CLONAL VARIATION OF WOOD DENSITY VARIABLES IN *PINUS RADIATA*

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ABSTRACT

Wood basic density was assessed on cuttings from 11 clones in a 16-year-old clonal trial of *Pinus radiata* D. Don, using breast-height increment cores, and wood disc samples from the butt, breast height (1.4 m), 6, 11, 16, and 20 m height. The cuttings came from 5-year-old trees and were thus physiologically "aged". The sample clones were chosen from the 120 clones in the trial, to cover the available range of wood density and tracheid length. Tree average wood density values were calculated from gravimetric measurements on the discs and within-tree trends were assessed using a scanning X-ray densitometer.

There were significant differences among clones, among trees within clones, among rings, and in interaction between rings and clones. The effects of clones and rings were dominant. There were also significant differences in pith-to-bark trends among clones, and in height up the stem at a given ring number from the pith in half of the clones. There were significant differences in the breast-height ring density profile between ring groups 1–5 and 11–15 due to increases in overall density, and in the amount and density of latewood, but there were no apparent differences in ring profile among clones. Mean ring density for rings outside ring 7 was highly correlated with weighted mean density at breast height and with weighted tree means. Estimates of clonal repeatability indicate a high degree of genetic inheritance for basic density, in agreement with results from earlier studies. All clones, however, were of below-average density compared to typical seedling stock at the same age, suggesting a physiological age effect in these clones, derived from 5-year-old trees. Using a corewood definition of <400 kg/m^3, only one of the clones reached this density level by ring 10 and most failed to reach it by ring 15.

Keywords: basic density; X-ray densitometry; clonal repeatability; cambial age; height; maturation; *Pinus radiata*.

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INTRODUCTION

Basic density is one of the principal determinants of wood quality in forest trees because of its association with cell dimensions, strength, stiffness, drying, machining, and hardness properties as well as various papermaking properties (Cown & Kibblewhite 1980; Kibblewhite 1980; Panshin & de Zeeuw 1980; Megraw 1985). In *P. radiata* the relationships between wood density and site, tree age, and silviculture have been extensively studied (Hughes & Mackney 1949; Loe & Mackney 1953, Harris 1965; Cown 1973, 1974, 1977; Cown & McConchie 1980, 1981, 1982; Bamber & Burley 1983; Cown *et al.* 1991). The recent development of equipment for rapid assessment of wood quality parameters using non-destructive sampling techniques (Evans 1994) will allow more detailed studies to be carried out relating these factors to wood quality.

In addition to defining the natural variability of wood density in *P. radiata*, several studies have been directed at determining its heritability (the fraction of phenotypic variance due to genetic as opposed to environmental effects on individuals) (Burdon & Harris 1973; Banister & Vine 1981; Burdon 1992; Burdon & Low 1992; Cown *et al.* 1992). Wood density has been shown to have a high heritability compared to other wood quality traits. Cown *et al.* (1992) reported a narrow-sense heritability (h^2) of 0.9–1.0 for density compared to values of 0.1 for ring width, 0.4–0.5 for resin content, 0.5 for percentage heartwood, and 0.6 for compression wood grade. Donaldson & Burdon (1995) reported the clonal repeatability (H^2—an estimate of broad-sense heritability) of microfibril angle in *P. radiata* to be 0.7. Burdon (1992) reported a value of 0.7 for narrow-sense heritability of density while Burdon & Low (1992), who examined a comprehensive range of *P. radiata* genotypes, including material from Californian mainland (Anõ Nuevo, Monterey, and Cambria) and island (Guadelupe, Cedros) populations as well as New Zealand land races, reported heritabilities of 0.6 or higher for breast-height density at ring 5.

The New Zealand tree breeding programme currently emphasises growth rate, stem form, and disease resistance in its selection procedures. Recently, however, there has been a greater interest in extending selection to include properties such as wood density. Given its natural variability and high heritability (Cown *et al.* 1992; Burdon & Low 1992) density is a good candidate for selection in *P. radiata*. The present study was undertaken in order to compare variation in wood density in trees derived from cuttings of elite clones of *P. radiata* with earlier results from seedlings. It involved 11 clones from a trial established in Kaingaroa Forest by the New Zealand Forest Research Institute.

