

WOOD DENSITY AND MICROFIBRIL ANGLE IN 10 *PINUS RADIATA* CLONES: DISTRIBUTION AND INFLUENCE ON PRODUCT PERFORMANCE

D. J. COWN, R. D. BALL, and M. J. C. RIDDELL

New Zealand Forest Research Institute,
Private Bag 3020, Rotorua, New Zealand

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ABSTRACT

A 27-year-old *Pinus radiata* D. Don clonal trial (with clones propagated from 7-year-old seedlings) was screened to identify clones with a wide range of branch size, internode length, and mature wood density (outer five rings at breast height). Four trees (ramets) from each of 10 such clones were subsequently chosen for use in wood processing/product performance studies, and wood properties were measured on discs taken from each end of 5-m logs up to the merchantable limit (200-mm small-end diameter). Properties assessed included wood density, microfibril angle, spiral grain, and incidence of compression wood.

Wood density values differed markedly between clones, but within each the overall patterns of density variation were consistent from pith to bark and between stem levels, indicating high heritability. Broad-sense heritability estimates were 0.6 and higher for wood properties, except compression wood (0.43) and knot area ratio (0.38). Over all wood samples, there was strong evidence for heritability of density and spiral grain, good evidence for heritability of microfibril angle, and weak evidence for heritability of compression wood and knot area ratio. In juvenile wood samples there was strong evidence for heritability of density and spiral grain, good evidence for heritability of microfibril angle and knot area ratio, and weak evidence for heritability of compression wood.

Values of Silviscan-2 variables were imputed for each piece of lumber on the basis of the actual sawing patterns for each log. Subsequent analyses examined the relationships between fundamental wood properties, predicted performance, and observed performance.

Two stems from each clone were processed into structural lumber and assessed for drying distortion and stiffness. The major effects on board stiffness were, in order of importance: density, board orientation, and knot area ratio. There was no evidence for an effect of microfibril angle. The major factors contributing to twist were spiral grain and density.

Keywords: wood density; microfibril angle; spiral grain; twist; stiffness; stability.

INTRODUCTION

A large proportion of the future forest establishment in New Zealand will be from progeny of seed-orchard clones. The parent trees have improved growth and form

characteristics compared with the trees that are currently being utilised. However, relatively little is known about the wood properties of these clones or the extent of variation between them in wood properties.

Basic wood density is often considered to be a major contributor to wood quality because it is demonstrably linked to the performance of a wide range of solid-wood and fibre products (Matheson *et al.* 1997; Zhang 1997; Zobel 1997; Cown & Kibblewhite 1980; Panshin & de Zeeuw 1980; Zobel & Jett 1995; Koga & Zhang 2001). Wood density is determined both by the anatomical characteristics of individual cells and the proportions of major growth-ring components (earlywood and latewood). Tree species have characteristic patterns of density within stems (Zobel *et al.* 1959; Pearson & Gilmore 1980), and in *Pinus radiata* the specific values are strongly influenced by a number of factors including tree age (Cown & McConchie 1982; Cown *et al.* 1992), position in the stem (Cown *et al.* 1991; Cown 1992; Tian *et al.* 1995), site (Cown *et al.* 1991; Cown 1999; Cown & Ball 2001), genotype (Harris 1965; Burdon & Harris 1973; Donaldson *et al.* 1995; Cown *et al.* 1992), and silviculture (Sutton & Harris 1974; Cown & McConchie 1981). Since the 1960s, increasing attention has been paid to microfibril angle as an important determinant of cell-wall and solid-wood behaviour, particularly shrinkage (transverse and longitudinal), stiffness, and growth stress development in the corewood and juvenile wood of pines (Wardrop 1951; Barber & Meylan 1964; Harris & Meylan 1965; Cave 1968; Donaldson & Burdon 1995; Astley *et al.* 1997; Booker *et al.* 1997; Harrington *et al.* 1998; Lindstrom *et al.* 2002; Megraw *et al.* 1999; Burdon *et al.* 2004). The apparent significance of microfibril angle has resulted in a strong call for this trait to be included in breeding programmes (Cave & Walker 1994; Walker & Butterfield 1995; Shelbourne 1997; Treacy *et al.* 2000).

The first-formed growth rings (surrounding the pith) in *P. radiata* have low density (normally about 300 kg/m³) and high microfibril angle. Each successive annual ring outwards from the pith increases in wood density (Cown 1999) and decreases in microfibril angle (Donaldson & Burdon 1995; Tsehaye *et al.* 1997). These trends have resulted in the general concept of the inner 10 growth rings being considered as comprising the juvenile wood in *P. radiata* (Cown 1992). It is now widely accepted that microfibril angles are steepest in the juvenile wood at the base of the stem in pines (Donaldson & Burdon 1995; Megraw *et al.* 1997). Since the early studies on microfibril angle (Cave 1969), research has shown that both wood density and microfibril angle are related to stiffness and shrinkage (Cown *et al.* 1999; Megraw *et al.* 1999; Evans & Ilic 2001; Xu & Walker 2004), but the exact nature of the relationships remains to be elucidated because of the confounding effects of site, silviculture, tree age, and genetics.

Analyses of the relationships between wood density, microfibril angle, and clearwood stiffness (based on “small clears” samples) in *P. radiata* have indicated that both average wood density and average microfibril angle contribute significantly to stiffness (Donaldson 1995; Cown *et al.* 1999; Beauregard *et al.* 2002). Recent developments in wood property assessment (SilviScan-2) have provided more detailed measures of density and microfibril angle patterns within stems (Evans *et al.* 1995; Evans & Kibblewhite 2002).

The current study was set up to assess within-stem trends in wood density and average microfibril angle in a “mature” crop (age 27 years at sampling), using SilviScan-2 technology. The study set out to examine the relative contributions of these basic wood

properties to predicted clearwood stiffness and compare with the actual results from a sawing study in which stiffness and drying distortion were assessed in full-length (5-m) lumber. The structure of the sample also allowed estimates of clonal effects and of heritabilities of some important wood properties.

MATERIALS AND METHODS

Wood samples were obtained from a clonal trial, originally containing 216 different clones, established in clonal blocks using cuttings from 7-year-old trees grown from seed collected from visually selected parent trees in the forest. The trial was established in 1968 at 1370 stems/ha, thinned at ages 7 and 13 to a final stocking of 350 stems/ha, and pruned to about 4 m in two lifts. Previous studies indicated that the effects of physiological ageing on wood properties (especially wood density) should not be a major concern in material of this type (Lausberg *et al.* 1995). However, Donaldson (1996) found some evidence of an ageing effect on microfibril angle, particularly in plants from ortets greater than 5 years old. In this study, the desire to use mature trees of clonal origin outweighed the possible influence of physiological age on microfibril angle.

