

WITHIN- AND BETWEEN-TREE VARIATION IN MICROFIBRIL ANGLE IN *PINUS RADIATA*

L.A.DONALDSON

New Zealand Forest Research Institute,
Private Bag 3020, Rotorua, New Zealand

(Received for publication 17 November 1992; revision 15 March 1993)

ABSTRACT

Microfibril angle was measured for every growth ring at butt, breast height, and 7, 12, 18, 23, and 30 m height in five 22-year-old trees of *Pinus radiata* D. Don. Mean angles varied from 9° to 55° with the highest angles occurring in the corewood of the butt log. Angles showed a curvilinear decline from pith to bark, which was more pronounced at the butt end of the stem. Significant variation was observed among trees and growth rings, with an interaction between rings and trees indicating some variation in pith-to-bark trends among trees. Microfibril angle declined rapidly with height within the tree, reaching more or less constant values beyond 7 m height, followed by small increases in the corewood of the top log.

Keywords: microfibril angle; within-tree variation; between-tree variation; *Pinus radiata*.

INTRODUCTION

Variation in microfibril angle in the S2 layer of the cell wall among individual tracheids and among samples of wood from various positions within the tree stem and among individual trees, has been related to the strength and shrinkage properties of solid wood and to the tensile strength, stretch, and tear properties of paper and pulp fibres (Watson & Dadswell 1964; Harris & Meylan 1965; Mark 1967; Cave 1968, 1969; Mark & Gillis 1973; Kellogg *et al.* 1975). Using multiple regression techniques, Wimmer (1992) showed that microfibril angle, together with tangential diameter of latewood tracheids, is an important determinant of the strength properties of clearwood when the effect of specific gravity is excluded.

Microfibril angle is known to vary in a systematic fashion within the tree stem. Microfibril angle varies from pith to bark with the highest angles occurring in the first 5–10 rings from the pith (Phillips 1941; Preston 1948, 1949; Wardrop & Dadswell 1950; Pillow *et al.* 1953; Echolls 1955; Manwiller 1972; Erickson & Arima 1974; Bendtsen & Senft 1986; Pedini 1992). Variation with height has not been examined in great detail but studies indicate that microfibril angle declines with height in the stem in softwoods (Pillow *et al.* 1953; Manwiller 1972).

Microfibril angle in compression wood is generally higher than in normal or opposite wood of the same stem (Wardrop & Dadswell 1950; Park *et al.* 1980). However, Harris (1977) found no difference in microfibril angle between opposite and compression wood within the same growth ring in *P. radiata*. Microfibril angle is inversely related to tracheid length, with longer tracheids having smaller (steeper) angles (Preston 1948, 1949; Preston & Wardrop 1949; Wardrop & Dadswell 1950; Wardrop 1951; Echolls 1955). The variations in microfibril angle that occur within trees and in relation to tracheid length are thought to be controlled by the strains imposed on the cells at their time of differentiation (Boyd 1985).

The New Zealand *P. radiata* tree breeding programme has, in the past, concentrated on selection for such features as growth rate, internode length, and crown form. However, recently there has been renewed interest in selection based on wood-quality criteria such as basic density, tracheid length, and chemical composition. The present investigation was carried out in order to determine appropriate sampling strategies for microfibril angle, including the potential for non-destructive assessment from increment cores based on small sample sizes. A further aim of this study was to determine the potential for genetic selection by estimating the variation among trees.

MATERIALS AND METHODS

Discs were collected from five trees of *P. radiata* growing in Cpt 1013 of Kaingaroa Forest. These trees showed 22 growth rings on the butt disc. Discs were collected from the butt and at 1.4, 7.0, 12.0, 18.0, 23.0, and 30 m height. Samples of earlywood were taken from each of the growth rings on each disc and macerated in a 50:50 mixture of glacial acetic acid and hydrogen peroxide (130 vol.). Microfibril angle was measured 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 was also measured for each growth ring on the breast height and 23 m height discs.

Regressions between the mean microfibril angle for each growth ring among the five trees at breast height (1.4 m) and at the other six heights were calculated in order to provide prediction equations. Regressions between microfibril angle and ring number from the pith were also calculated. Variation among and within trees was compared using analysis of variance.

