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WITHIN-TREE VARIATION IN ANATOMICAL PROPERTIES OF COMPRESSION WOOD IN RADIATA PINE

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SUMMARY

Two trees of radiata pine, one showing severe lean, the other growing almost vertically, were assessed for the presence and anatomical properties of compression wood, including anatomy, lignin distribution, microfibril angle, basic density, radial and tangential lumen diameter and cell wall thickness. Both trees contained significant amounts of compression wood although the severity and amount of compression wood was greater in the leaning tree. Changes in lignin distribution seem to be characteristic of the mildest forms of compression wood with reduced lignification of the middle lamella representing the earliest change observed from normal wood. An increase in microfibril angle was associated with both mild and severe compression wood although examples of severe compression wood with the same or smaller microfibril angles than opposite wood, or with very small microfibril angles, were found. When segregated into mild and severe compression wood the average difference in microfibril angle was 4° and 8° respectively compared with opposite wood. Within-ring distribution of microfibril angle was different in severe compression wood compared to opposite wood with higher angles in the latewood.

Severe compression wood showed a 22% increase in basic density compared to mild compression wood and opposite wood. The increased density was accounted for in terms of a 26% increase in tracheid wall thickness throughout the growth ring, offset by a 9% increase in radial lumen diameter, slightly greater in the latewood. There were no significant changes in density or cell dimensions in mild compression wood compared with opposite wood.

Key words: Compression wood, *Pinus radiata*, anatomical properties, microfibril angle, lignin distribution, cell dimensions, basic density.

INTRODUCTION

Compression wood in conifers occurs in a range of gradations from near normal wood to the severe compression wood typical of branches and leaning stems (Pillow & Bray 1935; Pillow & Luxford 1937; Pillow et al. 1936, 1941; Low 1964; Shelbourne 1966; Shelbourne & Ritchie 1968; Burdon 1975; Nichols 1982; Yumoto et al. 1983). A detailed

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classification of different types of compression wood based on microscopic features has been produced by Yumoto et al. (1983) allowing compression wood to be classified from mild to severe.

In general mild compression wood forms a continuum between normal wood and severe compression wood. According to Yumoto et al. (1983) the first feature to occur in the mildest expression of compression wood is an increased lignification of the outer S_2 region of the cell wall (S_{2L}), occurring first in the corners and later forming a continuous layer in more severe grades. The circularity of cells increases and eventually helical cavities may form in the most severe compression wood. The absence of an S_3 layer and the presence of intercellular spaces are variable in the mildest forms.

In radiata pine (*Pinus radiata* D. Don), compression wood is most commonly found in the juvenile wood, partly because of the high rate of growth in this region of the stem (Pillow & Luxford 1937; Burdon 1975; Harris 1977). Compression wood in radiata pine often has abnormally high longitudinal shrinkage, especially in the juvenile wood, although this seems to be accounted for more as a result of increased density than from increased microfibril angles. Harris (1977) found no significant difference in microfibril angle between compression wood and opposite wood in the same tree, even though significant differences in longitudinal shrinkage were observed. In the same study it was found that the relationship between longitudinal shrinkage and microfibril angle was different in compression wood compared to normal or opposite wood, with shrinkage in compression wood being much more sensitive to changes in microfibril angle. Donaldson and Burdon (1995) found that on average microfibril angle was higher in compression wood compared to normal wood but this trend was highly variable among different rings and trees.

Mild compression wood may occur throughout the growth ring and is often not limited to one side of the stem as is severe compression wood in radiata pine (Harris 1977). This more pervasive distribution, combined with a less distinctive visual appearance often makes mild compression wood more difficult to avoid by applying grading rules to timber. A tendency towards a patchy type of distribution around the circumference of the stem means that small pockets of mild compression wood can occur in clear timber, for example mouldings, where significant distortion may result from an uneven response to changing moisture content (Donaldson & Turner 2001).

As part of a study of the distribution of wood properties in relation to stem form we have carried out a detailed assessment of the anatomical properties of compression wood in two clonal trees, one with severe lean, the other with near vertical growth. This report describes within-tree variation in anatomical properties of compression wood including, lignin distribution, microfibril angle, density and cell dimensions.

MATERIALS AND METHODS

Two trees were selected from a clonal trial planted at Rotorua, New Zealand, in 1985. One tree was bent to the ground at an early age and was swept as a result of the trees response to lean. The other tree of the same clone had a similar dbh (diameter at breast height) and was considered to be growing vertically. The trees were felled in the spring of 2000 and discs were cut for measurement of anatomical and solid wood properties. Matched samples were assessed for microfibril angle, density and cell dimensions using Silviscan (Evans 1994, 1997). Solid wood properties for these samples will be described elsewhere.

Radial strips from pith to bark were collected at butt, 1 m, 2 m, 3 m, 7 m, 12 m, 17 m, and 23 m height in both north/south and east/west orientations for the leaning tree, and at northeast/southwest orientation for the vertical tree. Anatomical features for each growth ring (classified from bark to pith) from each disk were recorded by examination with polarised light and fluorescence microscopy of unstained sections. The following features were recorded:

1) Presence of a highly lignified S_{2L} layer
2) Presence of intercellular spaces
3) Absence of an S_3 layer
4) Presence of helical checks

Compression wood was ranked as mild (1 and/or 2) or severe (1, 2, 3, and 4) based on the number of characteristics shown. Some samples were examined in detail using confocal microscopy as described by Donaldson et al. (1999) (Knebel & Schnepf 1991). Transverse sections approximately 60 μm in thickness were mounted in 70% glycerol and examined with a Leica TCS/NT confocal microscope using 488 nm as excitation wavelength, and imaged using a 515 nm longpass filter (green-yellow fluorescence). Visible light autofluorescence is primarily due to lignin and thus shows the distribution of lignin across the tracheid cell wall, increased autofluorescence corresponding to increased lignin (Kutscha & McOrmond 1972; Donaldson et al. 1999).