In 1995, field screening for breast-height outerwood wood density (five growth rings) was undertaken on a total of 46 clones, and 10 clones were selected to represent a range in both visible characteristics (stem size and branching) and wood density. Two members of each of the 10 clones were felled in 1996 and discs (50 mm thick) were obtained from the base, the top of the pruned butt log (generally *ca* 4 m), and the top of subsequent 5-m log lengths to a top diameter of approximately 200 mm. The discs were measured for spiral grain using the method of Young *et al.* (1991) and a radial pith-to-bark strip was removed for a SilviScan-2 study of wood properties, avoiding any obvious defects such as knots and compression wood. All radial strips were resin-extracted in acetone and precision-machined to a tangential thickness of 2.0 mm. The radial strips were conditioned at 20°C and 40% RH (7% moisture content) before SilviScan-2 analyses, with a radial resolution of 0.2 mm (Evans *et al.* 1995, 2000; Evans 1997). The following variables were assessed for each growth ring:

- (1) Ring width (RW — mm)
- (2) Ring density (Density — kg/m³)
- (3) Ring microfibril angle (MFA — degrees)
- (4) Spiral grain (SG — degrees)
- (5) Predicted clearwood stiffness (E_p — GPa)

In a sawmill, 80 logs (10 clones × 2 stems × 4 log height classes) were processed to structural lumber (40 × 90 mm finished size) using two sawing patterns (50% using a central cant — 100 or 200 mm; and 50% random width — subsequently resawn to structural dimensions) yielding about 800 boards. Individual logs were treated separately, with the juvenile (inner 10 rings) and mature wood zones identified with paint. All lumber was dried to 10% m.c. under a high temperature schedule (120/70°C) with weight restraint, as is normal commercial practice in New Zealand. Each piece was given a unique number to identify the source log and assessed for drying distortion (New Zealand Grading Rules) before machine grading into stiffness classes. Juvenile wood and compression wood scores were allocated to each board.

Lumber measures included:

- (1) Distortion (twist, crook, bow — mm)
- (2) Stiffness (MoE as a plank — E_p)
- (3) Knot area ratio (KAR — %)
- (4) Growth ring position and orientation (Pos; Angle)
- (5) Spiral grain (SG — degrees)
- (6) Proportion of juvenile wood (JW — %)
- (7) Compression wood score (CW — %)

The sawing patterns for each log were recorded to allow subsequent allocation of SilviScan-2 properties to each individual board on the basis of ring width patterns and growth ring properties at the log ends. Assuming symmetry about the longitudinal axis of each log, SilviScan properties were assigned to the rectangle covered by the end of each board in the sawpattern (Fig. 1) to give a value for both ends of each board. The board average was then calculated as the average of the values from each end. Some of the results have been reported by Cown *et al.* (2002).

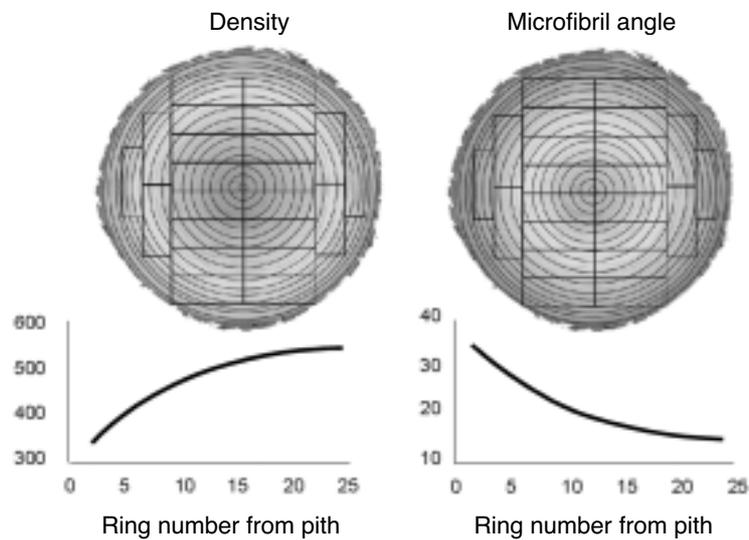


FIG. 1—Allocation of data to boards (using individual stem data).

Statistical Methods

Heritability estimation and tests for clonal effects

For each wood property or performance characteristic, Linear Mixed Effects models (LME, Pinheiro & Bates 2000) with random clone effects were fitted to tree-mean data to estimate variance components. The broad-sense heritability (ratio of clonal to total variance) was estimated as:

$$\hat{H}^2 = \hat{\sigma}_c^2 / (\hat{\sigma}_c^2 + \hat{\sigma}_e^2) \quad (1)$$

where \hat{H}^2 is the heritability estimate and $\hat{\sigma}_c^2, \hat{\sigma}_e^2$ are clone and residual (tree-within-clone) variance components. Posterior distributions for parameters, including estimates and 95% credible intervals were estimated using a Bayesian approach with parameters estimated using Gibbs sampling, a computationally intensive Markov Chain Monte Carlo (MCMC) method (*see, e.g., Gelfand et al. 1990*).

To assess evidence for a clonal effect the model (H_1) with a clonal variance component, representing the alternative hypothesis, was compared to a model (H_0) with no clonal variance component, representing the null hypothesis. Posterior probabilities for each model were estimated by first estimating the Bayes factor then combining this with prior probabilities for the models to posterior probabilities. Prior probabilities of 0.5 were used effectively assuming each model was *a priori* equally likely. With this prior, a posterior probability value greater than 0.5 is interpreted as evidence for a real effect, while a value less than 0.5 is evidence against a real effect.

An MCMC sampler was implemented using the BUGS system (Spiegelhalter *et al.* 1995). Posterior probabilities ($\Pr(H_1 | y)$, where y represents the data) and Bayes factors (B) were estimated for each trait. Bayes factors were estimated using the a modification of the Savage-Dickey density ratio (Dickey 1971; *see also Raftery 1996*) for nested models.

The *Bayes factor*, given by the ratio of the probability of observing the data under H_1 to that under H_0 , i.e.:

$$B = \Pr(y | H_1) / \Pr(y | H_0) \quad (2)$$

gives a more rigorous measure of evidence than the classical P -value, which has no interpretation as strength of evidence for H_1 independent of sample size (*see, e.g., Berger & Berry 1988*). One way to estimate the Bayes factor (B) for nested models is to use the Savage-Dickey density ratio given by:

$$B = \frac{\pi(\theta = 0)}{f(\theta = 0 | y)} \quad (3)$$

where θ is the variable being tested. For testing for non-zero clonal effects $\theta = H^2$, $\theta \geq 0$ in H_1 , and $\theta = 0$ corresponds to H_0 . The expression $\pi(\theta = 0)$ denotes the prior distribution for θ in H_1 evaluated at $\theta = 0$, and $f(\theta = 0 | y)$ is the marginal posterior distribution for θ evaluated at $\theta = 0$. A Beta(0.7,0.7) distribution was used as a prior for H^2 . Marginal posterior distributions for one or more variables are estimated from the Gibbs sampler output by simply ignoring values of unwanted variables. Our modification to the Savage-Dickey ratio is to replace $\theta = 0$ with $0 \leq \theta \leq \varepsilon$ in (3), where ε is a small positive real number, giving

$$B \cong \frac{\Pr_\pi(0 \leq \theta \leq \varepsilon)}{\Pr_f(0 \leq \theta \leq \varepsilon)} \quad (4)$$

where $\Pr_\pi(0 \leq \theta \leq \varepsilon)$ and $\Pr_f(0 \leq \theta \leq \varepsilon)$ denote the probabilities that $0 \leq \theta \leq \varepsilon$ under the densities π, f respectively. We do this because there may not be many posterior samples near zero for some traits. We use $\varepsilon = 0.05$ for most traits. Higher values $\varepsilon = 0.1$, or even $\varepsilon = 0.2$, were used where necessary for the higher heritability traits (density and spiral grain), in order to obtain a reasonable number of samples for the estimate. This is somewhat conservative, especially when $\varepsilon = 0.1$ or $\varepsilon = 0.2$; however, for the traits where $\varepsilon \geq 0.1$ is used the Bayes factor estimates are large even with the larger values of ε .

