

SHRINKAGE AND DENSITY OF *RADIATA* PINE COMPRESSION WOOD IN RELATION TO ITS ANATOMY AND MODE OF FORMATION

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ABSTRACT

Compression wood (c.w.) in 40-year-old *Pinus radiata* D. Don is described. Both cambial age (number of rings from the pith) and visually assessed severity were related to its anatomical and shrinkage characteristics. Because c.w. frequently finds its fullest expression in corewood, further observations were restricted to 8-year-old trees for which some results were available of stem deviations from vertical and their subsequent recovery. Some of these stems had "over-corrected" an initial lean, and resultant c.w. formation was often more severe than that evinced by the original toppling.

All visual grades of c.w. were examined, from intermittent discontinuous crescents of slightly darker wood to very dark c.w. that occupied the entire annual growth layer radially and more than one-quarter of its circumference. Certain of the commonly accepted anatomical characteristics of c.w. were not consistently present in c.w. zones. Among all grades of c.w. intercellular spaces occurred in some samples but not in others, and a degenerate residual S3 layer was occasionally detected under polarised light microscopy and scanning electron microscopy, though less frequently in the more severe grades.

Within the corewood zone, visual grade of c.w. was little guide to its shrinkage behaviour. The regressions of longitudinal shrinkage on microfibril angle were steeper in c.w. than in normal wood, particularly when visual grade of c.w. was severe, but there was little difference in mean microfibril angle between c.w. and the corresponding opposite wood. Within a given visual grade of c.w., microfibril angle accounted for about one-third of the observed variance in longitudinal shrinkage. Much of the remainder appeared to be related to the degree of cell wall thickening associated with c.w. formation — dense c.w. with thick cell walls tended to shrink more longitudinally than c.w. of the same grade and microfibril angle in which cell walls were little thicker than in normal wood.

INTRODUCTION

Compression wood is, in many respects, the most insidious defect commonly encountered in sawn radiata pine (*Pinus radiata* D. Don), in that it reduces strength and can cause distortion in apparently "clear" timber. Because of its high lignin content and other undesirable attributes, it is equally disadvantageous for pulping and many other uses. Yet casual inspection of log piles from almost any forest in New Zealand

will reveal batches of logs in which compression wood occupies up to 20% of the total log volume.

Reviews by Westing (1965; 1968) describe the formation and function of compression wood. Classically it can be regarded as a geotropic response to an inertial force, one which is virtually restricted to the secondary xylem of the Coniferae and of *Ginkgo*. Compared with normal wood, compression wood characteristically has:

1. Tracheids more circular in cross section so that intercellular spaces are formed;
2. Wood of darker colour, often with a distinct brown or reddish-brown tinge, and of greater opacity to transmitted light when the wood is green;
3. Less cellulose and more lignin and galactan;
4. Higher wood density;
5. Greater longitudinal shrinkage but less transverse shrinkage;
6. A different relationship between microfibril angle and shrinkage;
7. Larger microfibril angle in the S2 layer of the cell wall;
8. Helical splits or striations in the S2 layer; slit-like pit apertures;
9. No. S3 layer.

On the other hand, compression wood is known to vary in intensity from isolated crescents of slightly darker-coloured wood to extensive areas totally involving many annual growth layers, over one-quarter or more of their circumference. It has also been shown (Shelbourne *et al.*, 1969) that the various grades of compression wood differ in their relationships to stem straightness, and that the propensity to form compression wood is highly heritable. These conclusions have been supported for *Pinus radiata* by Burdon (1975). However, Burdon also makes the point that "although the genetic variation in visually rated compression wood is better understood now, its overall technical significance is uncertain". The technical properties of compression wood are, in fact, highly unpredictable; for example, what appears to be severe compression wood may or may not give rise to excessive longitudinal shrinkage or abnormally high wood density.

This report examines variability in certain physical and anatomical features of radiata pine compression wood in relation to the cambial age of the xylem in which it forms and to its mode of origin, and attempts to relate severity of compression wood (as indicated by longitudinal shrinkage) to its anatomical characteristics.

MATERIAL

To study the effects of cambial age on the wood properties of compression wood, one cross-sectional disc was cut from each of four radiata pine logs selected at Waipa Sawmill. Because most interest attached to the corewood regions of these discs (as will be described later) further samples were cut from 10 young trees, 8 years old from planting as 1/0 stock. These trees were from a provenance trial of radiata pine in Compartment 1333 in northern Kaingaroa Forest (Burdon and Bannister, 1973). This planting had proved particularly prone to tree toppling (Chavasse and Balneaves, 1971) and was of particular interest because records were made of the condition of the trees in 1966 (2 years after planting) and in 1970. Thus, something was known of the history of the stem deviations which had given rise to the compression wood within them. Cross-sectional discs were cut from various heights along these stems to examine the effects of toppling or stem kinks, as observed at the time of cutting or as previously

recorded. Samples were numbered using the grid notation for the tree in the provenance trial, followed by the height (in m) in the stem from which a disc was cut — 40/107/2 refers, therefore, to a disc cut at a height of 2 m in tree 40/107. Details of sample trees are presented in Table 1.