MATERIALS AND METHODS

Breast height increment cores and wood discs were collected from each of 11 clones produced from cuttings of genetically select (for growth rate and form) *P. radiata* growing in a 16-year-old clonal trial in Kaingaroa Forest. Clones were selected to cover the full range of basic density and tracheid length available among the 120 clones within the trial based on prior increment core sampling. Two trees for each clone were sampled using a 5-mm increment borer at breast height and discs were collected from the butt, breast height, 6, 11, 16, and 20 m. Increment cores and samples for wood densitometry were resin-extracted by refluxing in methanol in a Soxhlet apparatus for 24 hours, followed by conditioning to 10% moisture content by storage in a controlled atmosphere (20°C and 50% relative humidity).

Distortion of cores during drying was prevented by the use of drying racks. Cores and radial wood samples were then prepared for X-ray densitometry by reduction to samples of 2 mm tangential thickness using a twin-blade saw.

Gravimetric density was also determined on five-ring groups for each disc at each height and a tree mean density was calculated after weighting ring groups by their relative cross-sectional areas.

The machined and conditioned cores were scanned in an X-ray densitometer similar to that described by Cown & Clement (1983), equipped with a ^{55}Fe X-ray source. Cores were scanned radially at 0.3-mm intervals and data summarised using the density analysis program IDAS were transferred to Microsoft Excel for detailed analysis. Density measurements were calibrated by calculating an attenuation factor as described by Cown & Clement (1983). Analyses were performed on data for samples of equal ring number from the pith, aligned at the outermost ring and excluding partial and missing growth rings near the pith. Analyses of variance were performed using the format described by Donaldson & Burdon (1995) as reflected in Table 1. Comparisons of earlywood density, latewood density (>400 kg/m^3), and percentage latewood were carried out on five-ring group weighted averages. A multiple regression using both clonal averages and individual tree averages, comparing weighted breast-height density against weighted earlywood density, latewood density, and percentage latewood, was carried out in order to estimate the relative contributions of these factors. Multiple regressions were also performed for clonal mean data and for individual tree data, using mean ring density as the dependent variable. Independent variables included height and various exponents of ring number required to give the best fit. The density analysis program IDAS was also used to calculate 20 within-ring point averages for each ring group × clone combination to provide a comparison of within-ring density profiles on a uniform five-percentile increment scale.

TABLE 1–Form of main analysis of variance and expected mean squares

Source	Expected mean square	
Clones	$= \sigma^2_{RT(C)}$	$+ 11\sigma^2_{T(C)} + 22\sigma^2_C$
Trees within clones	$= \sigma^2_{RT(C)}$	$+ 11\sigma^2_{T(C)}$
Rings	$= \sigma^2_{RT(C)} + 2\sigma^2_{RC} + 22\theta^2_R$	
Rings × clones	$= \sigma^2_{RT(C)} + 2\sigma^2_{RC}$	
Rings × trees within clones	$= \sigma^2_{RT(C)}$	

σ^2_C and $\sigma^2_{T(C)}$ are variances among clones and trees-within-clones respectively.

σ^2_{RC} and $\sigma^2_{RT(C)}$ are the rings × clones and the rings × trees-within-clones interaction variances respectively.

θ^2_R is the fixed-effect "variance" among rings.

Data were analysed using analysis of variance to yield estimates of the variance components according to the format given in Table 1. Clonal repeatabilities were then estimated (at the individual tree level) according to the following relationships:

$$\text{Biological repeatability} = \sigma^2_C / (\sigma^2_C + \sigma^2_{T(C)}) \quad (1)$$

$$\text{Observational repeatability} = \sigma^2_C / (\sigma^2_C + \sigma^2_{T(C)} + (\sigma^2_{RC}/11) + (\sigma^2_T/11) \quad (2)$$

It is assumed that selection of trees within clones was random. The selection of clones to include extremes of density on the basis of prior sampling means that clonal repeatabilities for density are inherently overestimates of broad-sense heritability (H^2).

RESULTS

Gravimetric Density

There was generally good agreement between weighted whole-tree basic density values for individual trees within each clone (Table 2). An analysis of variance confirmed a highly significant clonal variance component ($F_{10,11} = 133, p = 0.000$). Correlations between mean ring density for each ring against either weighted tree means or weighted breast height means were significant for all rings outside ring 3 from the pith, although correlations for breast-height data reached a maximum at ring 7 (Fig. 1).