RESULTS

Mean microfibril angles varied from 9° to 55° and showed a consistent pith-to-bark trend of declining angles (Fig. 1) as well as a general decline in angle with increasing height, especially within the butt log (Fig. 2). Significant variation occurred among individual trees with some trees showing above or below average angles growth ring by growth ring. An analysis of variance in Table 1 indicates significant variation among trees and among growth rings, and an interaction between growth rings and trees reflecting differences in pith-to-bark trends among trees.

Variation in microfibril angle among trees at breast height on a growth-ring-by-growth-ring basis (Fig. 3) indicates large differences among trees.

Volume-weighted microfibril angles for the corewood and outerwood at breast height among trees are shown in Fig. 4, as well as estimated values for the butt log, the toplog, and for the whole tree calculated using growth increment at breast height.

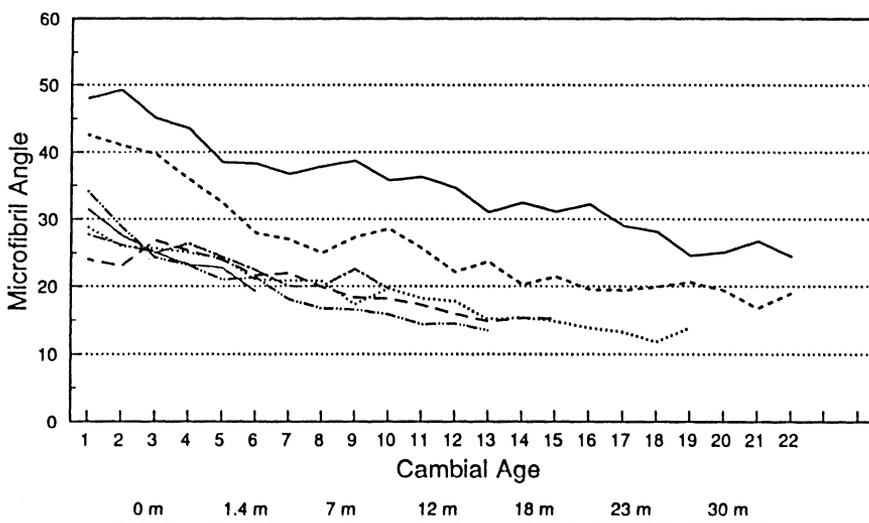


FIG. 1—Variation in mean microfibril angle with cambial age and height.

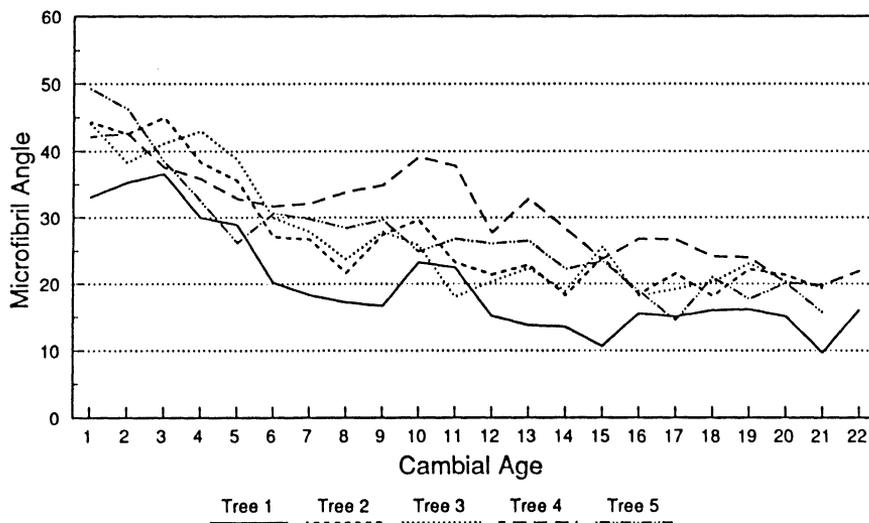


FIG. 2—Variation in volume-weighted microfibril angle for corewood (rings 1–10) and outerwood with height.