Anatomical features were related to microfibril angle, density and cell dimensions determined from Silviscan analysis using both growth ring averages and within-growth ring distributions on a % of growth ring width basis. Data were segregated on the basis of classification into mild and severe compression wood groups. All comparisons were made with the same growth ring in opposite wood. Opposite wood is defined as non-compression wood from a compression wood containing growth ring, usually on the side of the stem opposite to the compression wood zone. Normal wood is defined as wood from a growth ring that does not contain any compression wood. Growth rings where compression wood was present on both sides of the stem were excluded from this analysis.

RESULTS AND DISCUSSION

Between tree comparison

The leaning tree contained large amounts of compression wood near the base, which was most severe at 1 m height. This corresponded to the region of most severe lean in the stem (Fig. 1). The mildest compression wood that could be detected contained sporadic cells with an S_{2L} layer, and adjacent cells with reduced lignification of the middle lamella as detected by lignin autofluorescence (Fig. 2 & 3). Intercellular spaces occurred sporadically in some juvenile rings (Fig. 3) without any other indications of

Fig. 1. Sample trees growing in a clonal trial at Longmile, Rotorua, New Zealand. The vertical tree is shown at left while the leaning tree is shown at right.

compression wood and on both sides of the stem so this feature was considered less characteristic of compression wood than for example an S_{2L} layer. In most cases compression wood could be recognised macroscopically by its darker colour. However, some mild compression wood could not be distinguished in this way. Screening the samples using fluorescence microscopy was found to be a rapid and effective way of identifying and classifying the compression wood.

The second tree was almost vertically grown (Fig. 1) and contained smaller amounts of compression wood, almost exclusively of the mild type. Compression wood of an extremely mild type was observed in this tree. The only recognisable anatomical feature of this material was a reduced lignification of the middle lamella detected by fluorescence microscopy (Fig. 3). This is assumed to be a precursor to the increased lignification of the S_{2L} region and sometimes the wood contained a mixture of the two cell types as in the leaning tree. In these cells the autofluorescence intensity of the middle lamella was similar to that of the secondary wall even though an S_{2L} layer could not be distinguished. This confirms that lignin distribution gradually changes from normal wood to compression wood, initially with a reduction in middle lamella lignin followed by increased lignification of the outer S_2 region.

Anatomical properties for both trees are shown in Table 1. In general the leaning tree shows larger differences between compression wood and opposite wood compared to the vertical tree because of the greater amount of severe compression wood. The leaning tree contained a total of 63 growth ring samples with severe compression wood and 56 growth ring samples containing mild compression wood out of a total of 317 growth rings sampled throughout the tree. In contrast the vertical tree contained only 2 growth ring samples with severe compression wood and 42 growth ring samples containing mild compression wood out of a total of 158 growth rings sampled. Of these 475 growth ring samples, only 274 were used for compression wood/opposite wood comparisons, the remaining samples were excluded because there was no appropriate comparison either due to missing growth rings near the pith or to the distribution of compression wood around the stem.

The two trees showed similar differences in microfibril angle between severe and mild compression wood compared with opposite wood, the values for mild compression wood being about half those for severe compression wood (Table 1). The differences for density, radial diameter and wall

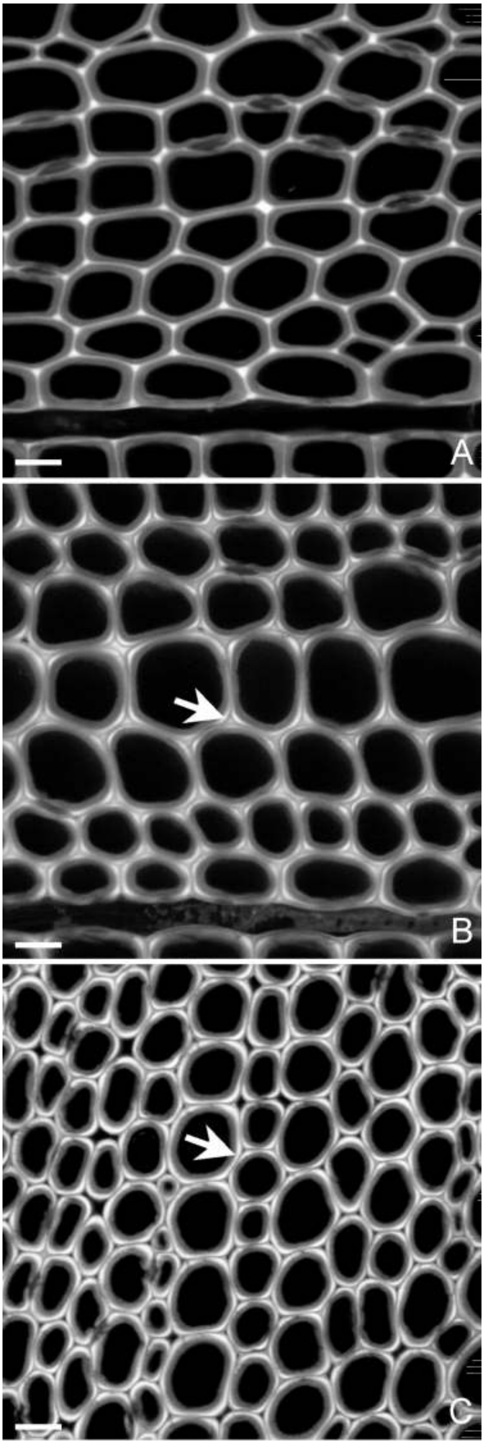

Fig. 2. Typical examples of opposite, A, mild, B, and severe compression wood, C, as seen by lignin autofluorescence at 515–600 nm. The most consistent features that distinguish the two compression wood types in cross-sectional view are the extent of the S_{2L} region (arrows), which is restricted to the cell corners in mild compression wood, and the rounded shape and consistent presence of intercellular spaces in severe compression wood. Lignification of the middle lamella is reduced in the mild sample compared to opposite wood. Scale bars = 49 μm (A and B), and 24 μm (C).