Posterior probabilities for non-zero clonal variances (represented by $\Pr(H_1 | y)$) are given, assuming a prior probability of $\pi(H_1) = 0.5$ for each trait. The posterior probabilities are related to the Bayes factors and prior probabilities by

$$\Pr(H_1 | y) / \Pr(H_0 | y) = B \times \pi(H_1) / \pi(H_0) \quad (5)$$

i.e.,

$$\text{posterior odds} = \text{Bayes factor} \times \text{prior odds} \quad (6)$$

We have used a prior probability of $\pi(H_1) = 0.5$ for each trait, mainly for convenience. This gives posterior probabilities that do not use information from previous studies. Readers may wish to use different values reflecting results from other studies. Noting that $\Pr(H_0 | y) = 1 - \Pr(H_1 | y)$, and $\pi(H_0) = 1 - \pi(H_1)$, readers can substitute their own values for $\pi(H_1)$ to obtain their own posterior probabilities for heritability.

The Bayesian approach is recommended for heritability estimation because of the inherent skewness in heritability estimates (as exemplified in our results) unless sample sizes are large (since heritability is bounded between 0 and 1). Additionally, our approach avoids the problem with REML estimation when variance components are small (some packages give meaningless negative estimates, while others arbitrarily set small variance components to zero), which is an obvious serious limitation when testing a hypothesis that a variance component is non-zero. A further (related) advantage of the Bayesian approach with estimates using MCMC sampling is the removal of reliance on “asymptotic” assumptions which require large sample sizes for validity of inference.

Note:

Common analyses based on maximum likelihood or REML, and confidence limits implicitly assume a prior probability of 0 for zero heritability — logically, to test for non-zero heritability one must have a non-zero probability for zero heritability. Just because a lower 95% confidence limit is greater than zero need not imply evidence for non-zero heritability. With LME models this is always the case, since LME models use an “unconstrained parameterisation” for the variance structure which means that only physically possible, i.e., positive and non-zero values for variance estimates will be obtained, when confidence intervals are back-transformed to the original scale. With other statistical software negative values can be obtained for estimates and confidence limits, which is problematic for interpretation since heritability cannot be negative.

Estimation and evidence for effects on performance characteristics

The square root transformation was used for twist, crook, and bow to give approximately normally distributed errors.

Multiple regression was used to obtain estimates of effects and indicative estimates of proportions of variability, either overall or partitioned by strata, e.g., within and between trees. Since sums of squares depend on the order of fitting, various models and orders of fitting were examined. It is impractical to present all orders, and so only one is presented here.

To avoid problems with order of fitting and correlated predictors, or bias from stepwise regression from selecting a single best-fitting model or analysis of variance, we used a Bayesian hierarchical model approach (cf. George & McCulloch 1993; Smith & Kohn

1996). Each model involves fitting of a selected subset of the variables being tested. Each parameter was assumed to be equally likely to have an effect as not, i.e., had a prior probability 0.5, so all models were considered equally likely. An adaptation of the Gibbs sampler of George & McCulloch (1993) designed to improve convergence with correlated predictors was run for 11 000 iterations per analysis, giving estimates of posterior probabilities for the most probable models. The MCMC sampler moves around the space of all possible models. Moves are generated, randomly adding or dropping variables, and either accepted (in which case the sampler moves to the new model) or rejected (in which case the sampler remains at the same model). Probabilities of rejection are designed so that in the long run the samples generated are from the posterior distribution.

Marginal posterior probabilities for individual variables (wood properties, and board orientation) which represent the probability that an individual wood property has a real effect, were then estimated for each variable by summing the probabilities of models where the variable was selected. Calculations used Splus (Becker *et al.* 1988). The Gibbs sampler for multiple linear regressions used code developed by R.D.Ball. These analyses were done at the board level and also at the tree-mean level, with the same variables except board orientation.

Analyses were performed on both the juvenile wood (rings 1–10) and all material combined (All) and in order to get more information on microfibril angle some tests were done using specific modulae (${}_sE_p = E_p/\text{density}$).

RESULTS

Wood Properties

The within-stem patterns of variation in wood density and microfibril angle for the 10 clones are illustrated in Fig. 2. The trends conformed to the patterns already established for *P. radiata* (Cown *et al.* 1991; Harris & Cown 1991; Matheson *et al.* 1997; Tsehaye *et al.* 1997; Cown 1999; Zamudio *et al.* 2001).

Means and ranges for wood properties and performance traits by clone are shown in Tables 1a–b.

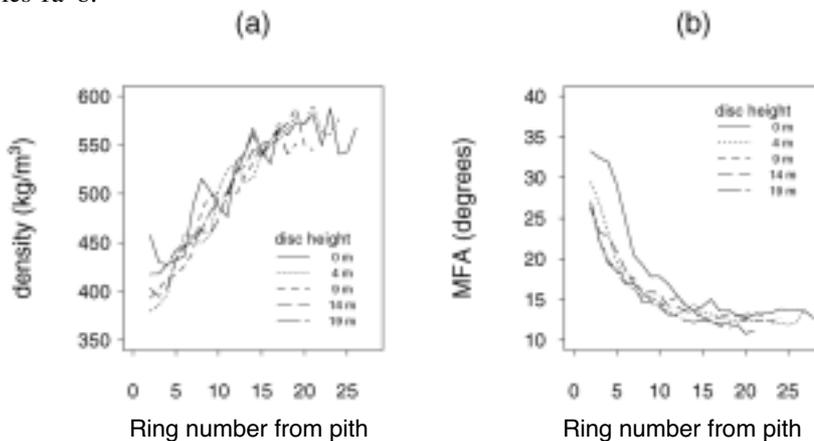


FIG. 2—Overall trends in density and microfibril angle at various levels in the stem.

TABLE 1a—Clonal means (ranges) of wood properties*

Clone	Density (kg/m ³)	MFA (°)	KAR (% of section)	SG (°)	CW (%)
1	539 (442–622)	15.3 (10.2–21.0)	45.6 (0–99)	3.37 (1.19–7.06)	10.94 (5.00–20.40)
2	468 (406–538)	18.6 (13.2–28.4)	43.3 (0–92)	2.65 (0.22–6.11)	8.43 (2.85–12.83)
3	499 (401–553)	16.2 (11.3–30.5)	36.1 (0–90)	2.26 (0.69–3.78)	6.46 (0.00–10.00)
4	563 (431–701)	13.2 (9.2–24.7)	36 (0–84)	6.12 (3.28–10.06)	4.2 (0.00–5.00)
5	516 (401–617)	15.1 (10.2–23.4)	38.7 (0–100)	5.45 (0.42–9.62)	5.28 (2.75–7.93)
6	442 (350–505)	16.1 (11.9–25.6)	37.1 (0–83)	5.32 (2.47–8.07)	3.39 (0.00–7.80)
7	488 (387–608)	16.5 (10.9–27.4)	43 (0–83)	4.06 (1.76–7.44)	4.19 (0.00–7.78)
8	444 (347–505)	16.1 (12.1–26.1)	36.7 (0–98)	4.09 (2.52–7.21)	5.77 (0.00–10.00)
9	537 (403–647)	17.9 (10.7–31.1)	36.1 (0–78)	5.48 (0.64–11.93)	9.86 (5.00–15.00)
10	482 (387–552)	13.3 (10.6–27.6)	39.1 (0–100)	3.63 (1.41–6.95)	7.85 (2.15–12.69)
Average	497	15.8	39.2	4.24	6.63
CV(%) [†]	8.5	21.5	60.1	37.1	48.5

* MFA microfibril angle; KAR knot area ratio; SG spiral grain; CW compression wood

[†] Within-clone coefficient of variation, as a percentage, averaged over clones.