TABLE 1—Details of sample trees and history of toppling

| Tree* | Height (cm) | | Angle of topple (°) | | Condition when felled (1972) |
|--------|-------------|------|---------------------|------|----------------------------------|
| | 1966 | 1966 | 1966 | 1970 | |
| 14/11 | 121 | 50 | 5 | | Whole stem sinuous. |
| 20/69 | 127 | 0 | 0 | | Violent stem kink at 4 m. |
| 22/87 | 145 | 75 | 5 | | Straight above 2 m. |
| 22/89 | 139 | 45 | 5 | | Minor sinuosity. |
| 22/95 | 150 | 15 | 30 | | Butt sweep: straight above 3 m. |
| 24/89 | 152 | 20 | 5 | | Kinks from competing vegetation. |
| 40/91 | 131 | 35 | 5 | | Butt sweep. straight above 3 m. |
| 40/98 | 179 | 0 | 90 | | Some roots exposed: tree prone. |
| 40/107 | 146 | 45 | 5 | | Fairly straight stem. |
| 54/95 | 290 | 0 | 0 | | Very vigorous tree. |

* See Burdon and Bannister (1973)

METHODS

Wood density was measured in two ways: gravimetrically (using either a mercury volumeter or water immersion for volume measurements), and with a beta-ray densitometer (Harris, 1969). Tracheid lengths were measured on 50 macerated tracheids from each growth layer, by pairs of observers (Harris, 1966). A shrinkage comparator (Dadswell and Nicholls, 1959) was used to measure longitudinal shrinkage of small samples with dimensions approximately 28 mm longitudinally \times 10 mm tangentially \times 2 mm radially. A Zeiss Photomicroscope II was used for microscopy and photomicrography, and microfibril angles in tracheid cell walls were measured by the method of Cousins (1972) using polarised light. Microfibril angles were measured in 20 tracheids from each sample examined. This gave 95% confidence limits of approximately $\pm 2^\circ$ for the mean values so obtained, as coefficients of variation were about 9%.*

Compression wood was classified visually, primarily on the basis of its darker colouration, into the following grades (*see also* Fig. 1):—

- Grade 1. Small crescents and isolated patches of darker wood within an annual growth layer, but discontinuous and not occupying more than half of the growth layer as measured radially.
- Grade 2. Darker wood terminating an annual growth layer for at least 45° of arc, but not extending radially to the inner limit of the earlywood.
- Grade 3. Darker wood occupying the entire radial width of a growth layer, from first-formed earlywood to the outer limit of the latewood.
- Grade 0. Wood of "normal" appearance wherever it occurs around the circumference.

* I am indebted to Mr B. A. Meylan of the Physics and Engineering Laboratory, DSIR, for measuring microfibril angles by X-ray diffraction for comparison.

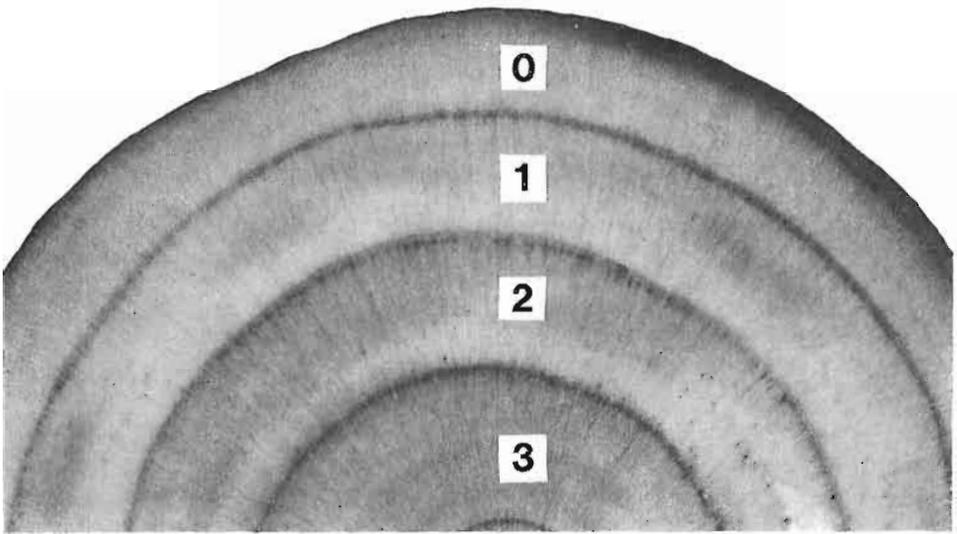


FIG. 1.—Cross-sectional disc of radiata pine illustrating the various grades of compression wood visually assessed in this study.

RESULTS

Old Logs

Logs with compression wood were selected at the mill. All had grown eccentrically for many years, suggesting that a constant deviation of the stem from vertical had been responsible for their condition. Yet the macroscopic and microscopic evidence of compression wood was always less in the narrow outer growth layers than in the inner growth layers, so that it was often difficult to decide which should be regarded as compression wood and which as simply "well-developed latewood" in the outer wood of old trees. For example, intercellular spaces were often absent, and slit-shaped pits in latewood tracheids were the only remaining characteristic of the compression wood anatomy readily detectable in the inner growth layers (R. N. Patel, pers. comm.). Engler (1918), Pillow and Luxford (1937), and Burdon (1975) have noted that development of compression wood may be governed in part by tree vigour, so that, as growth rings become narrower and rate of cambial division decreases in outer wood, the factors conducive to compression wood formation may no longer exceed the threshold required for its fullest manifestation.

Where compression wood was fully developed it showed many of the expected features. For example, tracheids were consistently shorter than those of the corresponding growth layers on the opposite side of the stem outside the first five growth layers (Table 2). On the other hand, although compression wood was often denser than "opposite" wood, this was not invariably so. Similarly, compression wood shrinkage longitudinally was often very high in the central growth layers but it was usually less in outer wood. Also, the *mean angle* of cellulose microfibrils in tracheid cell walls (as measured with polarised light) was not significantly larger than in tracheids from opposite wood. This last feature will be discussed in greater detail later.