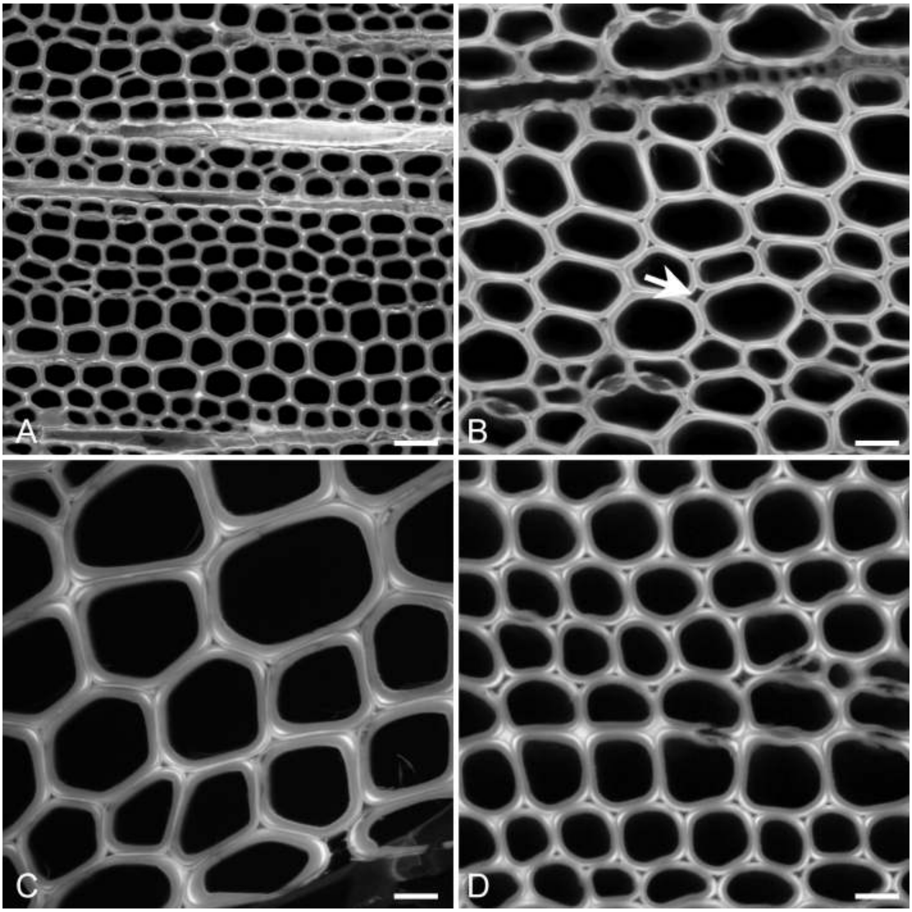

Fig. 3. Examples of very mild compression wood as seen by lignin autofluorescence at 515–600 nm. – A: In this example there are sporadic intercellular spaces and the autofluorescence of the cell corner middle lamellae is reduced but there is no evidence of an S_{2L} region. Scale bar = 49 µm – B: This example of juvenile wood contains intercellular spaces (arrow) but no other evidence of compression wood. Scale bar = 49 µm. – C: This example has small intercellular spaces and an S_{2L} region restricted to the cell corners. Compare this sample with Fig. 2B where the S_{2L} extends further from the corners but is not continuous around the cell wall. Scale bar = 16 µm. – D: This example of mild compression wood has well developed intercellular spaces (arrow) compared to Fig. 2B from the same growth ring. The S_{2L} is more extensive than in C sometimes extending between adjacent cell corners but not continuous around the circumference. Scale bar = 49 µm.

thickness for severe compression wood, were about half as big in the vertical tree. However, because there were only 2 severe compression wood samples, both near the base of the tree, compared to 63 in the leaning tree this comparison is of limited accuracy. The difference for density in mild compression wood was also about half in the vertical tree compared to the leaning tree suggesting a weaker compression wood

Table 1. Anatomical properties of compression wood and opposite wood in leaning and vertical trees showing the confidence interval and the p-value from analysis of variance. Measurements are recorded from continuous scans of radial strips by Silviscan averaged by growth ring. Significant differences are shown in bold. In the case of the vertical tree no test is possible for the severe compression wood because there were only two samples.

	Leaning tree		Vertical tree	
	Mean	Difference	Mean	Difference
MFA				
Severe	30° ± 1.9[1]	**7.8** ($p < 0.001$)	26° ± 0.9	9.5
Opposite	22° ± 1.9		16° ± 0.9	
Mild	23° ± 1.5	**4.0** ($p < 0.001$)	26° ± 1.8	**4.9** ($p < 0.001$)
Opposite	19° ± 1.5		21° ± 1.8	
Density				
Severe	572[2] ± 15.1	**95.4** ($p < 0.001$)	516 ± 15.6	35.9
Opposite	477 ± 15.1		480 ± 15.6	
Mild	463 ± 18.4	8.8 ($p = 0.511$)	44 5 ± 16.6	4.6 ($p = 0.703$)
Opposite	455 ± 18.4		440 ± 16.6	
Radial diameter				
Severe	33.6[3] ± 0.7	**2.2** ($p < 0.001$)	36.4 ± 2.0	1.2
Opposite	31.4 ± 0.7		35.2 ± 2.0	
Mild	35.0 ± 0.6	0.2 ($p = 0.611$)	36.2 ± 0.6	**1.1** ($p = 0.013$)
Opposite	34.8 ± 0.6		35.1 ± 0.6	
Tangential diameter				
Severe	26.3[3] ± 0.8	-0.4 ($p = 0.864$)	26.8 ± 1.4	-0.3
Opposite	26.7 ± 0.8		27.1 ± 1.4	
Mild	27.1 ± 0.3	-0.4 ($p = 0.058$)	27.2 ± 0.3	0.1 ($p = 0.837$)
Opposite	27.5 ± 0.3		27.1 ± 0.3	
Wall thickness				
Severe	3.13 ± 0.1	**0.6** ($p < 0.001$)	2.9 ± 0.1	0.3
Opposite	2.5 ± 0.1		2.6 ± 0.1	
Mild	2.6 ± 0.1	0.1 ($p = 0.517$)	2.5 ± 0.1	0.1 ($p = 0.356$)
Opposite	2.5 ± 0.1		2.4 ± 0.1	

