Breeding for wood properties of radiata pine in New Zealand

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Abstract

Two genetic trials were sampled for studying variation and inheritance of wood properties and diameter at breast height (DBH) in radiata pine (*Piuns radiata* D. Don). The study involved: (1) Five female testers with 56 pollen parents, *ca* 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 (LS), collapse on drying, and resin pockets (as resin bleeding - ERB).

Coefficients of variation (CVs) for density, velocity and DBH were about 7%, 11% and 13%, respectively. Estimated broad-sense heritabilities (H^2) around age 8 were around 0.6 for all wood properties except ERB, but narrow-sense (h^2) estimates were much lower for all except density. For DBH estimated h^2 and H^2 were ≈0.25 and ≈0.3 respectively. DBH showed generally adverse genetic correlations with wood properties. Notable correlations between wood properties involved Velocity and LS ($r_g \approx$ -0.9), and density and collapse (-0.3 to -0.6). Even allowing for some very indirect measures of traits, and generally adverse genetic correlations with DBH, the prospects for genetic improvement of the wood properties are encouraging.

Key words

Pinus radiata, breeding strategy, clonal test, genetic correlation, growth, wood properties

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, could have serious effects on the quality of radiata pine timber. However, New Zealand breeders working with radiata pine (*Pinus radiata* D. Don) have been proactive in trying to improve wood quality. A High Wood Density breed was formulated in 1991, and recently an updated breeding strategy, including the formation of a Structural breed and an Appearance / Clear-cuttings breed, has been put in place (Jayawickrama and Carson 2000).

While the inheritance of wood density in radiata pine is generally well understood (e.g. Burdon and 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 can strongly influence stability which itself is much affected by differential longitudinal shrinkage. Collapse on drying, and incidence of resin pockets can also be important. Preliminary studies on small numbers of entries have shown moderate-to-high heritabilities of wood stiffness and strength in radiata pine (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 radiata pine. First, stronger estimates of genetic parameters, including genetic correlations with density and growth rate, are needed for properties other than density, based on more entries and a broader sample. Second, genetic expression of different economic traits often varies with the environment, such that genetic parameter estimation should be conducted on more than one site.

The purpose of this paper is to report results from a number of research projects that were recently undertaken to investigate: (i) the variances and heritabilities of various wood properties, including wood density, stiffness, longitudinal shrinkage, internal checking, and external resin bleeding; (ii) genetic correlations among wood

properties, and between diameter (DBH) and wood properties. A comparison of parameter estimates obtained from seedling progeny trial with those obtained from clonal test was also made.

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 North Island, New Zealand: and Warrengong in NSW, Australia) using a single-tree-plot sets-in-replicates design (P.A. Jefferson et al. 1993 - unpublished). The purpose of this trial was to obtain breeding-value estimates of promising untested parents in the breeding population, and to confirm and strengthen 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). The "875" parental series were selected individuals from the first-generation open-pollinated progeny of the "268" series. Selection of the "875" series emphasized tree volume, stem straightness, branch quality and wood density. More details are given in King et al. (1998). For this exploratory study, only the Esk site (Hawke's Bay) was considered. In addition to various form traits, diameter at breast height (DBH) and external resin bleeding (ERB) were measured, at age 8, on all surviving trees. In addition to growth and form traits, a subset of replicates (10 out of 30) were also measured for basic density (DEN) and acoustic velocity (using FAKOPP).

At age 13 from planting, a subset of 56 (out of 189) pollen-parent families, chosen to represent a wide range of variation for both growth and form traits, was assessed for DBH and wood properties. Fifteen replicates (individual trees) of each the 56 pollen-parent families were assessed for DBH, DEN and acoustic velocity (using TreeTap^{TM}). The replicates assessed for DEN and acoustic velocity (VEL) 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 DEN and VEL. 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. Assessment details of these wood properties are provided later.

