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ABSTRACT

Breast height pith-to-bark 10-mm increment cores were collected from eight individual stems from each of 10 families of *Pinus radiata* D. Don (+ control seedlot) at seven sites after 22 years of growth. The sites ranged from Taringatura, in the deep south of New Zealand (lat. 46°S; mean annual temperature 10.1°C), to Woodhill (lat. 35°S; mean annual temperature 14.6°C), and covered an altitudinal range of 650 m. The cores were resin-extracted and scanned in a wood densitometer to yield a continuous density trace across all annual growth rings. Sample data were analysed by family and site to determine the influence of genotype and environment on growth ring density components.

There were significant site effects for both growth rate and wood density, which broadly corresponded to expected patterns, but little correlation between the two variables. Average wood density at Woodhill reached "mature" levels (defined as 400 kg/m^3) well before age 10 years whereas the southernmost site, Taringatura, failed to reach this level even after 20 years. Percentage latewood proved to be the most sensitive variable in both juvenile and mature wood, and was reflected in the site values for average wood density. Site differences in earlywood and latewood density were comparatively small.

Family ranks for density traits averaged across all sites maintained a high degree of consistency and moderate-to-high heritabilities, but analyses of variance also revealed a significant G×E component. The range in family density means of about 50 kg/m^3 remained consistent from pith to bark across sites. There were large differences in the ability of individual families to reach "mature" levels of wood density. Families varied in the period required for mature wood initiation (8 to 20 years).

Keywords: density; families; site; wood densitometry; genotype × environment interaction; heritability; residual maximum likelihood; Bayesian hierarchical models; Gibbs sampler; Trellis graphics; *Pinus radiata*.

INTRODUCTION

Among the various fundamental wood properties, basic wood density is widely considered to be the most important because of its influence on the quality of a wide range of solid wood and fibre products. It is widely acknowledged as the single best predictor of performance attributes (Zobel & Jett 1995). Solid wood density is determined both by the density of individual cells and the proportions of growth ring components (earlywood and latewood). Most authors agree that, within a species, the latewood component is the most sensitive to environmental influences (Cown 1977) and has the strongest effect on mechanical properties (Rozenberg *et al.* 1999). Knowledge of the factors influencing wood formation at the growth ring component level is useful for better understanding of product performance.

A progeny trial based on 25 parent trees, mated in a series of disconnected half-diallel crosses, was established at 11 varied sites throughout New Zealand in 1975 (Carson 1991). Seedlings were obtained from 25 parents originally selected for superior growth and form ("850" series). The objectives of the trial included documentation of the extent of genotype × environment interactions and assessment of expected genetic gains at contrasting sites, defined on the basis of differing soil and climatic conditions. Carson (1991) reported the results of an analysis of diameter growth at all 11 sites to age 15 years and concluded that, while regionalisation of trials promised only modest enhancement of genetic gains in stem growth, there could be significant advantages when dealing with tree form traits, such as internode length. A similar argument could be used for wood density, in that it may be more critical in areas where structural lumber is an important consideration, as opposed to lumber for clearwood products.

The existence of such a comprehensive "mature" trial provided excellent material for a study of wood density, which is considered a major parameter affecting most wood uses (Cown 1999). Wood densitometry has been used in several countries to document the within-ring patterns of wood density variation and to compare the effects of silvicultural, environmental, and genetic influences (Harris 1969; Ohta 1981; Nicholls 1984; Hapla 1985; Cleaveland 1986; Jozsa & Brix 1989; Malan & Marais 1991; Abdel-Gadir *et al.* 1993; Hodge & Purnell 1993; Vargas-Hernandez *et al.* 1994a, b; Vargas-Hernandez & Adams 1994; Barbour *et al.* 1996; Donaldson *et al.* 1996; Fujisawa *et al.* 1996; Rozenberg *et al.* 1999). Previous research has confirmed that average wood density and density of growth ring components (earlywood and latewood) in New Zealand are influenced by both environmental factors (Cown & McConchie 1983) and genotype (Cown *et al.* 1992). The availability of study material at diverse locations across New Zealand provided a good opportunity to further explore both site and genotype effects on some wood properties.