1) 95% confidence interval; 2) kg/m^3; 3) µm.

response in this tree. Tangential lumen diameter showed no significant variation and was not examined in any further detail.

In mild compression wood, changes in lignin distribution were the most characteristic anatomical feature. In some cases a reduced lignification of the cell corner middle lamella was the only feature that could be detected, representing the very earliest sign of a compression wood response (Fig. 2 & 3). This feature was only observed in juvenile wood (within 5 rings of the pith) and so may be a characteristic of juvenile compression wood. Intercellular spaces were of highly variable occurrence often occurring as solitary features or in small patches within a growth ring (Fig. 3). Even in severe compression wood, intercellular spaces occurred only sporadically (Fig. 2). The absence of an S_3 layer as well as helical checking, and a significantly rounded shape, were only found in severe compression wood. However it was sometimes difficult to detect an S_3 layer even in normal or opposite wood indicating variability in the thickness of this cell wall layer. In some cases wood varied from normal, to mild, to severe compression wood, within a single growth ring. Compression wood also occurred as bands within a growth ring, a pattern which was identified as zonate compression wood. In other cases compression wood cells with an S_{2L} layer at the cell corners were dispersed amongst otherwise anatomically normal cells as a special type of mild compression wood.

Microfibril angle

Compression wood is generally considered to have increased microfibril angles compared to opposite wood from the same growth ring (Timell 1986). Many early studies have reported high microfibril angles in compression wood without providing comparative data for opposite wood, or reporting the cambial age (growth ring number from the pith) of the growth rings examined. Since the microfibril angle is known to show significant variation both with cambial age and height in the stem (Donaldson 1992) it is essential to provide the location of the sample when reporting microfibril angles, or at least to provide a reference value for opposite wood at the same location in the stem.

Wardrop and Dadswell (1950) measured microfibril angles along radial profiles in radiata pine wood and showed increased microfibril angles in compression wood growth rings compared to both adjacent normal wood and to opposite wood from the same growth rings. The increased microfibril angle continued in the growth rings beyond the compression wood zone and was associated with a decrease in tracheid length.

We did not observe any extension of increased microfibril angles beyond the zone of compression wood in our samples. In fact we have noted that microfibril angles tend to be lower than in opposite wood in growth rings just outside the compression wood zone (Fig. 4).

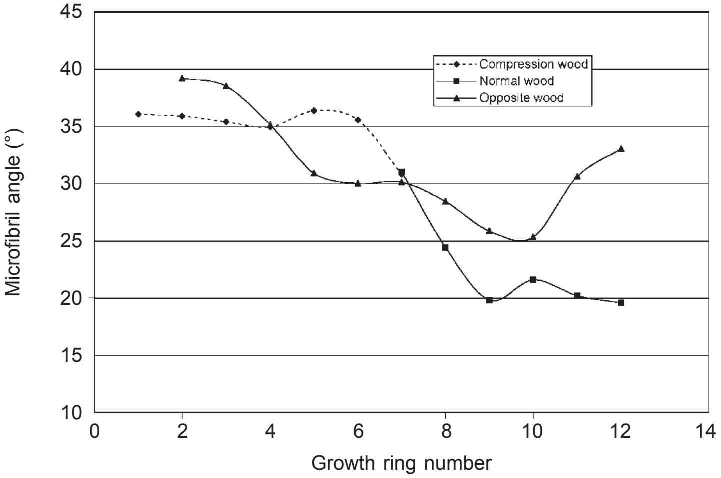

Fig. 4. MFA trends (growth ring averages) from pith to bark among compression, normal and opposite wood for the leaning tree at 0.5 m height. Compression wood in the juvenile wood at the butt tends to have the same microfibril angle as opposite wood. In this example only rings 5 and 6 containing compression wood have higher microfibril angles when compared to opposite wood. Normal rings post compression wood tend to have lower microfibril angles when compared to opposite wood in this example.

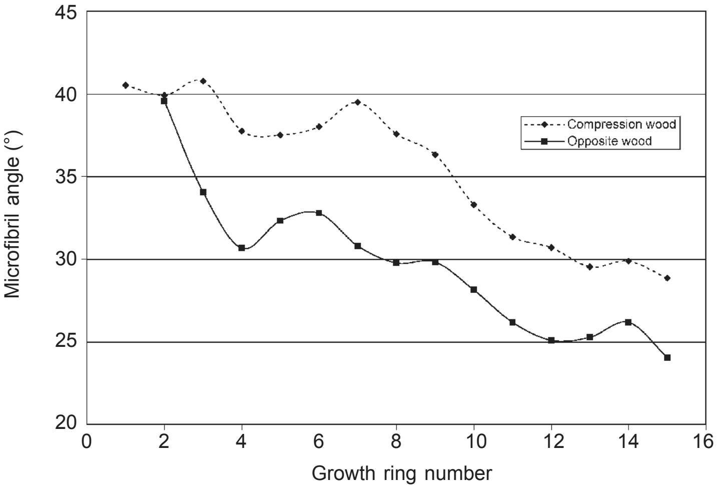

Fig. 5. MFA trends (growth ring averages) from pith to bark among compression and opposite wood for the leaning tree at 1 m height. In this example compression wood has consistently higher microfibril angles except at ring 2 adjacent to the pith.

