Dbh	–0.23 (0.09)	–0.30 (0.08)	0.12 (0.09)	0.33 (0.09)	0.23 (0.10)
VEL		0.18 (0.08)	–0.92 (0.01)	–0.10 (0.10)	–0.07 (0.11)
DEN			0.13 (0.08)	0.16 (0.09)	–0.59 (0.07)
LS				0.10 (0.10)	–0.07 (0.11)
ERB					–0.15 (0.11)

shrinkage and velocity ($r_g \approx -0.9$) was especially noteworthy, but velocity was used (along with density) in deriving the measure of longitudinal shrinkage. Also of note was consistently negative r_g between density and collapse.

Age-age genetic correlation estimates for individual traits were all close to +1 (Table 4). Compared with age-8 estimates of between-trait correlations, those for age 13 were not clearly different, most of the estimates being clearly very imprecise.

DISCUSSION

The study was intended to explore the possibilities for improving various wood properties, rather than obtaining unbiased estimates of genetic parameters. The use of 56 families representing a wide range of variation (Experiment 1) would tend to inflate heritability estimates of diameter at breast height (and correlated traits) and, to some degree, of genetic correlations involving diameter. However, the estimated h^2 of diameter, obtained from all 189 families of Experiment 1, was 0.14 which is similar to that obtained in this study (0.19). Although the set of 33 parents involved in the clonal test (Experiment 2) represented average-to-high performing parents from different selection series, the estimated h^2 of diameter (0.32) was relatively high — suggesting large genetic variation.

The genetic samples represented in the two experiments were somewhat restricted, which could reduce the inherent precision of the results. However, the level of agreement between the results from the two experiments, and the overall precision of the results, were reassuring. Also reassuring was the level of agreement between results for broad-sense heritability obtained with very different genetic classifications, and between different measurement tools for the same variable (velocity). Agreement between different velocity measurement tools supports earlier results (e.g., Kumar *et al*. 2002; L.Guenole, C-L.Huang, M.Kimberley, M.Lausberg, & D.McConchie unpubl. data). The increase in average basic density between the two ages in the female-tester trial appeared modest, but it accords with previous studies (e.g., Kumar & Lee 2002).

For acoustic velocity, estimates of h^2 were similar at ages 8 and 13 but tended to drop for H^2. Previous studies (e.g., Kumar *et al*. 2006) reported generally lower h^2 of modulus of elasticity in the outerwood than in the corewood. The agreement between broad-sense and narrow-sense heritability estimates for density was unsurprising. Not expected was the apparent drop in heritability in the female-tester trial for density between the two samplings, but the limited overlap in samples within families could have led to a considerable random sampling difference. Analysis of only those trees that were common to age-8 and age-13 density assessments revealed h^2 estimates 0.58 and 0.46 respectively (results not tabulated). In contrast to the results for density, the lower narrow-sense heritability estimates for several wood properties are noteworthy and could have important implications for clonal

forestry. The presence of relatively large non-additive genetic variance for wood properties (other than wood density) could favour selection and deployment of clones as opposed to seedling families (open-pollinated or control-pollinated).

Some of the genetic parameters, e.g., coefficient of variation and heritability of average density, were already well-known, providing a cross-check on the value of our results. Previous estimates of heritability of stiffness (Matheson *et al.* 1997, 2002; Kumar *et al.* 2002; Kumar 2004; Fujimoto *et al.* 2006; Baltunis *et al.* 2007) were in close agreement with those found in this study. Our heritability estimates for collapse (or internal checking) were similar to those reported in *P. radiata* (Kumar 2004) and *Picea abies* (L.) H.Karst. (Hannrup *et al.* 2004). Age-8 H^2 estimates of longitudinal shrinkage from this study are similar to that reported (0.54) from an earlier study (Dadswell *et al.* 1961), but the estimated h^2 were somewhat higher than those reported by Gapare *et al.* (in press).