EXPERIMENTAL METHODS

A group of 10 unrelated full-sib families was selected for sampling at seven sites over the period 1997 to 1999. At each site (Fig. 1, Table 1) pith-to-bark 10-mm breast-height (1.4 m) increment cores were obtained from 10 stems in each family and a "control" seedlot ("Kaingaroa Bulk" – R69/654). In all, 770 cores were collected over a 2-year period and processed according to standard densitometric procedures (Cown & Clement 1983).

Wood density is such an important wood characteristic and also so variable that it has been proposed as a useful criterion for demarcation of juvenile wood (Diáz-Vaz 1981; Cown 1992; Abdel-Gadir & Krahmer 1994; Vargas-Hernandez *et al.* 1994a, b; Danborg 1994). Several distinctly different approaches have been suggested for selection of the transition position based on densitometric values:

(1) Change of slope in the radial density trend

(2) Nomination of an absolute wood density value

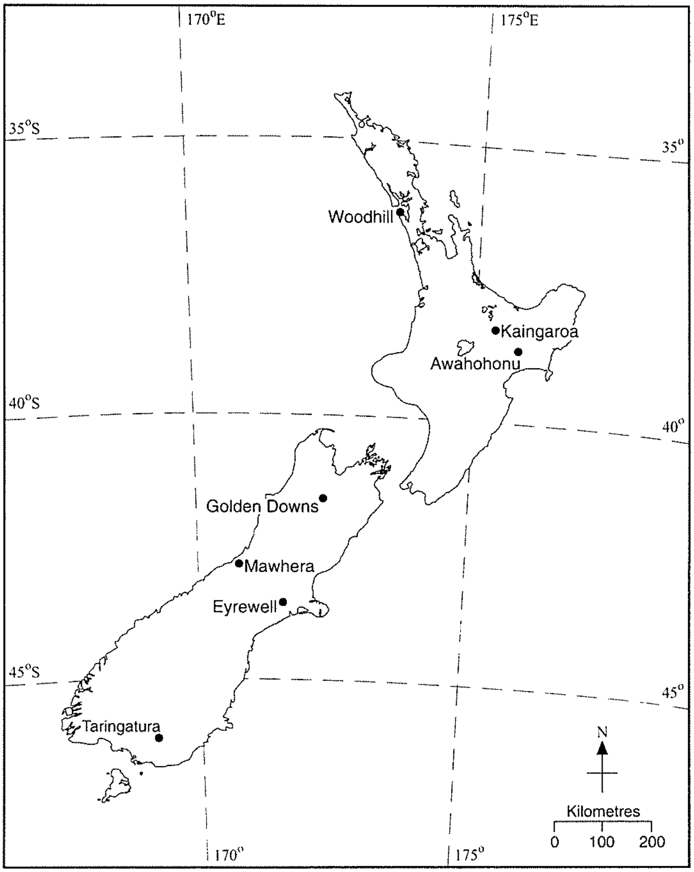

FIG. 1–Location of seven test sites.

TABLE 1–Sample site data (from Carson 1991)

Site	Latitude (S)	Altitude (m)	Mean annual temperature (°C)	Mean annual rainfall (mm)
1. Woodhill	35°00′	20	14.6	1300
2. Kaingaroa Cpt 327	38°30′	560	10.7	1490
3. Awahohonu	39°10′	500	11.9	1750
4. Golden Downs	41°43′	670	10.5	1300
5. Mawhera	42°27′	100	11.3	1890
6. Eyrewell	43°25′	180	11.0	850
7. Taringatura	45°59′	350	10.1	840

(3) Fixed number of growth rings from the pith.

There have been advocates for all approaches, but no universal acceptance of a standard densitometry method. The commonest (and simplest) way of defining juvenile wood is simply to assign a ring number from the pith at all stem levels (Method 3 above), normally 10 rings for *P. radiata* in New Zealand (Cown 1992). Such an approach was used in this study, and "juvenile" and "mature" values were calculated on this basis, weighted by ring area. The earlywood/latewood transition value was set at 400 kg/m^3, and the within-ring density contrast (latewood density minus earlywood density) labelled "uniformity" (Cown & Clement 1983).