We also confirm that not all compression wood rings show an increase in microfibril angle, especially compression wood in the first few juvenile growth rings adjacent to the pith (Fig. 4, 5) where there was often no difference between compression wood and opposite wood. In general the difference in microfibril angle between compression and opposite wood tended to increase with height up to about 3 m followed by a gradual decline towards the crown. Typically growth rings with high microfibril angles in opposite wood, such as the juvenile wood in the butt log, showed little or no increase in the corresponding severe compression wood. The effects of juvenility and compression wood on microfibril angle can thus be regarded as non-additive.

Harris (1977) measured microfibril angle in compression wood and opposite wood of radiata pine and found very similar high angles in both wood types. Nečesaný (1955) also found similar angles in the compression and opposite woods of juvenile wood from *Abies alba* Mill. It is likely that when microfibril angles are already high (for whatever reason) that compression wood does not result in any further increase, as we have observed for juvenile wood. We observed several examples of severe compression wood (and many examples of mild compression wood) with a microfibril angle essentially the same as that in opposite wood (35° vs. 35°, 38° vs. 36°, in juvenile wood at 0.5 m height, and 12° vs. 10° in mature wood at 7 m height).

We have also described severe compression wood with low microfibril angles (less than 20°). In one case we confirmed that the severe compression wood had a low microfibril angle by measuring the orientation of the helical checks giving a comparable result to the Silviscan measurement (20° cf. 19° respectively compared to 12° for opposite wood) (Fig. 6). These results confirm the observations by Donaldson and Burdon (1995) that compression wood is not always associated with high microfibril angles.

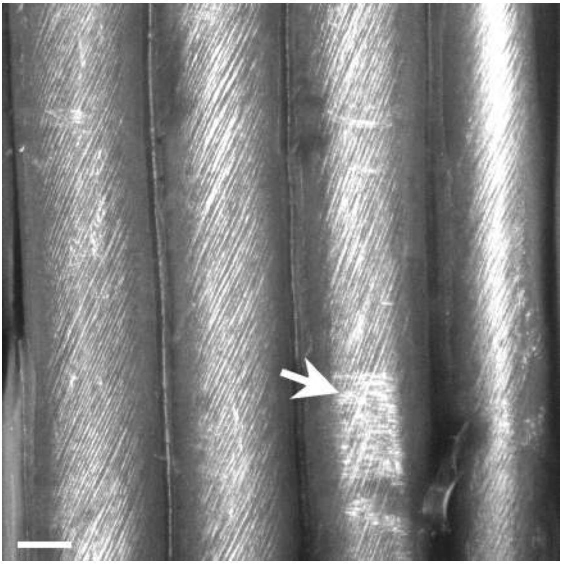

Fig. 6. Confocal reflectance image showing a longitudinal view of helical cavities in severe compression wood tracheids, which illustrate the microfibril orientation. Measurements on this sample confirmed microfibril angle measurements by Silviscan (X-ray diffraction) giving values of 20° and 19° respectively showing that severe compression wood can have low microfibril angles depending on its position within the tree. A small area of S_1 layer (arrow) shows a near horizontal S-helix compared to the steep Z helix of the S_2. Scale bar = 17 μm.

Table 2. Anatomical properties of compression wood and opposite wood – overall values.

	MFA	Density (kg/m^3)	Radial (μm)	Tangential (μm)	Wall thickness (μm)
Severe	31°	580	34.3	26.8	3.1
Opposite	22°	477	31.5	26.7	2.5
Mild	24°	456	35.5	27.1	2.5
Opposite	20°	444	34.4	27.0	2.4

Severe compression wood had a microfibril angle 8.4° higher on average than opposite wood from matched growth rings (Table 2) while mild compression wood showed a 4.6° increase compared to opposite wood. The largest compression wood microfibril angle was 41° compared to 34° in opposite wood of the same growth ring. The largest difference in microfibril angle between severe compression wood and opposite wood was 17°.

Relatively few studies have examined variation in microfibril angles within growth rings, especially in relation to compression wood occurrence. Hiller (1964) found that the microfibril angle decreased from earlywood to latewood in both opposite and compression woods (Nečesaný 1955; Park et al. 1980). Park et al. (1980) observed the highest microfibril angles in the centre of the growth ring. In normal wood microfibril angles are high in the earlywood and decline gradually towards the ring boundary with a more abrupt decline in the last few latewood tracheids (Paakkari & Serimaa 1984; Evans 1997; Donaldson 1998; Anagnost et al. 2002). In the present study we have found that

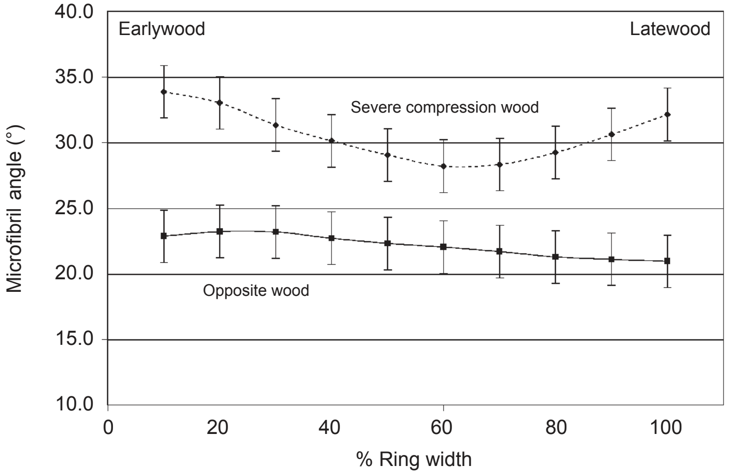

Fig. 7. Within-ring variation in microfibril angle between severe compression wood and opposite wood averaged for a sample of 56 growth rings. Severe compression wood shows consistently higher microfibril angles. While opposite wood shows a gradual decline in microfibril angles across the growth ring, severe compression wood shows a decline across the earlywood with a subsequent increase in the latewood. Error bars represent the 95% confidence interval.