Longitudinal shrinkage and wood density for a typical disc from a leaning 40-year-old

TABLE 2—Tracheid length (mm) in compression wood and opposite wood

| Type of wood | No. of growth layers from the pith: | | | | | | | | | | | |
|-------------------------|-------------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| Compression Wood | | | | | | | | | | | | |
| Earlywood | 1.9 | 2.0 | 2.1 | 2.3 | 2.4 | 2.4 | 2.4 | 2.5 | 2.6 | 2.7 | 2.5 | 2.5 |
| Latewood | 2.1 | 2.1 | 2.4 | 2.4 | 2.5 | 2.5 | 2.6 | 2.7 | 2.6 | 2.8 | 2.7 | 2.6 |
| Opposite Wood | | | | | | | | | | | | |
| Earlywood | 1.9 | 2.0 | 2.4 | 2.4 | 2.6 | 2.6 | 2.9 | 2.9 | 3.1 | 2.9 | 3.2 | 3.2 |
| Latewood | 2.1 | 2.2 | 2.6 | 2.6 | 2.8 | 3.1 | 3.1 | 3.2 | 3.2 | 3.3 | 3.3 | 3.3 |

tree are summarised in Fig 2. Growth of this stem had been markedly eccentric from the fourth growth layer onwards. Rings 5-16 contain strongly developed Grade 2 compression wood, extending some way into the earlywood but not completely across it. Rings 17-30 contain compression wood that is clearly Grade 2 but not extending far into the earlywood. Rings 31-35 in any situation other than a strongly eccentric stem would probably be described as normal wood containing a high percentage of latewood.

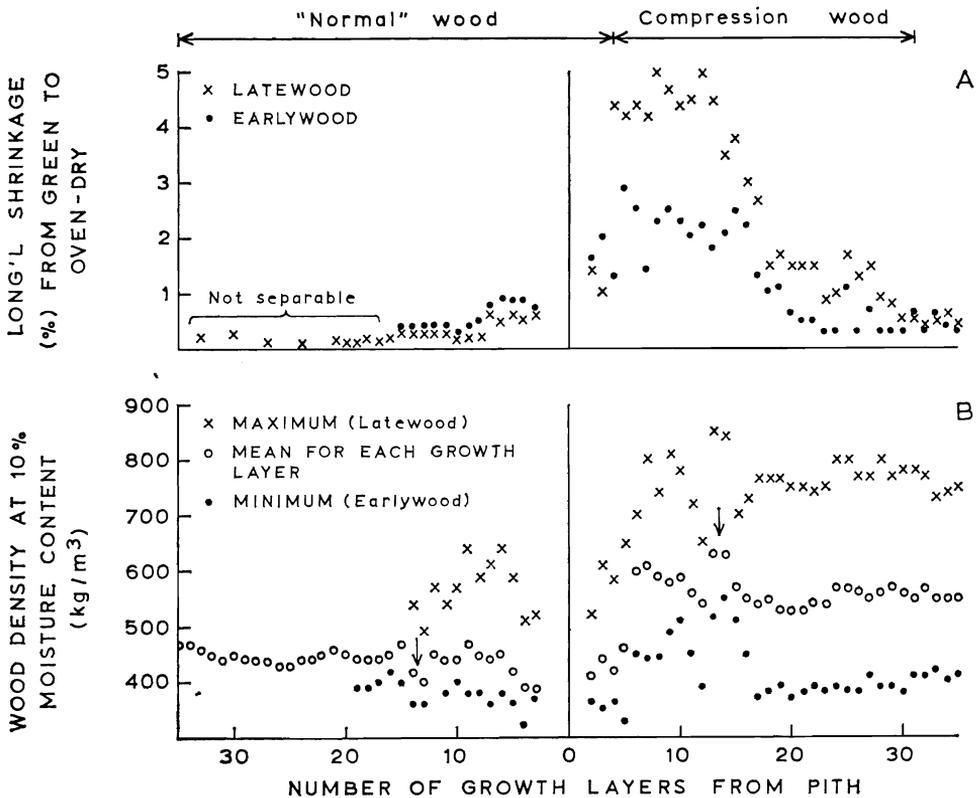


FIG. 2—A. Longitudinal shrinkage in earlywood and latewood from the compression and opposite sides of a disc containing 35 annual growth layers, in which strongly eccentric growth has been maintained from the fourth growth layer onwards. B. Wood density, in the same disc as A, measured with a beta-ray densitometer.

In the inner growth layers prior to the onset of visible compression wood, longitudinal shrinkage (Fig. 2A) is higher in earlywood than latewood (the usual situation), though even here shrinkage values are high in the side destined to produce compression wood. In rings 4-16 longitudinal shrinkage of latewood varies from 3 to 5% in compression wood and is frequently greater than 2% in earlywood. As compression wood ceases to extend far into the earlywood zone, in rings 17-30, longitudinal shrinkage of earlywood returns slowly to values approaching normal, although latewood shrinkage remains high. In the outermost five growth layers longitudinal shrinkage is not excessive and can be said to be at a technically acceptable level.

Thus, longitudinal shrinkage in compression wood in a particular tree can be related to some extent to the macroscopic appearance of the wood, but additionally appears to be dependent partly on the cambial age of the wood in which it occurs.

Radial patterns of wood density in this particular cross-section (Fig. 2B) clearly reflect the presence of compression wood. Mean density is consistently higher in compression wood, even in the outer growth layers where the wood appeared almost completely normal. Latewood density is also unusually high in compression wood, though no direct comparison can be made with the opposite wood because growth layers were too narrow to permit complete resolution with the densitometer (Harris, 1969). Apart from the growth layers in which compression wood could be seen to extend well into the earlywood zones (rings 5-16) earlywood density on both sides of the stem appeared to be about average for this species.

Opposite wood usually appears normal in all respects other than its slow rate of growth, but there are some indications that extreme compression wood on one side of the stem can affect wood properties on the "tension" side. In the data of Fig. 2B, for example, growth layers 13 and 14 (arrows) show extremely high density on the compression wood side and correspondingly low density on the opposite side.

Because compression wood appears to develop most characteristically in inner wood, and because it was obviously desirable to know something of the mode of formation of each sample of compression wood, the remainder of this study concentrated on young trees on which some observations of stem deviations had been made.

Young Trees from a Provenance Trial

How compression wood forms

Distribution of compression wood within the young trees is summarised in Table 3. The most severe compression wood in a particular cross-section is listed in the columns to the right of "pith" in Table 3 but, because compression wood does not develop exclusively along one radius, the columns to the left of "pith" are used to describe the incidence of compression wood in the opposite side of the stem.