A mixed effects model was fitted to each response variate, with site effects fixed, and random effects of family, replicates within site, plus interactions, giving the following decomposition of total variance (var(y)):

$$\mathrm{var}(y) = V_F + V_{R(S)} + V_{FS} + V_{FR(S)} + V_E \qquad (1)$$

where V_F, $V_{R(S)}$, V_{FS}, $V_{FR(S)}$, V_E are the variance components for family, replicate within site, family × site, family × replicate within site, and residual error (incorporating micro-environmental variation and within-family genetic variation measurement error) respectively. The models were fitted using REML (Patterson & Thompson 1971) implemented in Splus (Becker *et al.* 1988). An overall estimate of heritability (expressed as the ratio of twice the family variance to total variance*) was obtained from the full dataset, and within-site heritabilities were also estimated from separate analyses for each site. For the within-site analyses the variance decomposition reduces to:

$$\mathrm{var}(y) = V_F + V_R + V_{FR} + V_E \qquad (2)$$

Note: these estimates may be slightly greater (due to non-additive effects) than the estimates of heritability defined as the proportion of total variation which is *additive* genetic variation (which cannot be estimated from the data of this paper) to which we compare our results below.

To investigate the distribution of the heritability estimates, the ring density response variate was re-analysed by fitting a Bayesian hierarchical model with random effects corresponding to the variance components above. Inverse gamma prior distributions (the standard conjugate prior distributions) were used for the variance components. The priors were chosen to be nearly flat over the expected range of the parameter, representing prior ignorance. Posterior distributions for model parameters were estimated by Gibbs sampling using the computer program BUGS (Spiegelhalter *et al.* 1995). It should be noted that this method, in contrast to the traditionally used REML method, has no problem with estimates tending to zero or becoming negative in the iterative process, and then being arbitrarily set to zero. Additionally, estimation using Gibbs sampling is simulation consistent, meaning that the validity of variance estimates and standard errors does not depend on large sample sizes, but arbitrarily accurate estimates of the posterior distribution can be obtained with any given data-set by simply running the Gibbs sampler long enough.

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* It is common practice among geneticists (to avoid selecting families merely because of their occurrence in extreme replicates) to treat the replicate within-site effects as fixed effects which does not contribute a variance, or else drop the term $V_{R(S)}$ from Eqn 1. The same applies in respect of V_R in Eqn 2. The impact of this was examined and found to make no difference to the heritability estimates. The family-by-replicate-within-site variation may be dominated by local microsite influences, but was generally small. The choice of how to treat these effects in formulating var(y) was, for the purposes of heritability estimation, immaterial.

RESULTS AND DISCUSSION

Site Effects

The growth and wood density data are summarised in Table 2, for all families across all sites.

TABLE 2–Site means: annual ring growth and density components

Site	Ring width (mm)	EW width (mm)	LW width (mm)	LW (%)	Ring density (kg/m^3)	EW density (kg/m^3)	LW density (kg/m^3)	Uniformity (kg/m^3) *
Juvenile wood (rings 1–10)								
Woodhill	13.4	12.1	1.33	10	400	368	570	202
Kaingaroa, Cpt 327	15.6	14.7	0.84	6	343	327	546	219
Awahohonu	15.9	15.8	1.30	8	357	336	556	220
Golden Downs	11.5	10.6	0.83	7	349	327	573	246
Mawhera	12.5	11.9	0.53	4	345	333	542	209
Eyrewell	10.4	9.5	0.91	9	358	335	570	236
Taringatura	14.0	13.3	0.67	5	339	326	549	235
Average	**13.5**	**12.6**	**0.92**	**7**	**356**	**336**	**558**	**222**
S.E.D. †	0.7	0.7	0.03	1	70	42	52	81
Mature wood (rings 11+)								
Woodhill	4.1	2.3	1.78	45	496	397	614	217
Kaingaroa, Cpt 327	5.6	4.6	0.99	19	397	357	567	210
Awahohonu	6.2	5.0	1.20	20	409	362	591	229
Golden Downs	6.9	6.0	0.89	13	371	341	569	228
Mawhera	7.8	7.0	0.86	13	385	361	545	184
Eyrewell	4.7	3.7	1.00	21	412	367	574	207
Taringatura	8.5	8.0	0.49	6	351	339	550	211
Average	**6.3**	**5.2**	**1.03**	**20**	**403**	**361**	**573**	**212**
S.E.D. †	0.6	0.5	0.04	12	206	73	89	86