TABLE 1—Analysis of variance for growth rings and trees for microfibril angle at breast height

Source	df	MS	F
Trees	4	8 633.23	99.02 ***
Rings	20	7 159.42	23.59 ***
Interaction	80	303.54	3.48 ***
Residual	2520	87.19	
Total	2624		

Trees = random; rings = fixed

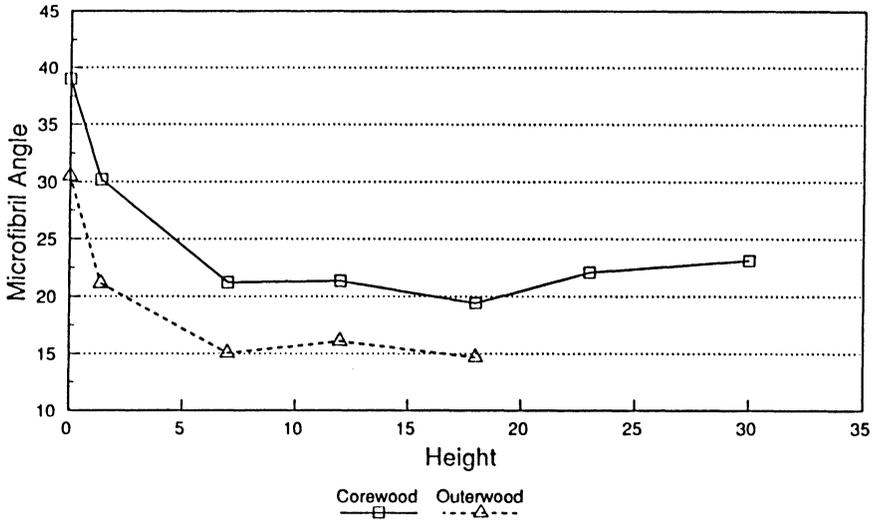


FIG. 3—Variation in microfibril angle among trees at breast height.

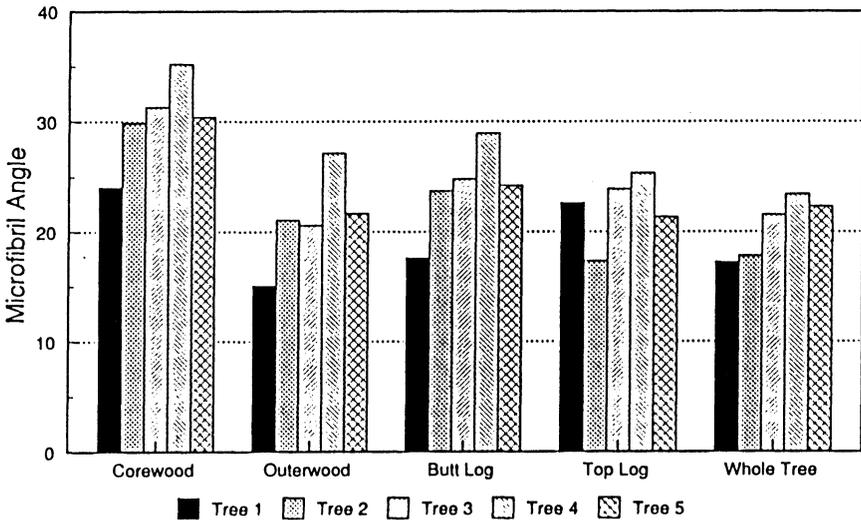


FIG. 4—A comparison of volume-weighted microfibril angle among trees for corewood and outerwood at breast height, the butt log (0–7 m), the top log (23–30 m), and the whole tree.

DISCUSSION

The patterns of variation within trees for *P. radiata* are similar to those reported in previous studies for both *P. radiata* and a range of other softwood species (Phillips 1941; Preston 1948, 1949; Wardrop & Dadswell 1950; Pillow *et al.* 1953; Echolls 1955; Manwiller 1972; Erickson & Arima 1974; Bendtsen & Senft 1986; Pedini 1992). Little information has previously been available on variation with height in the stem. Pillow *et al.* (1953) measured microfibril angle in three trees of *P. taeda* L. (loblolly pine), both at breast height and at 9–

12 m where values were considerably lower. Manwiller (1972) also found a decline in microfibril angle with height in *P. glabra* Walter (spruce pine). In *P. radiata*, microfibril angle declines rapidly with height within the first 7 m (Fig. 2). Angles then remain more or less constant but may show a slight increase in the corewood of the top log where values can reach those at breast height. Pith-to-bark trends tend to become flatter with height so that corewood is not as sharply defined beyond 7 m (Fig. 1 and 2). This pattern of variation for microfibril angle is the inverse of the variation in tracheid length described by Cown (1975).