TABLE 1b—Clonal means (ranges) of performance characteristics

Clone	Avg. E_p (GPa)	Avg. sE_p ×1000	Crook (mm)	Bow (mm)	Twist (mm)
1	10.32 (5.84–16.7)	19.2 (11.2–27.9)	3.40 (0–16)	7.37 (0–52)	2.16 (0–14)
2	9.38 (4.54–14.5)	20.0 (11.1–30.3)	6.57 (0–28)	9.91 (0–40)	2 (0–16)
3	9.81 (4.35–17.2)	19.6 (10.5–32.6)	3.37 (0–14)	7.17 (0–53)	1.64 (0–12)
4	10.89 (5.90–18.6)	19.4 (10.9–29.6)	4.54 (0–20)	6.34 (0–31)	5.62 (0–20)
5	10.03 (4.86–19.7)	19.4 (10.1–36.7)	4.83 (0–17)	12.56 (0–40)	6.18 (0–17)
6	9.14 (4.13–14.3)	20.6 (10.8–18.9)	4.68 (0–26)	8.25 (0–27)	3.92 (0–12)
7	10 (4.29–15.7)	20.6 (10.6–30.9)	3.76 (0–17)	6.59 (0–20)	3.30 (0–12)
8	8.84 (4.62–13.6)	19.9 (9.9–31.1)	3.57 (0–16)	6.86 (0–37)	3.34 (0–14)
9	9.62 (4.92–16.9)	18.0 (10.7–27.9)	4.81 (0–17)	10.46 (0–34)	4.69 (0–20)
10	9.61 (4.88–19.6)	19.9 (10.0–38.5)	4.04 (0–31)	8.45 (0–52)	3.37 (0–16)
Average	9.76	19.7	4.36	8.40	3.62
CV(%) [*]	24.1	20.1	87.1	82.4	99.2

* Within-clone coefficient of variation, as a percentage, averaged over clones.

Correlations at the clone, tree, and board level are shown in Tables 2a–c. There were no statistically significant correlations at the clone or tree levels, mainly reflecting the fact that the minimum significant correlations at these levels are quite large (0.63, 0.44 for $p = 0.05$, respectively), meaning that only large correlations could be detected. At the board level the main correlations were between density and microfibril angle (–0.62, –0.64 for juvenile wood and all-wood samples respectively), and between density and knot area ratio (–0.32 for all-wood samples), with all other correlations less than 0.3 .

TABLE 2a—Clone-level correlations between wood properties for juvenile wood samples (above diagonal) and all-wood samples (below diagonal).

	Density	MFA	KAR	SG	CW
Density	1.00	–0.31	–0.05	0.22	0.37
MFA	–0.33	1.00	–0.22	–0.16	0.27
KAR	0.01	–0.20	1.00	–0.34	0.41
SG	0.34	–0.31	–0.46	1.00	–0.17
CW	0.32	0.27	0.41	–0.41	1.00

Minimum statistically significant correlations: 0.63 ($p = 0.05$), 0.77 ($p = 0.01$), 0.87 ($p = 0.001$)

TABLE 2b—Tree-level correlations between wood properties for juvenile wood samples (above diagonal) and all-wood samples (below diagonal).

	Density	MFA	KAR	SG	CW
Density	1.00	–0.31	–0.03	0.21	0.29
MFA	–0.35	1.00	–0.14	–0.14	0.16
KAR	0.00	–0.17	1.00	–0.29	0.35
SG	0.31	–0.26	–0.34	1.00	–0.13
CW	0.25	0.16	0.41	–0.31	1.00

Minimum statistically significant correlations: 0.44 ($p = 0.05$), 0.56 ($p = 0.01$), 0.68 ($p = 0.001$)

TABLE 2c—Board level correlations between wood properties for juvenile wood samples (above diagonal) and all wood samples (below diagonal).

	Density	MFA	KAR	SG	CW
Density	1.00	–0.62	–0.19	–0.02	0.10
MFA	–0.64	1.00	0.07	0.04	0.16
KAR	–0.32	0.22	1.00	0.06	–0.08
SG	–0.24	0.23	0.27	1.00	–0.10
CW	0.14	0.09	–0.20	–0.18	1.00

Minimum statistically significant correlations 0.05 ($p = 0.05$), 0.07 ($p = 0.01$), 0.08 ($p = 0.001$)

Variance component estimates (shown as standard deviations) are shown in Table 3a. The last column of Table 3a gives the posterior probability for a non-zero clone variance component (i.e., evidence for non-zero heritability) assuming a prior probability of 0.5 for non-zero heritability. Heritability estimates in Table 3a were estimated in a model with random clone effects for the data consisting of tree averages of attributes. This model was used because working with tree averages is similar to the common situation where single-trait measurements are made on trees, and it also simplifies the calculation of confidence

limits for the heritability estimates. Alternative heritability estimates can also be obtained from the variance components in Table 3a, using the fact that there were approximately four log classes per tree and 16 boards per log-height class. Posterior summary statistics for heritabilities, Bayes factors, and posterior probabilities for a non-zero clone variance component from the Gibbs sampling model are shown in Table 3b.

TABLE 3a—Square roots of variance components, and heritability estimates* for wood properties. The variance components are estimated in a model allowing for fixed effects of log height class (in four groups: first, second, third/fourth, fifth and higher logs), with random effects for clones, trees within clones, logs within trees, and boards within log.

		Clone	Tree	Log	Board	\hat{H}^2 (95% c.i.)
Juvenile wood	Density/100	0.37	0.00	0.10	0.39	0.96(0.86–0.99)
	MFA	1.66	0.86	1.38	3.08	0.69(0.32–0.92)
	KAR	4.67	2.91	0.82	16.56	0.62(0.23–0.89)
	CW	1.86	2.21	NA†	2.29	0.43(0.09–0.87)
	SG	1.29	0.23	0.74	1.40	0.87(0.64–0.96)
All-wood	Density/100	0.39	0.07	0.11	0.44	0.93(0.79–0.98)
	MFA	1.46	0.89	1.46	3.05	0.66(0.28–0.90)
	KAR	2.83	2.24	1.99	19.00	0.38(0.06–0.87)
	CW	1.94	2.29	NA†	2.19	0.43(0.09–0.85)
	SG	1.29	0.23	0.74	1.40	0.87(0.64–0.97)

* Estimated as $\hat{H}^2 = \hat{\sigma}_c^2 / (\hat{\sigma}_c^2 + \hat{\sigma}_e^2)$ in a mixed model for tree-averaged trait values with random clone effects. This is an estimate of broad-sense heritability. Estimates are probably upwardly biased for density, since clones were sampled to give a range of outer-wood densities; 95% confidence intervals were estimated by simulation from the asymptotic covariance structure for variance parameters.

