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ABSTRACT

A 27-year-old *Pinus radiata* D. Don clonal trial 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 property studies. Gravimetric wood property measurements were made on discs taken from each end of 5-m logs up to the merchantable limit (200 mm small-end diameter) and samples for densitometry obtained from specific positions in the stems. Structural lumber was recovered from four logs from each of two ramets/clone, assessed for drying distortion, and graded mechanically.

The discs were used to derive unextracted density for the juvenile (growth rings 1–10) and mature (rings 11+) portions of the stems at all levels, and samples for X-ray densitometry at 5 m and 20 m. For each annual ring, a number of wood density variables were recorded, including earlywood and latewood measures. Within each of the 10 clones, the overall patterns of density variation were quite consistent from pith to bark and between stem levels, and demonstrated distinct clonal differences. Indicative estimates of heritabilities, age-age correlations, and predictability of final average tree and log densities were derived using linear mixed-effects models from the densitometric data. Both average wood density and intra-ring density component patterns were highly consistent within clones, and heritability estimates were high for most properties assessed. Latewood characteristics were particularly strongly related to growth ring density.

For *P. radiata*, juvenile wood is often conveniently described as the first 10 growth rings from the pith. On this basis, clonal means for juvenile wood volume varied from 39% to 61%. The actual wood properties for this zone, in terms of wood density, differed markedly between clones. Using an alternative technical definition for juvenile wood (proportion of the stem with annual average basic density < 400 kg/m^3), the percentage of juvenile wood varied from 15 to 64%, or from 5 to 13 growth rings. This suggests that clonal selection may be an effective way of controlling the impact of juvenile wood properties.

Keywords: clones; wood density; earlywood; latewood; densitometry; juvenile wood; heritability.

INTRODUCTION

A large proportion of the future forest establishment in New Zealand will be from progeny of the best seed-orchard clones. This select group of parents has better growth and form characteristics than the trees that are now being utilised. However, relatively little is known about the wood properties of these clones or the extent of variation in wood properties between them.

Basic wood density is often considered to be the single most important wood property because of its strong influence on the quality of a wide range of solid-wood and fibre products (Matheson, Spencer, Nyakuengama, Yang, & Evans 1997; Zhang 1997; Zobel 1997; Cown & Kibblewhite 1980; Panshin & de Zeeuw 1980; Megraw 1985; 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 *P. radiata* the specific values are strongly influenced by a number of factors including tree age (Cown & McConchie1982a; Cown *et al.* 1992), position in the stem (Cown 1974, 1980, 1992), site (Cown 1999), genotype (Harris 1965; Burdon & Harris 1973; Donaldson *et al.* 1995; Cown *et al.* 1992), and silviculture (Sutton & Harris 1974; Cown & McConchie 1981). In several species, the latewood component is the most sensitive to environmental influences (Cown 1977) and its variation has the strongest effect on mechanical properties (e.g., Rozenberg *et al.* 1999). Aspects of wood density which can influence utilisation include:

(1) Average stem basic density
(2) Radial density gradient (pith to bark)
(3) Latewood percentage
(4) Earlywood-latewood density contrast.

The first-formed growth rings (surrounding the pith) in *P. radiata* have low density (normally about 300 kg/m^3) and, on average, each successive annual ring outwards from the pith increases by about 6–7 kg/m^3. At the macroscopic level this is often expressed in softwoods as visible changes in the earlywood-latewood ratio (or latewood percentage). Typically, average earlywood density increases from around 300–320 kg/m^3 at the pith to 350–400 kg/m^3 in "mature" wood — often defined as rings 11+ from the pith (Cown *et al.* 1992; Donaldson *et al.* 1995; Cown & Ball 2001). On the other hand, average latewood density increases from 420–460 kg/m^3 near the pith to around 450–550 kg/m^3 in the outer rings (Cown *et al.* 1992). At the same time, there is typically a steep increase in the latewood percentage outwards from the pith at all stem levels, and this is accompanied by a corresponding increase in the average basic wood density of successive growth rings, particularly over the first 10 or so rings (often termed juvenile wood or corewood — Harris & Cown 1991). Typically, average ring basic wood density increases from around 300–320 kg/m^3 at the pith to between 400 and 500 kg/m^3 in mature wood (Cown & McConchie 1983), with a corresponding increase in latewood percentage from 20% to around 60% (Cown *et al.* 1992). These trends contribute to the strong expression of juvenile wood in *P. radiata*.

Several studies have examined the wood density of genetic material (Bannister & Vine 1981; Burdon & Bannister 1973; Burdon & Harris 1973; Burdon & Low 1992; Burdon *et al.* 1992; Donaldson *et al.* 1995; Shelbourne *et al.* 1997; Matheson, Ngakuengama, Yang, & Spencer 1997; Cown & Ball 2001). Estimated heritabilities have generally been relatively high (0.5 to 0.7), and the degree of natural variation such that the potential gains from breeding were estimated to be moderate. Average growth ring wood density has been shown to be highly heritable, and the range of variation described thus far indicates that there is every likelihood that genotypes can be identified which have desirable within-ring or between-ring wood density characteristics.

Bannister & Vine (1981) assessed family density gradients from increment core samples and calculated a narrow-sense heritability for the density gradient as 0.3. Densitometric analyses of thirty 20-year-old half-sib families also revealed strong family differences in average wood density, as well as earlywood and latewood densities, and a radial density increase, which was related mostly to latewood percentage (Cown *et al.* 1992). The spread in family means was dramatic, ranging from 50 kg/m^3 at the pith to 100 kg/m^3 at the bark, suggesting a strong genetic component to the radial gradient. Families with high latewood percentage tended to have high density and a steeper pith-to-bark gradient.

Nyakuengama (1997) also documented radial differences in the gradients of wood density and latewood trends in *P. radiata* progeny. Average earlywood density in the 20-year-old families increased slightly from pith to bark, from an average of around 310 to 360 kg/m^3. Average latewood density similarly increased from 450 to 520 kg/m^3. Latewood percentage, on the other hand, increased from 20% to 60% over the same age, and was much more variable between families. The average difference between earlywood and latewood density is a measure of uniformity. Family means in the trial (EW/LW difference) ranged from 145 to 175 kg/m^3.

A densitometric study of eleven 16-year-old *P. radiata* clones revealed significant differences between clones in several density-related variables (Donaldson *et al.* 1995). Interestingly, a number of clones exhibited within-tree density patterns different from the "norm" in having greater or lesser radial density gradients. Significant clonal differences in ring density components confirmed that there is strong genetic control over within-tree density patterns. There was little difference in the pattern of within-ring density variation between clones, but large differences in the density levels. Earlywood density and latewood percentage contributed most to clonal differences.

The current study set out to document within-stem trends in intra-ring wood density components in a relatively "mature" crop (age 27 years at sampling) and to examine the contribution of genotype.

MATERIALS AND METHODS

Wood samples were obtained from a clonal trial, originally containing 216 different clones (266 series), established in clonal blocks using cuttings from 7-year-old trees grown from seed collected from mass-selected "old crop" trees. 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).

