VARIATION IN WOOD CHARACTERISTICS OF 20-YEAR-OLD HALF-SIB FAMILIES OF *PINUS RADIATA*

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ABSTRACT

Increment core samples were collected at breast height (1.4 m) from 20-year-old trees of 30 of the top-ranked wind-pollinated progenies from the '268' series of *Pinus radiata* D.Don plus trees, and their wood properties were examined. The objectives were to establish the extent of any possible shift in average wood properties caused by intensive selection for growth rate and stem straightness, and to estimate genetic parameters (variances, narrow-sense heritabilities, and genetic correlations). Samples were also collected from control trees, representing a "felling select" seedlot, within the same progeny trial.

Properties examined included growth rate, wood density, and resin content (all by five-ring core segments), heartwood percentage and compression wood rating (whole cores), and tracheid length (outerwood only).

Although wood density was variable (coefficient of variation about 0.07), the average for the progenies overall was almost identical to that of the control trees. On the other hand, there were slight indications that, along with the improved growth rate of the progenies, compression wood and heartwood resin content levels increased whereas tracheid length decreased. Heritability estimates for all the actual wood properties were high, ranging from 0.4 upwards, and coefficients of variation for resin content variables and heartwood content were very high (0.4 or higher), suggesting good prospects for genetic manipulation.

Keywords: wood properties; tree breeding; *Pinus radiata*.

INTRODUCTION

It is accepted that the utilisation potential of any timber species is determined largely by the anatomical and chemical nature of the woody cells, which confer the basic physical and mechanical properties and processing characteristics, as well as the presence or absence of "defects". Classification of the latter depends to some extent on the specific end-use, but for *Pinus radiata* they commonly include features such as knots, compression wood, and spiral grain. Fortunately, the presence of internal checks and decay is negligible in this species, although resin pockets can be a nuisance.

Research on the relationships between wood characteristics and processing economics and product values is rarely definitive, owing to the large number of interacting factors.

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However, reviewers looking for common themes almost invariably select wood density as the single most influential variable. This is because density is a general indicator of cell size and is a good predictor of strength, stiffness, ease of drying, machining, hardness, and various papermaking properties (Panshin & de Zeeuw 1980; Megraw 1985).

Wood properties in *P. radiata* have been extensively researched, particularly in relation to site, tree age, and silvicultural effects in New Zealand and Australia (Harris 1965; Bamber & Burley 1983; Cown *et al.* 1991). A reasonable body of work has also indicated that a number of wood properties of *P. radiata*, as in other timber species, may be highly heritable. Characteristics covered so far in New Zealand research include wood density (Burdon & Harris 1973; Bannister & Vine 1981), compression wood (Burdon 1975), and spiral grain (Harris 1989; Burdon & Low in prep.). Characteristics for which little or no information exists in the New Zealand resource include tracheid length, heartwood development, and resin content. Research results on *P. radiata* from Australia, however, have suggested that these should also be heritable (Dadswell *et al.* 1961).

Despite the direct relationships between some wood properties and wood uses, there has been little real progress in breeding for specific wood properties in *P. radiata*. This can be attributed to:

(a) The relatively high cost of assessing wood traits in progeny trials.

(b) The lack of hard cost/benefit data for wood properties.

(c) The negative genetic correlation between wood density and diameter growth.

(d) The uncertainty about whether breeds with high or with low wood density are more desirable for general-purpose plantations, in combination with a past lack of propagation technology for producing conveniently a multiplicity of specialised breeds.

At present the New Zealand tree breeding programme concentrates on growth rate, stem form, and disease resistance but also keeps a watching brief on wood density to prevent unwanted changes that may result from adverse genetic correlations with other traits.

Changes in *P. radiata* silviculture and genetic improvements have dramatically shortened commercial rotations to around 30 years or less. At the same time, forest management tools have been developed to enable much better assessment of the impact of consequent changes in wood properties. The computer model SAWMOD, for example, permits evaluation of the effect of changes in wood density (which depends very strongly on rotation length) on the recovery of machine stress-graded timber (Cown *et al.* 1987).

Most of the plantations in New Zealand will be established using progeny from the best seed-orchard clones, selected almost entirely on the basis of growth rate and tree form in addition to general health. It is important to assess the wood characteristics of these seed sources to ensure that the utilisation potential is not adversely affected, and to obtain information on the potential for manipulation of wood properties.

MATERIALS AND METHODS

The Trial

The '268' clonal series represents a key source of genetic material from which improved seed can be obtained. A trial established in Kaingaroa Forest in 1969 contained openpollinated progenies of 588 plus trees from the '268' series. The trial also contained a control representing a "felling select" seedlot obtained by collecting seed from 25 trees chosen per hectare in a generation of stands preceding that wherein the '268' parents were selected. The trial had five block replicates with one 10-tree row-plot per progeny per replicate, but with the control lot represented in 150-tree subblocks of 15 adjacent 10-tree row-plots. The plots were thinned to five trees per row-plot at age 5 years and the blocks received a commercial thinning to 300 stems/ha without regard to progenies at age 18 years. At the time of sampling the trees were 20 years old.

