CLONAL VARIATION AND REPEATABILITY OF MICROFIBRIL ANGLE IN *PINUS RADIATA*

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ABSTRACT

Microfibril angle was measured at breast height on growth rings 1, 5, 10, and 15 from the pith, for two trees from each of 11 clones of *Pinus radiata* D. Don. Average breast-height values for both trees and clones were calculated by weighting individual ring values by relative growth ring area. Significant variation was observed both among clones, and within and between trees for each clone. The clonal repeatability (an estimate of broad-sense heritability) of unweighted microfibril angle was 0.7. The corresponding single ring values were high for rings 1 and 15 but were much lower for rings 5 and 10. Differences between trees within clones could be attributed to the presence of compression wood in some cases. Compression wood was associated with larger angles on average, although this was a variable effect for individual ring comparisons. Microfibril angle in ring 5 was the best predictor of average weighted breast-height microfibril angle for individual trees, indicating a potential for screening of young trees if required. The poor correlation of ring 15 values with weighted tree means suggests that outerwood microfibril angle is independent of corewood microfibril angle, or that the relationship varies among clones.

Keywords: microfibril angle; clonal repeatability; broad-sense heritability variation; compression wood; *Pinus radiata*.

INTRODUCTION

The microfibril angle of the S2 layer in the tracheid cell wall is acknowledged as one of the main determinants of the mechanical properties of wood, especially modulus of elasticity (Wardrop 1951; Cave 1968, 1969) and shrinkage anisotropy (Harris & Meylan 1965). Microfibril angle is known to interact with density (Wimmer 1992) and may also interact with spiral grain in relation to the strength and stiffness of clearwood. The microfibril angle in individual tracheids has been related to the tensile strength and stretch properties of pulp fibres, with small microfibril angles resulting in greater tensile strength and large microfibril angles resulting in greater elasticity (Watson & Dadswell 1964; Mark 1967; Mark & Gillis 1973; Kellogg *et al.* 1975).

Microfibril angle varies within the stem, with large angles in the corewood and small angles in the outerwood (Phillips 1941; Preston 1948, 1949; Preston & Wardrop 1949; Wardrop & Dadswell 1950; Pillow *et al.* 1953; Echols 1955; Manwiller 1972; Erickson &

Arima 1974; Bendtsen & Senft 1986; Pedini 1992; Donaldson 1993). Microfibril angle may also vary with height and, in *P. radiata*, shows a rapid decline from the butt to 7 m height at rings of comparable cambial age. Subsequent small increases may occur near the crown in 20-year-old trees (Donaldson 1993). Variation in microfibril angle with both cambial age and height can differ considerably among trees. In a study comparing microfibril angles in three half-sib groups of *P. radiata*, Donaldson (1993) found differences in corewood angles and differences in variation with height but these differences were not statistically significant because of a large variation among trees within groups.

Heritability is defined as the fraction of the phenotypic variation in a trait that is due to genetic differences as opposed to environmental effects on individuals (Ayala & Kiger 1980). Heritability can be measured as biological heritability where sampling errors are effectively excluded from phenotypic variation, or as observational heritability which includes sampling errors in phenotypic variation and is thus lower. Heritability can vary with site because of variation in the size of micro-environmental effects, and interaction between the genotypic effect and site. Heritability is therefore a site-specific as well as a population-specific parameter. Despite its specificities, heritability is useful because, when combined with variability, it indicates the amount of response that can be expected in artificial selection for desirable traits. In tree crops, if heritability is high an improvement in wood quality may be readily achievable by selective breeding. If heritability is low then a silvicultural approach may sometimes be more successful. In practice, a combination of breeding and silviculture may yield the optimum improvement.

In order to estimate the clonal variation and clonal repeatability (which ideally is broad-sense heritability, denoted H^2) of microfibril angle, and hence the potential for improvement of clearwood strength properties by selection for lower microfibril angles, an assessment was made on 11 clones from a clonal trial established in Kaingaroa Forest by the New Zealand Forest Research Institute.