In 1995, field screening for breast height outerwood wood density (five growth rings) was undertaken on 46 clones, and 10 clones were selected to represent a range in both visible characteristics (stem size and branching) and wood density. Two ramets 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 used both for gravimetric measurement of wood density (juvenile wood = rings 1–10; mature wood = rings 11+) and to yield samples for a study of intra-ring density components. In 1997, a further two ramets were felled from each clone and discs were collected from the top of the butt log and the 19-m level only. Pith-to-bark strips were cut from all discs, avoiding any obvious defects such as knots and compression wood. All samples were resin-extracted by refluxing in methanol in a Soxhlet apparatus to extract resin, and conditioned to 10% moisture content. The strips were then precision-machined to a tangential thickness of 1.5 mm prior to scanning with a radioactive source (Fe^{55}) and a scintillation counter (Cown & Clement 1983). Density data were collected in radial increments of 0.3 mm and processed to yield equivalent basic density values. The transition from earlywood to latewood in *P. radiata* may be gradual or steep depending largely on location in the stem. In this study, the boundary was arbitrarily set at a wood density threshold of 500 kg/m^3 (Cown & Clement 1983; Jozsa *et al.* 1989; Koga & Zhang 2001). The following parameters were assessed for each growth ring:

(1)	ring width	(RW)
(2)	earlywood and latewood widths	(EWW; LWW)
(3)	latewood percentage	(LW%)
(4)	ring density	(RD)
(5)	maximum ring density	(Max)
(6)	minimum ring density	(Min)
(7)	intra-ring density range (Max – Min)	(Range)
(8)	earlywood and latewood density	(EWD; LWD)
(9)	intra-ring density uniformity (latewood density – earlywood density)	(UNIF)

Densitometric data allow alternative interpretations of juvenile wood, both biological and technological (Cown 1992), and a related variable to be calculated as the difference in average wood density between juvenile and mature wood (JMDIFF). In this case there were 24 growth rings at breast height and the JMDIFF was defined as the area-weighted average density of rings 16–20 less that for rings 1–5, and was calculated at each of two sample heights (nominally 5 m and 19 m).

Statistical Methods

Linear mixed-effects models were fitted using LME (Pinheiro & Bates 2000). Confidence intervals for genetic and phenotypic age-age correlations and heritabilities were obtained semi-empirically by simulating values of variance model parameters from the asymptotic variance-covariance matrix estimated by LME, and recalculating the quantity of interest. As a check on the asymptotics, confidence intervals for heritabilities (H^2) were also estimated using the standard error of Falconer (1961).

In the LME modelling framework (Pinheiro & Bates 2000) various covariance and correlation structures are possible at each level of "grouping". For the grouping structure we have the clone level, ramets within clones, and discs within ramets, and rings within discs, although we have modelled each height separately, avoiding the need for the disc level of grouping. At each level of grouping it is possible to specify sets of random effects and a variance structure for each set of random effects. At the clone level this implies a separate set of effects for each clone, at the ramet level a separate set of effects for each ramet within clone, etc. Each of these sets of random effects is assigned a covariance or correlation structure. Some common structures are:

(1) Identity (ID): representing the identity matrix, corresponding to independent identically distributed random effects.

(2) Autoregressive of order 1 (AR(1)): representing an autoregressive process for some ordering of the random effects.

(3) Unstructured (UNSTR) representing a general positive definite symmetric matrix.

In the LME framework, models with different covariance structures or fixed effects are compared using the Akaike Information Criteria (AIC) and Bayesian Information Criteria (BIC). Models with lower values of the AIC are likely to give better predictions on future data, while models with lower values of the BIC are more likely to be the "true" model. Models can be fitted with either maximum likelihood or residual maximum likelihood (REML). The REML method (which gives better estimates of variance parameters) is generally used, except when comparing models with different fixed effects, models are fitted using maximum likelihood to give a valid comparison.

Estimation of genetic and phenotypic age-age correlations.

A linear mixed effects (LME) model was fitted to the data from 5 m (height 5) with two levels of grouping: clone, and ramet within clone. Within each ramet were area-weighted density values for the ring groups 1 – 6, 7 – 12, 13 – 18, respectively. In terms of the LME framework, the selected model had random effects at both the clonal level (unstructured model with random effects for ring groups for each clone) and the ramet level (identity model, with a single random effect for each ramet), plus a within-ramet correlation structure (AR(1)). Let *i,j,k* index clone, ramet, and ring group, respectively. In terms of parameters and distributions the model fitted was:

$$y_{ijk} = \mu + b_{ik} + c_{ij} + e_{ijk}; \qquad (1)$$

where μ is the overall average value
y_{ijk} is the area-weighted average density value for clone i, ramet j, ring group k,
b_{ik} is the random effect for ring class k within clone i,
c_{ij} is the random effect for ramet j within clone i,
and e_{ijk} is the residual for ring class k.

The covariance of the random effects is given by

$$\{e_{ijk} : k = 1,2,3\} \sim N(0,V_r); \{c_{ij} : j = 1,2,3,4\} \sim N(0,I_4\sigma_R^2); \textit{ for each } i = 1,2,\ldots 10; \qquad (2)$$

and

$$\{e_{ijk} : k = 1,2,3\} \sim N(0,C_r\sigma^2) \textit{ for each } i = 1,2,\ldots,10; j = 1,2,3,4; \qquad (3)$$

where "~" is short for "is distributed as";
V_r is a general 3×3 positive definite symmetric matrix, representing the covariance of $\{b_{ik} : k = 1,2,3\}$;
I_4 is the 4×4 identity matrix, representing the covariance of $\{c_{ij} : j = 1,2,3,4\}$;
and C_r is a 3×3 positive definite symmetric matrix, representing the correlation of $\{e_{ijk} : k = 1,2,3\}$.

In the selected model, C_r was assumed to have a first-order autoregressive correlation structure (denoted by AR (1)), which implies the following correlation matrix:

$$C_r = \begin{bmatrix} 1 & \phi & \phi^2 \\ \phi & 1 & \phi \\ \phi^2 & \phi & 1 \end{bmatrix} \tag{4}$$

The genetic age-age correlation estimates are given by the correlations corresponding to V_r, which can be read off directly from the LME fitted model output. The phenotypic correlations are the correlations between observations of densities for any two ring groups k_1, k_2 within the same tree, so are given by

$$\frac{\sigma_C^2 + \sigma_R^2 + \phi^{|k_1 - k_2|}\sigma^2}{\sigma_C^2 + \sigma_R^2 + \sigma^2} \tag{5}$$

where the clonal variance, σ_C^2, is arbitrarily obtained from the average of the diagonal elements of the matrix which are separately estimated clonal variances for each ring group.

N.B.: (1) LME uses the marginal likelihood (with the random effects parameters b_{ik}, c_{ij} integrated out), and so the asymptotic covariance matrix is a much better approximation than would be the case if inference was based on the joint distribution of variance components and random effects. Furthermore, LME uses an unconstrained parameterisation for the variance parameters, so there is no problem with estimated variances becoming negative or hitting the boundary (zero).

(2) Other models were tried, but the model described gave the best fit (according to the AIC or BIC). In particular, while a general symmetric matrix of random ring class effects was needed at the clone level, at the ramet level only a single random effect was supported by the data. The AR(1) correlation structure best fitted the within-ramet errors. This model posits that, for example, the correlation between e_{ij1} and e_{ij2} is equal to that between e_{ij2} and e_{ij3}.

(3) There was insufficient data to distinguish this model from the more general unstructured correlation model. The latter when fitted gave seemingly random pairwise correlations, including some negative correlations.

Prediction of tree component densities

For each of the predictors, outerwood density at breast height (ODBH), and area-weighted average densities d_{1-6}, d_{7-12}, d_{13-18}, d_{19-24}, for rings 1 to 6, 7 to 12, 13 to 18, and 19 to 24, respectively, a model of the form:

$$y_{ij} = a + a_i + b(x_{ij} - \mu_x) + e_{ij};\ a_i \sim N(0,\sigma_C^2);\ e_{ij} \sim N(0,\sigma_e^2) \tag{6}$$

was fitted, where x_{ij}, μ_x, y_{ij} are, respectively, the predictor value, the overall average value of the predictor, and the tree component (whole tree or log) density for ramet j of clone i. The parameters a and b represent the mean and the slope respectively, while the parameter a_i represents random clone effects on the mean.

Neglecting the error in estimating the coefficients a, b (since our interest here is in potential accuracy in predicting values for a clone — in practice, more accurate estimates of these coefficients would be obtained from a larger and unbiased dataset), the error variance for predictions is $\sigma_C^2 + \sigma_e^2$.

N.B.: Models with random slopes b_i were also tried but the model above was preferred with lower BIC and lower or similar AIC values. Furthermore, estimates for b_i were highly negatively correlated with those of a_i.