TABLE 2–Variation in whole-tree gravimetric density among clones

Clone	Tree A	Tree B	Mean
1	329	328	329
2	292	287	289
3	344	346	345
4	346	346	346
5	346	353	349
6	381	394	388
7	303	300	301
8	369	368	369
9	328	332	330
10	357	356	357
11	367	369	368

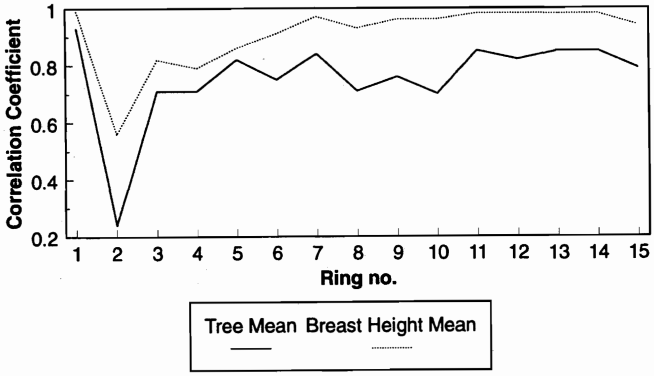

FIG. 1–Correlation coefficients for individual ring density with whole-tree or breast-height mean density. Values from ring 3 outwards are significant. Each correlation is based on 22 values except for ring 1 (n=3), ring 2 (n=16), and ring 3 (n=21).

Densitometry

In general, density increased with cambial age and decreased slightly with height (Fig. 2), in accordance with documented trends. These results were based on multiple regressions of clonal ring averages against height and cambial age. About half the clones showed a significant effect of height (Table 3). Within each clone, multiple regressions for each tree were not significantly different in all but two of the clones. Pith to bark trends for clonal averages at breast height showed significant variation among clones (Fig. 3). Only four of the clones reached an average density of 400 kg/m^3 by ring 15.

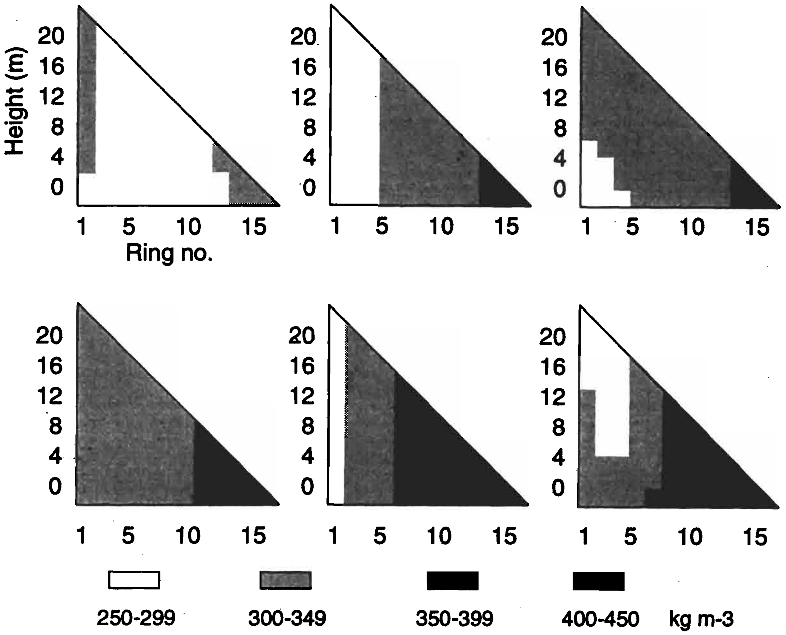

FIG. 2–Density class distribution within stems with height and distance from the pith for a selection of clones representing the range from lowest to highest overall density. These plots assume equivalent growth ring width at different heights and with distance from the pith, and are thus not volume weighted.