MATERIALS AND METHODS

Discs were collected at breast height from 11 clones produced from cuttings of genetically select (for growth rate and tree form) *P. radiata*, growing in a 16-year-old clonal trial in a single compartment of Kaingaroa Forest. The clones were chosen on the basis of density and tracheid length to give a diverse sample for the purpose of relating wood properties to pulp and paper properties. Clones were sampled on the basis of two trees per clone, giving a total of 22 trees sampled. Samples of earlywood were taken from rings 1, 5, and 10 from the pith, and the outermost ring for each tree. The outermost ring was usually ring 14 or 15 and was designated as ring 15 in the data tables and analyses. These samples were macerated in a 50:50 mixture of glacial acetic acid and hydrogen peroxide (130 vol.). Microfibril angle was recorded on 25 tracheids for each growth ring by measuring the maximum extinction position of single cell walls under polarised light using the technique described by Donaldson (1991). Growth increment and the presence or absence of visual compression wood were also recorded for each growth ring on the samples examined.

In addition to this sampling, two clones were assessed in more detail by measuring microfibril angle for every growth ring. The sample from one clone contained significant visual compression wood in one of the trees, while the sample from the other clone did not

contain significant visual compression wood in either tree. It should be noted that compression wood assessments relate only to the samples examined, which were segments of the breast height disc. The occurrence of compression wood will vary around the circumference of the disc so that the samples examined are unlikely to be representative of whole stems at breast height.

Tree and clonal averages for microfibril angle at breast height were calculated by weighting values for individual growth rings by their relative cross-sectional areas.

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

Clonal coefficient of variation $= \sigma_C / \bar{x}_C$ ($\bar{x}_C$ = grand mean of all clones) (1)

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

Observational repeatability $= \sigma^2_C / (\sigma^2_C + \sigma^2_{T(C)} + (\sigma^2_{RC}/4) + (\sigma^2_T/100)$ (3)

Assuming *inter alia* that the choice of clones entailed no indirect selection for microfibril angle, such a repeatability may be accepted as an estimate of broad-sense heritability, which is relevant to selecting on individual-tree data for vegetative propagation systems.

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

Clones	$= \sigma_e^2 + 25\sigma^2_{RT(C)}$	$+ 100\sigma^2_{T(C)} + 200\sigma^2_C$
Trees within clones	$= \sigma_e^2 + 25\sigma^2_{RT(C)}$	$+100\sigma^2_{T(C)}$
Rings	$= \sigma_e^2 + 25\sigma^2_{RT(C)} + 50\sigma^2_{RC} + 550\theta^2_R$	
Rings × clones	$= \sigma_e^2 + 25\sigma^2_{RT(C)} + 50\sigma^2_{RC}$	
Rings × trees within clones	$= \sigma_e^2 + 25\sigma^2_{RT(C)}$	
Residual	$= \sigma_e^2$	

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.

σ_e^2 is the residual variance.

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

RESULTS

Microfibril angle for individual tracheids varied from 0.2 to 72.2° (Table 2). The tree and clonal values were weighted by relative growth ring cross-sectional area. Some clones showed good agreement between trees while others did not. Clonal microfibril angles varied over a range of about 12° from 20° to 32°. Analysis of variance for the unweighted data for individual tracheids indicated significant variation among clones, among rings, and significant interactions between rings and clones, and between trees and rings within clones (Table 3). The estimated variance component for trees within clones, although not statistically significant ($p = 0.11$), was still considered sufficiently large to be used to test the effect of clones, thus allowing a realistic assessment of repeatability. The major variance components were for rings, and for tracheids within rings (residual). Clonal (biological) repeatability estimated using the unweighted data was 0.7.