It will be noticed that the milder forms of compression wood (predominantly Grade 1) frequently occur on both sides of the stem in growth layers 1 and 2. These obviously arise during minor corrections to maintain an erect leading shoot, and are commonly seen as random irregular crescents of compression wood near the centre of the stem. In these particular trees minor stem deviations had been caused by competing weed growth, especially lupin, in the early years of establishment.

Of far greater concern are the trees which, having toppled within a year or so of

TABLE 3—Distribution of compression wood in sample discs

| Tree no. | Disc ht (m) | Diam. i.b. (mm) | Compression wood grade in growth layers numbered from the pith: | | | | | | | | | | Remarks | | |
|----------|-------------|-----------------|-----------------------------------------------------------------|---|---|---|---|---|------|---|---|--------------------|-------------------------------|------------------------------|--------------------------------|
| | | | 6 | 5 | 4 | 3 | 2 | 1 | Pith | 1 | 2 | 3 | | 4 | 5 |
| 14/111 | 1 | 184 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 2 | 1 | 0 | At first correction. |
| | 2 | 147 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | Centre of correction. | | |
| | 3 | 131 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | Wind stress? (tree on ridge). | | |
| 20/69 | 3 | 101 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 2 | 3 | Straight lower stem. | | |
| | 4 | 96 | 0 | 0 | 1 | 1 | 2 | 3 | 1 | 2 | 3 | Below severe kink. | | | |
| | 6 | 75 | 0 | 0 | 0 | 1 | 3 | 3 | 1 | 3 | 3 | Horizontal region. | | | |
| 22/87 | 0 | 119 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 3 | 2 | 0 | Reaction to over-correction. |
| | 1 | 106 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 3 | 3 | 2 | Reaction to over-correction. |
| | 2 | 96 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 2 | 2 | 1 | Below stem kink. | | |
| 22/89 | 0 | 193 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | At first correction. |
| | 1 | 165 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | Centre of correction. | | |
| | 3 | 152 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | Stem kink. |
| 22/95 | 0 | 174 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 3 | 2 | 3 | 3 | Increasing toppling. |
| | 1 | 155 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 3 | 2 | 2 | 2 | Increasing toppling. |
| | 2 | 130 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 2 | 1 | Increasing toppling. | | |
| | 3 | 112 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 1 | Reaction to over-correction. | |
| 24/89 | 0 | 217 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 3 | 2 | 2 | 2 | Kink from competition. |
| | 1 | 193 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 2 | 2 | Kink from competition. | | |
| | 3 | 160 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 1 | Correction to straighten stem. |
| 40/91 | 0 | 197 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 3 | 3 | 0 | Reaction to over-correction. |
| | 1 | 174 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 3 | 2 | 1 | 0 | Effective straightening. |
| | 3 | 151 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 2 | 2 | 0 | Effective straightening. |
| 40/98 | 1 | 173 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 3 | 3 | 3 | Tree prone. |
| 40/107 | 0 | 201 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 1 | 3 | 3 | Reaction to over-correction. |
| | 1 | 183 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 3 | 3 | 3 | 3 | Reaction to over-correction. |
| | 2 | 103 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | Reaction to over-correction. | | |
| 54/95 | 1 | 237 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | Comp. wood all round. |

planting, return to an approximately erect state but actually "overcorrect" and end up with, say 5° of opposite lean. The compression wood response required to "reorrect" a stem of rapidly increasing diameter is greater and of longer duration than that evinced by the original toppling. This can be seen, for example, in tree 22/87 (discs 0 and 1) and in tree 40/107 (discs 0 and 1). The apparent recovery of a toppled tree does not mean that no further harm will arise; wood properties may be affected for several years.

One further cause of compression wood should be mentioned at this point. Westing (1968) refers to the compression wood that is occasionally produced by exceedingly

rapidly-growing gymnosperms. This may arise without the stimulus of any observable external stress, but may nevertheless affect almost the entire circumference of certain growth layers. Tree 54/95 (Table 2) was one such tree. It had no record of toppling and was growing in a sheltered position, yet this very vigorous straight stem was producing what appeared to be Grade 1 or Grade 2 compression wood around most of its circumference at the end of each year's growth. Subsequent examination confirmed that the anatomical and physical characteristics of this abnormal wood justified its classification as true compression wood. Westing (loc. cit.) suggests that such compression wood may result from an over-production of endogenous auxin.

Grade of compression wood and longitudinal shrinkage

Longitudinal shrinkage (green to oven-dry) was extremely variable within compression wood samples of the same grade. Yet average shrinkage values within each grade did reflect the visual assessment as follows:—

- Grade 0 (samples from the side of the stem containing most compression wood but from growth layers which were themselves free of it) 0.60%;
- Grade 1, 1.62%;
- Grade 2, 2.46%;
- Grade 3, 2.67%.

Microfibril angle and longitudinal shrinkage

A theoretical model for the shrinkage of wood (Barber and Meylan, 1964) was examined by Harris and Meylan (1965) for its application to radiata pine. The relationship between microfibril angle (of the S2 layer as determined by X-ray diffraction) and longitudinal shrinkage was found to be curvilinear, but with a rapid and nearly linear increase in shrinkage for microfibril angles above 25°. However, longitudinal shrinkage of compression wood increased much more rapidly with increasing angle than did the shrinkage of normal wood. For example, at a microfibril angle of 40° longitudinal shrinkage of normal latewood was approximately 1% whereas shrinkage of compression wood was approximately 2.5%. This anomalous shrinkage of compression wood can be explained in terms of its abnormal structure (Dadswell, 1958).