For this study it proved possible to ignore the block-replicate classification without causing appreciable bias which, in view of imbalance in numbers within family/block subclasses, simplified the statistical analysis.

Sample Collection

From 30 top-ranking progenies, selected for growth and form, two bark-to-pith 5-mm increment cores were collected per tree from breast height (1.4 m). Sample numbers per family varied from nine to 15, depending on availability, but averaged 11. Six control trees were also sampled from each of the five block replicates. All cores represented radii at right angles to any obvious sweep or lean in the stem, to avoid bias caused by compression wood—Harris (1977) documented significant increases in wood density associated with this phenomenon. In addition, 10-mm cores were collected from the outerwood of a subsample of the above trees (≤10 trees per progeny) for tracheid length determination on the outer five growth rings.

Growth Rate (Ring Width)

The pith-to-bark radii of the increment cores were measured and expressed as millimetres per ring to give data on growth rate.

Heartwood Content

The heartwood radius was measured visually on each 5-mm core, and expressed for each tree as a percentage of the cross-sectional area at breast height.

Compression Wood

As in previous studies (Harris 1977; Cown & McConchie 1981) a method of visual assessment of compression wood was applied to whole cores, and a rating given from 0 (nil) to 5 (severe) for each increment core sample, an average for the two being calculated for each tree.

Basic Density

Of the two increment cores per tree, the one that better represented the complete pith-to-bark ring sequence was selected for density determination. Basic wood density was assessed gravimetrically for all cores (rings 1–5, 6–10, and the outer five rings) by the maximum moisture content method (Smith 1954) both before and after resin extraction. The results discussed in this report refer to the extracted densities. The weighted average densities for the ring 1–5 and ring 6–10 segments has been adopted as a measure of the corewood density in *P. radiata* (Cown 1980).

Average wood density is made up of several components, each of which may be important to some form of wood utilisation. The most important of these are earlywood density, latewood density, and latewood percentage. In order to examine the relationships between families, six were selected on the basis of the gravimetric data to represent three low- and three high-density examples. The control trees were also sampled. The pith-to-bark cores were analysed in the wood densitometer (Cown & Clement 1983). As before, the data from all cores were combined to give family means. Latewood was arbitrarily defined as that portion of the growth ring with basic density exceeding 400 kg/m^3.

Resin Content

All core segments were extracted in methanol in a Soxhlet reflux condenser for 72 hours, to remove wood extractives. The difference in oven-dry weight before and after extraction gave a measure of resin content, expressed as a percentage of the extracted dry wood weight.

Tracheid Length

The outermost two complete growth rings were removed from the 10-mm cores, and macerated in 50:50 glacial acetic acid and hydrogen peroxide. Because of time constraints, trees within families were bulked and microscope slides prepared and assessed by two operators according to the method of Harris (1966).

Statistical Analyses

Differences between families were studied using standard analyses of variance (ANOVA) which were used as a basis for least significant difference (LSD) comparisons. Genetic parameters (variances, narrow-sense heritabilities, and genetic correlations) were estimated from the ANOVAs of family data and corresponding analyses of cross-products between variables. Standard procedures (e.g., Becker 1984) were used, assuming half-sib families. A preliminary report by Burdon & Young (1991) contains some more detailed genetic statistics. Several variables showed considerable departures (positive skewness) from the normal distribution, but normalising transformations had little impact on estimates of heritability or genetic correlations.

RESULTS AND DISCUSSION

Growth Rate

The '268'-series families had originally been selected on the basis of growth rate, and the groups sampled in this trial were top-ranking families for this trait. Almost all of the families showed significantly faster growth rates than the control, although the absolute differences were modest on a per-ring basis (Table 1), and tree-to-tree variations were large within families (Fig. 1). The difference between families and the control, while it could still translate into large differences in per-hectare volume production, is likely to have been biased downwards by differences in the level of among-tree competition between the two categories of material.

TABLE 1–Selected statistics for increment core variables

Variable	Group means			Estimated heritability‡	Phenotypic coefficient of variation§
	Control	Families	Difference†		
Ring width (mm/ring)	8.15	9.45	1.30***	0.13*	0.16
Heartwood (%)	16.0	17.5	1.5^{NS}	0.49***	0.39
Compression wood grade	1.25	1.52	0.27^{NS}	0.64***	[0.68]
Basic density (kg/m^3)					
Rings 1–5	311	312	1^{NS}	0.92***	0.07
Rings 6–10	364	364	0^{NS}	1.02***	0.08
Rings 1–10	332	333	1^{NS}	1.02***	0.07
Outer 5	438	435	3^{NS}	1.10***	0.09
Tracheid length (mm)	3.86	3.70	0.16^{NS}	N.A.	N.A.
Resin content (%)					
Rings 1–5	6.75	9.75	3.00*	0.51***	0.37
Rings 6–10	1.73	1.69	0.04^{NS}	0.45***	0.65
Outer 5	1.65	1.20	0.45^{NS}	0.37***	0.69

NS difference non-significant ($p>0.05$)
* difference significant at $p<0.05$
** difference significant at $p<0.01$
*** difference significant at $p<0.001$
† Standard error of families group mean based on families mean square
‡ From Burdon & Young (1991)
§ Phenotypic variance divided by the overall mean for the families sample