* Uniformity = difference between latewood (LW) density and earlywood (EW) density
† S.E.D. = standard error of difference between means within a column

Radial growth

Growth ring width followed a decreasing trend with age at most sites after an increase over the first few rings from the pith (Fig. 2). Juvenile wood radial growth (inner 10 rings) was greater at Awahohonu and Kaingaroa than at other sites ($p<0.05$), but in the mature wood (rings 11+) both Mawhera and Taringatura outperformed the northern sites. Woodhill produced narrower mature wood rings than the other sites.

Wood density

The general patterns of average wood density variation in New Zealand have been demonstrated (Harris 1969; Cown & McConchie 1983), and generally conform to a pattern dictated by mean annual temperature, rainfall, and site nutrient status. The sites covered by the Diallel represent all three broad site classes (high, medium, and low density — Cown 1999).

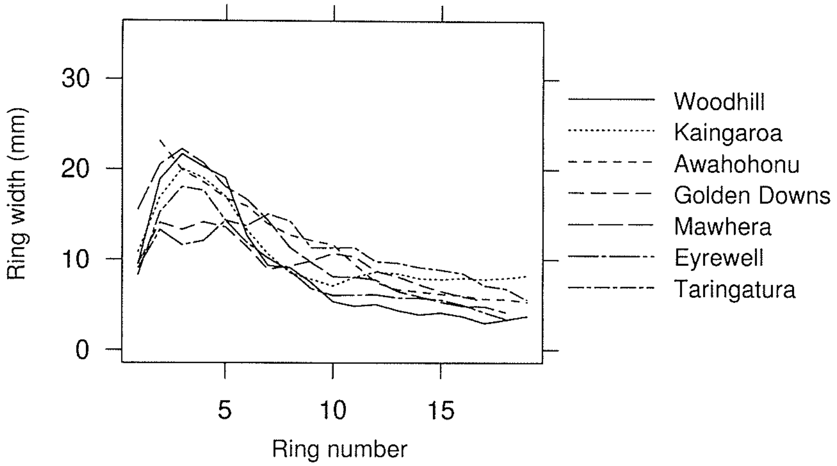

FIG. 2–Site means for ring width: pith-to-bark trends.

Pith-to-bark trends in average ring density and latewood percentage at each site are shown in Fig. 3 and 4. As expected, there were differences in wood density between the sites. Broadly, the variation corresponded to the known pattern of decrease from north to south — Woodhill gave the highest values and Taringatura the lowest — but there was no clear latitudinal trend among the other sites (not unexpected, given the restricted range of mean annual temperature applying to the selected sites). Woodhill stands out with higher overall rate of increase in density (Fig. 3) and latewood percentage (Fig. 4) with age. Historically, this forest was recognised to be a "hard" site, with variable soil conditions (sand overlaying clay) and nutrient limitations (phosphorus and nitrogen deficiency).

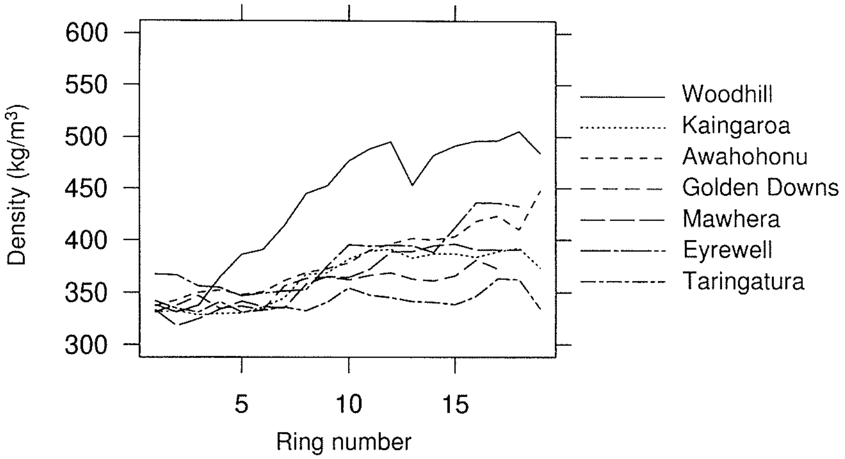

FIG. 3–Site means for ring density: pith-to-bark trends.