RESULTS AND DISCUSSION

Gravimetric Data

Average clone growth and wood density

Clone means for stem volume and basic density, based on disc values, are given in Table 1. The difference in the growth rates (volume) of the clones was dramatic (1.08 to 5.26 m^3) and the range in average clone density (354 to 438 kg/m^3) was also relatively wide, reflecting the sampling strategy aimed at covering the range available. However, in this dataset, growth was not obviously related to tree average density. Others, including Wilcox *et al.* (1975) and Cown *et al.* (1991) have documented a weak negative phenotypic correlation in *P. radiata* between density and diameter or volume.

Analyses of the unextracted disc basic wood densities showed all clones corresponding to the generally accepted pattern of a density increase from juvenile (rings 1–10) to mature wood (rings 11+) and a slight decrease in average density with height in the stem (Table 2). Clonal trends are shown in Fig. 1, clearly demonstrating that all clones conformed to the overall pattern and that quantitative differences were maintained at all stem levels.

TABLE 1–Average clone stem volume and basic density

Clone	Volume (m^3)	Unextracted basic density (discs) (kg/m^3)
1	3.05	429
2	2.51	383
3	5.26	406
4	2.17	434
5	2.94	397
6	2.33	358
7	1.08	411
8	2.24	354
9	1.59	438
10	4.14	397
Means	2.73	401

TABLE 2–Average unextracted area-weighted density by stem levels

Nominal height (m)	No. of samples	Unextracted basic density (kg/m^3)		
		Juvenile (rings 1–10)	Mature (rings 11+)	Disc
0	20	405	451	431
4	20	368	445	404
9	20	361	442	398
14	20	360	439	392
19	20	361	440	391
24	18	367	424	387
28	8	399	432	404
Mean		374	439	401

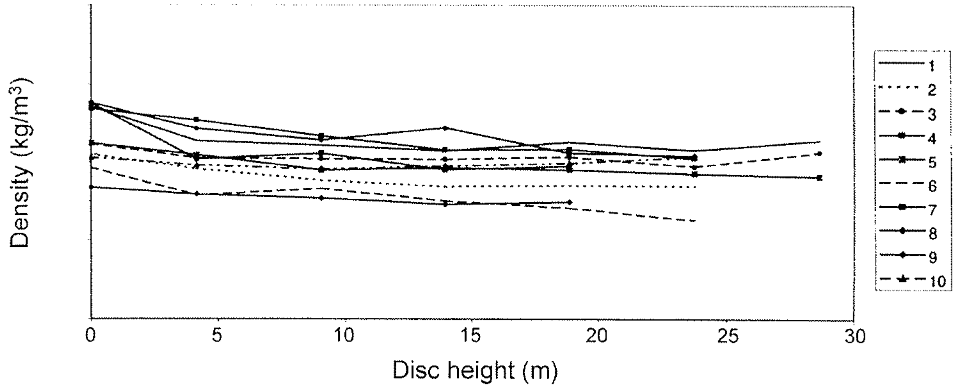

FIG. 1–Clonal variation in disc density (unextracted) with height

At each height level, there was a range of about 100 kg/m^3 in clonal means. The relationships between outerwood density at breast height (outer five rings) and specific tree components are shown in Table 3. The overall relationship between breast height outerwood density, whole-tree density, and specific log classes was high, in agreement with several other reports on *P. radiata* (Cown & McConchie 1982b; McKinnell 1970; Evans *et al.* 1995; Tian *et al.* 1995; Cown 1999). The relative magnitude of clonal variance components indicates a substantial genetic component to the relationships.

TABLE 3–Relationships between outerwood density at breast height (five rings) and stem component densities.

Log height class	Coefficient of determination*		Standard deviations of residuals (kg/m^3)	
	Clone R^2_C (%)	Ramet R^2_e (%)	Clone $\hat{\sigma}_C$	Ramet $\hat{\sigma}_e$
Butt	80	87	9.4 (4.0–22.4)	13.1 (10.1–17.1)
Second	77	84	7.8 (3.0–20.7)	12.7 (9.5–16.6)
Third	69	82	11.3 (5.6–22.8)	13.2 (10.2–17.1)
Fourth	69	82	14.7 (7.7–28.0)	13.4 (10.3–17.4)
Whole tree	73	85	11.1 (5.2–23.8)	12.2 (9.3–15.9)

* $R^2_C = 1(\hat{\sigma}^2_C + \hat{\sigma}^2_e) / \mathrm{var}(y)$, $R^2_e = 1 - (\hat{\sigma}^2_e / \mathrm{var}(y)$, where var($y$) denotes the phenotypic variance of the trait under consideration. R^2_C gives the overall proportion of variance explained; R^2_e gives the proportion of variance explained if the clonal component is controlled, and var(y) denotes the phenotypic variance of the trait in question.

Densitometric Data

Clonal growth ring components

The ring density trends are shown in Fig. 2 and components summarised for each clone (at the top of the pruned log) in Table 4. Although the pruned butt logs varied somewhat in length (nominally 4 m), the number of complete growth rings at this level varied only from 23 to 24.

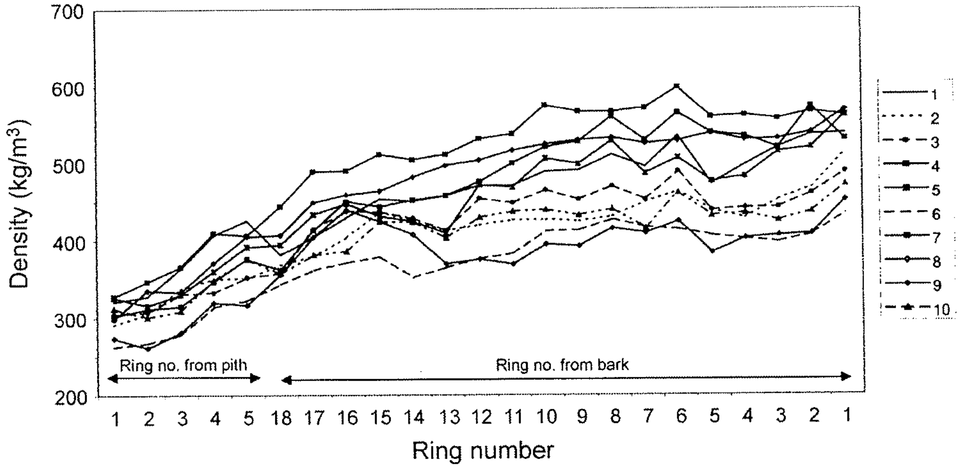

FIG. 2–Clonal mean density trends (4 m height)

TABLE 4–Arithmetic means of growth-ring width and density components at 4 m.

Clone No.	Width (mm)				Density (kg/m³)						
	RW	EW	LW	LW%	RD	ED	LD	UNIF	Min.	Max.	Range
1	8.8	6.8	2.0	29	449	372	619	253	314	723	409
2	9.7	8.4	1.3	18	408	376	524	167	325	591	266
3	11.3	9.5	1.8	20	405	357	568	224	300	648	348
4	7.8	5.6	2.2	42	500	410	616	213	363	749	386
5	8.1	6.5	1.6	27	442	378	588	224	317	682	365
6	7.8	6.8	1.0	16	370	332	550	229	266	613	347
7	5.8	4.7	1.1	33	465	382	598	228	336	670	334
8	8.3	7.6	0.7	12	367	341	455	172	278	569	291
9	6.9	5.2	1.7	39	475	385	609	229	332	713	381
10	10.3	9.0	1.3	16	392	357	567	217	295	637	343

Overall, clonal ring density means averaged around 300 kg/m³ (range 75 kg/m³) at the pith, increasing to around 475 kg/m³ (range 150 kg/m³) at the bark (ring No. 23 from the pith) (Fig. 2). The density profiles in these samples indicated that the differences between clones were quite consistent from pith to bark, in that the clones with the highest-density juvenile wood also had the highest-density mature wood. Cown *et al.* (1992) reported similar results when they compared the pith-to-bark density profiles for six 20-year-old families. However, three of the 11 clones studied by Donaldson *et al.* (1995) had pith-to-bark density profiles that did not follow the expected pattern for *P. radiata*. Similarly, Zamudio *et al.* (2001) demonstrated striking family differences in densitometric trends in *P. radiata* in Chile. If the density patterns from pith to bark are consistent between clones, as in this study, then density screening at an early age could be used to rank clones.