In the present study, microfibril angles were measured on compression wood samples and on samples from the same annual growth layer on the opposite side of the stem. The method used measures the average microfibril angle in all layers of the cell wall, including the S1 (and S3 if present), in which microfibrils are orientated approximately at right angles to the tracheid axis. Therefore angles tend to be 10-15° greater than when measured from the spread of the (002) diffraction arcs on X-ray diffraction patterns, because this latter technique measures microfibril angle only in the S2 layer. In all other respects the two methods are usually in close agreement (B. A. Meylan, pers. comm.) though extreme development of the S1 layer can cause larger deviations (El-Hosseiny and Page, 1973). Results are summarised in Table 4 for the three grades of compression wood by growth layers numbered from the pith. Only in Grade 1 compression wood are microfibril angles consistently higher than in the corresponding opposite wood. In other respects the data of Table 4 show no marked trends within the "corewood" type of material provided by these young trees.

There were, however, distinct trends when longitudinal shrinkage was compared with microfibril angle (Fig. 3). Longitudinal shrinkages grouped into 5° classes of

TABLE 4—Mean microfibril angle ($^{\circ}$) in compression wood and opposite wood

| Grade of compression wood | No. of annual growth layers from pith | | | | | | | | Average | |
|---------------------------------|---------------------------------------|------|-------|------|-------|------|-------|------|---------|------|
| | 2 | | 3 | | 4 | | 5 | | Comp. | Opp. |
| | Comp. | Opp. | Comp. | Opp. | Comp. | Opp. | Comp. | Opp. | Comp. | Opp. |
| 1 | 49 | 45 | 51 | 49 | 48 | 42 | 51 | 48 | 50 | 46 |
| 2 | 45 | 48 | 45 | 46 | 48 | 49 | 48 | 44 | 46 | 47 |
| 3 | 51 | 54 | 52 | 52 | 47 | 48 | 41 | 44 | 48 | 50 |
| Average | 48 | 49 | 49 | 49 | 48 | 46 | 47 | 45 | 48 | 48 |

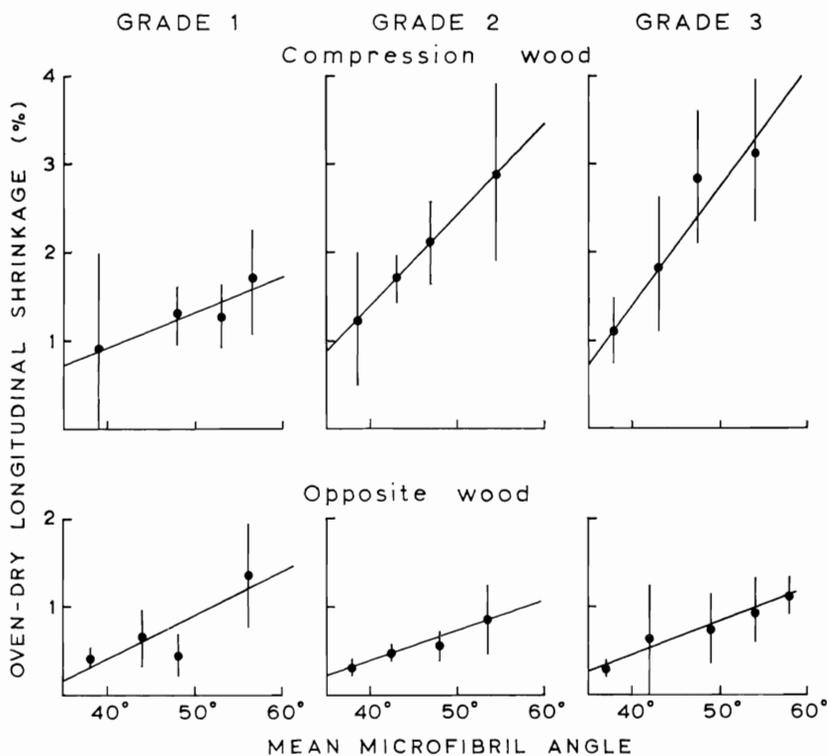


FIG. 3—Effect of microfibril angle on longitudinal shrinkage in compression wood of all grades and in the corresponding opposite wood.

microfibril angle are plotted for compression wood of each grade and for the corresponding opposite wood. Linear regressions were clearly appropriate for each group of observations, a feature which was to be expected because angles are not less than 33° in these young trees. Confidence limits could not be fitted readily to the regressions because there is some evidence that shrinkage variance increases with microfibril angle. Instead, the calculated 95% confidence limits for the microfibril angle class means have been included in each figure.

Being based on an average of only five results in each class (sometimes as few as two), the confidence limits are inevitably rather broad, but certain trends are clearly present:—

1. Longitudinal shrinkage of wood from the side of the stem opposite to compression wood is unaffected by the severity of the compression wood.
2. The relationship between microfibril angle and longitudinal shrinkage in compression wood is distinctly different from that in opposite wood. This confirms the observations of Harris and Meylan (1965).
3. There are strong indications that severity of compression wood affects the slope of the regression relating microfibril angle to longitudinal shrinkage: that Grade 3 compression wood having a microfibril angle of 50° , for example, shrinks more than Grade 1 compression wood with the same microfibril angle.

The coefficients of correlation between microfibril angle and longitudinal shrinkage had the same average value for the compression wood and opposite wood samples, both being 0.55. Thus approximately 30% of the variance in longitudinal shrinkage can be accounted for in terms of the mean angles of the cellulose microfibrils within cell walls, when compression wood and opposite wood are considered separately.

Microscopy of wood with extremes of shrinkage

The extremes of longitudinal shrinkage that were measured in earlywood samples where grade of compression wood, cambial age, and microfibril angle were the same, were well beyond anything that might have arisen through experimental error. To examine the causes of variability, five pairs of compression wood samples were selected in which longitudinal shrinkage represented the extremes for a particular combination of compression wood grade, ring number, and microfibril angle. Transverse microscopic sections were viewed by normal transmitted light and polarised light microscopy. Some of the features detected in this study were also confirmed by scanning electron microscopy.

In Table 5 the paired results are presented, with the sample having highest longitudinal shrinkage followed by the corresponding compression wood sample with lower shrinkage. It should be noted that "lower shrinkage" in this connection is a purely relative term: all samples have higher longitudinal shrinkage than normal, so that they all behave like compression wood in this respect.