TABLE 3–Regressions for ring density among clones for height and ring number from the pith

Clone	R^2 (%)	Observations	Density at ring 1 at breast height (kg/m^3)	Height (m)	N*	N^2	N^3	N^4
1	72	56	292			0.322		
2	71	62	297	1.088	–32.790	4.290	–0.146	
3	57	60	314	–2.842	3.148			
4	62	57	298	–2.813	6.108			
5	63	57	294	1.434		0.377		
6	78	58	294		10.282			
7	69	60	353	–1.274	–84.916	15.479	–1.074	0.026
8	65	63	311			0.468		
9	68	57	278		5.263			
10	70	61	301		0.482			
11	88	59	316	–1.436	–23.846	5.173	–0.206	

* Ring number from the pith

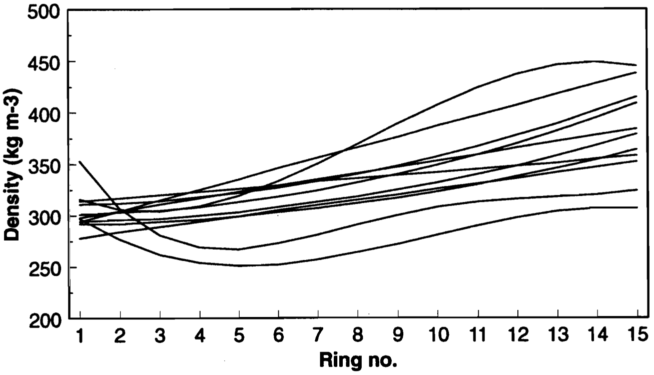

FIG. 3–Variation in breast-height density from pith to bark among 11 clones based on the regressions shown in Table 3.

Analysis of variance for breast-height density indicated significant effects for clones, trees within clones, rings, and rings × clones (Table 4). The major variance components were clones and rings. Biological repeatability was 0.91 while observational repeatability was 0.90 (Table 4).

TABLE 4–Analysis of variance and estimation of variance components for breast-height mean ring density for clones, trees within clones, and rings

	df	MS	F	p	$\hat{\sigma}^2$
Clones	10	29144.3	18.7	0.000	1253.7
Rings	10	19845.9	32.0	0.000	873.9 (θ^2)
Trees within clones	11	1561.3	6.5	0.000	120.0
Rings × clones	100	619.8	2.6	0.000	189.4
Rings × trees within clones	110	241.0			241.0
Biological repeatability (Eq. 1)		0.91			
Observational repeatability (Eq. 2)		0.90			

Mean within-ring density profiles in five-percentile increments for ring groups 1–5, 6–10, and 11–15 showed no apparent differences in within-ring density patterns among clones, other than those related to overall ring density (Fig. 4, 5, and 6). The percentage of latewood (density >400 kg/m^3) increased with increasing cambial age. There was negligible variation among clones in the ratio of earlywood to latewood density. For average within-ring density profiles, the amount of latewood did not increase between ring groups 1–5 and 6–10, but there was a slight increase in density of the latewood in rings 6–10 (Fig. 7). Both the amount and density of latewood showed a significant increase in rings 11–15, indicating a transition from corewood to outerwood within this ring group.

Based on five-ring groups, earlywood density had a significant clonal variance component ($p = 0.01$) (Table 5) as did latewood density ($p = 0.03$) (Table 6), while percentage latewood had a marginally significant clonal variance ($p = 0.07$) (Table 7). For both latewood density and percentage latewood, the ring groups variance was the dominant component and there was no significant interaction with clones. The estimated biological repeatabilities for earlywood density, latewood density, and percentage latewood were 0.68, 0.62 and 0.49 respectively. Multiple regression analysis for weighted breast-height density against weighted

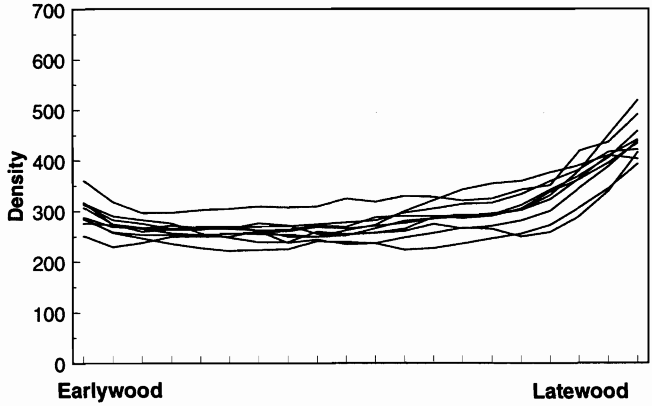

FIG. 4–Variation in within-ring density profile at breast height averaged for rings 1–5 among 11 clones on a standardised five-percentile incremental scale.