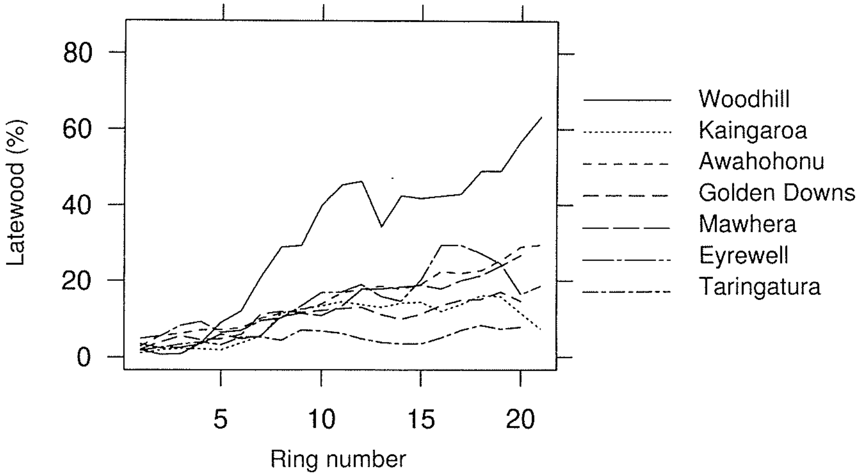

FIG. 4–Site means for percentage latewood: pith-to-bark trends.

Growth ring density components

The average values of ring density components (ring mean density, earlywood density, and latewood density and uniformity) for juvenile and mature wood are shown in Fig. 5.

Growth ring components (earlywood and latewood) have a strong influence on average density values. Mature wood latewood percentage (Fig. 6) was very high at Woodhill (50%

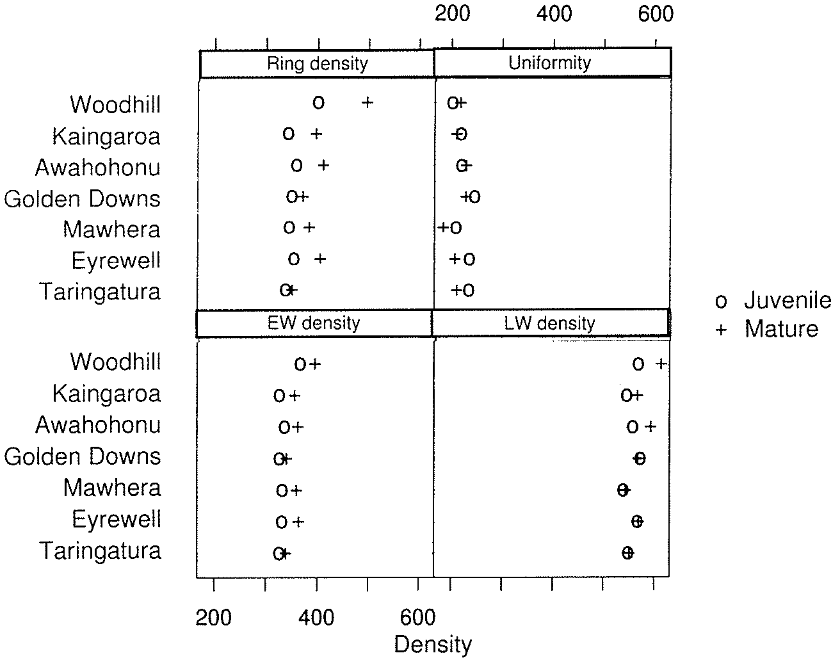

FIG. 5–Site means: ring density components.