The anatomical features which have been accepted as characteristic of compression wood were, however, by no means consistently present. Intercellular spaces were absent from one or more samples in all grades of compression wood, and this particular feature seems to occur largely independently of the other characteristics of compression wood. For example, intercellular spaces were a prominent feature of Grade 1 compression wood in disc 40/107/2 that contained few other characteristic features (Fig. 4B). Yet intercellular spaces were absent from Grade 2 and Grade 3 compression wood in discs 22/87/0 and 40/107/1 in which all other features were present. Even when intercellular spaces were absent, tracheid lumina often appeared to be much more rounded than in normal wood. Consequently, the corners of tracheids as viewed in cross-section were very thick indeed (Fig. 4A and 4C).

As shown in Fig. 4B and 4C, faint traces of the S3 layer could be detected under polarised light in one or more samples in all grades of compression wood, though less frequently in Grades 2 and 3 than in Grade 1. With scanning electron microscopy the

TABLE 5—Anatomical features of paired samples having similar cambial age, grade of compression wood, and microfibril angle but contrasted longitudinal shrinkages

| Tree no. | Disc ht (m) | Ring no. | Comp. wood grade | Microfib. angle (°) | Longl. shrink. (%) | Anatomical features* | | | | Other features |
|----------|-------------------|-------------|------------------------|---------------------------|--------------------------|----------------------|----|------|------|------------------------------|
| | | | | | | I.s. | S3 | S.S. | T.w. | |
| 22/95 | 2 | 2 | 1 | 47 | 2.25 | 2 | 2 | 1 | 1 | |
| 40/107 | 2 | 2 | 1 | 49 | 0.62 | 2 | 2 | 0 | 0 | |
| 22/89 | 3 | 2 | 1 | 52 | 2.30 | 1 | 2 | 1 | 2 | |
| 14/111 | 2 | 2 | 1 | 51 | 0.83 | 0 | 2 | 1 | 0 | Thin-walled angular cells |
| 22/95 | 0 | 3 | 3 | 54 | 4.31 | 2 | 0 | 2 | 2 | Classical comp. wood |
| 40/107 | 1 | 3 | 3 | 55 | 1.98 | 1 | 1 | 1 | 0 | |
| 40/98 | 1 | 4 | 3 | 53 | 4.49 | 2 | 0 | 1 | 2 | |
| 40/107 | 1 | 4 | 3 | 51 | 1.64 | 0 | 0 | 1 | 1 | Lumina rounded |
| 22/87 | 0 | 5 | 2 | 58 | 4.46 | 0 | 0 | 1 | 2 | Lumina rounded |
| 24/89 | 0 | 5 | 2 | 51 | 1.81 | 0 | 1 | 1 | 1 | Lumina rounded |

* 0 = absent; 1 = occasional; 2 = frequent. I.s., intercellular spaces; S3, presence of S3 layer; S.S., spiral slits in S2; T.w.; thickened cell walls.

S3 layer could be seen to consist of only a few strands of microfibrils at a wide angle to the tracheid axis, sometimes bridging spiral slits in the S2 layer (Fig. 5).

The feature that most consistently distinguished samples with high longitudinal shrinkage from those with lower shrinkage was the presence of thick cell walls in the former. In some extreme examples of compression wood with high longitudinal shrinkage cell diameters also appeared to be smaller than normal (Fig. 4D) but this was not a constant feature.

Another aspect of compression wood anatomy in radiata pine was that not all cells in a zone were equally affected. This is contrary to the views of Westing (1965) who claimed that in any one area of compression wood all of the tracheids are affected similarly, although all gradations in structure between normal wood and pronounced compression wood can occur in different areas. In the present study it was found that even adjacent cells in a radial file might or might not contain any one of the characteristics of compression wood, though there was admittedly a strong tendency for whole zones of cells to share many features in common. In Fig. 4 features such as presence or absence of an S3 layer and spiral checks in the S2 layer are seen as discontinuous features between adjacent cells. The same was sometimes true of intercellular spaces.

Wood density and longitudinal shrinkage

The possibility that cell wall thickness contributes to the longitudinal shrinkage in compression wood suggested that wood density might be used to assess this feature. In particular, the increase of wood density in compression wood could be measured