The ring width data reflected large differences in wood production between the clones. The faster-growing clones (e.g., Clones 3 and 10) had average ring widths exceeding 10 mm.

The slowest-growing clones (e.g., Clones 7 and 9) had ring widths averaging 5 to 7 mm. However, these clones were sampled from a relatively densely stocked trial where the slower-growing clones may have been suppressed by adjacent clones that were growing more rapidly. It is therefore very likely that the differences in growth rate between these clones were exaggerated by the trial design.

Clone 4 had the highest average ring density (500 kg/m^3) at this stem level. This clone also had the highest earlywood density (410 kg/m^3), the second highest latewood density (616 kg/m^3), and the most latewood (42%). In contrast, Clone 8 had the lowest average ring density (367 kg/m^3), the second lowest earlywood density (341 kg/m^3), the lowest latewood density (455 kg/m^3), and the least latewood (12%). Clones 2 and 8 had the most uniform wood (<200 kg/m^3 between earlywood and latewood and the lowest range values). Individual tree and clonal mean correlations between ring density components at heights 4 m and 19 m are given in Table 5.

Variation in density by height level

Density patterns at each of the heights sampled are plotted in Fig. 3. This graphically illustrates that the patterns for extracted values at each level are practically identical. The pattern is similar to that described for loblolly pine (*Pinus taeda* L.) by Megraw & Leaf (1997). This is a convenient feature of pines, allowing density characteristics from any part of the stem to be related to any other.

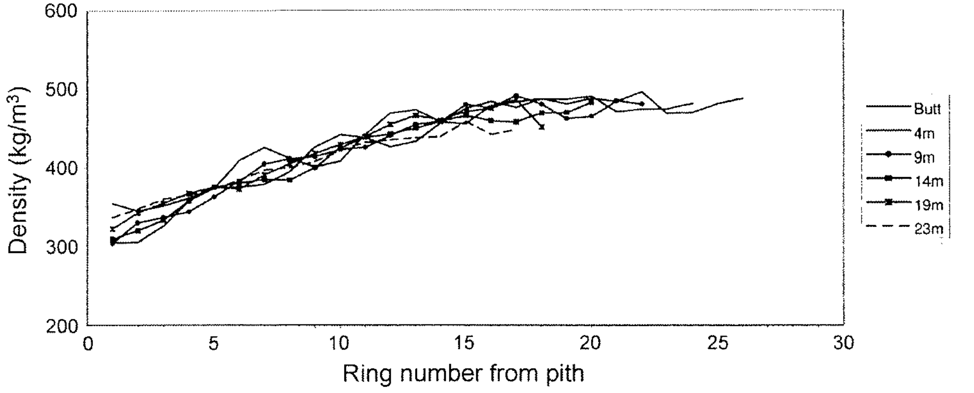

FIG. 3–Overall density/height relationship

The pith-to-bark density profiles (while differing widely among clones) remained very consistent among stem levels for undividual clones. In Clones 4 and 8, illustrated in Fig. 4, the contrasting JMDIFF characteristics are very apparent.

Earlywood and latewood density trends

Earlywood and latewood density levels (Fig. 5) were similar to those in previous studies (Cown *et al.* 1992; Donaldson *et al.* 1995; Cown & Ball 2001) and indicated progressive small increases with tree age, along with some regular differences between clones and a notable consistency in average values at the various stem levels (Fig. 6). Clone 2, which had

TABLE 5–Tree and clone level correlations between ring density components at nominal heights 4 m and 19 m.

	RD	ED	LD	LW %	UNIF	JMDIFF
(a) 4 m						
Individual-tree level						
RD	1.00					
ED	0.88	1.00				
LD	0.81	0.52	1.00			
LW %	0.97	0.78	0.79	1.00		
UNIF	0.41	0.02	0.83	0.43	1.00	
JMDIFF	0.56	0.37	0.44	0.65	0.29	1.00
Clonal-mean level						
RD	1.00					
ED	0.89	1.00				
LD	0.84	0.56	1.00			
LW %	0.97	0.79	0.84	1.00		
UNIF	0.46	0.08	0.85	0.51	1.00	
JMDIFF	0.69	0.49	0.52	0.81	0.30	1.00
(b) 20 m						
Individual-tree level						
RD	1.00					
ED	0.89	1.00				
LD	0.79	0.5	1.00			
LW %	0.95	0.73	0.80	1.00		
UNIF	0.34	–0.08	0.82	0.46	1.00	
JMDIFF	0.38	0.23	0.43	0.44	0.35	1.00
Clonal-mean level						
RD	1.00					
ED	0.90	1.00				
LD	0.83	0.53	1.00			
LW %	0.95	0.74	0.88	1.00		
UNIF	0.34	–0.08	0.80	0.51	1.00	
JMDIFF	0.48	0.22	0.62	0.62	0.55	1.00

Observations:

- The correlations between individual-tree and clonal-level results were very similar.
- Average ring density was highly correlated with both earlywood and latewood densities, but was consistently even more highly associated with latewood percentage. This confirms the visual observation that density and latewood percentage are related, and the observation of Koga & Zhang (2001) in balsam fir. (On the other hand, Donaldson *et al.* (1995) found earlywood values more closely related to average density than latewood values in a different set of clones.)
- Mean ring density, intra-ring contrast (UNIF), and juvenile-mature difference (JMDIFF) were not strongly related. This suggests that average density and inter- and intra-ring uniformity are largely independent — offering more choices for breeders.

the lowest intra-ring density range (Uniformity – Table 4) combined relatively low latewood values with comparatively high earlywood values. This suggests the potential to breed clones with "designer" properties, e.g., high uniformity.

The situation with latewood percentage is illustrated in Fig. 7. Latewood percentage in all clones started low at the pith (0–10%) and increased rapidly thereafter with ring number