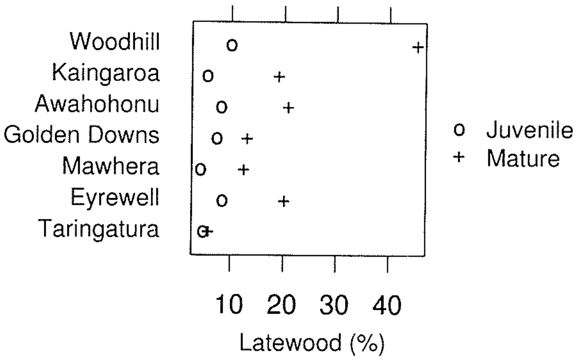

FIG. 6–Site means: latewood percentage.

vs. 10–25% at other sites, except for Taringatura, where the latewood percentage for mature wood remained very low) and this, combined with the latewood density level of about 600 kg/m^3, has contributed to the site density. Comparison of growth parameters (e.g., dbh at age 20 years) failed to reveal a simple relationship with latewood percentage. The most obvious trend was the decreasing latewood percentage with increasing latitude. This accords with the acceptance of southern lumber as an excellent source of light-coloured wood with uniform density and superior machining properties.

Families

The average values for each family — separated into juvenile and mature phases — are shown across all sites in Table 3. Individual-family ring density trends are shown in Fig. 7 and the results of an analysis of variance in Table 4.

TABLE 3–Annual ring density components, all families

Family	Juvenile wood (rings 1–10)				Mature wood (rings 11+)			
	Ring density (kg/m^3)	EW density (kg/m^3)	LW density (kg/m^3)	Uniformity (kg/m^3) *	Ring density (kg/m^3)	EW density (kg/m^3)	LW density (kg/m^3)	Uniformity (kg/m^3) *
1	360	337	560	223	415	369	572	203
2	332	315	561	246	382	348	571	223
3	357	332	570	238	409	353	589	236
4	380	355	576	221	431	379	592	213
5	343	326	550	224	385	352	561	209
6	343	332	541	209	374	347	554	207
7	361	343	546	203	402	362	566	204
8	373	351	563	212	429	378	581	203
9	358	340	556	216	406	364	576	212
10	342	323	557	234	386	345	571	226
Mean	356	335	558	223	402	360	573	213
S.E.D.†	4	3	4		9	5	6	
Control	370	345	564	219	422	374	578	204

* Uniformity = difference between latewood (LW) density and earlywood (EW) density
† S.E.D. = standard error of difference between means within a column

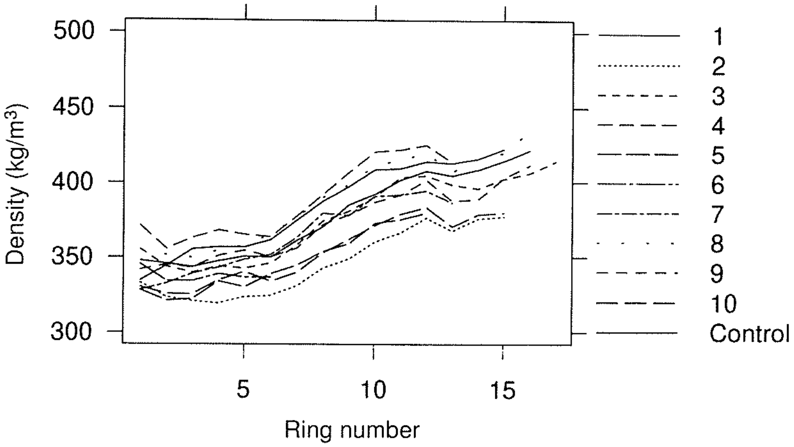

FIG. 7–Family means for ring density: pith-to-bark trends.