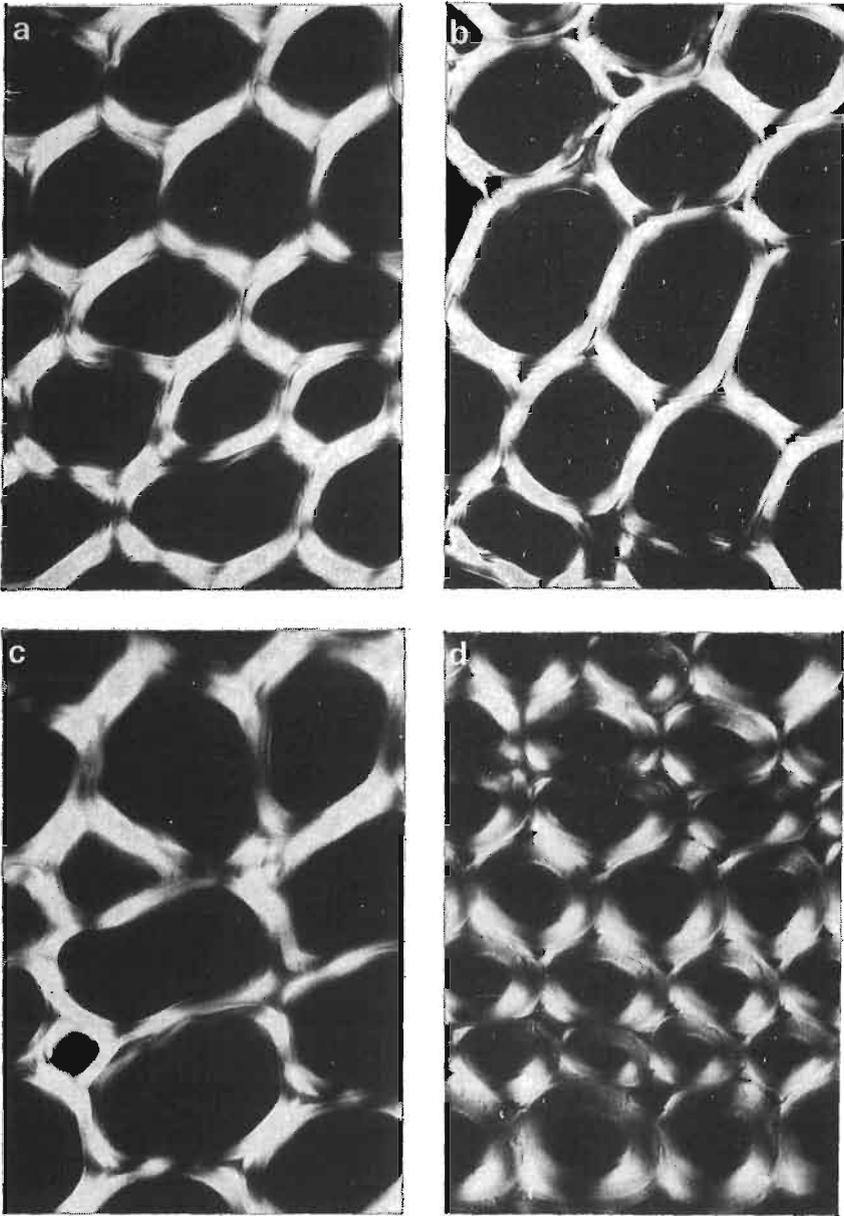


FIG. 4—Transverse sections of radiata pine compression wood viewed under polarised light.

- a. 40/107/1, Ring 4. Grade 3 compression wood without intercellular spaces.
- b. 40/107/2, Ring 2. Grade 1 compression wood. S3 present in some tracheids. Intercellular spaces present.
- c. 24/89/0, Ring 5. Grade 2 compression wood without intercellular spaces and S3 present in some tracheids.
- d. 40/98/1, Ring 4. Grade 3 compression wood with all classical compression wood features.

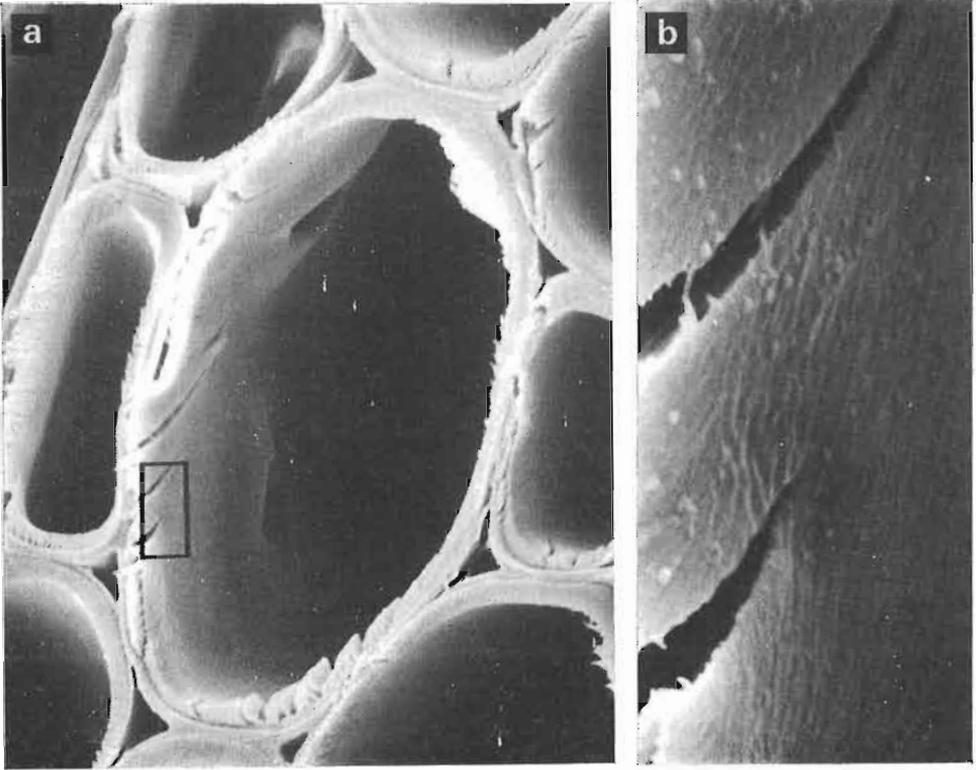


FIG. 5—Scanning electron micrographs of radiata pine compression wood.

- a. $\times 2000$, showing general view of Grade 2 compression wood with intercellular spaces: cracks in the cell wall are probably cutting artifacts but indicate microfibril orientation in S2.
- b. $\times 16000$, from area inset above. Showing microfibrils at a wider angle to the cell axis than slits in S2, and also some warts. These are believed to represent a residual S3 layer.

against "normal" density in opposite wood of the same annual growth layer. Table 6 summarises wood density of the five pairs of compression wood samples examined for microscopic features, and also the density of the corresponding opposite wood samples. In each case the increase in wood density due to the presence of compression wood in a growth layer is much greater for the sample with high longitudinal shrinkage.

DISCUSSION AND CONCLUSIONS

There are several features of compression wood in radiata pine that emerge quite clearly from the foregoing results.