Experiment 2: Control-pollinated clonal test

A group of 33 full-sib families was selected on the basis of GF value from the total number of 137 families that were available. The selected full-sib families were based on 33 parents of various selection series: "850" (3 parents), "268" (17 parents), "875" (5 parents) and "880" (8 parents). On average, each parent was involved in two crosses, but this number varied from one to five. 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 (cf Schutz and 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 six ramets of each clone were assessed for DBH and form traits, but the wood properties (DEN, acoustic velocity (using TreeTap™), internal checking, and ERB) were measured only on three ramets of each clone. Data from only one site (Tarawera) were available for this report.

Assessment techniques of wood properties

Basic density: For assessment of DEN, a 5-mm bark-to-bark core was collected at breast height (1.4 m), but only one pith-to-bark radius, with the least compression wood, was used for measuring DEN by the water-displacement method.

Acoustic velocity: For assessing a standing-tree acoustic velocity using FAKOPP, two transducers were driven a few cm into the stem and 1 m apart, with the lower transducer about 1 m above ground level. The start transducer was then tapped gently and a reading recorded. What is measured, by use of an amplification device, is the time for the sound wave to travel from the start transducer to the stop transducer. Details on FAKOPP procedure are given in the FAKOPP user guide (Anonymous, 2000). Assessment of standing-tree velocity using TreeTap™ requires two probes to be inserted into solid wood through the bark layer, at 45º angle facing downwards. The top probe is approximately 2 m from the base of the tree, while the distance between the top and the bottom probe is kept at 1 m. A third probe (facing upward) is

also inserted directly below (within about 20 cm) the bottom probe. A steel hammer is used to hit the third probe, and the time taken for the sound wave to travel between the top and the bottom probes is recoded. Further information on TreeTap^{TM} can be found at: http://www.cant.canterbury.ac.nz/docs/treetap_1pg.pdf.

Longitudinal shrinkage: A mathematical model developed using data from various unpublished studies was used to predict LS from DEN and MoE measurements. One of the assumptions of this model is that DEN and MoE are measured on dry (say, air-dried) samples. The basic density (DEN) measurements in our study fulfilled this assumption. MoE was not measured as such in this study, but assuming a constant green density of 1000 kg/m^3 the VEL^2 would provide a reasonable approximation of MoE of green lumber. Results from unpublished studies showed a very high correlation (>0.9) between MoE of green- and dry pieces of lumber. Thus, DEN and VEL^2 obtained from this study were suitable for using as independent variables in the model for predicting LS. The mathematical model that was used in our study predicts the "maximum" LS for a given set of DEN and MoE values.

Internal checking: Collapse, which is considered as a surrogate trait for internal checking, was measured using a non-destructive technique. A 12-mm bark-to-bark breast-height increment core was collected from each pre-selected tree, and put through a drying schedule prescribed by D. McConchie et al. 2006 (unpublished). After drying, each core was assessed for severity of collapse. Both qualitative and quantitative assessment has 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 the actual collapse using callipers. Our unpublished results have shown that estimated genetic correlation between qualitative and quantitative assessments were high (about 0.8).

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

Assessment criteria for different traits are summarised in Table 1.

Table 1. Assessment criteria for various traits.

Trait	Units	Description
DBH	cm	Measured at 1.4 m above ground level
DEN	Kg/m^3	Measured using 5-mm breast-height cores
VEL	Km/sec	Acoustic velocity measured on standing trees using FAKOPP or TreeTap™
Checking	Collapse (0-3 scale)	Measured on 12-mm breast-height cores in Experiment 1.
	Collapse (%)	Measured on 12-mm breast-height cores in Experiment 2.
ERB	0 to 3 scale	0 = no resin bleeding, to 3 = severe resin bleeding
LS	percentage	Obtained from a function of DEN and VEL

Data Analysis

Experiment 1: Female-tester trial

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

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

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 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. **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_a^2 ($\approx \sigma_A^2$), σ_f^2 ($\approx \sigma_{SCA}^2$), and σ_e^2 respectively. σ_A^2 and σ_{SCA}^2 ($\approx 0.25\,\sigma_D^2$) are the variances due to additive genetic effects, and specific combining ability (SCA) of the pair-crosses. σ_e^2 represents the remaining non-additive genetic variance, and environmental variance. Epistasis variance was assumed to be zero. Multivariate analyses were also conducted, using Model 1, to estimate genetic correlations between different traits.