† A model with random log effects could not be fitted for CW, probably due to limited sample size and a number of missing values.

TABLE 3b—Posterior statistics for heritability*. Posterior distributions for heritabilities were estimated using Gibbs sampling. Columns shown are the mode (maximum marginal posterior estimate), median, 95% credible interval, the Bayes factor (*B*), and $\text{Pr}(H_1: \sigma_c^2 > 0)$ the posterior probability for a non-zero clone variance component.

		Mode	Median	95% ci	B	$\text{Pr}(H_1: \sigma_c^2 > 0)$
Juvenile wood	Density	0.94	0.92	0.74—0.98	23053	>0.999
	MFA	0.70	0.62	0.15—0.88	73	0.982
	KAR	0.63	0.55	0.12—0.85	36	0.973
	CW	0.34	0.38	0.07—0.77	11	0.917
	SG	0.87	0.83	0.49—0.95	1701	>0.999
All-wood	Density	0.92	0.89	0.67—0.97	4913	>0.999
	MFA	0.71	0.63	0.16—0.88	54	0.987
	KAR	0.24	0.34	0.07—0.74	9	0.899
	CW	0.34	0.38	0.07—0.77	11	0.917
	SG	0.87	0.83	0.49—0.95	1958	>0.999

* Estimated as $\hat{H}^2 = \hat{\sigma}_c^2 / (\hat{\sigma}_c^2 + \hat{\sigma}_e^2)$ in a model for tree-averaged trait values with random clone effects. Bayes factors were estimated using the Savage-Dickey density ratio estimated from 1 000 000 iterations of the Gibbs sampler for each attribute. Broad-sense heritability estimate of density is possibly upwardly biased since clones were sampled to give a range of outerwood densities.

The heritability estimates for density are high and there is strong evidence for heritability of density (estimates 0.96, 0.93 in juvenile and all-wood, respectively, in Table 3a, and posterior probability greater than 0.999 in Table 3b). From an Splus multistratum analysis of variance with tree and log error terms (not shown) and fixed clone effects, we found that clones explained 88% of the tree-level variation in all-wood density. It should be noted, however, that the original clone selection ensured a range of outerwood density, and so the heritability estimates for density will be biased upwards.

Slightly lower estimates and lower limits for the confidence intervals were obtained from the Gibbs sampler (Table 3b) than from the REML estimation (Table 3a). This may be due to the inherent skewness of the posterior distribution for heritability shown in Fig. 3. This skewness is expected except with very large sample sizes since the values are limited to the interval from 0 to 1.

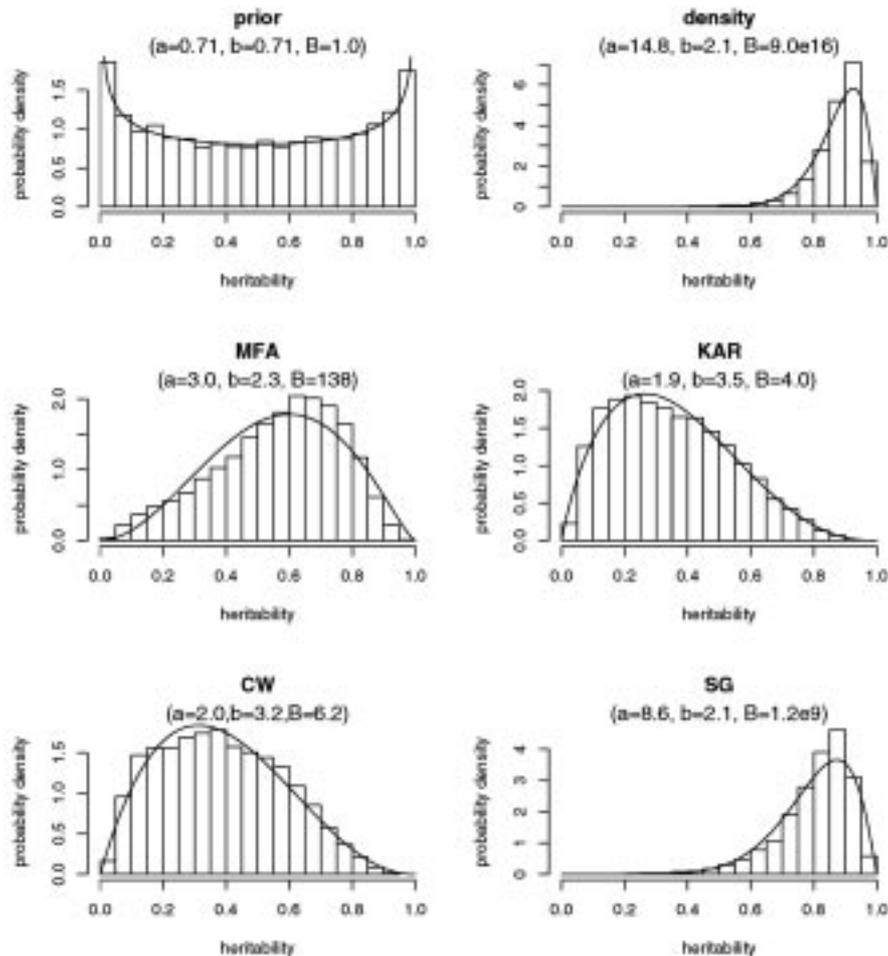


FIG. 3—Posterior density estimates for broad-sense heritabilities of wood properties. In each panel, the values a, b are parameters of a Beta distribution approximating the posterior, and the value B is the Bayes factor for testing for a non-zero clonal variance component (and hence heritability).

The marginal posterior distributions for heritabilities are shown in Fig. 3. Interestingly, most marginal posterior distributions were well approximated by Beta distributions. Bayes factors and parameters of the approximating Beta distributions are also shown. These approximations could also be used to estimate the probability of low heritability values for use in the Bayes factor calculation (Eq. 4). The Bayes factors indicate strong evidence for heritability of density and spiral grain (posterior probability > 0.999), as well as good evidence for heritability of microfibril angle (posterior probabilities of around 0.98 for both juvenile wood and all-wood) in both the all-wood and juvenile wood data-sets, and good evidence for knot area ratio with posterior probability 0.98 (juvenile wood only). There was moderate evidence for knot area ratio (all-wood) and compression wood (juvenile wood and all-wood), with posterior probability around 0.9.

Previous studies of wood properties in this trial (four trees/clone) confirmed a strong clonal effect, with high heritabilities for average wood density and within-ring density components (Cown & Ball 2001; Riddell *et al.* 2002). In this study, partitioning some of the effects also revealed evidence of significant genetic control over several important variables. Square roots of variance components at the clone, tree, log, and board levels estimated by REML, and broad sense heritability estimates and 95% confidence limits are shown in Table 3a.