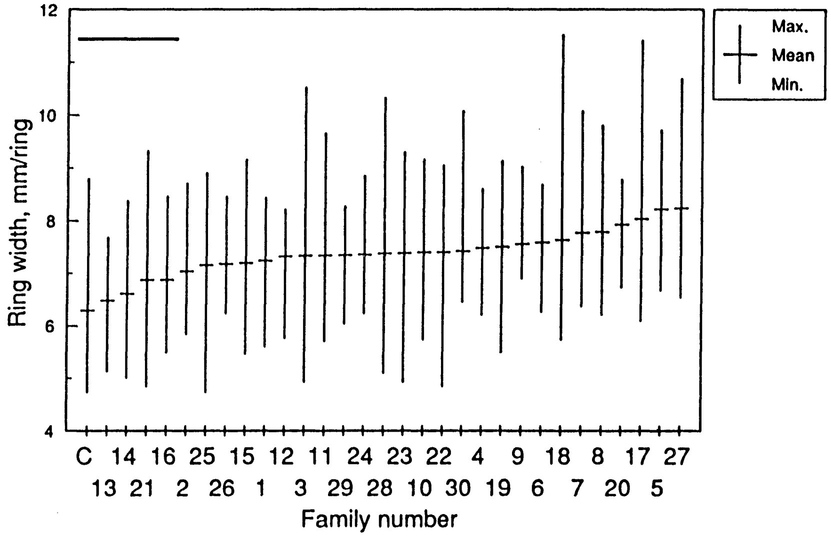

FIG. 1–Within- and between-family variation in growth rate (mm/ring). The bold horizontal line brackets families that are not significantly different from the control (LSD test, α = 0.05).

Heartwood Content

Heartwood development at breast height starts at about 12 years and continues to expand at a rate of 0.5 rings per year (Cown *et al.* 1991). Heartwood percentage in trees at 20 years of age is expected to average 10% of the stem volume and about 20% of the cross section at breast height. Family means in this trial (Fig. 2) ranged from 12% to 29%, with an average of 17.5% (control 16%). The individual-tree coefficient of variation of 39% (Table 1) is very high.

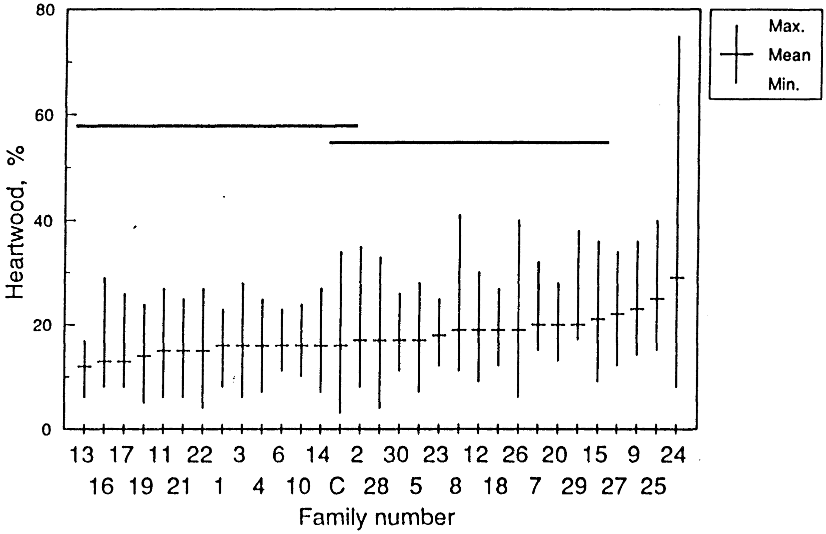

FIG. 2–Within- and between-family variation in heartwood content (%). The bold horizontal line brackets families that are not significantly different from the control (LSD test, α = 0.05).

The data thus show that differences in family means are significant in a trait which is little understood at present. Traditional wisdom holds that heartwood is preferable because it is more durable and has better stability and often a more attractive appearance. However, plantation species such as *P. radiata* can have a large proportion of sapwood, non-durable heartwood, and a small colour difference. Plantation softwoods commonly require some form of preservative treatment for most solid wood end-uses. For pulp and paper, low heartwood content is a distinct advantage as it contributes to low resin content and fewer pitch problems.

The estimated heritability (0.49), along with the high variability (phenotypic coefficient of variation), indicates that significant genetic manipulation of heartwood development is possible.

Compression Wood

The families had been selected for superior form (straightness) as well as growth, so inherited stem crookedness can be discounted as a cause of compression wood, particularly as the sampling procedure was designed to avoid the lower side of stems which had a perceptible lean. Nevertheless, family means ranged from 0.7 (trace) to 2.5 (moderate) (Fig. 3) although only six families differed significantly from the control lot.