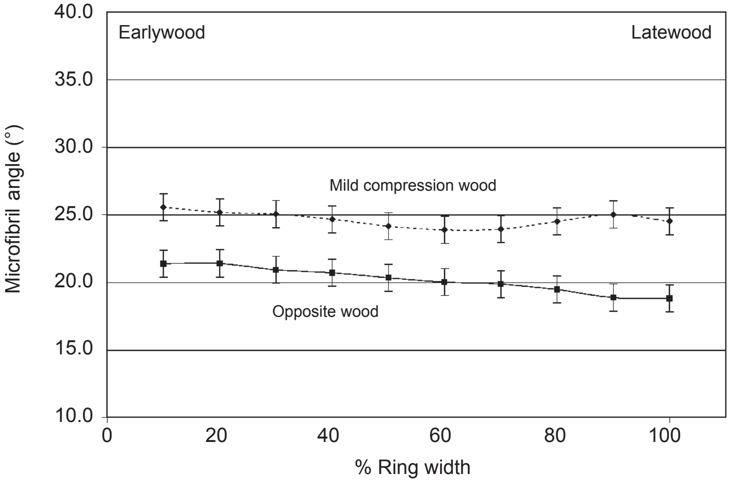

Fig. 8. Within-ring variation in microfibril angle between mild compression wood and opposite wood in a sample of 82 growth rings. Data are shown as a percentage of ring width. Mild compression wood shows consistently higher microfibril angles with a similar within-ring distribution in both wood types. Error bars represent the 95% confidence interval.

for severe compression wood, microfibril angles decline across the earlywood but then increase again in the latewood when averaged over 56 growth ring samples (Fig. 7). For mild compression wood the pattern of within-ring variation is essentially the same as opposite wood (Fig. 8). Although this within-ring pattern for severe compression wood disagrees with the findings of Park et al. (1980) this may be due to variation among

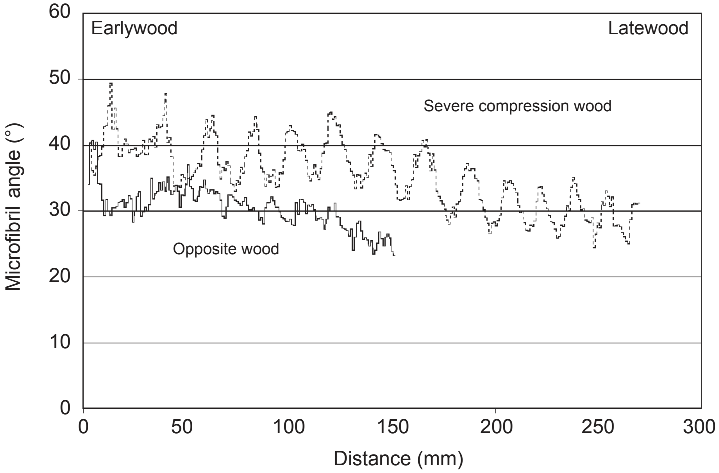

Fig. 9. Pith to bark variation in MFA in severe compression wood and opposite wood for the leaning tree at 1 m height (shown as growth ring averages in Fig. 5). The most notable feature is the greater within-ring variation in MFA in compression wood compared to opposite wood, which tends to accentuate the growth related pattern in compression wood. Growth rings are indistinct as defined by MFA variation in the opposite wood.

individual growth rings. Our result represents the average pattern for a large sample (56 growth ring samples) with acknowledgment that individual rings may show different patterns. The within-ring pattern for mild compression wood was essentially similar to opposite wood when averaged over 82 growth ring samples. However, it was noted that some individual growth rings did show a pattern similar to that for more severe compression wood. The amount of variation in microfibril angle within growth rings tends to be greater in compression wood compared to opposite wood resulting in a more clearly defined growth ring pattern in the pith to bark plot (Fig. 9). Wimmer et al. (2002) have examined within-ring variations in microfibril angle in *Eucalyptus nitens* (Deane & Maiden) Maiden, and found that microfibril angles increase in response to water stress and wind. Growth rates on a short time scale (several days) also affect microfibril angles although other studies have shown that on larger time scales, growth rate has only a weak affect on microfibril angle (Erickson & Arima 1974; Lindström et al. 1998; Herman et al. 2000). It would be interesting to examine the interaction of these factors with compression wood occurrence in radiata pine.

Lignin distribution

Many studies have shown that compression wood contains more lignin than opposite or normal wood. Not only does the amount of lignin increase but its location in the cell wall also changes (Donaldson et al. 1999; Singh & Donaldson 1999; Donaldson 2001). There is a shift in lignin distribution away from the middle lamella and into the secondary wall forming a highly lignified outer S_2 region known as the S_{2L} layer (Lange 1954; Wardrop & Bland 1961; Côté et al. 1966, 1968; Wood & Goring 1971;

Fukazawa et al. 1974; Fujita et al. 1978). In mild compression wood the S_{2L} layer is restricted to the corners of cells but becomes continuous around the circumference in severe compression wood (Yumoto et al. 1983; Donaldson et al. 1999).