TABLE 2–Microfibril angle among clones

Clone	Tree	Ring				Means (°)	
		1	5	10	15	Tree	Clone
1	1	32.0	41.3*	27.3	14.2	33.5	
	2	35.3	28.1	23.9	13.8	25.6	29.6
2	1	44.5	35.4	22.6	24.2	29.8	
	2	47.1	35.8	26.9	26.9	30.8	30.3
3	1	41.6	42.1	27.1	23.2	32.5	
	2	42.6	44.6	21.8	21.3	30.9	31.7
4	1	42.1	37.1	17.1	19.3	27.0	
	2	39.2	29.7	14.7	14.8	23.4	25.2
5	1	41.7	31.7	20.9	20.9	24.3	
	2	33.9	27.3	22.2	24.6	24.6	24.4
6	1	39.5	32.4	16.5	17.8	25.0	
	2	33.5	35.0	23.2	24.4	26.7	25.9
7	1	38.9	28.1	24.2	22.5	25.8	
	2	40.3	35.5	26.0	22.3	28.5	27.2
8	1	44.9	35.9	28.0	14.4	30.1	
	2	37.9	39.3	9.4	9.4	27.1	28.6
9	1	31.8	25.7	15.4	24.2	20.0	
	2	30.9	22.1	18.0	19.1	19.9	20.0
10	1	39.9	29.1	20.7	23.3	24.3	
	2	35.0	32.5	11.9	17.5	23.3	23.8
11	1	40.5	36.3	16.0	20.8	27.7	
	2	41.5	28.6	18.8	19.6	23.0	25.4

* Underlined values represent compression wood

TABLE 3–Analyses of variance for unweighted microfibril angle (individual tracheid measurements) and estimates of clonal repeatabilities and the clonal coefficient of variation.

Source	df	MS	F	p	$\hat{\sigma}^2$
Clones	10	1588.9	2.87	0.049	5.18
Trees within clones	11	553.1	1.71	0.114	2.30
Rings	3	48920.4	73.26	0.000	87.73
Rings × clones	30	667.8	2.07	0.022	6.90
Rings × trees within clones	33	322.7	3.37	0.000	9.07
Residual	2112	95.9			95.88
Clonal coefficient of variation (Eq. 1)	8.1%				
Biological repeatability (Eq. 2)	0.69				
Observational repeatability (Eq. 3)	0.56				

Variation in microfibril angle with cambial age for clone 5 where neither tree had significant compression wood (Fig. 1) was compared with that for clone 6 where the sample from one tree had abundant compression wood while the other did not (Fig. 2). In this particular comparison, compression wood did not seem to account significantly for between-tree variation within clones. Mean microfibril angles weighted by ring cross-sectional areas, agreed closely between trees within each of these two clones, with values of 23.3 and 23.5 for clone 5, and 24.8 and 24.8 for clone 6.

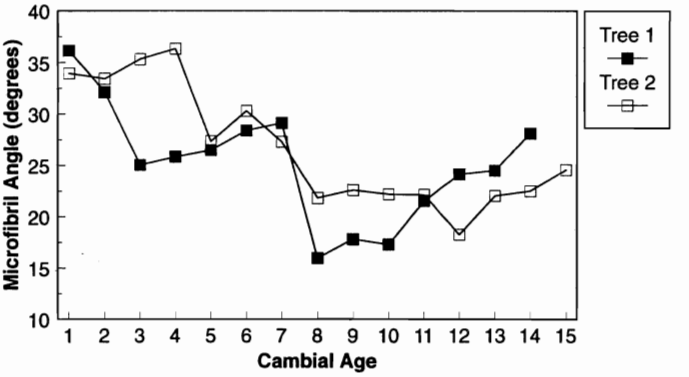

FIG. 1–Variation in microfibril angle with cambial age for normal wood of two trees, for clone 5.