Estimated epistatic variances varied from 5% (for diameter at breast height) to 24% (for longitudinal shrinkage) of the total phenotypic variance in our study. The small number of full-sib families, along with unequal representation of parents, plus possible C-effects could result in unreliable estimates of epistatic effects. To our knowledge, there are no published estimates on the magnitude of epistatic variances for wood properties in *P. radiata* or other pine species, but such estimates for diameter have been reported to be zero in *Pseudotsuga menziesii* (Mirb.) Franco (Stonecypher & McCullough 1986) and *Pinus taeda* L. (Paul *et al.* 1997; Isik *et al.* 2003).

Genetic correlation estimates from Experiment 2 would have involved all the non-additive gene effects as well as the additive ones. However, this seems unlikely to have caused appreciable bias, because of the agreement between estimates from the two experiments, and the findings of Burdon *et al.* (1992) for seedling and clonal material respectively. Using three different estimation methods involving varying levels of non-additive genetic variances, Cahaner & Hillel (1980) showed that estimated genetic correlations were similar — suggesting that estimates of genetic correlations are generally not biased by non-additive effects.

Various estimated genetic correlations among wood properties were predictable, notably the strong correlation between velocity and longitudinal shrinkage. Superficially, that augurs very well for measuring velocity as a multi-purpose screening procedure, but the fact that velocity was used along with density in predicting longitudinal shrinkage means that this finding remains to be validated. It is also important to note that reliability of the function used for predicting longitudinal shrinkage remains to be tested. A study is currently under way to investigate the relationship of our predicted longitudinal shrinkage with that obtained from using near infrared resonance (NIR) on the same samples. The

NIR technique has shown great potential for predicting longitudinal shrinkage in *P. radiata* (A. Thumn unpubl. data).

There are only few published studies on genetic interrelationships of wood properties. Our estimates of genetic correlation between density and modulus of elasticity were in accord with those reported earlier (Matheson *et al.* 1997; Kumar 2004; Fujimoto *et al.* 2006; Baltunis *et al.* 2007). Our results on genetic correlation between density and collapse (surrogate for internal checking) are in good general agreement with other findings (e.g., Kumar 2004). Hannrup *et al.* (2004) also reported negative genotypic correlations between average wood density and internal checking, but the magnitude of estimated correlations was lower than that found in this study. Similar to the findings of this study, adverse genetic correlation of diameter at breast height with density and stiffness has been reported previously (Kumar 2004; Fujimoto *et al.* 2006; Baltunis *et al.* 2007). A review of genetic parameters of wood properties of *P. radiata* (Wu *et al.* 2008) does not cover the key appearance-grade related properties.

Genotype-by-environment (G×E) interaction was not addressed in this study. It is well known that within-site estimates of genetic parameters could be upwardly biased in the presence of G×E. While G×E for diameter can be substantial in *P. radiata* (Burdon *et al.* 1997 and references therein), it tends to be minimal for density (e.g., Burdon & Harris 1973; Burdon & Low 1992; Kumar 2004). For the other wood properties, there is an indication that G×E for stiffness, internal checking, and resin bleeding is far less than that for diameter (Kumar 2004, 2006). Overall, there are good prospects of simultaneous genetic improvement of a suite of wood properties, although this is likely to be at some cost in potential genetic gain for stem volume production.

CONCLUSIONS

Moderate-to-high heritability estimates suggested great potential for genetic improvement of structural and appearance-related wood properties, but adverse genetic correlation with diameter could result in loss in volume production.

The presence of relatively large non-additive genetic variance for wood properties (other than wood density) could need changes in selection and deployment strategies in order to capture this variation.

Genetic correlation estimates from seedling and clonal experiments were in close agreement, suggesting that estimates of genetic correlations are generally not biased by non-additive effects.

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REFERENCES

ANONYMOUS 2000: "FAKOPP User's Guide". ALNUS Bt., H-9400 Sopron, Feher D. u. 22, Hungary.

——2008: TreeTap™ Wood Quality Censor [online]. Available: http://www.cant.canterbury.ac.nz/docs/treetap_1pg.pdf.

BALTUNIS, B.S.; WU, H.X.; POWELL, M.B. 2007: Inheritance of density, microfibril angle, and modulus of elasticity in juvenile wood of *Pinus radiata*. *Canadian Journal of Forest Research 31*: 2164–2174.