TABLE 4–Variance components for juvenile and mature ring density components

Variance component	Juvenile wood (rings 1–10)				Mature wood (rings 11+)				J-M diff.
	Ring density (kg/m³)	EW density (kg/m³)	LW density (kg/m³)	Uniformity (kg/m³) *	Ring density (kg/m³)	EW density (kg/m³)	LW density (kg/m³)	Uniformity (kg/m³) *	
V_F	198	136	98	3.7	330	145	105	13	31
$V_{R(S)}$	18	13	<0.1	0.6	7	9	6	<0.1	<0.1
$V_{F(S)}$	19	12	24	1	165	43	64	9	97
$V_{FR(S)}$	20	3	13	1	31	<0.1	29	4	22
V_E	408	254	268	14	888	367	388	53	562
$h^2_{overall}$	0.60	0.66	0.48	0.36	0.46	0.52	0.36	0.34	0.08
h^2_{within}†	0.62	0.70	0.62	0.44	0.68	0.64	0.56	0.54	0.32
SEM of h^2_{within}	0.08	0.06	0.06	0.08	0.06	0.06	0.04	0.06	0.06
GxE (%)	10	9	25	28	50	30	61	71	314
F GxE	1.4	1.5	1.8	1.6	2.7	2.2	2.4	2.5	2.6
P GxE	0.03	0.03	0.001	0.004	<0.001	<0.001	<0.001	<0.001	<0.001

* Uniformity = difference between latewood (LW) density and earlywood (EW) density

† Arithmetic average of within-site heritabilities. Adding $2V_{FS}$ to the numerator while using Eqn (1) for the denominator for estimating a pooled within-site heritability (h^2_{within}) gave comparable figures.

Averaged across all sites, the family trends showed a high degree of consistency in average density, with individual families maintaining their rank (e.g., 8 is high and 40 low). The same families also tended to have high and low earlywood density respectively.

The estimated pooled within-site heritability h^2_{within} and its standard error SEM(h^2_{within}) are given in Table 4. Note: this SEM shows the variability in the estimate of heritability when the experiment is repeated at a different site, *with the same families*. This does not incorporate a major component of uncertainty in heritability, namely the genetic sampling of a random set of families, as can be seen by comparison with the results of the Bayesian analysis below. The row G×E(%) in Table 4 is the estimated G×E variance component, expressed as a percentage of the family variance. $F_{G\times E}$, $P_{G\times E}$, denote the F-statistic for testing G×E (i.e., ratio of mean squares for family × site and family × replicate within site), and the associated P-value respectively.

The overall heritabilities in Table 4 are mostly slightly lower than the corresponding within-site values except for the variable J-M Diff., defined as the difference between mature and juvenile wood density, where the overall heritability is much lower than the within-site value, and G×E(%) is high. This may be a result of different responses to the Woodhill environment (cf. Fig. 8).

Heritability estimates here are comparable to previous estimates (cf. Dadswell *et al.* 1961; Burdon & Harris 1973; Bannister & Vine 1981; Dean 1990; Burdon & Low 1992; Cown *et al.* 1992).

The Bayesian hierarchical model gave an estimated h^2 of 0.62 for the heritability of ring density with a posterior standard deviation of 0.18 and a 95% posterior credible interval of 0.34–1.00.

Overall, the density trends were very similar between families, but there were clearly consistent differences in the average values. Family 1, for instance "matured" (exceeded 400 kg/m^3) after 10 growth rings, whereas Families 5 and 6 barely exceeded this level at about age 18 years. The spread between high- and low-density families is about 50 kg/m^3 from pith to bark, and in contrast to the site effects, these differences do not become appreciably larger as the trees mature.

An Splus trellis graphics plot is depicted in Fig. 8 (Becker & Cleveland 1996). Each panel is a plot of trends in ring mean wood density *vs.* ring number from the pith for each site for a given family. The family number is given at the top of the panel. Note that some families (e.g., 3, 10, and control) show a greater rate of increase in density with age at the Woodhill site than others, (e.g., 5, 8), where the density at Woodhill is higher than other sites, but the difference between Woodhill and the other sites is nearly constant with age for these families. This is consistent with the high percentage of G×E variation for the juvenile-mature difference trait in Table 4.

CONCLUSIONS

Site had the greatest effect on growth and wood density parameters, and broadly agreed with previous findings of environmental effects (average wood density decreasing southwards and with increasing altitude). Site differences became more marked with increasing stand age. Based on a nominated wood density level (400 kg/m^3), the average age of onset of mature wood formation varied from about 5 years at the most northerly site (Woodhill) to 20+ years at the most southerly sites (Eyrewell, Mawhera, Taringatura).