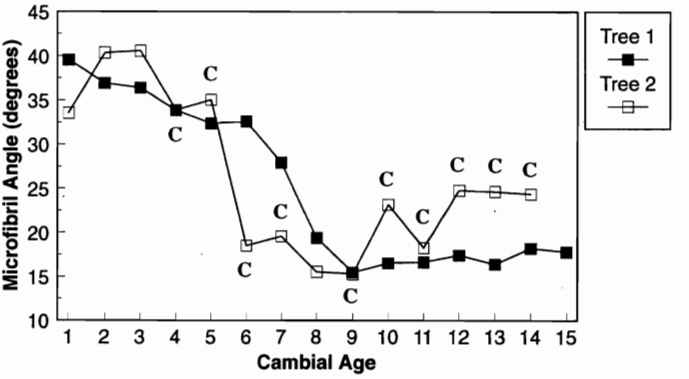

FIG. 2–Variation in microfibril angle with cambial age for normal wood and compression wood of two trees, for clone 6. Compression wood rings in Tree 2 are marked with a C.

Analysis of variance was used to compare reaction wood in compression wood rings with normal wood rings in alternative trees within clones (Table 4). Compression wood had significantly larger microfibril angles (27.9 *v.* 24.0), although there was a significant interaction with rings, indicating that this effect was variable. The effect labelled as reaction wood in this analysis also contained a variance component due to interaction between rings and trees within clones, which was significant in Table 3. An over-conservative test of reaction wood against its interaction with rings is nevertheless statistically significant ($p = 0.03$).

While there appeared to be some correlations for consecutive rings between residuals about the effects of clones and rings (Fig. 1 and 2), this appeared unlikely to invalidate the

TABLE 4–Analyses of variance for reaction wood.

Source of variation	df	MS	F	p
Rings	18	3834.9	5.80	0.000
Reaction wood	1	3743.0	5.66	0.029
Rings × reaction wood	18	661.4	7.62	0.000
Residual	912	86.8		

assumption, implied in Table 1, that the interactions between trees within clones and the four rings involved in the main study were essentially random.

Correlation coefficients of tree means between individual ring values and the weighted or unweighted breast height means ($r_{[df = 20, \alpha = 0.05]} = 0.42$) are given in Table 5, as well as the clonal repeatability (biological repeatability) among growth rings.

TABLE 5–Correlation coefficients ($r_{[df = 20, \alpha = 0.05]} = 0.42$) between individual rings and weighted or unweighted tree means, and estimates of biological clonal repeatability for individual growth rings (Eq. 3).

	Ring			
	1	5	10	15
Correlations				
Weighted mean	0.62	0.91	0.73	–0.12
Unweighted mean	0.79	0.75	0.70	0.43
Biological repeatability	0.71	0.47	0.09	0.72

DISCUSSION

A number of wood properties in *P. radiata* are known to be heritable. In a recent study involving several wood properties, Cown *et al.* (1992) reported h^2* estimates as follows: resin content 0.4–0.5, percentage heartwood 0.49, compression wood grade 0.64, and basic density 0.9–1.0.

Burdon & Low (1992), reporting on a more extensive study involving wood density, recorded $\hat{h}^2 = 0.7$, with a similar figure, based on less extensive data, for spiral grain. These figures agree with other published results (Burdon 1992).

Reported additive genetic coefficients of variation for wood properties within populations of *P. radiata* vary widely ranging, for instance, from around 7% for wood density and tracheid length to 40% or more for heartwood, resin content, and spiral grain (Cown *et al.* 1992; Burdon & Low 1992).

Fujisawa *et al.* (1992) studied broad-sense heritability (H^2) of modulus of elasticity (MOE) in clones of *Cryptomeria japonica* D. Don, yielding estimates of 0.59–0.86. Fujisawa *et al.* (1993) studied the broad-sense heritability of wood density and percentage latewood in *C. japonica* growth rings with values ranging from 0 to 0.4. The estimated clonal repeatability (broad-sense heritability) of 0.7 for clonal microfibril angle compares favourably with $\hat{H}^2$ values of these other properties. Since MOE is significantly correlated with microfibril angle (Wardrop 1951; Cave 1968, 1969; Cave & Walker 1994), it is not surprising to note that both have a significant genetic component to their variation.