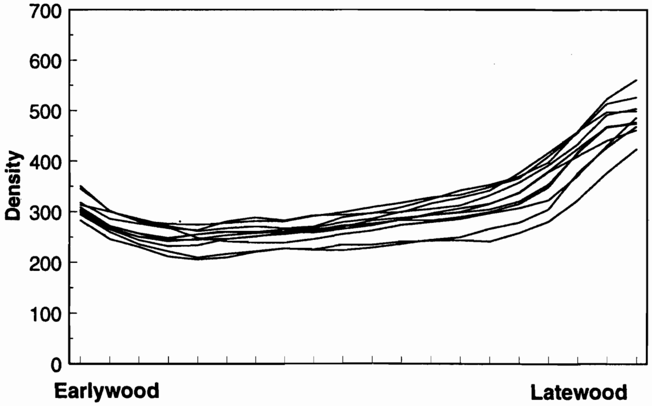

FIG. 5–Variation in within-ring density profile at breast height averaged for rings 6–10 among 11 clones on a standardised five-percentile incremental scale.

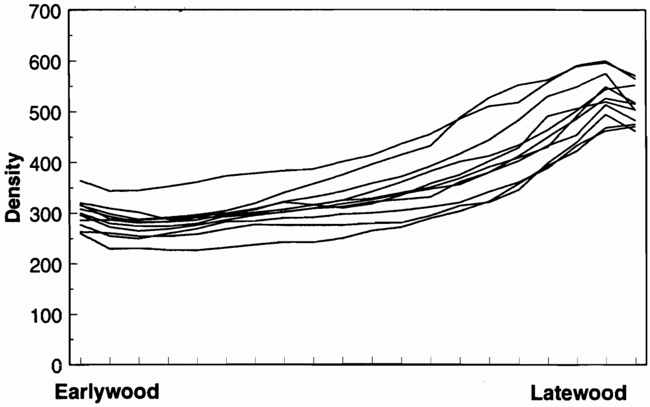

FIG. 6–Variation in within-ring density profile at breast height averaged for rings 11–15 among 11 clones on a standardised five-percentile incremental scale.

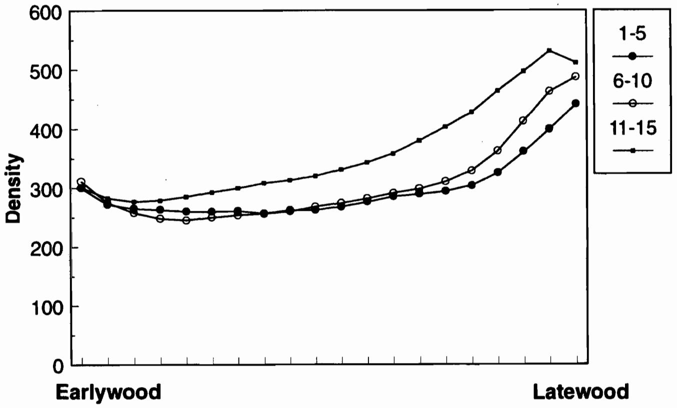

FIG. 7–Variation in mean within-ring density profile at breast height for five-ring groups averaged among 11 clones on a standardised five-percentile incremental scale.

TABLE 5–Analysis of variance and estimation of variance components for earlywood density among ring groups for clones, trees within clones, and ring groups

	df	MS	F	p	$\hat{\sigma}^2$
Clones	10	2107.0	4.38	0.011	271.0
Ring groups	2	6193.0	63.39	0.000	276.9 (θ^2)
Trees within clones	11	481.0	4.92	0.000	127.7
Ring groups × clones	20	100.6	1.06	0.446	2.8
Ring groups × trees within clones	22	95.0			95.0
Pooled residual*	42	97.7			97.7
Biological repeatability (Eq. 1)		0.68			
Observational repeatability (Eq. 2)		0.68			

*Based on Ring groups × clones and Ring groups × trees within clones.

TABLE 6–Analysis of variance and estimation of variance components for latewood density (>400 kg/m^3) among ring groups for clones, trees within clones, and ring groups

	df	MS	F	p	$\hat{\sigma}^2$
Clones	10	1536.7	3.5	0.025	183.1
Ring groups	2	6899.4	49.0	0.000	305.4 (θ^2)
Trees within clones	11	438.1	3.1	0.004	99.1
Rings × clones	20	179.9	1.7	0.112	37.4
Rings × trees within clones	22	105.2			105.2
Pooled residual*	42	140.8			140.8
Biological repeatability (Eq. 1)		0.65			
Observational repeatability (Eq. 2)		0.62			

*Based on Rings × clones and Rings × trees within clones.

earlywood density, latewood density, and percentage latewood for either individual trees or clones indicated that earlywood density was the dominant factor followed by percentage latewood (Table 8).