1. All samples visually assessed as compression wood proved to possess some anatomical features and physical properties (wood density or longitudinal shrinkage) that would justify the distinction from "normal" wood.
2. The development of compression wood in a stem is not necessarily indicated by its

TABLE 6—Density (at 10% m.c.) of compression wood and opposite wood for samples of similar cambial age, grade of compression wood, and microfibril angle but contrasted longitudinal shrinkages

| Tree no. | Disc height (m) | Ring no. | Compression wood grade | Longitudinal shrinkage (%) | Wood density (kg/m ³) | Density increase in compression wood |
|----------|-----------------|----------|------------------------|----------------------------|-----------------------------------|--------------------------------------|
| 22/95 | 2 | 2 | 0 | 0.45 | 402 | |
| | | | 1 | 2.25 | 438 | 36 |
| 40/107 | 2 | 2 | 0 | 0.36 | 338 | |
| | | | 1 | 0.62 | 356 | 18 |
| 22/89 | 3 | 2 | 0 | 0.58 | 350 | |
| | | | 1 | 2.30 | 441 | 91 |
| 14/111 | 2 | 2 | 0 | 0.74 | 293 | |
| | | | 1 | 0.83 | 346 | 48 |
| 22/95 | 0 | 3 | 0 | 0.95 | 445 | |
| | | | 3 | 4.31 | 598 | 153 |
| 40/107 | 1 | 3 | 0 | 0.87 | 356 | |
| | | | 3 | 1.98 | 361 | 5 |
| 40/98 | 1 | 4 | 0 | 1.70 | 409 | |
| | | | 3 | 4.49 | 633 | 224 |
| 40/107 | 1 | 4 | 0 | 0.30 | 357 | |
| | | | 3 | 1.64 | 358 | 1 |
| 22/87 | 0 | 5 | 0 | 0.37 | 418 | |
| | | | 2 | 4.46 | 504 | 86 |
| 24/89 | 0 | 5 | 0 | 0.69 | 411 | |
| | | | 2 | 1.81 | 414 | 3 |

external appearance, although severe compression wood invariably arises where there are violent deviations from verticality. Stems that are relatively straight may produce compression wood in response to overcorrection to a former deviation, to external stimuli (e.g., exposure to wind), or even, apparently, to excessive "vigour".

- When measuring mean microfibril angle the inclusion of S1 and S3 layers naturally gives higher values than when the angle in the S2 layer alone is measured. Conversely the absence of an S3 layer in compression wood tends to make the mean microfibril angle less. As a result, only Grade 1 compression wood in the present study had microfibril angles larger than the corresponding opposite wood, and only in this grade of compression wood was there frequent and distinct evidence of the presence of an S3 layer. Where the S3 layer was detected in Grade 2 and Grade 3 compression wood it tended to be very faint and was probably reduced to a few residual strands, as shown in Fig. 5.
- Visual assessment of compression wood grade has some meaning in terms of *average* wood properties, but variability within each grade is so wide that grading could not be used advantageously, for example, on the sorting table of a wood-processing plant.
- Longitudinal shrinkage has been used in this study to measure what might be called the "technical severity" of compression wood. Other properties could well have been used, but abnormal shrinkage along the grain is undoubtedly a serious defect in

- sawn timber, and is probably a fair reflection of compression wood development in a more general sense. The influence of cambial age on longitudinal shrinkage can be explained in terms of microfibril angle. Differences in microfibril angle between compression wood and opposite wood are quite small — negligible in core wood formed before differences in tracheid length begin to show up (Tables 2 and 4). But when large microfibril angles are present in opposite wood, the correspondingly large angles in compression wood of the same growth layer result in much greater longitudinal shrinkage because of the unique relationship between microfibril angle and shrinkage in compression wood. On the other hand, in outer wood where microfibril angles are small, compression wood will not have large longitudinal shrinkage if the resultant mean microfibril angle does not exceed approximately 30° .
6. It is important to realise that the full range of classical anatomical compression wood features is likely to be encountered only in very well-developed examples and all will not inevitably be present together, even in Grade 3 compression wood as defined in this study. Indeed, the absence of many anatomical features in all grades of compression wood raises the question as to what features enable its visual recognition. Westing (1965) concludes that the distinctive colouration can be attributed to the added amount of lignin present. Bland (1961) found that lignin in compression wood is only loosely associated with the cellulose framework because it is easy to extract. On the other hand, he found no evidence that compression wood and normal lignins differ in *basic* structure or types of linkages. However, because compression wood lignin yields considerable amounts of p-hydroxy-benzaldehyde whereas normal wood yields none, Bland believes that compression wood lignin is abnormal due to the failure of the methylation mechanism during synthesis and deposition. On balance it would seem that, if anatomical features are ruled out as inconsistent, it must be either the amount of lignin or its structure that enables compression wood to be so readily recognised visually.

When it comes to assessing the causes of variability in the properties of compression wood, the issues are more confused. By defining grade of compression wood and microfibril angle, we can apparently account for only about one-third of the total variance in longitudinal shrinkage, even within the corewood region where expression of compression wood properties is relatively uninhibited. Results from the 10 young trees — despite the restrictions of such a limited sample — do nevertheless suggest that it is cell wall thickness that largely determines the influence of compression wood on shrinkage. What is not at all clear is just why thick-walled cells should have higher longitudinal shrinkage than thin-walled cells. Is it simply the additional volume of S2 layer with its abnormal structure that increases longitudinal shrinkage? Or do thick cell walls contain a higher proportion of S1 layer in which microfibril orientation would theoretically favour longitudinal shrinkage? Or are there more direct, geometrical, reasons why a large amount of cell wall per unit volume should have this effect?

From a practical viewpoint these results do little more than confirm previous observations (which are nevertheless worth reiterating) that tree planting is an important operation with serious consequences for wood formation as well as tree growth; and that, although erect stems do not preclude the possibility of compression wood, they are less prone to the (visually and technically) most severe forms of compression

wood. To this extent these conclusions also confirm priorities for tree establishment and tree improvement research in New Zealand.

Unfortunately no easy remedies can be suggested to meet the existing situation in which compression wood is an all-too-frequent defect of sawn radiata pine timber. For critical uses where straightness, stability, and strength of sawn timber are paramount, there is no alternative to outright rejection of pieces containing compression wood, unless some form of non-destructive test is available to detect those pieces in which the technical properties of compression wood are adequate for a particular purpose.

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