There is significant variation among trees in breast height values (Table 1, Fig. 3). Values at breast height do not give a good indication of whether values will be high or low in other parts of the stem for individual trees. Only when averaged over a number of trees does breast height microfibril angle adequately predict variation with height.

Echolls (1955) identified a genetic component to variation in microfibril angle in *P. elliotii* Engelm. (slash pine). The between-tree variation shown in Fig. 3 may represent genetic variation, at least in part, suggesting that there may be some potential for a selective breeding programme. Examination of multiple trees of the same genotype (clones) should confirm the extent of genetic control of microfibril angle in *P. radiata*.

In order to assess correctly the impact of variation in microfibril angle on wood properties, it is necessary to weight the values for individual growth rings by their relative volume. Volume-corrected microfibril angles for corewood (rings 1–10) and outerwood at breast height, and similar values for the butt log (0–7 m), the toplog (23–30 m), and the whole tree are shown in Fig. 4. From this graph it can be seen that differences among whole trees can be up to 6° while larger differences of 10° or more occur among trees in the butt log. This variation occurs in both the corewood and, to a slightly greater extent, in the outerwood.

Growth increment at breast height was used to calculate the volume-corrected microfibril angles (Fig. 2 and 4). Growth increment was also measured on samples at 23 m height and substitution of these values in the volume-weighting procedure gave identical results, indicating that breast height increment is adequate for estimating volume corrections.

When considering the impact of variation in microfibril angle on wood properties, the magnitude of the angle is important. Assuming that 30° is the cut-off point between acceptable and unacceptable wood quality (MOE <1000 kg/mm², longitudinal shrinkage >0.5%—Harris & Meylan 1965; Cave 1968), then only the corewood of the butt log will be classified as unacceptable (Fig. 2 and 4). It is this region of the stem which would have the potential for improvement in wood quality by genetic selection for low microfibril angles, representing from 14% to 18% of the total wood volume for the trees examined in this study. Because this region of the stem usually also contains large numbers of defects including knots, spiral grain, and compression wood, selection for low microfibril angle may not result in any significant gain in wood quality within the defect core of pruned logs.

Outside of the corewood, some gains in strength may also be achieved. According to Cave (1969), longitudinal Young's Modulus should increase from 1000 kg/mm² to 4000–5000 kg/mm² for microfibril angles less than 30°. Longitudinal shrinkage shows negligible change within this range, while tangential shrinkage almost doubles from 4% to 7% (Harris & Meylan 1965).

Assuming that a programme of genetic selection for microfibril angle in *P. radiata* is considered worthwhile, there would be considerable difficulty in screening large numbers

of genotypes because of the tedious nature of the measurement procedure. It is therefore of interest to examine possible strategies which minimise the sampling required. If measurements are made on every growth ring at six different heights (total = 85 growth rings) at 0.75 h per growth ring, the cost in operator time will be 63.8 h. If measurements are made at five-ring intervals from the pith at six different heights (total = 21 rings), operator time will be 15.8 h. If measurements are made at five-ring intervals from the pith on a single sample at breast height (total = 5 rings), operator time will be just 3.8 h.

Microfibril angle at breast height is significantly correlated with growth ring number from the pith and this may be useful for predicting missing values in minimal sampling. Regression equations for the five trees examined indicated that a large proportion of the variance is accounted for by this relationship (Table 2). It is interesting to note that Tree 4 shows a markedly different gradient from the other trees, which relates to the significant interaction between trees and growth rings shown in Table 1.

Predicted and actual values for Tree 1 at breast height are plotted in Fig. 5, based on the third sampling strategy above, where rings 1, 5, 10, 15, 20, and 22 were measured. The prediction equation is $37.06 - 2.30X + 0.059X^2$ with an r^2 value of 88.0%. Adding growth

TABLE 2—A regression analysis for microfibril angle against growth ring number from the pith for individual trees at breast height

Tree No.	Regression equation	$r^2_{y,1,2}$
1	$Y_p = 39.24 - 2.96X + 0.09X^2$	82.8%
2	$Y_p = 49.23 - 3.51X + 0.10X^2$	88.8%
3	$Y_p = 48.96 - 3.49X + 0.10X^2$	87.7%
4	$Y_p = 40.51 - 0.66X - 0.01X^2$	80.5%
5	$Y_p = 47.03 - 2.78X - 0.07X^2$	85.8%