Overall, clones explained 88% of the tree-level variation in density (it should be noted that the original clone selection ensured a range of outerwood wood density). On the same basis, clones accounted for only 17% of the variance in microfibril angle, and within-log variation accounted for 74%. Clone explains 65% of the tree-level variation in microfibril angle.

Performance Characteristics

The individual boards had a wide range of stiffness values (4.1–19.7 GPa) (Table 1b) and some drying distortion outside the allowable grade limits. The overall results conform to the generally known patterns of wood properties relating to position within stems (Cown *et al.* 1994) as well as genetic influences (Cown & Ball 2001). Approximate posterior probabilities for a clone effect on performance traits (assuming a prior probability of 0.5), are shown in Table 4a. The proportions of clonal variance (possibly biased estimates of broad-sense heritability) for performance traits are shown in Table 4b.

As with wood properties, the confidence limits for heritabilities of most performance traits are quite wide. There was good evidence for heritability of $avg.E_p$, \sqrt{bow} and \sqrt{twist} for both juvenile wood and all-wood, and for ${}_sE_p$ (all-wood). The heritability for $avg.E_p$ is high, reflecting the influence of density. The estimated heritability of specific modulus is lower especially in juvenile wood, with only weak evidence for heritability (estimated heritability of 0.27, and posterior probability of 0.84).

Drivers for Performance

Stiffness

A previous study of small samples from this trial (Cown *et al.* 1999) revealed effects of both wood density and microfibril angle in the juvenile wood zone (within 10 rings from the pith, $R^2 = 59\%$), but a dominating effect of wood density in the mature wood (>10 rings from the pith, $R^2 = 74\%$).

TABLE 4a—Square roots of variance components, and heritability estimates* for performance characteristics. The variance components are estimated in a model allowing for fixed effects of log height class (in four groups: first, second, third/fourth, fifth and higher logs), with random effects for clones, trees within clones, logs within trees, and boards within log.

		Clone	Tree	Log	Board	\hat{H}^2 (95% c.i.)
Juvenile wood	E_p	0.56	0.33	0.003	2.00	0.61 (0.22–0.90)
	sE_p	0.42	0.70	0.004	3.70	0.23 (0.01–0.90)
	Sqrt(crook)	0.19	0.04	0.29	0.92	0.34 (0.04–0.86)
	Sqrt(bow)	0.28	0.00	0.29	1.28	0.66 (0.28–0.91)
	Sqrt(twist)	0.52	NA†	NA†	0.93	0.92 (0.76–0.98)
All-wood	E_p	0.50	0.20	0.20	2.27	0.72 (0.37–0.92)
	sE_p	0.60	0.21	0.40	3.87	0.59 (0.19–0.89)
	Sqrt(crook)	0.18	0.10	0.25	0.94	0.42 (0.07–0.86)
	Sqrt(bow)	0.30	0.003	0.29	1.25	0.74 (0.39–0.93)
	Sqrt(twist)	0.40	0.04	0.14	0.95	0.86 (0.61–0.96)

* Estimated as $\hat{H}^2 = \hat{\sigma}_c^2 / (\hat{\sigma}_c^2 + \hat{\sigma}_e^2)$ in a mixed model for tree-averaged trait values with random clone effects. This is an estimate of broad sense heritability. Estimates are probably upwardly biased for density, since clones were sampled to give a range of outerwood densities; 95% confidence intervals were estimated by simulation from the asymptotic covariance structure for variance parameters.

† A model with random log effects could not be fitted for twist, juvenile boards, probably due to limited sample size and a number of missing values..

TABLE 4b—Posterior statistics for heritability of performance characteristics*. Posterior distributions for heritabilities were estimated using Gibbs sampling. Columns shown are the mode (maximum marginal posterior estimate), median, 95% confidence interval, the Bayes factor (B), and $\Pr(H_1: \sigma_c^2 > 0)$, the posterior probability for a non-zero clone variance component.

		Mode	Median	95% c.i.	B	$\Pr(H_1: \sigma_c^2 > 0)$
Juvenile wood	E_p	0.63	0.54	0.11–0.85	33	0.97
	sE_p	0.15	0.27	0.06–0.68	5	0.84
	Sqrt(crook)	0.19	0.31	0.06–72	7	0.88
	Sqrt(bow)	0.68	0.60	0.14–0.87	54	0.98
	Sqrt(twist)	0.92	0.88	0.64–0.97	759	0.999
All-wood	E_p	0.75	0.66	0.19–0.90	104	0.99
	sE_p	0.50	0.51	0.10–0.84	29	0.97
	Sqrt(crook)	0.30	0.36	0.07–0.76	10	0.91
	Sqrt(bow)	0.76	0.69	0.21–0.90	142	0.99
	Sqrt(twist)	0.87	0.82	0.47–0.95	381	0.997

* Estimated as $\hat{H}^2 = \hat{\sigma}_c^2 / (\hat{\sigma}_c^2 + \hat{\sigma}_e^2)$ in a model for tree-averaged trait values with random clone effects. Bayes factors were estimated using the Savage-Dickey density ratio estimated from 1 000 000 iterations of the Gibbs sampler for each attribute.

In this study, there was an opportunity to examine “clearwood” stiffness as predicted from SilviScan-2 density and microfibril angle, as well as to compare predictions with actual “in-grade” boards tested for stiffness. Overall, the clones with the highest average wood density also gave the highest stiffness values (Table 1). Observed *vs* predicted values

for two models for stiffness are shown in Fig. 4(a) and (b). The first model, in which stiffness is proportional to density/microfibril angle, gave a good fit to eucalypt data (Evans & Ilic 2001), but does worse than density alone here (panel (a)). Linear models in terms of density, microfibril angle, etc., do better (panel (b)), with $R^2 = 46\%$.

The data used in Fig. 4 panel (a) were derived from small clear samples. Lumber visual grades (as opposed to machine grades) recognise the known influence of branch size and location of lumber stiffness and strength. Therefore it is unreasonable to expect even highly accurate predictions of clearwood stiffness (Fig. 4, panel (a)) to be closely related to actual board stiffness (Fig. 4, panel (b)).

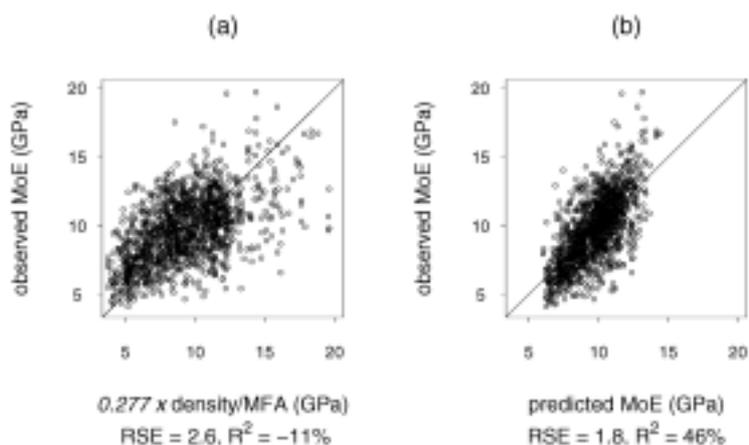


FIG. 4—Observed vs predicted board stiffness for a linear model. In panel (a) the model was of the form $E = \text{density/microfibril angle}$ suggested by Evans & Ilic (2001). In panel (b), the model fitted was a linear multiple regression model in terms of density, knot area ratio, microfibril angle, spiral grain, compression wood, angle, position, and ring width, and had $RSE = 1.8$, $R^2 = 46\%$. Clone and tree random effects were ignored.