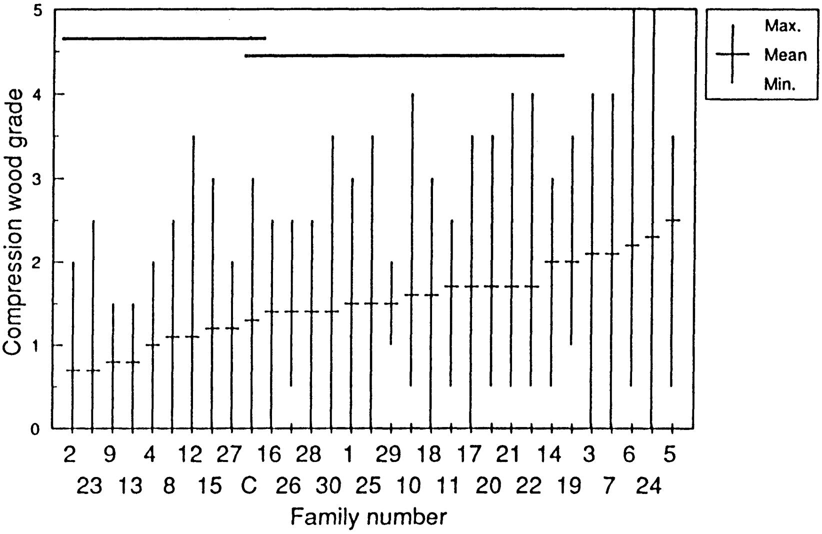

Fig.3–Within- and between-family variation in compression wood content (%). The bold horizontal line brackets families that are not significantly different from the control (LSD test, $\alpha = 0.05$).

The families overall did not have a significantly higher average compression wood rating than the control (Table 1). The estimated heritability (0.61) was remarkably high considering the nature of the samples and the relatively crude scoring scale that could be applied.

Compression wood is recognised as a "defect" in wood normally associated with sweep or lean in the stem (Timell 1986), hence the practice of sampling standing trees at right angles to any stem deviation. The collection of increment cores is designed to minimise the occurrence of compression wood in the sample so that wood density determinations are not unduly biased upwards because of the "abnormal" wood. In *P. radiata*, a form of visual compression wood can be found associated with rapid growth after thinning (Cown 1974), in which compression wood occurs right around the stem in apparently straight trees. This phenomenon is now commonly observed in intensively managed stands in New Zealand and elsewhere, but its practical importance is not known. Burdon (1975) observed a clonal component to the variation in compression wood incidence in *P. radiata* cuttings, which was not secondary to the clonal differences in stem crookedness.

Basic Wood Density

Gravimetric

Although some families were significantly higher or lower than the control (Fig. 4), the average for the select families was practically identical to that of the control, for both inner and outer growth rings (Table 1). This strongly suggests that the intensive selection for growth and form has not affected average wood density.

Individual families showed ranges in density of 290 to 343 kg/m^3 in rings 1–5 (Fig. 4a), 323 to 390 kg/m^3 in rings 6–10, and 384 to 477 kg/m^3 in outerwood (Fig. 4b). These data accord with the documented increase in density range with tree age (Cown 1980). Interestingly, the range in family-mean density on this medium-density site is roughly equivalent to the