Cambial age trends in density among clones were related to overall density and were more or less parallel (Fig. 8, 9, and 10). For percentage latewood, two clones showed above-average amounts of latewood from ring 7 (Fig. 11).

TABLE 7–Analysis of variance and estimation of variance components for percentage latewood among ring groups for clones, trees within clones, and ring groups

	df	MS	F	p	$\hat{\sigma}^2$
Clones	10	385.2	2.6	0.067	39.4
Ring groups	2	2165.2	90.4	0.000	97.3 (θ^2)
Trees within clones	11	148.6	6.2	0.000	41.5
Ring groups × clones	20	24.1	1.0	0.485	0.2
Ring groups × trees within clones	22	23.8			23.8
Pooled residual*	42	24.0			24.0
Biological repeatability (Eq. 1)		0.49			
Observational repeatability (Eq. 2)		0.49			

*Based on Rings × clones and Rings × trees within clones.

TABLE 8–Regression analysis for weighted (by ring cross-sectional area) breast-height density against weighted earlywood density, weighted latewood density, and weighted percentage latewood at breast height, for trees and clones (b' is the standard partial regression coefficient which gives a comparison of the relative importance of each factor in the combined regression)

	Coefficients	Standard error	p	b'	Cumulative R^2 (%)
Trees					
Intercept	–115.20	36.34	0.005		
Earlywood density	0.73	0.10	0.000	0.47	92.9
Latewood density	0.43	0.07	0.000	0.23	96.8
Percentage latewood	1.24	0.23	0.000	0.36	98.8
Clones					
Intercept	–72.00	47.03	0.157		
Earlywood density	0.83	0.12	0.000	0.51	96.1
Latewood density	0.27	0.12	0.043	0.15	97.6
Percentage latewood	1.36	0.26	0.000	0.37	99.5

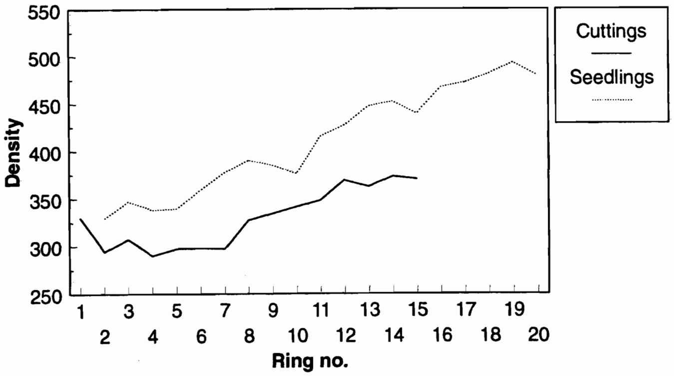

FIG. 8–A comparison of mean density at breast height for cuttings (based on 11 clones) and seedlings (typical values for *P. radiata*, Cown *et al.* 1992) of comparable age at planting but from different although comparable sites, and of different genotype. The effects of site and genotype are considered to be small in this comparison which is intended only to show the low densities of the clones in relation to typical values for *P. radiata*.

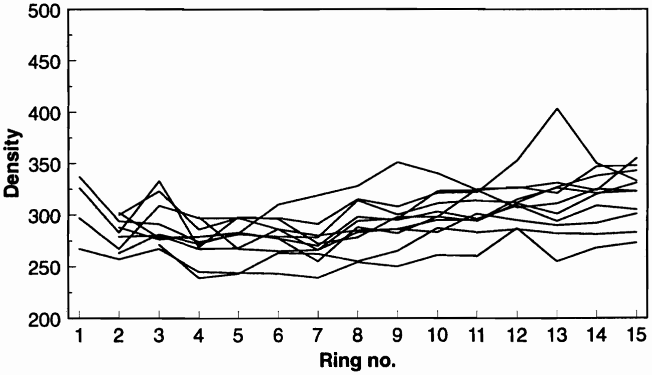

FIG. 9-Clonal trends in earlywood density with cambial age for 11 clones at breast height.