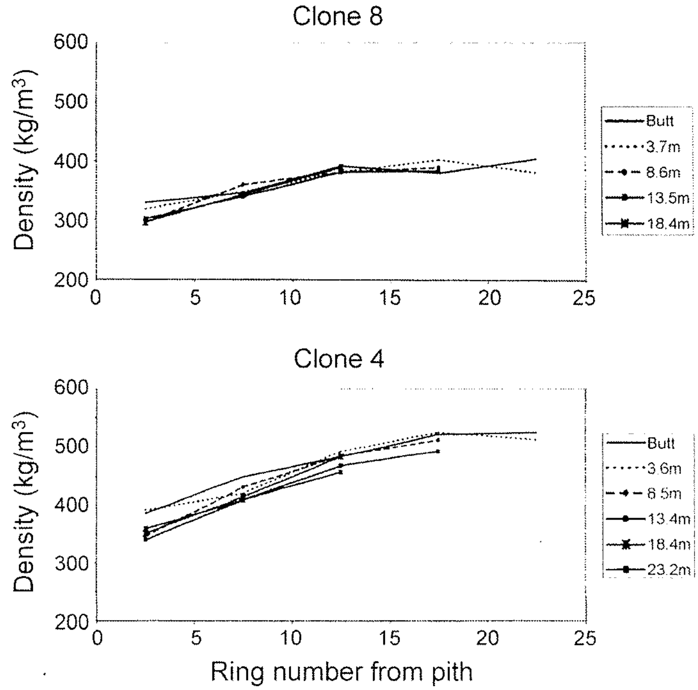

FIG. 4–Clonal variation in density profile

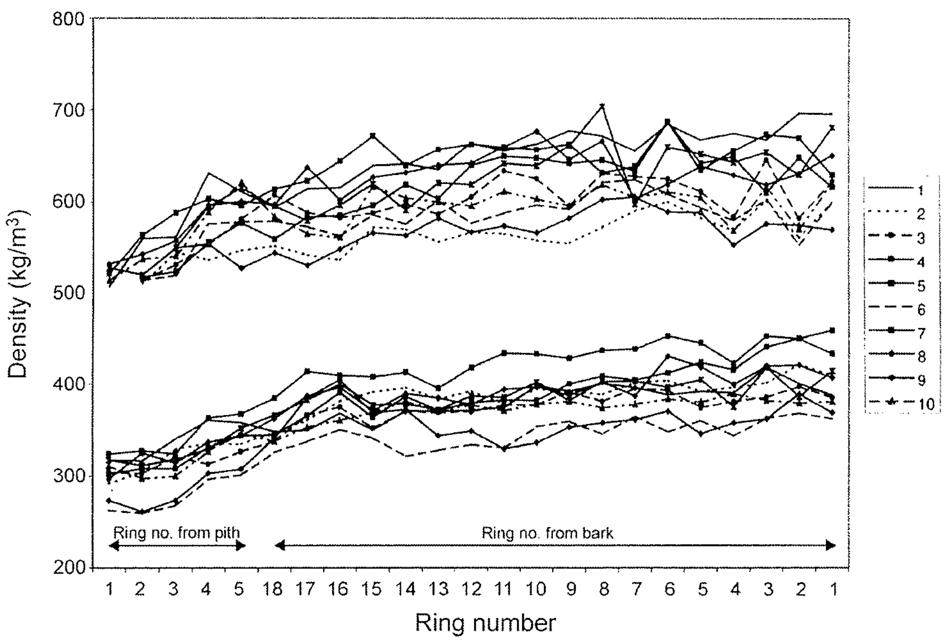

FIG. 5–Clonal earlywood and latewood density trends (5-m level)

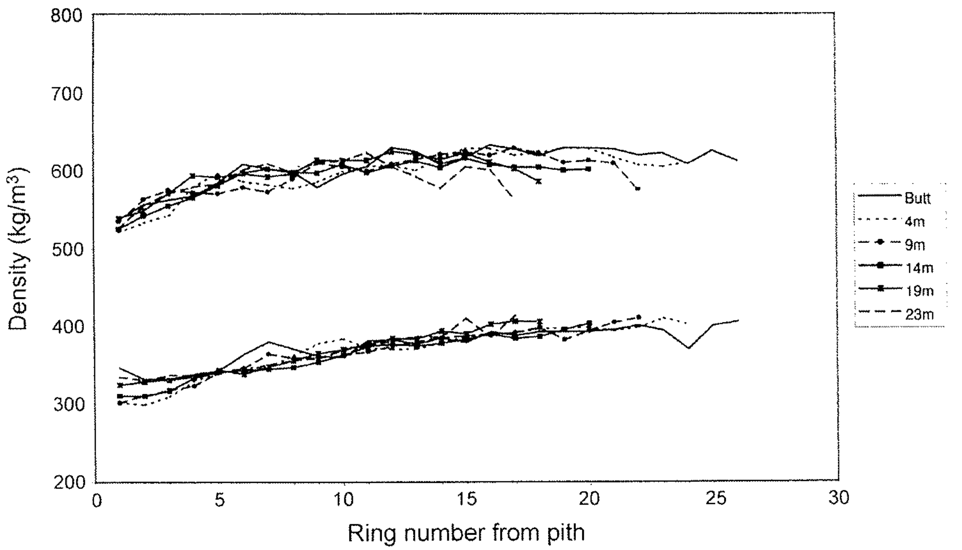

FIG. 6–Earlywood and latewood density trends by height classes, showing averages across clones

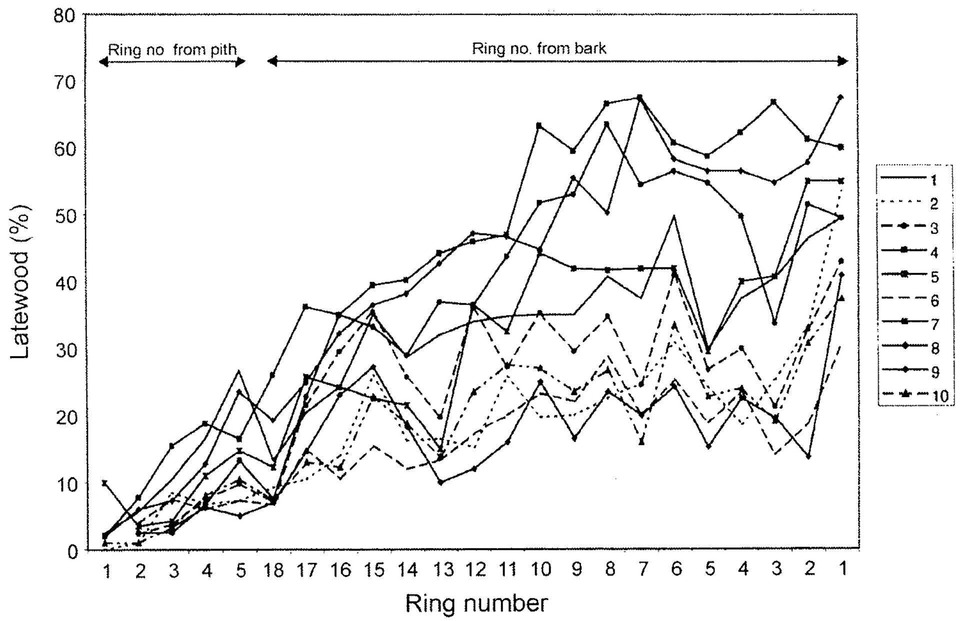

FIG. 7–Latewood percentage — clonal means by ring number (4 m height)

from the pith. Clones diverged from an early age, and in the outer wood ranged from 20% to 70% latewood. Again, there was a high degree of consistency between height levels overall (Fig. 8).

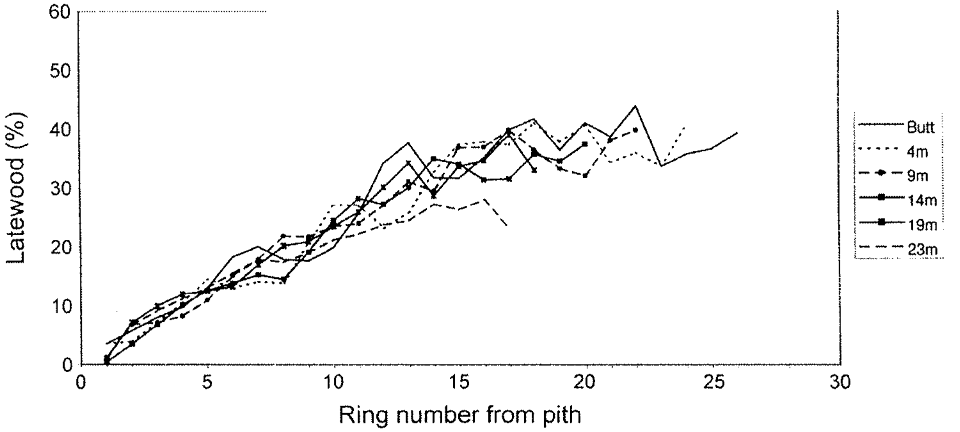

FIG. 8–Latewood percentage by stem height, averaged across clones

Clonal differences in intra-ring density for juvenile wood and mature wood are illustrated in Fig. 9. The wider growth rings in the juvenile wood tended to have lower latewood density and less latewood percentage, resulting in lower density.

Genetic Considerations

Variance components and heritabilities

Estimates of variance components and broad sense heritabilities for ring mean density (RD), earlywood density (ED), latewood density (LD), latewood percentage (LW%), uniformity (UNIF), and juvenile-mature difference (JMDIFF) are shown in Table 6. Estimates were based on four ramets from each of 10 clones at heights 5 and 19 m. Estimated heritabilities were high, with the possible exception of JMDIFF at 19 m.