The observation that the lignification of the cell corner middle lamella is reduced in mild compression wood, with or without intercellular spaces, even when there is no detectable S_{2L} layer at the cell corners (Fig. 3) confirms that there is a continuum of lignification changes associated with compression wood formation. Indeed lignin topochemistry seems to be a sensitive indicator of exposure to several types of stress including drought (Barnett 1976; Donaldson 2002), climate (Gindl et al. 2000) and nutritional status (Downes et al. 1991). We have observed that individual tracheids within close proximity may show either reduced lignification of the middle lamella and/or formation of an S_{2L} layer indicating that individual cells can show differing degrees of response to gravitropic stimulus. Donaldson (1985, 1986, 1993) has described the natural variations in lignification of the middle lamella among trees and clones. The reduced lignification in some of these examples may have reflected a very mild reaction wood response that is permanently active in some genotypes.

Density & cell dimensions

Timell (1986) has reviewed the physical and anatomical properties of compression wood. Numerous studies have shown that compression wood is more dense than opposite or normal wood in a wide variety of conifers including radiata pine (Du Toit 1963; Kibblewhite 1973; Harris 1977; Nicholls 1982).

X-ray densitometry on our samples confirms earlier reports of increased basic density in compression wood of radiata pine (Du Toit 1963; Kibblewhite 1973; Harris 1977;

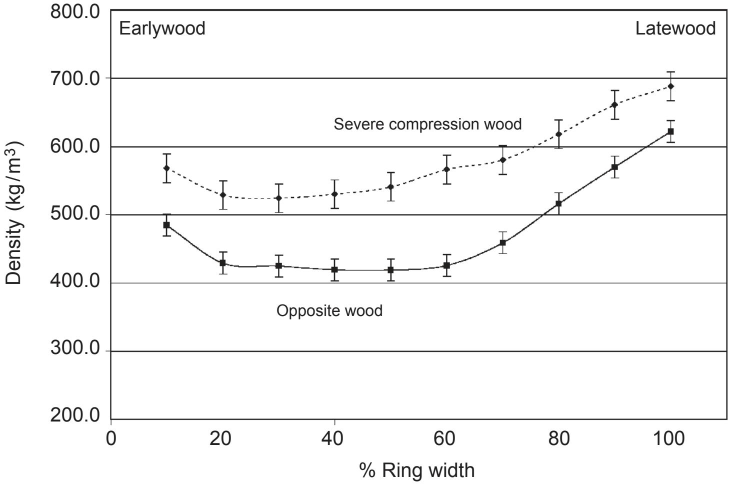

Fig. 10. Variation in basic density between severe compression wood and opposite wood in a sample of 56 growth rings. Data are shown as a percentage of ring width. Severe compression wood shows consistently higher density with a similar within-ring distribution in both wood types. Mild compression wood showed no difference in density when compared to opposite wood. Error bars represent the 95% confidence interval.

Nicholls 1982). On average severe compression wood had 22% higher density than opposite wood, an increase of 103 kg m^{-3} (Table 1). Mild compression wood had the same density as opposite wood. The within-ring density profile was essentially the same in severe compression wood and opposite wood, indicating that the density increase is not due to a change in the proportion of latewood (Fig. 10). Cell dimension measurements indicate that the increased density in severe compression wood is due to a 26% increase in cell wall thickness offset slightly by a 9% increase in radial lumen diameter. Mild compression wood shows no difference in cell dimensions when compared with opposite wood.

The size of the density difference varies greatly among species (Timell 1981, 1982). Wardrop (1951) determined the specific gravity of earlywood and latewood of both compression and normal wood for nine growth rings of radiata pine. These data indicate that the density difference between compression wood and normal wood occurs in both earlywood and latewood as found in the present study. In contrast Harris (1977) found that the density difference between compression wood and opposite wood was almost entirely restricted to the latewood. It is likely that these different results can be accounted for by differences in the severity of the compression wood examined in the two studies. A unique feature of the present study is the accurate classification of compression wood type allowing the distinction between mild and severe forms to be taken into account. Some earlier studies have attempted to take into account differences in severity of compression wood with confusing results. Shelbourne and Ritchie (1968) examined juvenile wood of *Pinus taeda* L. using opacity as a measure of severity. They found no difference in specific gravity between normal and compression wood and found that in latewood, specific gravity decreased with increasing compression wood severity.

The reasons for observations of increased density in compression wood, despite the reduced cell wall density resulting from altered chemical composition (Mayer-Wegelin 1931; Trendelenberg 1932; Onaka 1949), include increased tracheid wall thickness, and shorter tracheids. Observations of lower latewood density such as those of Shelbourne and Ritchie (1968) are explained by the increased radial diameter of tracheid lumens in the latewood of compression wood compared to normal wood. Our present results show that both increased tracheid wall thickness and increased radial lumen diameter occur throughout the growth ring in our samples (Fig. 11 & 12) although the increased radial diameter is slightly greater in the latewood region. This increase in radial diameter reflects the increasingly rounded shape of the tracheid lumen typical of severe compression wood.

A number of studies have examined differences in cell dimensions between compression wood and normal wood. Most have studied tracheid length, which is invariably shorter in compression wood (Timell 1986). Kienholz (1930) examined radial and tangential diameters of tracheids from compression, opposite, and side wood in *Tsuga mertensiana*. Radial diameters were slightly less in earlywood compression wood compared to opposite and side wood with no difference in latewood. Tangential diameters in latewood were similar in compression and opposite wood compared to side wood, which was slightly greater. This result is different from our result for radiata pine where we found a consistently higher radial diameter in compression wood. We found no difference in tangential diameter in agreement with Kienholz (1930). Onaka (1949) examined 10 conifer species, also reporting increased radial diameters for latewood tracheids in compression wood in most of the species examined.