BURDON, R.D.; HARRIS, J.M. 1973: Wood density in radiata pine clones on four different sites. *New Zealand Journal of Forestry Science 3*: 286–303.

BURDON, R.D.; LOW, C.B. 1992: Genetic survey of *Pinus radiata*. 6: Wood properties: variation, heritabilites, and interrelationship with other traits. *New Zealand Journal of Forestry Science 22*: 228–245.

BURDON, R.D.; BANNISTER, M.H.; LOW, C.B. 1992: Genetic survey of *Pinus radiata*. 5: Between-trait and age-age genetic correlations for growth rate, morphology, and disease resistence. *New Zealand Journal of Forestry Science 22*: 211–227.

BURDON, R.D.; HONG, S.O.; SHELBOURNE, C.J.A.; JOHNSON, I.G.; BUTCHER, T.B.; BOOMSMA, D.B.; VERRYN, S.D.; CAMERON, J.N.; APPLETON, R. 1997: International gene pool experiments in *Pinus radiata*: Patterns of genotype-site interaction. *New Zealand Journal of Forestry Science 27*: 101–125.

CAHANER, A.; HILLEL, J. 1980: Estimating heritability and genetic correlation between traits from generations F_2 and F_3 of self-fertilising species: a comparison of three methods. *Theoretical & Applied Genetics 58*: 33–38.

COSTA e SILVA, J.; BORRALHO, N.M.G.; POTTS, B. 2004: Additive and non-additive genetic parameters from clonally replicated and seedling progenies of *Eucalyptus globulus*. *Theoretical & Applied Genetics 108*: 1113–1119.

DADSWELL, H.E.; FIELDING, J.M.; NICHOLLS, J.W.P.; BROWN, J.P. 1961: Tree-to-tree variation and the gross heritability of wood characteristics of *Pinus radiata*. *Tappi 44*: 174–179.

FUJIMOTO, T.; AKUTSU, H.; NEI, M.; KITA, K.; KUROMARU, M.; ODA, K. 2006: Genetic variation in wood stiffness and strength properties of hybrid larch (*Larix gmelinii* var. *japonica* × *L. kaempferi*). *Journal of Forest Research 11*: 343–349.

GAPARE, W.J.; IVKOVIĆ, M.; WU, H.X.: Genetics of shrinkage in juvenile trees of radiata pine from two test sites in Australia. *Silvae Genetica* (in press).

GILMOUR, A.R.; THOMPSON, R.; CULLIS, B.R.; WELHAM, S.J. 1997: "ASREML User's Manual". New South Wales Agriculture, Orange, Australia.

HANNRUP, B.; CAHALAN, C.; CHANTRE, G.; GRABNER, M.; KARLSSON, B.; LE BAYON, I.; JONES, G.L.; MÜLLER, U.; PEREIRA, H.; RODRIGUES, J.C.; ROSNER, S.; ROZENBERG, P.; WILHELMSSON, L.; WIMMER, R. 2004: Genetic parameters of growth and wood quality traits in *Picea abies*. *Scandinavian Journal of Forest Research 19*: 14–29

HUANG, C.L.; LINDSTRÖM, H.; NAKADA, R.; RALSTON, J. 2003: Cell wall structure and wood properties determined by acoustics — A selective review. *Holz als Roh- und Werkstoff 61*: 321–335.

ISIK, F.; LI, B.; FRAMPTON, J. 2003: Estimates of additive, dominance and epistatic genetic variances from a clonally replicated test of loblolly pine. *Forest Science 49*: 77–88.

JAYAWICKRAMA, K.J.S.; CARSON, M.J. 2000: A breeding strategy for the New Zealand radiata pine breeding cooperative. *Silvae Genetica 49*: 82–90.

JAYAWICKRAMA, K.J.S.; CARSON, M.J.; JEFFERSON, P.A.; FIRTH, A. 1997: Development of the New Zealand radiata pine breeding population. Pp. 217–225 *in* Burdon, R.D.; Moore, J.M. (Ed.) "IUFRO '97 Genetics of Radiata Pine", Proceedings of NZ FRI-IUFRO Conference 1–4 December and Workshop 5 December, Rotorua, New Zealand. *FRI Bulletin No. 203*.