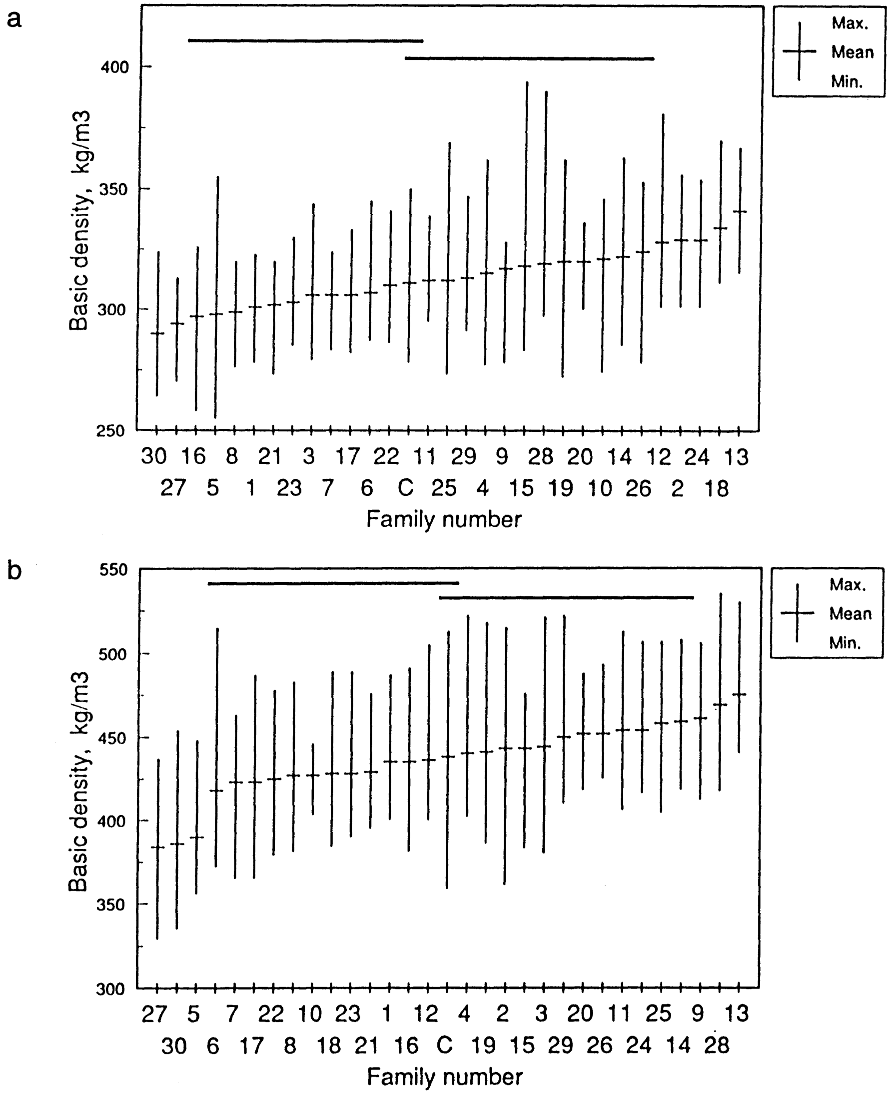

FIG. 4–Within- and between-family variation in wood density. The bold horizontal line brackets families that are not significantly different from the control (LSD test, $\alpha = 0.05$).

a: Variation of rings 1–5 from the pith.

b: Variation of outer five growth rings.

average range between the low- and high-density site classes described by Cown *et al.* (1991). The estimated heritabilities of around 1.0 (the values exceeding the theoretical bound of 1 being readily attributable to sampling errors) suggest that the potential for manipulating this characteristic is excellent, should the need arise, even though the coefficients of variation were only around 7–9 %.

An analysis of growth rate effects failed to show a strong correlation, except for rings 6–10. On the other hand, the correlation between the inner and outer core sections was high at

0.79. This confirms that selection for density at an early age can be highly efficient, particularly when the time saving is taken into account.

Densitometric

Several points emerge:

- The densitometric data closely mirror the gravimetric data for average density, with the high and low families on either side of the control (Fig. 5a). The family means for average density increase with age from 320 kg/m^3 at the pith to 475 kg/m^3 at the bark. The range of family means increases from about 50 kg/m^3 near the pith to around 100 kg/m^3 in the outerwood.

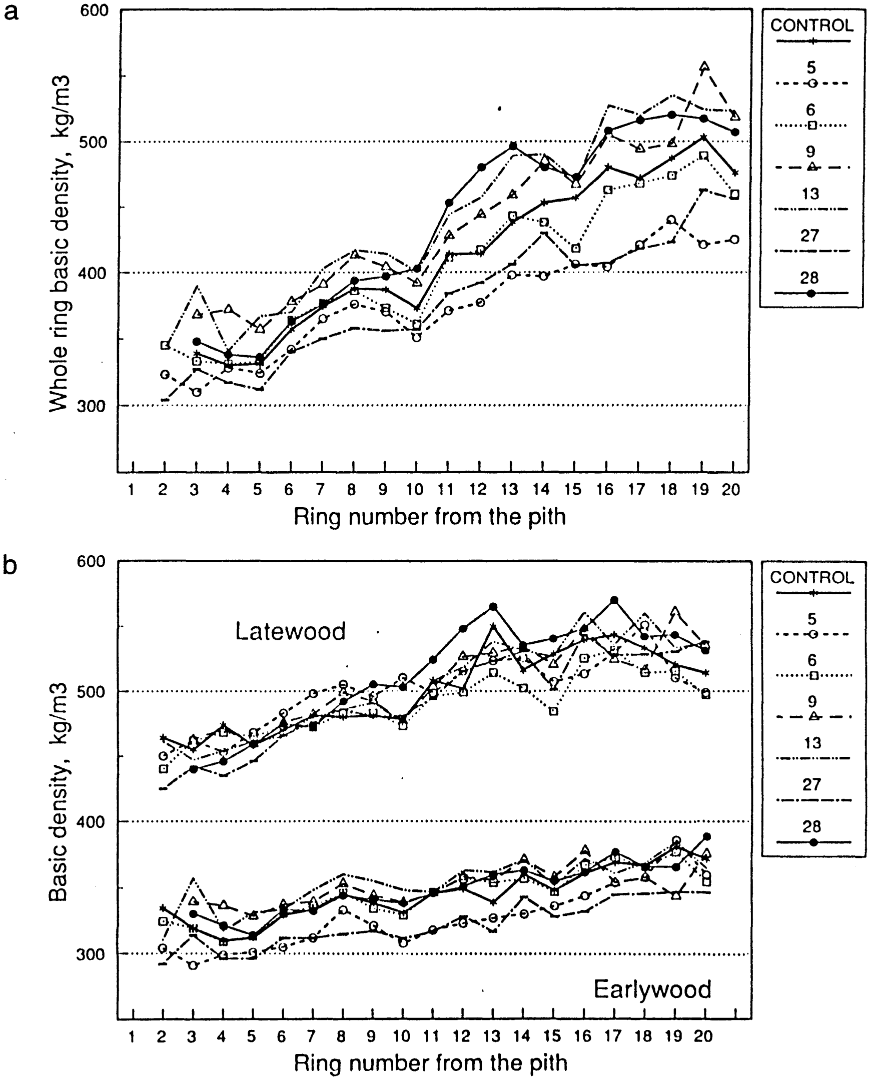

FIG. 5–Six selected families (three high-density and three low density).
a: Average whole-ring densities, ring by ring from the pith.
b: Average earlywood and latewood densities, ring by ring from the pith.