The “%SS_{seq}” column shows sequential sums of squares as variables are fitted in the order shown, while the “%SS_{last}” column shows sums of squares for each variable if it is fitted last. Looking at the “%SS_{seq}” column we see that density alone explains a substantial percentage of the variation (28% in juvenile wood boards, 34% in all boards) with smaller contributions to the remaining variation from knot area ratio, microfibril angle, angle, and ring width. Many variables are statistically significant with $P_{\text{seq}} < 0.001$ in the sequential analysis, but this may be an artefact of within-tree patterns of variation. Spiral grain and microfibril angle drop out, indicating there is no evidence of an independent effect of these variables.

The values in the “%SS_{last}” column are smaller, particularly density, reflecting the correlations due to within-tree patterns of variation. Marginal posterior probabilities are given in Table 5a for each of the likely causal variables on specific modulus, i.e., the wood property variables and board orientation (angle), at the board level. The corresponding marginal posterior probabilities are given in Table 5b for effects on specific modulus *at the tree level*. These marginal probabilities are interpreted as probabilities that each variable has a real effect. Thus from Table 5a, for juvenile wood boards there is strong evidence

TABLE 5a—Marginal posterior probabilities for effects of wood properties and board orientation on specific modulus (${}_sE_p$) of boards.

	Density	KAR	MFA	SG	CW	Angle
Juvenile wood	0.08	0.969	0.35	0.11	0.01	0.9995
All-wood	0.36	0.999	0.51	0.72	0.12	0.9990

TABLE 5b—Marginal posterior probabilities for effects of wood properties on tree-average specific modulus (${}_sE_p$).

	Density	KAR	MFA	SG	CW
Juvenile wood	0.42	0.39	0.33	0.33	0.29
All-wood	0.62	0.38	0.38	0.38	0.41

(with posterior probability 0.9996, i.e., nearly 1) for an effect of angle, and fairly good evidence for knot area ratio (probability 0.969), and for all boards there is strong evidence for effects of both angle and knot area ratio (probability >0.999), and possible effects (but very weak evidence) of microfibril angle (probability 0.51) and spiral grain (probability 0.72). At the tree level (Table 5b) there is no evidence for any effect on specific modulus (probabilities from 0.29 to 0.62).

After allowing for density and knot area ratio, microfibril angle accounted for only 3% and 1.6% of the variance in MoE for juvenile wood and all-wood respectively. The %SS_{seq} and %SS_{last} values for density in Table 6 were both around 10–20 times larger for density than microfibril angle. Knot area ratio accounted for a similar proportion of the variation to microfibril angle in juvenile wood when fitted sequentially before microfibril angle or

TABLE 6—Factors influencing board stiffness (multiple regression models for MoE).

	Coeff.	s.e.	%SS _{seq}	P_{seq}	%SS _{last}	P_{last}
Juvenile wood (RSE = 1.6, $R^2 = 41\%$, n = 785 boards)						
(Intercept)	5.20	1.07	*	*	*	*
Density	0.01	<0.01	28.2	<0.001	3.8	<0.001
KAR	-0.01	<0.01	3.0	<0.001	1.3	<0.001
MFA	-0.04	0.02	2.7	<0.001	0.2	0.12
SG	-0.04	0.03	0.8	0	0.1	0.2
CW	0.02	0.02	0.1	0.4	0.2	0.12
Angle	0.02	<0.01	3.6	<0.001	2.7	<0.001
Pos	0.01	<0.01	0.2	0.1	0.4	0.02
RW	-0.15	0.03	2.4	<0.001	2.4	<0.001
All-wood (RSE = 1.8, $R^2 = 46\%$, n = 1476 boards)						
(Intercept)	3.52	0.86	*	*	*	*
Density	0.01	<0.01	34.1	<0.001	5.6	<0.001
KAR	-0.02	<0.01	5.1	<0.001	1.6	<0.001
MFA	-0.01	0.02	1.6	<0.001	0	0.63
SG	-0.04	0.03	1.0	<0.001	0.1	0.2
CW	0.00	0.01	0.0	0.48	0.0	0.78
Angle	0.02	<0.01	2.6	<0.001	2.3	<0.001
Pos	0.00	<0.01	0.3	0.002	0.2	0.02
RW	-0.11	0.02	1.3	<0.001	1.3	<0.001

five times more when fitted last. If fitted first, microfibril angle accounted for about half of the variation in specific modulus that knot area ratio did.

Drying distortion

Some softwoods have a reputation for exhibiting significant drying degrade, particularly in the juvenile wood. The most prominent feature is often twist, which has been associated with spiral grain in logs and lumber (Cown *et al.* 1994; Johansson & Kliger 2002). Coefficients and sums of squares of a linear regression for $\sqrt{\text{twist}}$ are shown in Table 7. The column definitions and interpretations are as for Table 6. As expected, spiral grain accounts for the major part of the variation with a lesser contribution from density.

Marginal probabilities for effects of wood properties and board orientation on twist are shown in Tables 8a at the board level and 8b at the tree level. There is strong evidence for

TABLE 7—Influence of factors on twist. Linear model for $\sqrt{\text{twist}}$.

	coeff.	s.e.	%SS _{seq}	%SS _{last}
Juvenile wood (RSE = 0.8, $R^2 = 46\%$)				
(Intercept)	2.22	0.52	*	*
Density	0.00	<0.01	0.0	5.9
KAR	0.00	<0.01	0.6	2.9
MFA	-0.04	0.01	0.8	0.3
SG	0.22	0.02	15.2	29.2
CW	-0.01	0.01	0.2	0.6
Angle	0.00	<0.01	0.0	0.2
Pos	-0.01	<0.01	6.3	5.9
RW	0.04	0.01	0.7	0.7
All-wood (RSE = 0.9, $R^2 = 25\%$)				
(Intercept)	2.97	0.44	*	*
Density	0.00	<0.01	1.3	7.9
KAR	0.00	<0.01	0.0	1.0
MFA	-0.01	0.01	0.1	0.1
SG	0.19	0.01	9.4	15.2
CW	-0.01	0.01	0.1	0.2
Angle	0.00	<0.01	0.0	0.0
Pos	0.00	<0.01	0.8	0.7
RW	-0.01	0.01	0.1	0.1

TABLE 8a—Marginal posterior probabilities for effects of wood properties and board orientation on twist.

	Density	KAR	MFA	SG	CW	Angle
Juvenile wood	1.0000	0.92	0.24	0.9997	0.52	0.32
All-wood	0.9997	0.06	0.03	1.0000	0.23	0.08

TABLE 8b—Marginal posterior probabilities for effects of wood properties on tree-average twist.

	Density	KAR	MFA	SG	CW
Juvenile wood	0.52	0.44	0.38	0.9996	0.22
All-wood	0.48	0.45	0.63	0.9995	0.36

effects of density and spiral grain on twist in juvenile wood boards (marginal probability >0.999), moderate evidence for an effect of knot area ratio (probability 0.92), and possible effects (no evidence for or against) of compression wood and angle. There is strong evidence for effects of density and spiral grain on twist in all boards, with evidence against any of the other factors. At the tree level there is evidence of effect of spiral grain (probability >0.999), and possible effects (no evidence for or against) for the other variables including density.