Y_p = microfibril angle

X = growth ring from the pith

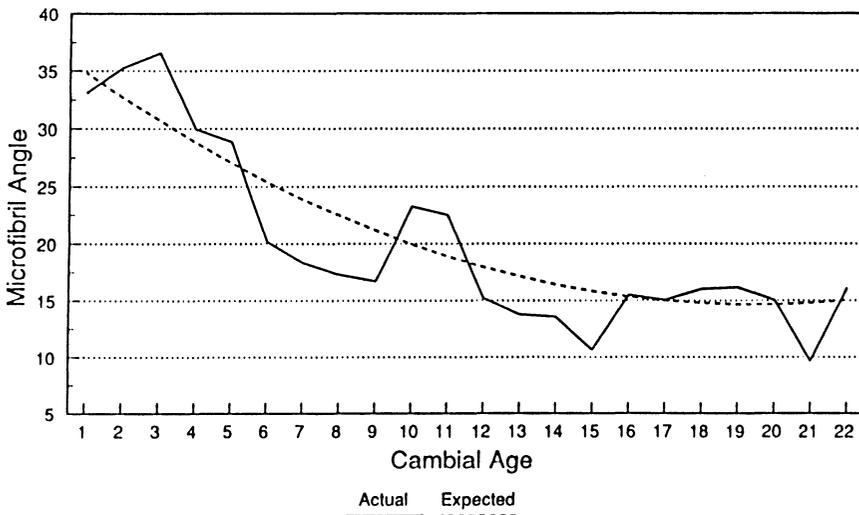


FIG. 5—Predicted and actual microfibril angle for Tree 1 at breast height based on a regression between microfibril angle and cambial age using rings 1, 5, 10, 15, 20, and 22.

rate to this regression did not significantly improve prediction. The peak shown in rings 10 and 11, which occurs in several other trees during the same two growth seasons, does not correspond with the known silvicultural history of the trees. This peak may reflect the influence of some unknown environmental factor.

Microfibril angle at breast height is significantly correlated with microfibril angle at other heights when values are averaged for the whole group of trees. This allows the possibility of predicting variation with height based on breast height measurements. Because microfibril angle at breast height and at other heights are both measured variables, there is no determinate variable and a standard regression analysis would be inappropriate. Prediction equations were therefore calculated by determining the first-principal axis of the bivariate scattergram using the method described by Sokal & Rohlf (1981). Prediction equations for each height are given in Table 3 and the observed and predicted values for the butt in Fig. 6. The mean deviation between observed and predicted values varies from 1° to 2°, with a maximum deviation of 5°. Predictions appear to be more or less equally accurate for all heights.

TABLE 3—Prediction equations based on the first principal axis of the bivariate scattergram between microfibril angle at breast height and at six other heights, using an average data set based on measurements from five trees

Height (m)	First principal axis	r ²
Butt	$Y_2 = 10.23 + 0.94Y_1$	87.6%
7	$Y_2 = 1.40 + 0.65Y_1$	90.3%
12	$Y_2 = 5.32 + 0.50Y_1$	75.3%
18	$Y_2 = -6.24 + 0.86Y_1$	88.6%
23	$Y_2 = 9.79 + 0.42Y_1$	81.5%
30	$Y_2 = -2.23 + 0.74Y_1$	85.9%

Y1 = Microfibril angle at breast height
 Y2 = Predicted microfibril angle

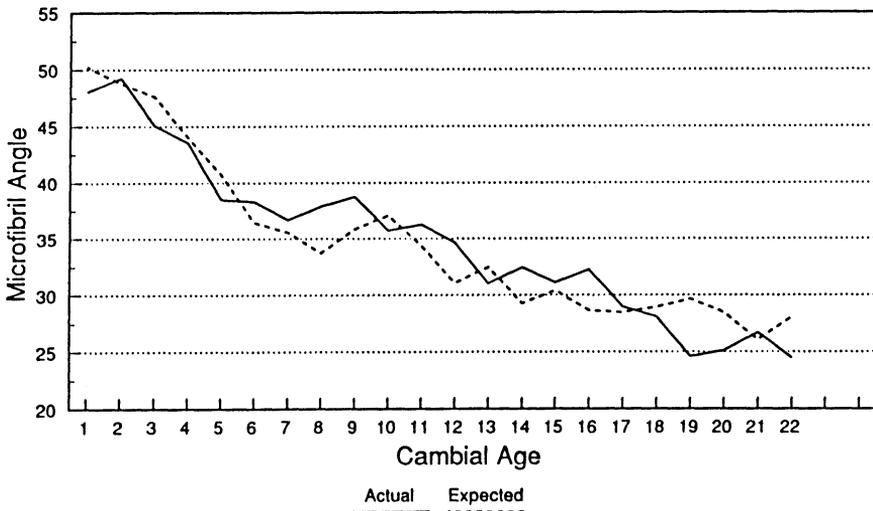


FIG. 6—Predicted and actual mean microfibril angles at the butt, based on mean microfibril angles measured at breast height.