- Earlywood and latewood densities measured separately are much less variable than the growth-ring averages, among families and years (Fig. 5b). Earlywood density rankings of both family means and year means varied in accordance with ring mean density, but latewood density variation was not as closely associated with changes in ring average density.
- Latewood percentage (wood with density over 400 kg/m^3—Fig. 6) proved highly variable both among families and with distance from the pith. Overall averages ranged from about 20% at the pith to between 50% and 90% at the bark. These figures, however, are likely to reflect an artifact of the accepted criteria of latewood (>400 kg/m^3).
- The average difference between earlywood and latewood densities is a measure of the uniformity of wood texture, an important property in wood machining. In these samples the family means ranged from 145 to 175 kg/m^3 and were not related to average density.
- On the basis of this analysis it would seem that family means for both earlywood density and latewood percentage are related to ring average density. Since only latewood percentage can be estimated visually, it could provide a rapid means of comparing wood density in small samples. Problems remain, however, in achieving a satisfactory objective distinction between earlywood and latewood because of the gradual transition from earlywood to latewood in *P. radiata*.

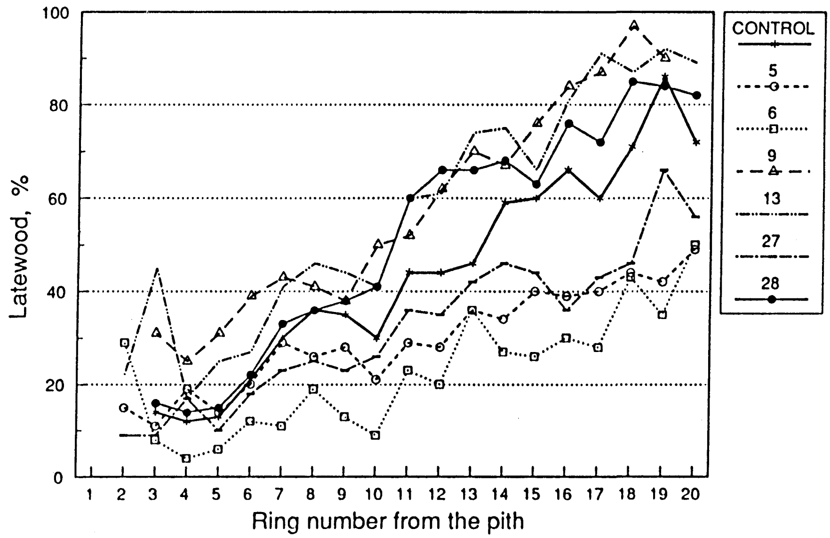

FIG. 6–Average latewood percentage, ring by ring from the pith, for six selected families.

Resin Content

Resin contents were highly variable within and between trees. Sapwood (outerwood) values for the families averaged 1.20% compared to 1.65% for the control (Table 1) although this difference is statistically non-significant ($p \approx 0.08$). The inner five growth rings (Fig. 7) showed large differences in heartwood resin content among families, with averages ranging from 3.3% to 15.9% (control 6.8%), the estimated heritability being 0.5. In all, 26 of the 30 families showed higher resin content in this zone than the control, which indicates that

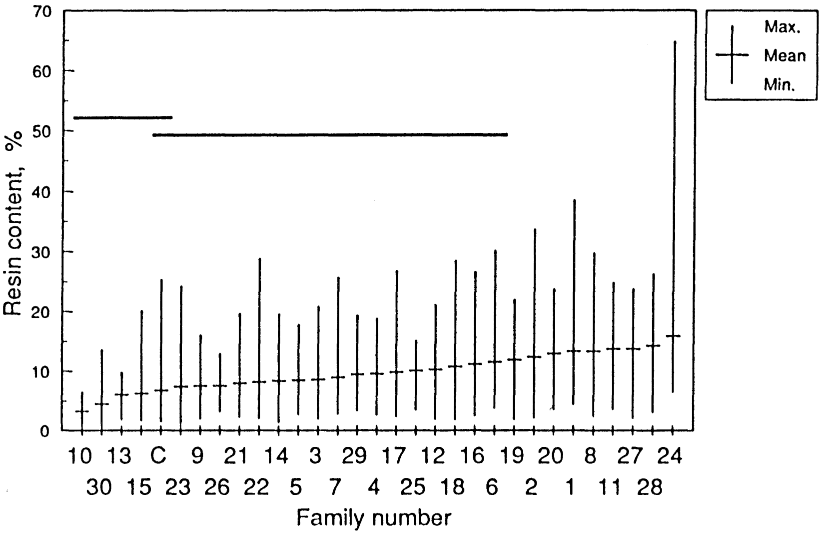

FIG. 7–Within- and between-family variation in resin content (%) of rings 1–5. The bold horizontal line brackets families that are not significantly different from the control (LSD test, $\alpha = 0.05$).

selection for growth and form may have favoured resinous heartwood, this being the one actual wood property for which the families overall differed significantly ($p \approx 0.02$) from the control lot (Table 1).