DISCUSSION

Evidence for Clonal Effects

Results are consistent with medium to high heritability of most traits. There was strong evidence for heritability of density, spiral grain, and twist, and good evidence for heritability of microfibril angle and knot area ratio (juvenile wood boards only), and weak evidence for heritability of knot area ratio (all boards) and compression wood. The confidence intervals for heritabilities for some traits are quite wide, e.g., (0.16–0.88) for microfibril angle, owing to the limited number of clones and limited number of ramets per clone; however, it was possible to obtain evidence for heritability of most traits.

It must be borne in mind, however, that there may be a possible moderating effect of maturation on the within-stem radial variation in microfibril angle, which could reduce the apparent impact in this particular material (M.I.Menzies, pers. comm.).

Evidence for Effects on Stiffness

There was strong evidence for an effect of density on stiffness of juvenile wood boards and all-boards, and evidence for effects of knot area ratio and board orientation on specific modulus for all boards. There was no evidence for effect of microfibril angle on specific modulus in this dataset. There was no evidence for effects of any variable on tree-average specific modulus.

It is difficult to separate out causal effects of the variation in wood properties because the within-tree variation in microfibril angle is confounded with other variables with pith-to-bark trends. Simply considering a regression model with a particular set of variables or an ANOVA table with a particular ordering may be misleading. To demonstrate a probable causal effect of one variable, statistical analyses need to show effects, independent of the other variables. Our analysis, calculating posterior probabilities from multiple models, does this.

Megraw *et al.* (1999) and Evans & Ilic (2001) considered *within tree variation*; however, their within-tree analyses did not show evidence for an independent effect of microfibril angle. The apparent effect of microfibril angle or the amount of variation explained may be wholly or in part due to correlations with other wood properties.

Effects on *between-tree variation* are more likely to be causal than effects on within-tree variation due to the confounding caused by within-tree trends in wood properties. Cown *et al.* (1999) found evidence for effects of microfibril angle on between-tree variation in specific modulus of juvenile wood, with a posterior probability greater than 0.99, with density and microfibril angle explaining comparable proportions of between-tree variation

in juvenile wood MoE. Megraw *et al.* (1999) also considered between-tree variation for fixed ring positions and heights, obtaining multiple R^2 values ranging from 62% to 95%, and comparable values of partial correlation coefficients for both density and microfibril angle. Note, however, the minimum significant correlations for $n = 24$ trees and $p = 0.05$, 0.01, 0.001 are 0.40, 0.52, 0.63, respectively, and the values at each ring/height are not independent. They did not quantify their evidence in terms of Bayes factors and posterior probabilities as we have; however, comparison of the p -values with posterior probabilities for a similar sample size here (Tables 2a, 3a, 4a) suggests that quite low p -values are needed for convincing evidence. Therefore, the evidence in terms of partial correlations by Megraw *et al.* (1999), while suggestive, may not represent strong evidence.

The results presented in this paper, and by Cown *et al.* (1999) and Megraw *et al.* (1999), are consistent with effects of microfibril angle on stiffness being smaller than the effects of density, especially when all boards are considered. Recent studies of maturation effects since the study reported here suggest that physiological ageing of the clones (cuttings from 7-year-old trees) in this study may have ameliorated the effects of microfibril angle, especially in the lower butt logs where the microfibril angle is largest (Menzies, pers. comm.). This may have reduced the effects of microfibril angle and hence made them more difficult to detect.

The formulae of Evans & Ilic (2001) showing that MoE is proportional to density/microfibril angle do not hold for our data. Evans & Kibblewhite (2002) compared results for eucalypts and pine, and also found density alone did better than models with MoE proportional to 1/microfibril angle or density/microfibril angle for the pine data. They showed that a direct measure of stiffness from SilviScan densitometry and diffractometry (MOE_{SS} , not yet tested on our data) apparently can provide good predictions for both, with values of R^2 of 86% for pine and 94% for eucalypts. We obtained $R^2 = 46\%$ and an RSE of 1.8 Gpa for a model with density, knot area ratio, microfibril angle, spiral grain, compression wood, angle, growth ring position, and ring width. By comparison, Evans & Kibblewhite (2002) obtained $R^2 = 47\%$ for a model for stiffness of small clears in terms of density alone. For the equivalent model (i.e., a model for stiffness of boards in terms of density alone, not shown), we obtained $R^2 = 34\%$ (35% if microfibril angle is fitted in addition to density; 39% if knot area ratio is fitted in addition to density). The comparison with the work of Evans & Kibblewhite (2002) gives an indication of the increase in error for predicting boards compared with small clear samples, which is to be expected given the additional errors in ascertaining properties of boards. The comparison between models gives an indication of the relative importance of density, microfibril angle, and knot area ratio.

Relative Importance of Effects of Basic Properties on MoE

The effect of density on stiffness is not in question. Theory predicts an effect of microfibril angle, and from other data there is some evidence of an effect of microfibril angle. Considering all boards, the results of this study suggest that density is by far the most important characteristic, with the greatest potential for improvement, as it is less expensive to measure, has higher heritability, and accounts for 10–20 times more variation in the average stiffness of all boards than microfibril angle. Furthermore, knot area ratio appears to be a more important factor than microfibril angle, accounting for 2–5 times more

variation than microfibril angle in all-wood and a similar amount of variation to microfibril angle in juvenile wood. For juvenile wood, the results of Cown *et al.* (1999) suggested that microfibril angle and density may contribute approximately equally to between-tree variation in specific modulus, but that result is not confirmed here, mainly because of the limited number of trees (20) and hence limited power to detect tree level effects.

The results of this paper, and those presented by Cown *et al.* (1999), are consistent with effects of microfibril angle on stiffness being smaller than the effects of density, especially when all boards are considered. To detect an effect of microfibril angle, a good sample size and the right experimental design and/or analysis are needed to avoid within-tree patterns of confounding. Evidence for effects of microfibril angle on modulus of elasticity were found by Cown *et al.* (1999) in a study of small clears looking at the between-tree error stratum for juvenile wood samples, and by Megraw *et al.* (1999) looking at samples from a fixed juvenile wood ring from each of many trees. Xu & Walker (2004) observed changes in stiffness in the longitudinal direction of machine-graded boards near the pith, which could not be explained by density since density was roughly constant in the longitudinal direction; hence they concluded the variation was probably due to microfibril angle.

No variable had a statistically significant effect on between-tree variation in specific modulus.

Twist

The material in this study showed a relatively low level of drying degrade. In common with several other studies, the major contributor to twist was spiral grain, accounting for about 9% of the variation in all wood. There was also evidence for an effect of density accounting for about 1% of the variation in all wood.

CONCLUSIONS

This study supports strong relationships between basic wood properties and board performance in terms of stiffness and stability, and offers further confirmation that the main characteristics (wood density and spiral grain) are under significant genetic control. On the basis of this analysis, there is little statistical evidence for a strong effect of microfibril angle. This may be at least partly attributable to the use of “aged” clones as the study material. In addition to these fundamental wood properties, the study identified a significant effect from knot area ratio on stiffness.

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