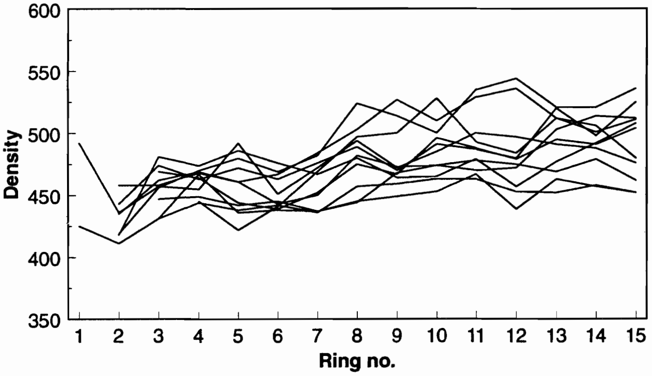

FIG. 10–Clonal trends in latewood density with cambial age for 11 clones at breast height.

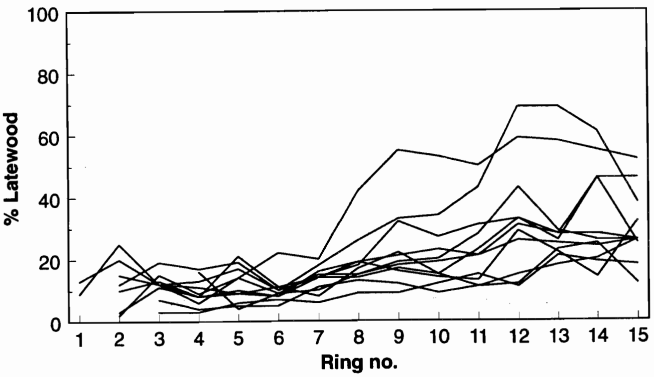

FIG. 11–Clonal trends in percentage latewood with cambial age for 11 clones at breast height. Two of the clones show above-average percentage latewood from ring 7 outwards.

DISCUSSION

The patterns of within-tree variation in basic density among clones (Fig. 2) were similar to those described in earlier studies (Cown & McConchie 1980; Cown *et al.* 1991), indicating increasing density with cambial age and, to a much lesser extent, decreasing density with height. Overall, densities for these clones were well below the expected average for typical seedling stock (cf. Cown *et al.* 1992), with only one clone reaching the corewood boundary of 400 kg/m^3 by ring 10 (Fig. 3 and 8). This finding supports earlier studies in which wood density in cuttings was lower than in seedlings (Nicholls & Brown 1971; Nicholls *et al.* 1974; Sweet & Harris 1976; Cown 1988). This effect is known to increase with the physiological age of the trees at the time cuttings are taken (Sweet & Harris 1976). Selection for higher density clones to overcome this possible physiological aging effect would seem to be highly justified if clonal forestry based on cuttings is implemented on a large scale.

There were quite marked differences in pith to bark trends in density at breast height (Fig. 3), with some clones showing a relatively rapid increase in density while the lowest density clones showed a decline in density over the first five rings and negligible increases over subsequent rings. The fact that trees within clones showed consistent pith to bark trends suggests that there is a large element of genetic control in this cambial age effect. Variation among clones in the size of the height effect on density (Table 3) also supports the presence of an additional component of genetic influence, although this is much smaller than the cambial age effect and probably would not warrant selection.

It was also apparent that clonal selection based on assessment of young trees will be difficult (Fig. 3). Not only was the range of variation among clones much smaller in the first few growth rings, as reported for families by Burdon & Harris (1973) and Cown *et al.* (1992), but the relative magnitude of density was only weakly related to density values observed in later growth rings. This was confirmed in the high correlations between density in individual rings and weighted averages seen only from ring 7 outwards (Fig. 1). Sampling of clones by collection of increment cores containing the outer five rings from trees 10–15 year old would therefore be a more reliable basis for selection than sampling of young (<5-year-old) trees. Sampling trees 5–10 years old might be an acceptable compromise between the time required to make a selection and the reliability of the selection. Other components of the density variation in the inner five rings may have potential to form a basis for selection, including a tendency for low-density trees to show declining rather than increasing density in the first few rings. However, a much larger sample of clones with greater replication covering a greater range of densities is needed to determine the efficacy of such trends as a basis for selection.