Age-age correlations

According to the BIC criterion, the model with AR(1) within-ramet errors best fitted the data (Model 2 in Table 7), although this could not be distinguished from a model with an unstructured within-ramet correlation matrix (Model 3 in Table 7). The unstructured model, however, gave seemingly random pairwise correlations, including some negative correlations. This indicates that there were insufficient data to reliably estimate all the correlations in the unstructured model. Estimates of genetic and phenotypic age-age correlations between densities of six-ring groups are shown in Table 8. When applied to the data at height 19 m, the AR(1) model had a singular asymptotic variance covariance matrix, so confidence intervals could not be calculated. Indicative confidence intervals, for the data at height 19 m, based on the model with independent within-ramet errors, can be obtained from Table 9.

Predictability of whole-tree density from various six-ring groups at 4 m height

Estimated clone- and ramet-level standard deviations (square root of variance components) are shown in Table 10 using Model (6), for predicting whole-tree average density from area-weighted average densities of six-ring groups at height 4 m. Note the clone-level component

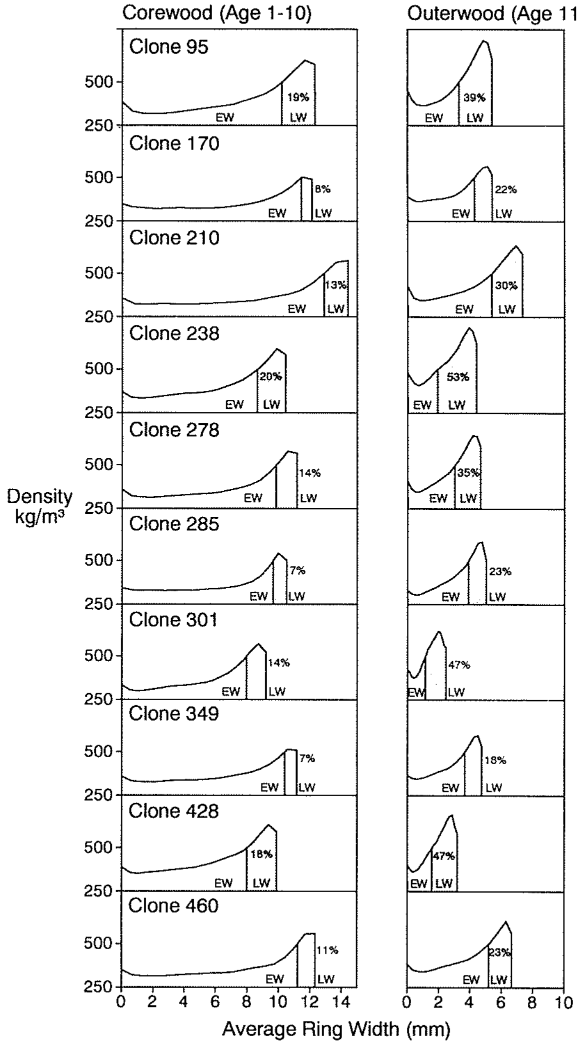

FIG. 9–Clonal variation in juvenile wood and mature wood intra-ring density profiles

σ_C was about twice the size of the ramet-level component σ_e, suggesting that clonal variation dominates the overall prediction error. The variance components for each of the six-ring groups were similar (to within the accuracy of the experiment, as shown by the 95% confidence intervals).

Predictability of whole-tree density from outerwood density

By comparison, the clone-level variance components for prediction of whole-tree density from the outer five rings (Table 3) were approximately the same as the ramet level components, suggesting that outerwood density may be a better predictor of whole-tree density than individual ring groups. However, considering the size of the confidence intervals, this difference would not be statistically significant.

TABLE 6–Variance components and heritability estimates* (95% confidence intervals)† for ring density components.

	Height 5 m			Height 19 m		
	$\hat{\sigma}^2_C$	$\hat{\sigma}^2_e$	$\hat{H}^2$	$\hat{\sigma}^2_C$	$\hat{\sigma}^2_e$	$\hat{H}^2$
RD	1235 (475–3210)	166 (100–275)	0.88 (0.72–0.96)	980 (364–2643)	285 (172–472)	0.78 (0.53–0.92)
ED	296 (112–781)	60 (36–100)	0.83 (0.62–0.94)	341 (127–920)	99 (60–164)	0.78 (0.53–0.92)
LD	643 (243–1698)	131 (79–217)	0.83 (0.62–0.94)	797 (299–2124)	193 (116–320)	0.81 (0.57–0.93)
LW %	63.1 (24.2–164.4)	9.3 (5.6–15.5)	0.87 (0.69–0.95)	33 (12.0–92.3)	13.7 (8.3–22.8)	0.71 (0.43–0.89)
UNIF	593 (218–1610)	191 (115–317)	0.76 (0.49–0.91)	571 (209–1557)	195 (118–324)	0.75 (0.49–0.90)
JMDIFF	1462 (540–3956)	449 (271–745)	0.77 (0.52–0.91)	557 (124–2503)	1321 (791–2206)	0.30 (0.07–0.69)

* $\hat{H}^2 = \hat{\sigma}^2_C / (\hat{\sigma}^2_C + \hat{\sigma}^2_e)$, an estimate of broad-sense heritability. Clonal variance components and heritability estimates are liable to be positively biased by the choice of clones to span a range of densities.

† Alternative confidence intervals based on the standard error of $\hat{H}^2$ (Falconer 1961), and transformation to a logistic scale, agreed with the values in Table 6 to within ±0.01.

TABLE 7–Comparisons between models for genetic and phenotypic covariance between densities of six-ring groups (1–6, 7–12, 13–18) at height 4 m.

Covariance model*	Within-ramet correlation structure	Df	AIC	BIC	LogLik†	Test	L.Ratio†	p-value
1	ID	11	–321.2	–290.8	171.6			
2	AR(1)	12	–336.7	–303.5	180.3	1 *v.* 2	17.48	<0.0001
3	UNSTR	16	–322.2	–278	177.1	2 *v.* 3	6.54	0.16

* Covariance/correlation structures tested are: unstructured (UNSTR), autoregressive order 1 (AR(1)) and independence (ID). Smaller values of AIC indicate a model is likely to have better predictive accuracy. Smaller BIC indicates a model is more likely to be the "true" model.

† LogLik = logarithm of likelihood
L.Ratio = logarithm of likelihood ratio

Juvenile Wood Analyses

For *P. radiata*, juvenile wood is often conveniently described as the first 10 growth rings, mainly on the basis of the known variation in wood density and other wood properties (Harris & Cown 1991). When pith-to-bark density data for many trees are averaged, the steep density gradient in the inner rings tends to level off at about 10 rings from the pith. Using this definition, the overall percentage of juvenile wood in the 10 clones varied from 39% to 61% (Table 11). However, since wood density has such an important influence on wood performance, there is a case for defining juvenile wood on a quantitative density basis (Cown 1992). The density values for the inner 10 rings are already known to differ markedly

TABLE 8–Age-age correlations between area-weighted average densities of ring groups, estimated in the model with AR(1) correlated within-ramet errors (Model 2 in Table 7).

Rings	Genotypic (95% confidence intervals)	Phenotypic (95% confidence intervals)
Height 4 m		
1–6 *v.* 7–12	0.77 (0.29–0.94)	0.99 (0.43–1.00)
1–6 *v.* 13–18	0.87 (0.52–0.97)	0.98 (0.37–1.00)
7–12 *v.* 13–18	0.92 (0.66–0.99)	0.99 (0.43–1.00)
Height 19 m		
1–6 *v.* 7–12	0.98	0.90
1–6 *v.* 13–18	0.96	0.87
7–12 *v.* 13–18	1.00	0.90

* Confidence intervals not estimated due to singular estimated asymptotic variance matrix.

TABLE 9–Age-age correlations between area-weighted average ring densities, estimated in the model with independent within-ramet errors (Model 1 in Table 7).