KUMAR, S. 2004: Genetic parameter estimates for wood stiffness, strength, internal checking and resin bleeding for radiata pine. *Canadian Journal of Forest Research 34*: 2601–2610.

—— 2006: Correlation between clonal means and open-pollinated offspring performance, and its implications for radiata pine breeding strategy. *Canadian Journal of Forest Research 36*: 1968–1975.

KUMAR, S.; LEE, J. 2002: Age-age correlations and early selection for end-of-rotation wood density in radiata pine. *Forest Genetics 9*: 323–330.

KUMAR, S.; DUNGEY, H.; MATHESON, C. 2006: Genetic parameters and strategies for genetic improvement of stiffness in radiata pine. *Silvae Genetica 55*: 77–84.

KUMAR, S.; JAYAWICKRAMA, K.J.S.; LEE, J.; LAUSBERG, M. 2002: Direct and indirect measures of stiffness and strength show high heritability in a wind-pollinated radiata pine progeny test in New Zealand. *Silvae Genetica 51*: 256–261.

LIBBY, W.J.; JUND, E. 1962: Variance associated with cloning. *Heredity 17*: 533–540.

LYNCH, M.; WALSH, B. 1998: "Genetics and Analysis of Quantitative Traits". Sinauer, Sunderland, MA, USA.

MATHESON, A.C.; DICKSON, R.L.; SPENCER, D.J.; JOE, B.; ILÍC, J. 2002: Acoustic segregation of *Pinus radiata* logs according to stiffness. *Annals of Forest Science 59*: 471–477.

MATHESON, A.C.: SPENCER, D.J.; NYAKUENGAMA, J.G.; YANG, J.; EVANS, R. 1997: Breeding for wood properties in radiata pine.Pp. 169–179 *in* Burdon, R.D.; Moore, J.M. (Ed.) "IUFRO '97 Genetics of Radiata Pine", Proceedings of NZ FRI-IUFRO Conference 1–4 December and Workshop 5 December, Rotorua, New Zealand. *FRI Bulletin No. 203*.

PAUL, A.D.; FOSTER, G.S.; CALDWELL, T.; McRAE, J. 1997: Trends in genetic and environmental parameters for height, diameter and volume in a multilocation clonal study with loblolly pine. *Forest Science 43*: 87–98.

SCHUTZ, W.M.; COCKERHAM, C.C. 1966: The effect of field blocking on gain from selection. *Biometrics 22*: 843–63.

SHELBOURNE, C.J.A. 1997: Genetics of adding value to the end-products of radiata pine. Pp. 129–141 *in* Burdon, R.D.; Moore, J.M. (Ed.) "IUFRO '97 Genetics of Radiata Pine", Proceedings of NZ FRI-IUFRO Conference 1–4 December and Workshop 5 December, Rotorua, New Zealand. *FRI Bulletin No. 203*.

SMITH, D.M. 1954: Maximum moisture method for determining the specific gravity of small wood samples. *USDA Forest Service, Forest Products Laboratory Report No. 2014*. 8 p.

STONECYPHER, R.W.; McCULLOUGH, R.B. 1986: Estimates of additive and non-additive variances from a clonal diallel of Douglas-fir (*Pseudotsuga menziesii*) (Mirb.) Franco. Pp. 211–227 *in* Proceedings IUFRO Joint Meeting of Working Parties on Breeding Theory, Progeny Testing and Seed Orchards, Williamsburg, Va., 13–17 October 1986. North Carolina State University-Industry Cooperative Tree Improvement Program, Raleigh.

WU, H.X.; IVKOVIC, M.; GAPARE, W.J.; MATHESON, A.C.; BALTUNIS, B.S.; POWELL, M.B.; McRAE, T.A. 2008: Breeding for wood quality and profit in *Pinus radiata*: A review of genetic parameters and implications for breeding and deployment. *New Zealand Journal of Forestry Science 38(1)*: 55–86.