Tracheid Length

Family average tracheid lengths ranged from 3.36 to 3.97 mm (Table 1, Fig. 8). Only five out of 30 families had average lengths longer (non-statistically significant difference) than

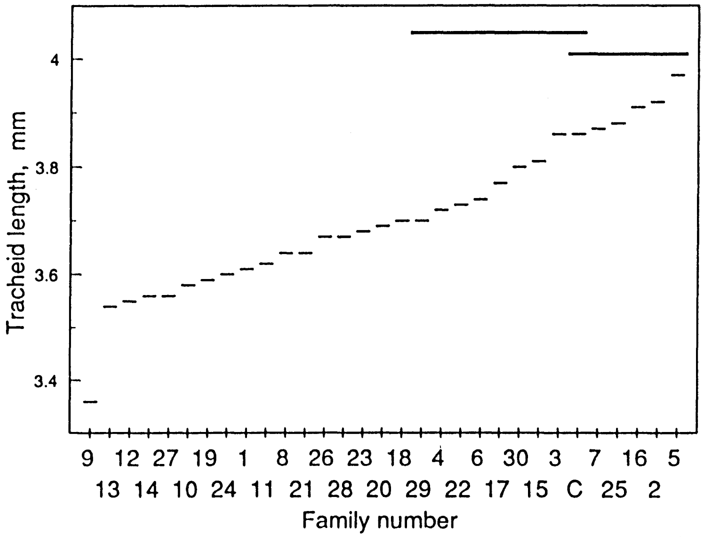

FIG. 8–Family means for tracheid length, based on a bulked sample for each family. The bold horizontal line brackets families that are not significantly different from the control (LSD test, $\alpha = 0.05$).

the control value of 3.86 mm; the families overall were almost significantly different ($p \approx 0.06$) from the control. This suggests that selection for growth and form may have resulted in a reduction in average tracheid length.

The between-family coefficient of variation was 3.5%, suggesting an additive genetic coefficient of variation of 7%. In conjunction with estimates of tree-to-tree phenotypic variation (Nicholls *et al.* 1964; Burdon & Low in prep.) this suggests a heritability of 0.7.

Genetic Correlations

Burdon & Young (1991) reported that genetic correlation estimates (r_g) were very imprecise because of the small number of families and so the estimates are not presented exhaustively in this paper. Nevertheless, several important indications emerged:

- Corewood density and outerwood density were highly correlated ($r_g = 0.79$).
- Resin percentage in outerwood was strongly correlated with that in rings 6–10 ($r_g = 0.82$) but not with that in rings 1–5 or with heartwood.
- The high correlation of compression wood score with ring width ($r_g = 0.82$) suggests that families superior for growth rate have more compression wood. The heritability estimate of 0.61 (Table 1) confirms that there is a strong genetic influence on the incidence of compression wood in *P. radiata.*
- A strong negative association (r_g approaching –1) between growth rate and density was apparent for rings 6–10 only. Likely reasons for such a pattern are discussed in a forthcoming publication (Burdon & Low in prep.).
- No other adverse genetic correlations were clearly evident.

CONCLUSIONS

The '268' series of families reflect intensive selection for growth and form which has given significant gains in these attributes (Carson *et al.* 1990; Johnson *et al.* 1992). This analysis has shown that there is no indication of a change in average wood density, despite the well-publicised negative genetic correlation between growth rate and density (e.g., Burdon & Low in prep.). There are indications, however, that some other properties may have "drifted" away from the control values, although the evidence that this has resulted from the selection *per se* is generally inconclusive. On average, the top-ranking '268' series families had higher average compression wood scores and heartwood resin contents and shorter tracheids. Some differences are small in relation to the overall variability and may not be significant unless further selection reduces the number of families and thereby increases sampling deviation from the base-population average for those properties.

The heritability estimates for wood density were broadly in line with previous research results (e.g., Bannister & Vine 1981; Burdon & Low in prep.). For the other variables, for which there was little if any prior information, the combinations of heritabilities and coefficients of variation appear particularly favourable.

The results, although preliminary, are very encouraging in indicating the scope for breeding for several wood properties. Perhaps it is fortuitous that the property most often considered worthy of alteration is wood density, for which very high heritability estimates have been confirmed. Equally important, selection of suitable genetic material could be used to reduce some unwanted variation in wood properties both within and between stands. In particular, clonal forestry systems could greatly reduce the tree-to-tree variation within stands, although they would not avert substantial variation between lower logs and top logs or the pith-to-bark gradient.

It has often been claimed that the importance of density overshadows that of other wood properties (Zobel & van Buijtenen 1989). As early as 1965 this property was identified as being in most need of improvement in *P. radiata* (Burdon & Thulin 1965). Our results point to a good juvenile/mature correlation (rings 1–5 *v.* the outer five rings at age 20 years) and the densitometric analysis of a small number of families indicated that density ranking remained almost constant from an early age. This suggests that a method could and should be developed for selecting for wood density at an early age.