Rings	Genotypic (95% confidence intervals)	Phenotypic (95% confidence intervals)
Height 4 m		
1–6 *v.* 7–12	0.88 (0.49–0.98)	0.86 (0.71–0.94)
1–6 *v.* 13–18	0.89 (0.57–0.98)	0.86 (0.71–0.94)
7–12 *v.* 13–18	0.98 (0.58–0.99)	0.86 (0.71–0.94)
Height 19 m, Model 2		
1–6 *v.* 7–12	0.98 (0.50–0.999)	0.80 (0.62–0.92)
1–6 *v.* 13–18	0.96 (–0.39–0.99)	0.80 (0.62–0.92)
7–12 *v.* 13–18	0.99 (0.28–0.99)	0.80 (0.62–0.92)

TABLE 10–Standard deviations* for prediction of whole-tree density from area-weighted average densities of six-ring groups at height 4 m.

Rings	Clone level: $\hat{\sigma}^2_C$ (95% confidence intervals)	Ramet level: $\hat{\sigma}^2_e$ (95% confidence intervals)
1–6	18.7 (8.5–40.9)	11.6 (8.7–15.7)
7–12	26.0 (15.4–44.1)	11.1 (8.6–14.5)
13–18	22.6 (10.0–51.3)	11.9 (8.7–16.2)
19–24	22.5 (10.2–49.8)	11.8 (8.7–16.1)

* Square root of variance components

TABLE 11–Comparison of juvenile wood criteria

Log height class	Clone number									
	1	2	3	4	5	6	7	8	9	10
Juvenile wood (%) — Using 10-ring definition										
Butt	34	36	35	44	35	36	51	39	47	33
Second	43	46	41	49	41	42	55	46	53	38
Third	45	52	49	51	53	49	64	51	58	39
Fourth	55	54	53	56	55	55	71	57	65	43
Fifth	66	60	56	64	56	64	75	68	75	51
Whole tree	45	46	45	51	47	48	61	50	57	39
Juvenile wood (%) — using 400 kg/m³ threshold										
Butt	8	24	24	14	21	45	30	40	21	26
Second	17	45	30	19	30	68	53	34	24	36
Third	21	75	37	24	44	67	62	42	23	34
Fourth	17	68	46	30	44	61	57	70	22	37
Fifth	19	57	47	33	32	84	49	93	36	32
Whole tree	15	48	35	22	33	64	50	51	24	33
Number of juvenile wood rings — using 400 kg/m³ threshold										
Butt	4	8	8	4	6	12	7	11	6	9
Second	5	10	8	5	8	14	10	8	5	10
Third	6	14	8	6	8	13	10	9	5	9
Fourth	5	13	10	6	9	12	9	12	4	9
Fifth	4	10	9	6	7	13	8	13	5	8
Whole tree	5	11	9	5	8	13	9	10	5	9

between individuals and sites (Cown & McConchie 1983; Cown & Ball 2001) and this was confirmed in this study. Although the generic trend of increasing wood density from pith-to-bark existed for all clones, the density values were extremely variable (Fig. 2 and 4).

The alternative definition for the juvenile wood zone of *P. radiata* proposed by Cown (1992) described the juvenile wood as the inner growth rings with average density less than 400 kg/m³. This is a technological definition with much more relevance when considering the suitability of wood for solid wood uses, as density is often described as the single most-important property affecting stiffness and strength of structural lumber, machining quality and surface hardness of appearance products, and pulp yield (wood consumption per unit product). Using this technical definition, the percentage of juvenile wood in these clones varied from 15% (Clone 1) to 64% (Clone 6), representing an average of 5 and 13 growth rings respectively (Table 11). The overall clonal ranking is shown in Table 12 using the two alternative methods.

These results show that the proportion of wood defined as juvenile depends very much on the measurement method and that the density method is much more discriminative. There are also indications that this approach gives a more consistent quantitative classification at different stem levels (Table 12).

This study indicated that there may be opportunities to significantly change the amount of juvenile wood in the resource using clonal selection.

TABLE 12–Ranking in terms of juvenile wood by alternative methods

Clone No.	Rank 400 kg/m^3	Rank 10 ring
1	1	3
4	2	8
9	3	9
10	4	1
5	5	5
3	6	2
2	7	4
7	8	10
8	9	7
6	10	6

CONCLUSION

This report provides a detailed description of the within-tree variation, not only in wood density, but also in traits derived from densitometry (earlywood and latewood). This makes it possible to identify the positions within a tree where timber can be sawn with predictable performance characteristics.

The clones used in this study are not used operationally today. However, the detailed wood property measurements on these clones provide insight into the range of wood properties between clones and, equally important, the consistency within clones. As in other studies, a high degree of variation and inheritance has been indicated for most wood density variables. Heritability and correlation estimates were presumably over-estimated on account of the sampling protocol which sought variation in outerwood density in the small number of clones. Nevertheless, the study suggests that clonal selection could be an effective way of modifying juvenile wood properties.

The high age-age correlations between ring groups, and similar values of variance components for prediction error when using any one of the ring groups to predict whole-tree density, suggest that both of these ring groups could be useful for selection. However, given the size of the confidence intervals, it is recommended that more accurate estimates be obtained, based on a larger dataset, before this information is used as a basis for selection decisions.

Outerwood density at breast height is used to predict densities of tree components (logs, or types of logs) in the Wood Density Prediction Model of the New Zealand Forest Research Institute (Tian *et al.* 1995). Previously there has been little evaluation of genetic sources of error variation. The results of this study suggest that genetic (clonal in this case) variation is an important component of prediction error variation, particularly when dealing with clones. This was also observed by Donaldson *et al.* (1995).

There were consistent density patterns from pith to bark and vertically within stems for these clones. Breast height samples were strongly representative of the stem as a whole for average wood density and growth ring density components.

Heritability estimates for ring-density components were high, as in previous studies. Although density patterns varied somewhat between genotypes, the strong degree of consistency within stems (low density core) may still allow ranking of clones for density at an early age.

The proportion of juvenile wood depends very much on the criterion used. The proposed density criterion is more quantitative and discriminative and also more accurately indicates the utilisation potential than the 10-ring threshold. However, neither approach is quantitative for other traits.

It is clear that wood density variables in *P. radiata* display highly consistent patterns as an expression mainly of genotypic and site effects (Cown & Ball 2001). The limited studies completed to date on material of known genotypes all indicate that wood density and its main components are also highly heritable. The extent to which this information can be used to improve the performance of the species will depend on acceptance by tree breeders and end users of the links to wood behaviour and value.

REFERENCES

BANNISTER, M.H.; VINE, M.H. 1981: An early progeny trial in *Pinus radiata*. 4. Wood density. *New Zealand Journal of Forestry Science 11(3)*: 221–243.

BURDON, R.D.; BANNISTER, M.H. 1973: Provenances of *Pinus radiata*: their early performance and silvicultural potential. *New Zealand Journal of Forestry 18*: 217–232.

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

BURDON, R.D.; LOW, C.B. 1992: Genetic survey of *Pinus radiata*. 6: Wood properties: Variation, heritabilities, and interrelationships with other traits. *New Zealand Journal of Forestry Science 22(2/3)*: 228–245.

BURDON, R.D.; YOUNG, G.D.; COWN, D.J. 1992: Evaluation of wood properties in highly select *Pinus radiata* progenies and preliminary estimates of genetic parameters. Pp. 168–169 *in* Proceedings IUFRO All-Division 5 Conference, Nancy, France, Wood Quality Group 5.01.

COWN, D.J. 1974: Wood density of radiata pine: its variations and manipulation. *New Zealand Journal of Forestry 19(1)*: 84–92.

——1977: Summary of wood quality studies in fertiliser trials. Pp. 307–310 *in* Ballard, R. (Comp.) "Use of Fertilisers in New Zealand Forestry". *New Zealand Forest Service, Forest Research Institute Symposium No.19*.

——1980: Radiata pine: wood age and wood property concepts. *New Zealand Journal of Forestry Science 10(3)*: 504–507.

——1992: Corewood (juvenile wood) in *Pinus radiata* — should we be concerned? *New Zealand Journal of Forestry Science 22(1)*: 87–95.