It should be emphasised that because of the small number of clones examined in this study, the confidence interval for clonal repeatability (Table 2) is very large, indicating considerable uncertainty in its exact value. It is nevertheless indicative of a significant genetic component to the variation in microfibril angle.

* h^2 = narrow-sense heritability, which is relevant to selection for propagation by seed production.

The estimates of clonal microfibril angle at breast height are based on values for just four growth rings and will therefore be subject to bias in favour of these particular rings, especially for the ring with the largest weighting. Corresponding weighted values for the two clones where measurements were made for all of the growth rings, indicate that this bias is approximately + 1 to 1.5°. Agreement between trees within clones was appreciably improved when all growth rings were used in the volume weighting procedure.

In several clones, the values for particular growth rings did not agree closely between the two trees and this could often be explained by the presence of compression wood in one of the samples (Table 2). Compression wood is often thought to have larger microfibril angles than opposite wood from the same tree (Wardrop & Dadswell 1950; Park *et al.* 1980), although in *P. radiata* Harris (1977) found no significant differences in microfibril angle in relation to visual compression wood grade. In the present study a comparison was made between compression wood and normal wood pooled among clones. These results indicated that, while compression wood rings had larger microfibril angles overall, there was also a significant interaction with rings, indicating a variable effect in agreement with Harris (1977). There are several grades of compression wood ranging from mild to severe and it is possible that microfibril angle is affected differentially among grades.

The nature of the samples examined in this study did not permit a comparison of microfibril angle in compression and opposite wood from the same tree. The analysis (Table 4) did not differentiate the random differences between trees within clones from a reaction wood effect. Notwithstanding, the reaction wood effect was significant ($p = 0.03$) even with a very conservative test, while trees-within-clone differences over all four rings were not significant (Table 3). In future studies an effort should be made to compare compression wood and opposite wood within trees within clones to differentiate these two effects more clearly.

There was a tendency not only for compression wood rings to have higher microfibril angles, but also for subsequent non-compression wood rings to have larger angles (Table 2). This suggests that the presence of compression wood, in one or several rings within a tree, may have an effect on microfibril angle in subsequently formed rings, whether or not these rings contain significant compression wood. Compression wood development may introduce growth stress in the stem which acts on tracheids during subsequent wood formation, affecting the microfibril angle of these tracheids (Boyd 1985). It is also possible that these rings contained mild compression wood which was not detected. There was an indication (Fig. 2, and to some extent Table 2) that microfibril angle is affected by compression wood more in the outerwood than in the corewood.

The correlation coefficients for individual rings against weighted or unweighted tree means indicated that for weighted means ring 5 was the best predictor, while for unweighted means rings 1–10 were the best predictors (Table 5). Apparently microfibril angle for ring 15 was poorly correlated with the tree mean and hence with corewood values in these trees. This may reflect the cumulative effects of micro-environmental factors acting independently on individual trees. However, the fact that repeatability was high for ring 15 suggests that the low correlation was due to significant differences in the effect of cambial age among clones. More detailed sampling would be needed to confirm this. Since microfibril angle is usually a problem only in relation to wood quality within the corewood, where values are often above

30°, this means that screening of clones for small angles could be carried out on young 1- to 5-year-old trees. This would be a considerable advantage in terms of the time delay for screening of progeny if such a screening programme was warranted.