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

[2] $$h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_{sca}^2 + \sigma_e^2)$$

[3] $$H^2 = (\sigma_a^2 + 4\sigma_{sca}^2)/(\sigma_a^2 + \sigma_{sca}^2 + \sigma_e^2)$$

[4] $$r_g = \sigma_{\text{cov}} / \sqrt{\sigma_{a1}^2 \times \sigma_{a2}^2}$$

In Equation 4, the additive genetic covariance between a pair of trait is denoted by σ_{cov}, and σ_{a1}^2 and σ_{a2}^2 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:

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

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. **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_a^2 ($\approx \sigma_A^2$), σ_f^2 ($\approx \sigma_{SCA}^2$), σ_c^2 ($\approx \sigma_{C(FS)}^2 - 2\sigma_{GCA}^2$), and σ_e^2 respectively. σ_A^2 ($\approx 4\sigma_{GCA}^2$), σ_{SCA}^2 ($\approx 0.25\sigma_D^2$), $\sigma_{C(FS)}^2$ ($\approx 0.5\sigma_A^2 + 0.75\sigma_D^2$), and σ_D^2 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. Epistatic variation was assumed to be zero. C-effects (these are persistent non-genetic effects which typically exaggerate the differences among ramets within a clone, and/or the differences among clones to beyond what would be expected from their purely genetic differences) introduced by cloning (Libby and Jund 1962) were 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. Estimates h^2 and H^2 were obtained as the ratio of additive variance (σ_a^2) to phenotypic variance, and total genetic variance ($=\sigma_a^2+\sigma_f^2+\sigma_c^2$) 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 simpler model:

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

where **g** is a vector of random total genetic effects of individual genotypes. Note that this model [6] is a shorter version of the model in [5] where the random effects **a**, **f**, and **c** are combined together as one random effect **g**. The variance associated with the random effects **g** was σ_g^2 (which represents total genetic variance, and could also be obtained by summing the three components, σ_a^2, σ_f^2 and σ_c^2). 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 and Walsh 1998, page 807) 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 (*ca* 7%), slightly higher for velocity, and generally much higher for LS, collapse and ERB.

At around age 8 all the actual wood properties showed high H^2 estimates (*ca* 0.6), ERB somewhat lower, and DBH lower again overall, but agreement between trials was generally close. Compared with the H^2 estimates, those for h^2 were similar for density and DBH but generally markedly lower for the other variables. The main exception to agreement between trials appeared to be much lower heritabilities for ERB in Experiment 2.

Compared with age-8 means, those for age 13 in the female-tester trial (Table 2) showed the expected increase in diameter, a notably modest increase in density, a

considerable increase in velocity, and a major drop in LS. Coefficients of variation increased slightly with age. The age trends in estimated heritabilities were not statistically clear, and were mixed. For DBH, age-13 heritability estimates were slightly higher, especially for H^2. For the other variables, however, the estimates tended to drop, more so in the case of H^2 than in h^2.

Genetic correlations

Estimated genetic correlations are shown for the respective trials in Tables 4 and 5. DBH 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 LS and velocity ($r_g \approx$-0.9) was especially noteworthy, but velocity was used (along with density) in deriving the measure of LS. 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. To this end, the study material was chosen to represent, if anything, an exaggerated level of variability for DBH (and strongly correlated traits) compared with a base population. That would tend to inflate heritability estimates of DBH (and correlated traits) and, to some degree, of genetic correlations involving DBH. If, however, there were zero heritability for traits such a choice of families would not incur any bias.

The genetic samples represented in the two experiments were somewhat restricted, which reduced 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).