——1999: New Zealand pine and Douglas-fir: Suitability for processing. *New Zealand Forest Research Institute, Forest Research Bulletin No. 216*. 72 p.

COWN, D.J.; BALL, R. 2001: Wood densitometry of 10 *Pinus radiata* families at seven contrasting sites: Influence of tree age, site, and genotype. *New Zealand Journal of Forestry Science 31(1)*: 88–100.

COWN, D.J.: CLEMENT, B.C. 1983: A wood densitometer using direct scanning with X-rays. *Wood Science and Technology 17(2)*: 91–99.

COWN, D.J.; KIBBLEWHITE, R.P. 1980: Effects of wood quality variation in New Zealand radiata pine on kraft paper properties. *New Zealand Journal of Forestry Science 10(3)*: 521–532.

COWN, D.J.; McCONCHIE, D.L. 1981: Effects of thinning and fertiliser application on wood properties of *Pinus radiata*. *New Zealand Journal of Forestry Science 11(2)*: 79–91.

——1982a: Rotation age and silvicultural effects on wood properties of four stands of *Pinus radiata*. *New Zealand Journal of Forestry Science 12(1)*: 71–85.

———1982b: Wood density prediction for radiata pine logs. *New Zealand Forest Service, FRI Bulletin No. 9*. 10 p.

———1983: Radiata pine wood properties survey (1979–1982). *New Zealand Forest Service, FRI Bulletin No. 50*.

COWN, D.J.; McCONCHIE, D.L.; YOUNG, G.D. 1991: Radiata pine wood properties survey. *New Zealand Ministry of Forestry, FRI Bulletin No. 50* (revised).

COWN, D.J.; YOUNG, G.D.; BURDON, R.D. 1992: Variation in wood characteristics of 20-year-old half-sib families of *Pinus radiata*. *New Zealand Journal of Forestry Science 22(1)*: 63–76.

DONALDSON, L.A.; EVANS, R.; COWN, D.J.; LAUSBERG, M.J.F. 1995: Clonal variation of wood density variables in *Pinus radiata*. *New Zealand Journal of Forestry Science 25(2)*: 175–188.

EVANS, R.; DOWNES, G.; MENZ, D.; STRINGER, S. 1995: Rapid measurement of variation in tracheid dimensions in a radiata pine tree. *Appita 48(2)*: 134–138.

FALCONER, D.S. 1961: "Introduction to Quantitative Genetics". Oliver and Boyd, Edinburgh and London.

HARRIS, J.M. 1965: The heritability of wood density. *In* Proceedings of IUFRO Meeting (Section 41) Melbourne, Australia, Vol. 1.

HARRIS, J.M.; COWN, D.J. 1991: Basic wood properties. Pp. 6-1 – 6-28 *in* Kininmonth, J.A.; Whitehouse, L.J. (Ed.) "Properties and Uses of New Zealand Radiata Pine". New Zealand Ministry of Forestry, Forest Research Institute, Rotorua.

JOZSA, L.A.; RICHARDS, J.; JOHNSON, S.G. 1989: Relative density. Pp. 5–22 *in* "Second Growth Douglas-fir: Its Management and Conversion for Value". Forintek Canada Corp. SP-32.

KOGA, S.; ZHANG, S.Y. 2001: Relationships between wood density and annual growth rate components in Balsam fir (*Abies balsamea*). *Wood and Fiber Science 34(1)*: 146–157.

LAUSBERG, M.; COWN, D.J.; GILCHRIST, K.; SKIPWITH, J.; TRELOAR, C.R. 1995: Physiological ageing and site effects on wood properties of *Pinus radiata*. *New Zealand Journal of Forestry Science 25(2)*: 189–199.

MATHESON, A.C.; YANG, J.; SPENCER, D.J. 1997: Breeding radiata pine for improvement of sawn product value. Pp. IV-19 to IV-26 *in* Zhang, S.Y.; Gosselin, R.; Chauret, G. (Ed.) "Timber Management Toward Wood Quality and End Uses", CTIA/IUFRO International Wood Quality Workshop, Quebec City, 18–22 August.

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*.

McKINNELL, F.H. 1970: Wood density studies in *Pinus radiata* D.Don. Ph.D. Thesis, Australian National University, Canberra, Australia.

MEGRAW, R.A. 1985: "Wood Quality Factors in Loblolly Pine: The Influence of Tree Age, Position in Tree, and Cultural Practice on Wood Specific Gravity, Fiber length and Fibril Angle". Tappi Press, Atlanta.

MEGRAW, R.A.; LEAF, G. 1997: A quantitative look at sources of specific gravity variation in loblolly pine. *In* Zhang, S.Y.; Gosselin, R.; Chauret, G. (Ed.) "Timber Management Toward Wood Quality and End Uses", CTIA/IUFRO International Wood Quality Workshop, Quebec City, 18–22 August.

NYAKUENGAMA, J.G. 1997: Quantitative genetics of wood quality traits in *Pinus radiata* D.Don. Ph.D. Thesis, University of Melbourne, 319 p.

PANSHIN, A.J.; de ZEEUW, C. 1980: "Textbook of Wood Technology", 4th Edition. McGraw-Hill, New York. 722 p.

PEARSON, R.G.; GILMORE, R.C. 1980: Effects of fast growth rate on the mechanical properties of loblolly pine. *Forest Products Journal 30(5)*: 47–54.

PINHEIRO, J.C.; BATES, D.M. 2000: "Mixed-effects Models in S and Splus". Springer-Verlag, New York. 528 p.

ROZENBERG, P.; FRANC, A.; MAMDY, C.; LAUNAY, J.; SCHERMANN, N.; BASTIEN, J.C. 1999: Stiffness of standing Douglas fir and genetic effects: from the standing stem to the standardised wood sample, relationships between modulus of elasticity and wood density parameters. Part 2. *Annals of Forest Science 56*: 145–154.

SHELBOURNE, C.J.A.; EVANS, R.; KIBBLEWHITE, R.P.; LOW, C. 1997: Inheritance of tracheid transverse dimensions and wood density in radiata pine. *Appita 50(1)*: 47–50.

SUTTON, W.R.J.; HARRIS, J.M. 1974: Effect of heavy thinning on wood density in radiata pine. *New Zealand Journal of Forestry Science 4(1)*: 112–115.

TIAN, X.; COWN, D.J.; McCONCHIE, D.L. 1995: Modelling of *Pinus radiata* wood properties. Part 2: Basic density. *New Zealand Journal of Forestry Science 25(2)*: 214–230.

WILCOX, M.D.; SHELBOURNE, C.J.A.; FIRTH, A. 1975: General and specific combining ability in eight selected clones of radiata pine. *New Zealand Journal of Forestry Science 5(2)*: 219–225.

ZAMUDIO, F.; BAETTI, R.; VERGARA, A.; GUERRA, F.; ROZENBERG, P. 2001: Genetic variation of wood density through cambial age in a radiata pine progeny test and its relationship with radial growth. P. 40 *in* Proceedings of "Wood, Breeding, Biotechnology and Industrial Expectations", 11–14 June, Bordeaux, France.

ZHANG, S.Y. 1997: Wood quality: its definition, impact, and implications for value-added timber management and end uses. Pp. 17–40 *in* Zhang, S.Y.; Gosselin, R.; Chauret, G. (Ed.) "Timber Management Toward Wood Quality and End Uses", CTIA/IUFRO International Wood Quality Workshop, Quebec City, 18–22 August.

ZOBEL, B.J. 1997: Genetics of wood – an overview. Pp. IV-3 to IV-9 *in* "Timber Management Toward Wood Quality and End Uses", CTIA/IUFRO International Wood Quality Workshop, Quebec City, 18–22 August. 7 p.

ZOBEL, B.J.; JETT, J.B. 1995: "Genetics of Wood Production". Springer-Verlag, Berlin. 337 p.

ZOBEL, B.J.; WEBB, C.; HENSON, F. 1959: Core of juvenile wood of loblolly and slash pine trees. *Tappi 42(5)*: 345–355.