Most clones showed a more-or-less linear decline in microfibril angle at breast height with cambial age, with a sharp reduction in the gradient at about 10 rings from the pith marking the corewood/outerwood boundary (Fig. 3). Two clones showed a continuing decline with no reduction in gradient up to ring 15, suggesting that in these clones the corewood/outerwood boundary occurred at a greater cambial age than the average of 10 rings from the pith. The effect of this was to markedly reduce outerwood microfibril angle. Apart from these two clones there was little evidence of variation in the size of the corewood zone as indicated by the gradient of microfibril angle decline. Donaldson (1993) also found a reduction in microfibril angle gradient at about ring 10 from the pith. This result is in contrast to studies on *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) by Abdel-Gadir & Krahmer (1993) who observed large variations in the age of demarcation of the corewood/outerwood boundary, as determined by changes in wood density. These variations were found to be under significant genetic control. Loo *et al.* (1985) found conclusive evidence for genetic control of the position of the corewood/outerwood boundary, as determined by density and tracheid length, in *Pinus taeda* L. (loblolly pine). Microfibril angle may also be a good indicator of the corewood/outerwood boundary. Indeed, selection for a reduction in the size of the corewood just by selecting for increased wood density and/ or tracheid length may be of limited benefit to mechanical properties if microfibril angles remain unchanged.

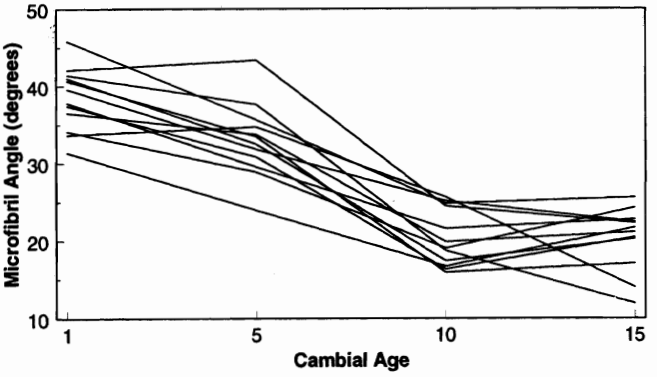

FIG. 3–Variation in clonal microfibril angle with cambial age. Note the abrupt reduction in gradient marking the corewood boundary at about ring 10 for all except two clones where microfibril angle continues a rapid decline beyond ring 10.

The possible influence of epigenetic factors, such as the physiological age of the seedling ortets from which cuttings were taken (approximately 5 years for the trees examined, C.J.A.Shelbourne pers. comm.), has been ignored in this study. Also, it is not known whether the variation in microfibril angle with cambial age reflects the changes in physiological age of the cambium, or is merely a consequence of changing stress patterns in the cambium as the stem becomes stiffer with increasing girth. It is likely that both factors may be involved, although there is evidence that the latter is the dominant factor (Boyd 1985). In comparing the pith to bark trends in microfibril angle of the cuttings examined in the present study with

seedlings examined in an earlier study (Donaldson 1992), there is no evidence for any physiological aging effect in the trees derived from cuttings.

CONCLUSIONS

Microfibril angle in the trees examined showed a clonal repeatability of 0.7 and an estimated coefficient of variation among clones of 8%, which indicates good potential for improvement by selective breeding. In the clones examined, microfibril angle in ring 5 from the pith was the best predictor of clonal (weighted) microfibril angle at breast height. Hence, clonal screening could be carried out on very young trees. Corewood microfibril angles appear to be independent of outerwood values in the same tree or clone, so that low corewood angles do not necessarily mean correspondingly low outerwood angles within a clone. The clonal repeatability of microfibril angle may be influenced by the occurrence of compression wood. Unfortunately, corewood microfibril angles do not vary as much as do outerwood angles and gains in wood quality (clearwood stiffness) for corewood may not be sufficient to justify selection, especially in short-rotation crops. There was little evidence of variation in corewood size as indicated by the reduction in pith-to-bark microfibril angle gradients which occurred more or less at ring 10 from the pith.

Further work is needed to identify the relative importance of basic density, microfibril angle, and spiral grain in determining clearwood stiffness and other properties so that the gain in wood quality from selective breeding for all or any of these properties can be quantified in economic terms.

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