Of the properties other than density that affect pulp and papermaking, tracheid length, heartwood content, and resin content are likely to be important, particularly if specialised pulpwood crops are to be seriously considered. All can manifestly be controlled to some degree by selective breeding.

While wood properties are comparatively expensive to evaluate in selection candidates, intensive selection does not appear to be necessary for achieving large genetic gains. Moreover, the substantial gains already achieved in tree-form traits (Carson *et al.* 1990) are shifting the focus towards new breeding goals.

Several wood characteristics influencing both solid wood and reconstituted products are capable of genetic manipulation. Good information on the economic impacts on processes and products is required now.

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REFERENCES

BAMBER, R.K.; BURLEY, J. 1983: "The Wood Properties of Radiata Pine". Commonwealth Agricultural Bureau, London. 84 p.

BANNISTER, M.H.; VINE, M.H. 1981: An early progeny trial in *Pinus radiata.* 4. Wood density. *New Zealand Journal of Forestry Science 11*: 221–43.

BECKER, W.A. 1984: "Manual of Quantitative Genetics". Fourth edition. Academic Enterprises, Pullman, Washington, USA. 188 p.

BURDON, R.D. 1975: Compression wood in *Pinus radiata* clones on four different sites. *New Zealand Journal of Forestry Science 5*: 152–64.

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

BURDON, R.D.; LOW, C.B. Genetic survey of *Pinus radiata* . 6. Wood properties: variation, heritabilities, and interrelationships with other traits (in prep.)

BURDON, R.D.; THULIN, I.J. 1965: The improvement of *Pinus radiata. New Zealand Forest Service FRI Symposium No. 6.* 92 p.

BURDON, R.D.; YOUNG, G.D. 1991: Preliminary genetic parameter estimates for wood properties from top-ranked *Pinus radiata* progenies and comparisons with controls. Pp. 137–40 *in* Proceedings, Australian Forestry Council Research Working Group No. 1 Meeting, Mt. Gambier, South Australia, March 1991.

CARSON, M.J.; BURDON, R.D.; CARSON, S.D.; FIRTH, A.; SHELBOURNE, C.J.A.; VINCENT, T.G. 1990: Realising genetic gains in production forests. Paper 3.1 *in* "Breeding and Genetic Resources". Proceedings of Joint Meeting of Western Forest Genetics Association and IUFRO Working Parties S2.02-05, S2.02-06, S2.02-12, and S2.02-14 on Douglas fir, contorta pine, Sitka spruce and *Abies* spp., Olympia, Washington, USA, August.

COWN, D.J. 1974: Comparison of the effect of two thinning regimes on some wood properties of radiata pine. *New Zealand Journal of Forestry Science 4*: 540–51.

———1980: Radiata pine: Wood age and wood property concepts. *New Zealand Journal of Forestry Science 10*: 504–7.

COWN, D.J.; CLEMENT, B.C. 1983: A wood densitometer using direct scanning with X-rays. *Wood Science and Technology 17*: 91–9.

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*: 79–91.

COWN, D.J.; KIMBERLEY, M.O.; WHITESIDE, I.D. 1987: Conversion and timber grade recoveries from radiata pine logs. Pp 147–61 *in* Kininmonth, J.A. (Ed.) Proceedings of the Conversion Planning Conference. *New Zealand Ministry of Forestry, FRI Bulletin No. 128.*

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

DADSWELL, H.E.; FIELDING, J.M.; NICHOLLS, J.W.P.; BROWN, A.G. 1961: Tree-to-tree variations and the gross heritability of wood characteristics of *Pinus radiata. Tappi 44*: 174–9.

HARRIS, J.M. 1965: A survey of wood density, tracheid length and latewood characteristics of radiata pine grown in New Zealand. *New Zealand Forest Service, Technical Paper No. 47.* 31 p.

———1966: A method of minimising observer bias in measuring tracheid length. *Journal of the Royal Microscopical Society 86(1)*: 81–3.

———1977: Shrinkage and density of radiata pine compression wood in relation to its anatomy and mode of formation. *New Zealand Journal of Forestry Science 7*: 91–106.

———1989: "Spiral Grain and Wave Phenomena in Wood Formation". Springer-Verlag, Berlin. 214 p.

JOHNSON, G.R.; FIRTH, A.; BROWN, P.C. 1992: Value gains from using genetically improved radiata pine stock. *N.Z. Forestry 36(4)*: 14–8.

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.

NICHOLLS, J.W.P.; DADSWELL, H.E.; FIELDING, J.M. 1964: The heritability of wood characteristics of radiata pine. *Silvae Genetica 13*: 68–71.

PANSHIN, A.J.; de ZEEUW, C.E. 1980: "Textbook of Wood Technology". McGraw-Hill, New York. 643 p.

SMITH, D.M. 1954: Maximum moisture method for determining the specific gravity of small wood samples. *USDA, Forest Service, Forest Products Laboratory Report No. 2014.* 8 p.

TIMELL, T.E. 1986: "Compression Wood in Gymnosperms". Springer-Verlag, Heidelberg. 2150 p.

ZOBEL, B.J.; van BUIJTENEN, J.P. 1989: "Wood Variation: Its Causes and Control". Springer-Verlag, Berlin. 363 p.