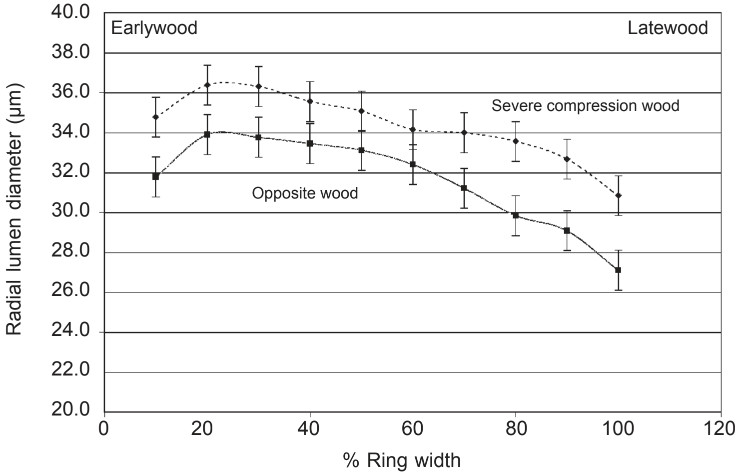

Fig. 11. Variation in radial tracheid diameter between severe compression wood and opposite wood in a sample of 56 growth rings. Data are shown as a percentage of ring width. Severe compression wood shows consistently higher radial diameter, especially in the latewood, with a similar within-ring distribution in both wood types. Mild compression wood showed no difference in radial diameter when compared to opposite wood. Tangential tracheid diameter showed little or no variation. Error bars represent the 95% confidence interval.

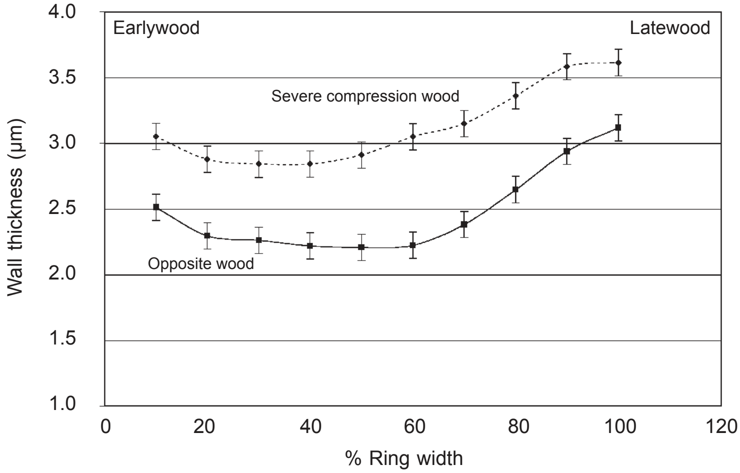

Fig. 12. Variation in tracheid wall thickness between severe compression wood and opposite wood in a sample of 56 growth rings. Data are shown as a percentage of ring width. Severe compression wood shows consistently greater wall thickness with a similar within-ring distribution in both wood types. Mild compression wood showed no difference in wall thickness when compared to opposite wood. Error bars represent the 95% confidence interval.

In many cases our measurements of cell dimensions show the same pattern from early to latewood in compression wood rings as in opposite wood. It is important to note that severe juvenile compression wood tends to be quite uniform across the growth ring making growth ring boundaries very indistinct in some cases. In some samples it was almost impossible to tell where the growth ring boundaries were located especially when considering only basic density variation.

Tracheid wall thickness increases in compression wood, especially in relation to earlywood of normal or opposite wood but to less an extent for latewood (Onaka 1949; Ollinmaa 1955, 1959). Our results are similar to those of Kibblewhite (1973), who found thicker tracheid walls in both earlywood and latewood of compression wood in radiata pine. In contrast Harris (1977) found much higher densities and cell wall thickness in radiata pine latewood compared to earlywood for growth rings containing severe compression wood. Park et al. (1979) also found an increase in tracheid wall thickness in compression wood compared to opposite wood but wall thickness in latewood was less than comparable values for normal wood.

It seems likely that anatomical differences between species in relation to latewood characteristics can account for slight differences in patterns of diameter and wall thickness variation in compression wood among species. Species with an abrupt earlywood-latewood transition may show a more pronounced difference between compression wood and opposite wood in the latewood (Pillow & Luxford 1937). Interpretation of these results is also somewhat affected by definitions of earlywood and latewood. Timell (1986) considers that true earlywood is confined to the first few tracheid rows in compression wood, an observation which is not supported by our within-ring measurements. Our data are measured across each growth ring without any formal distinction between early and latewood, thus avoiding any problem of definition. On this basis density, radial diameter and cell wall thickness all show the same pattern of variation between earlywood and latewood for either severe compression wood or opposite wood.

CONCLUSIONS

On average compression wood has an increased microfibril angle compared to opposite wood but we describe several examples where this is not the case, especially in the first few juvenile rings or in mild compression wood, but also occasionally in severe compression wood. Within-ring microfibril angle distribution is different in severe compression wood compared to mild compression wood or opposite wood. In severe compression wood microfibril angles decrease across the earlywood and increase again in the latewood, whereas in mild compression wood or opposite wood, microfibril angles decline from earlywood to latewood. Reduced lignification of the middle lamella is the earliest detectable sign of reaction wood formation in radiata pine. Intercellular spaces are a feature of juvenile wood even in the absence of any detectable compression wood. Severe compression wood shows an increase in basic density compared to opposite wood, which can be attributed to increased tracheid wall thickness throughout the growth ring, counteracted by an increase in radial lumen diameter. Our results confirm the distinction between mild and severe forms of compression wood indicating that changes in lignin distribution which are the first symptoms of compression wood, can occur independently of changes in microfibril angle and density.

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