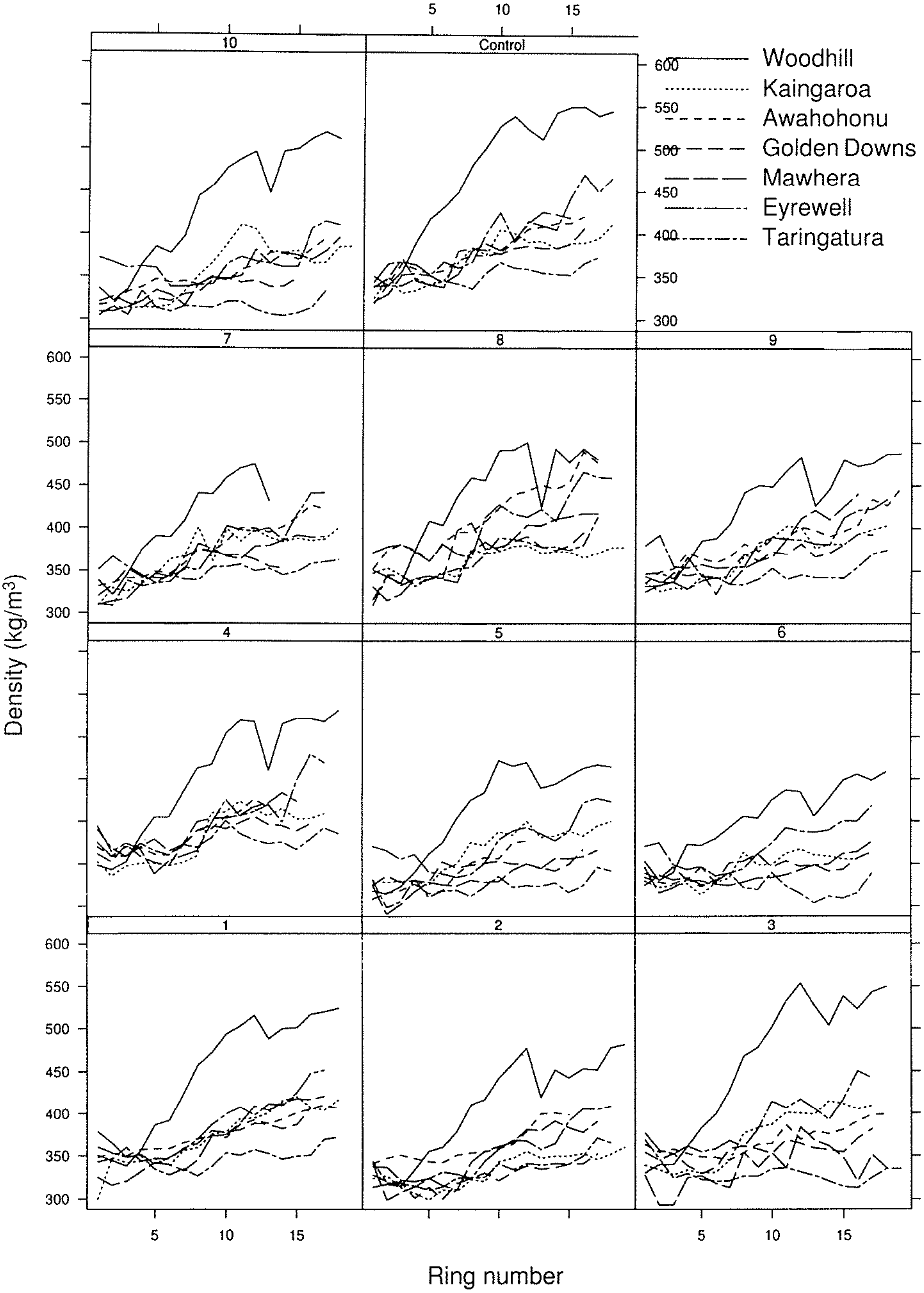

FIG. 8–Ring density trends by site by family.

The predominant influence on average growth ring density was latewood percentage (wood >400 kg/m^3). Growth ring component densities (earlywood and latewood), by comparison, varied to a minimal extent. In contrast to site effects, family density differences remained consistent throughout the period of the trial. Over all sites, families averaged from 8 to 20 years in the period required for mature wood initiation.

Heritabilities of wood density traits were moderate to high, confirming that early selection for wood density parameters is a sound strategy.

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