Applying the same procedure to data pooled from individual trees gave a poor result. Differences among trees in the relationship between microfibril angle at breast height and at other heights probably reflect variation in height growth, which produces variation in physiological height among trees. This procedure should therefore be used to predict values for groups of trees rather than for individual trees, where predictions will be inaccurate. Since the above equations are based on a relatively small sample size of five trees, they should be used with caution until their applicability to the general population has been determined. Since the amount of height growth may vary with site and genotype, patterns of microfibril angle variation with height may depend on tree growth rate, making prediction more difficult.

In order to assess the use of predicted microfibril angles, both on a pith-to-bark basis and with height, volume-weighted values for corewood and outerwood were compared at breast height, and for butt logs, top logs, and whole trees based on observed and predicted data (Table 4). These calculations are based on among-tree averages to enable prediction of variation with height. The model for the predicted data at breast height is $43.98 - 2.18X + 0.05X^2$ and this produces excellent agreement between the observed and predicted values. The inclusion of ring 22 in the sampling for this regression did not significantly improve the accuracy of the model, the r^2 value increasing from 98.0% to 98.5%. Further investigation is needed to determine the applicability of these prediction equations to an independent sample of trees.

TABLE 4—A comparison of observed and predicted volume-weighted microfibril angles based on sampling from pith to bark (rings 1, 5, 10, 15, 20, and 22)

	Observed	Predicted
Corewood	29.9	31.6
Outerwood	21.0	22.6
Butt log	23.1	24.5
Top log	22.6	23.6
Whole tree	21.4	21.3

While discs were used as samples in this study, increment cores could have been used equally well to enable non-destructive sampling. This would be essential for screening potential parents in any genetic selection programme. However, because of the prominent pith-to-bark trends in microfibril angle, especially the rapid decline within the first few rings from the pith, it is essential that increment cores contain either the pith or a large fraction of the innermost growth ring in order to be able to make correct comparisons among trees or groups of trees which need not be of the same age.

Any comparison of trees for purposes of selecting breeding stock must be made on comparable growth rings. From Table 1 the least significant difference between trees within rings must be based on the residual MS, and for measurements based on 25 tracheids the appropriate value is $\pm 5.5^\circ$. However, when comparing clonal trials with replicated trees within each clone, a comparison of clones (or any other tree group) must be made using the variance among trees within groups, which is estimated by the trees MS in Table 1. This value is quite large in the present group of trees. If microfibril angle is strongly genetically controlled, this variance may be substantially reduced among trees within clones, thus

avoiding the need for large sample sizes which could otherwise make such studies impractical.

CONCLUSIONS

Microfibril angle varies from pith to bark, with height in the stem, and among trees. The variation among trees suggests that there is potential for selection of low microfibril angle to improve wood quality. However, the volume of timber likely to be significantly affected by selection for low angles, primarily the corewood of the butt log, is less than 20% of the timber volume for a single tree. In addition, the presence of other timber defects such as knots, spiral grain, and compression wood in this region of the stem may render selection for microfibril angle ineffective in terms of improved wood quality. Microfibril angle can be assessed by measuring every fifth growth ring from the pith. Measurement on increment cores collected at breast height can provide an adequate basis for comparison among trees or tree groups. Regression analysis of breast height measurements against measurements at other heights suggests that microfibril angles can be predicted with acceptable accuracy based on data averaged among trees. The use of this model to predict microfibril angle for individual trees is not advisable and its applicability to a wider sample of trees needs to be examined.

ACKNOWLEDGMENTS

The author acknowledges the assistance of G.D. Young, D.J. Cown, J.M. Uprichard, S.O. Hong and I.A. Andrew during this investigation.