The modest increase in density between the two ages in the female-tester trial was surprising, and it suggests that some partial suppression may have led to choosing, within families, trees of larger stem diameter but lower density for the age-13 sampling. Any such effect, however, was clearly insufficient to mask either a major increase in stiffness (as measured by velocity) or a dramatic drop in predicted longitudinal shrinkage. Nor does it appear to have invalidated estimates of genetic correlations, either between traits or between ages for individual traits. Using x-ray densitometry data from open-pollinated families of '268'-series at Kaingaroa Compartment 1350, Kumar and Lee (2002) reported the average DEN of first five growth rings at breast height as 331 kg/m^3, which increased to 349 kg/m^3 when the first 10 growth rings were analysed. Thus, the increase in average DEN from age 8 to age 13 in this study accords with previous results.

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 DEN 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.

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.

Various estimated genetic correlations among wood properties were predictable, notably the strong correlation between velocity and LS. 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 LS means that this finding remains to be validated. Also noteworthy was the relatively strong observed negative genetic correlation between density and the measure of collapse.

Genotype-by-environment (G × E) interaction was not addressed in this study. While it can be substantial in radiata pine for DBH (Burdon et al. 1997 and references therein), it tends to be minimal for density (e.g. Burdon and Harris 1973; Burdon and Low 1992; Kumar 2004). For the other wood properties, there is an indication that G × E for stiffness, internal checking and ERB is far less than that for DBH (Kumar 2004, 2006).

Some of the genetic parameters, e.g. coefficient of variation and heritability of 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) were in close agreement with those found in this study. Our heritability estimates for collapse (or internal checking) are similar to those reported in radiata pine (Kumar 2004) and spruce (Hannrup et al. 2004). There are only few published studies on genetic interrelationships of wood properties. Our estimates of genetic correlation between density and MoE were in accord with those reported earlier (Matheson et al. 1997; Kumar 2004; Fujimoto et al. 2006). Our results on genetic correlation between density and internal checking are in good general agreement with other findings (e.g. Kumar 2004). Hannrup et al. (2004) also reported negative genotypic correlations between wood ensity 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 DBH with density and stiffness has been reported previously (Kumar 2004; Fujimoto et al. 2006). Overall, there are good prospects of simultaneous genetic improvement of a suite of wood properties, although this is likely to be at appreciable cost in potential genetic gain for stem volume production.

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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.

Age 8				
Trait	Mean	CV (%)	h^2	H^2
DBH (cm)	24.94	12	0.19 (.06)	0.23 (.08)
VEL (km/sec)	1.75	10	0.38 (.13)	0.74 (.22)
DEN (kg/m^3)	342	6	0.60 (.13)	0.60 (.13)
LS (%)	1.04	35	0.33 (.13)	0.68 (.23)
ERB (0 - 3 scale)	1.62	50	0.38 (.08)	0.49 (.09)
Age 13				
DBH (cm)	38.01	14	0.24 (.09)	0.38 (.13)
VEL (km/sec)	2.93	12	0.37 (.10)	0.43 (.13)
DEN (kg/m^3)	354	7	0.32 (.10)	0.49 (.13)
LS (%)	0.20	49	0.29 (.09)	0.38 (.13)
Collapse (0 – 3 scale)	0.90	103	0.16 (.08)	0.60 (.12)

Table 3. Trait meanss (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 (.10)	0.37 (.04)
Velocity (km/sec)	2.59	9	0.35 (.12)	0.56 (.04)
DEN (kg/m^3)	328	6	0.58 (.14)	0.63 (.04)
LS (%)	0.26	39	0.27 (0.15)	0.51 (.04)
Collapse (%)	8.3	36	0.21 (.12)	0.35 (.05)
ERB (0-3 scale)	0.79	74	0	0.27 (.03)

Table 4. Estimates of genetic correlations between DBH 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)	-.12 (0.31)	-

Table 5: Estimates of genotypic correlations between DBH 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 (.09)	-0.30 (.08)	0.12 (.09)	0.33 (.09)	0.23 (.10)
VEL		0.18 (.08)	-0.92 (.01)	-0.10 (.10)	-0.07 (.11)
DEN			0.13 (.08)	0.16 (.09)	-0.59 (.07)
LS				0.10 (.10)	-0.07 (.11)
ERB					-0.15 (.11)