Analyses of variance in Tables 5, 6, and 7 confirmed that earlywood density is the dominant factor in determining overall clonal density at breast height. Earlywood density is 1.4 times more important than percentage latewood (Table 8), due in part to the greater proportion of earlywood in the growth ring, which in turn is 2.5 times more important than latewood density in contributing to clonal differences. However, in spite of a significantly larger clonal repeatability for latewood density compared to percentage latewood, the high overall correlation between earlywood and latewood densities ($R^2 = 79\%$) means that selection for reduced density contrast between earlywood and latewood to produce wood with a more uniform within-ring density profile is likely to be of limited success. Visual observations of reduced optical contrast between earlywood and latewood in some of the clones examined in this study probably result from an overall reduction in density, making the latewood less prominent without affecting the appearance of the earlywood. Both latewood density and percentage latewood were substantially lower than in typical seedlings of comparable age (Cown *et al.* 1992) (assuming any site and genotype effect was negligible in this comparison) but this was related to an overall reduction in density rather than just a reduction in the amount and/or density of latewood. It is worth pointing out that the above analysis has been influenced by the use of 400 kg/m^3 as a cut-off value for latewood density which means that percentage latewood will be correlated to overall ring density to some extent. Nevertheless, these results seem to be biologically meaningful even though the relative magnitudes of the contributions from latewood density and percentage latewood may be biased.

Within-ring trends were more or less parallel among clones (Fig. 4, 5, and 6), indicating the absence of any genetic effect on within-ring density variation apart from overall density level. There was evidence of a significant genetic component to the variation in latewood density and, to a lesser extent, percentage latewood (Tables 6 and 7), but the effect of ring groups (a combination of cambial age and environmental effects related to seasonal variations) was substantially larger than the clonal effect, indicating that cambial age and environment, rather than genotype, are dominant factors in determining the amount and density of latewood.

Within-ring density changed from ring 10 outwards, with an increase in earlywood density and an increase in the density and amount of latewood (Fig. 7). This result suggests that the corewood, normally considered to include rings 1–10 in *P. radiata*, was not larger than normal in these trees, as discussed above in relation to the overall low density of the clones examined. A change in corewood size thus depends on whether corewood is defined by overall density (<400 kg/m^3) or by within-ring density profile. Donaldson & Burdon (in press) also found that the corewood in the same group of trees ended at about ring 10 on the basis of microfibril angle trends, suggesting that within-ring density profile may be a better definition for corewood than overall density, at least in a biological sense.

Trends in earlywood and latewood density with cambial age among clones were more or less parallel (Fig. 9 and 10). However, the same trends in percentage latewood indicated the presence of two clones which had above-average amounts of latewood from ring 7. This may reflect an interaction between rings and clones for percentage latewood even though this was not detected in the analysis of Table 7, possibly because ring groups were used. An analysis using individual ring data for percentage latewood confirmed the presence of an interaction between rings and clones for percentage latewood ($F_{100,110} = 2.2$, $p = 0.000$).

The results of this study confirm those of earlier studies (Burdon & Harris 1973; Burdon 1992; Burdon & Low 1992; Cown *et al.* 1992) indicating that density has a high degree of variability and inheritance. However, both these parameters are likely to be over-estimates in this study because of the selection procedure applied to the clones used, which tended to maximise σ^2_C and make it a fixed variance component rather than a random effect, as assumed in Table 1. The range of variation among the clones sampled was large (289–388 kg/m^3), although this was influenced by the preselection process used to screen all of the 120 clones in the trial examined here. These clones represent only the low to medium density range for *P. radiata* at this age (Cown *et al.* 1991).

CONCLUSIONS

The clones examined in this study showed significant variation in overall basic density and for within-tree trends in mean ring density with cambial age and height. There was little variation of within-ring density patterns among clones. Mean ring density for growth rings outside ring 7 was highly correlated with weighted mean density at breast height which, combined with a high clonal repeatability of 0.9, indicates that selection on the basis of mean ring density of rings 5–10, determined from increment cores, is feasible. Earlywood density was the major component in variation of basic density among clones, due in part to earlywood being the dominant component of each growth ring, with percentage latewood also contributing. Latewood density contributed relatively little to overall density variation among clones, probably because the amount of latewood in these trees was so small. This was due in part to the low overall density in these trees.

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