REFERENCES

- BENDTSEN, B.A., SENFT, J. 1986: Mechanical and anatomical properties in individual growth rings of plantation grown eastern cottonwood and loblolly pine. *Wood and Fiber Science* 18: 23–38.
- BOYD, J.D. 1985: "Biophysical Control of Microfibril Orientation in Plant Cell Walls". Martinus Nijhoff/Dr W. Junk Publishers, Boston. 200 p.
- CAVE, I.D. 1968: The anisotropic elasticity of the plant cell wall. *Wood Science and Technology* 2: 268–78.
- 1969: The longitudinal Young's modulus of *Pinus radiata*. *Wood Science and Technology* 3: 40–8.
- COWN, D.J. 1975: Variation in tracheid dimensions in the stem of a 26-year-old radiata pine tree. *Appita* 28: 237–45.
- DONALDSON, L.A. 1991: The use of pit apertures as windows to measure microfibril angle in chemical pulp fibres. *Wood and Fiber Science* 23: 290–5.
- ECHOLLS, R.M. 1955: Linear relation of fibrillar angle to tracheid length and genetic control of tracheid length in slash pine. *Tropical Woods* 102: 11–22.
- ERICKSON, H.D.; ARIMA, T. 1974: Douglas fir wood quality studies. Part II. Effects of age and stimulated growth on fibril angle and chemical constituents. *Wood Science and Technology* 8: 255–65.
- HARRIS, J.M. 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.
- HARRIS, J.M.; MEYLAN, B.A. 1965: The influence of microfibril angle on longitudinal and tangential shrinkage in *Pinus radiata*. *Holzforschung* 19: 144–53.

- KELLOGG, R.M.; THYKESON, E.; WARREN, W.G. 1975: The influence of wood and fiber properties on kraft converting-paper quality. *Tappi* 58: 113–6.
- MANWILLER, F.G. 1972: Wood and bark properties of spruce pine. *USDA Forest Service Research Paper SO-78*.
- MARK, R.E. 1967: "Cell Wall Mechanics of Tracheids". Yale University Press, New Haven. 310 p.
- MARK, R.E.; GILLIS, P.P. 1973: The relationship between fibre modulus and S2 angle. *Tappi* 56: 164–7
- PARK, S.; SAIKI, H.; HARADA, H. 1980: Structure of branch wood in Akamatsu (*Pinus densiflora* Sieb. et Zucc.). II. Wall structure of branch wood tracheids. *Memoires of the College of Agriculture Kyoto University* 115: 33–44
- PEDINI, M. 1992: The variation in the microfibrillar angle within the juvenile wood of sitka spruce. *IWA Bulletin n.s.* 13: 261.
- PHILLIPS, E.W.J. 1941: The inclination of fibrils in the cell wall and its relation to the compression of timber. *Empire Forestry Journal* 20: 74–8.
- PILLOW, M.Y.; TERRELL, B.Z.; HILLER, C.H. 1953: Patterns of variation in fibril angles in loblolly pine. *USDA Forest Service FPL Report No. D 1935*.
- PRESTON, R.D. 1948: The fine structure of the walls of the conifer tracheid. III. *Biochim et Biophys Acta* 2: 370–83.
- 1949: The organisation of the cell wall in relation to the structure of fibres. Pp. 218–47 in Preston, J.M. (Ed.) "Fibre Science". Manchester.
- PRESTON, R.D.; WARDROP, A.B. 1949: The fine structure of the walls of the conifer tracheid. IV. *Biochim et Biophys Acta* 3: 549–59.
- SOKAL, R.R.; ROHLF, F.J. 1981: "Biometry", 2nd Edition. W.H. Freeman and Company, San Francisco. 859 p.
- WARDROP, A.B. 1951: Cell wall organisation and the properties of the xylem. I. Cell wall organisation and the variation of breaking load in tension of the xylem in conifer stems. *Australian Journal of Scientific Research B-4*: 391–414.
- WARDROP, A.B.; DADSWELL, H.E. 1950: The nature of reaction wood. II. The cell wall organisation of compression wood tracheids. *Australian Journal of Scientific Research B-3*: 1–13.
- WATSON, A.J.; DADSWELL, H.E. 1964: Influence of fibre morphology on paper properties. 4. Micellar spiral angle. *Appita* 17: 151–6.
- WIMMER, R. 1992: Multivariate structure property relations for pinewood. *IWA Bulletin n.s.* 13: 265.