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Anatomical Comparison of Compression, Opposite, and Lateral Woods in New Zealand Rimu (*Dacrydium cupressinum* Lamb.) *[1]

Young Geun Eom*[2] and Brian G. Butterfield*[3]

ABSTRACT

Compression, lateral, and opposite woods in the stem and branch of rimu (*Dacrydium cupressinum* Lamb.), a softwood species indigenous to New Zealand, were described and compared in the anatomical aspects. Qualitatively, growth rings were wide in the compression wood, intermediate in the lateral wood, and narrow in the opposite wood. Tracheid transition from early wood to late wood was very gradual in the compression wood but was more abrupt in both the lateral and opposite woods. When viewed transversely, compression wood tracheids showed a roundish outline except at the growth ring boundary but lateral and opposite wood tracheids were angular to rectangular in outline. Intercellular spaces were occasionally detected in the compression wood except in the late wood at the growth ring boundary but were absent from both the lateral and opposite woods. Slit-like extensions of the bordered pit openings caused by the location of pit apertures within short and narrow helical grooves were observed in the compression wood tracheids but not in the opposite or lateral wood tracheids. In the compression wood tracheids, fine striations in the form of fine checks or grooves were observed on the lumen surfaces and the innermost S_3 layer of secondary wall was absent. In the tracheids of lateral and opposite woods, the S_3 layer was sometimes absent but occasionally highly developed. Cross-field pits in the compression wood appeared to be piceoid due to slit-like pit apertures but those in the lateral and opposite wood tracheids showed cupressoid to taxodioid. Quantitatively, compression wood tracheids were somewhat shorter than those of opposite or lateral wood in stem but not different from the opposite or lateral wood tracheids in branch. The walls were thicker in the compression wood than in the lateral or opposite wood. Uniseriate rays in the compression wood were fewer than in the lateral or opposite wood.

Keywords : rimu (*Dacrydium cupressinum*), compression wood, lateral wood, opposite wood, branch wood, stem wood, anatomical features

1. INTRODUCTION

Eccentric growth with well-developed compression wood to the lower side and suppressed opposite wood to the upper side is commonly displayed in the inclined stems and branches of

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[1] Received on March 13, 2001; accepted on May 7, 2001

[2] Department of Forest Products, College of Forest Science, Kookmin University, Seoul 136-702, Korea

[3] Department of Plant and Microbial Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

gymnosperms. This radial growth eccentricity may be the result of auxin redistribution caused by the action of gravity (Yamaguchi *et al.* 1983) or may also be induced by stress, wind, snow, *etc.* (von Pechmann 1973; Fengel & Wegener 1984; Timell 1986). Compression wood can be found in Ginkgoales, Coniferales, and Taxales among gymnosperms (Westing 1968; Timell 1978; Yoshizawa *et al.* 1982) and even in some primitive angiosperms such as *Buxus* (Onaka 1949; Timell 1981, 1982).

Compression wood, when viewed macroscopically in transverse surface, can be easily distinguished from surrounding tissues by its darker colour. Most of its anatomical features in a wide variety of species have been thoroughly investigated. Few studies, however, have focused on the opposite or lateral wood itself or have compared the opposite and/or lateral wood with the compression wood. In earlier studies, many anatomical differences were found between compression and opposite wood (Timell 1973, 1986; Park *et al.* 1979, 1980; Yoshizawa *et al.* 1981; Lee & Eom 1984, 1988; Eom & Lee 1985; Eom & Butterfield 1997). Lateral or side wood was considered as normal wood or as an intermediate between opposite wood and compression wood (Timell 1973).

In New Zealand, the family Podocarpaceae is represented by 17 species belonging to 8 genera. Of these, rimu (*Dacrydium cupressinum*) is probably the best known and most easily identified tree because of the weeping habit induced by its slender and pendulous branchlets in the forests. Rimu grows throughout New Zealand from sea level to 600 m, and usually reaches 20 to 35 m but sometimes 60 m in height and can grow up to 1.5 m in diameter. Its stem is generally straight and its darkish grey bark peels off in long and thick flakes (Clifton 1994). The wood anatomy of rimu has been described by Garratt (1924), Orman and Reid (1946), Patel (1967), and Pocknall (1977). This paper details anatomical comparisons of compression, opposite, and lateral woods in the stem and branch of rimu (*Dacrydium cupressinum* Lamb).

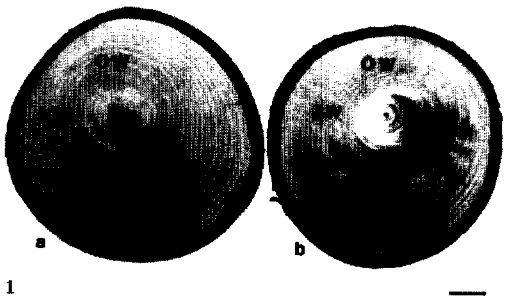

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Fig. 1. Compression (CW), opposite (OW), and lateral (LW) woods in the stem (A) and branch (B) of rimu (*Dacrydium cupressinum*). Scale bar = 1 cm.

2. MATERIALS and METHODS

A 31-year-old stem and a 28-year-old branch of rimu (*Dacrydium cupressinum*) containing compression, lateral, and opposite wood (Figure 1) were obtained from Kumara, West Coast, South Island, New Zealand. Small cubes of about 1~2 cm per side were softened in water for 90 minutes. For light microscopy, transverse, radial, and tangential sections of 20~30 μm thick were cut with a sliding microtome, and permanent slides were prepared following standard laboratory techniques (Japan Wood Research Society 1985).

For scanning electron microscopy, wood blocks of about 5 mm per side were prepared from the above softened blocks and the final cuts were made with single-edged, hard-backed razor blades. After removal of unwanted wood, the clean cut specimens were air-dried, glued to specimen stubs with double-sided carbon tabs, sputter-coated with gold to a thickness of 50 nm (Exley *et al.* 1974, 1977), and observed in a Leica S440 scanning electron microscope at 10 kV.

For transmission electron microscopy, small wood blocks of about 1.5×1.5×1 mm^3 were cut and fixed at room temperature with 2.5% glutaraldehyde in phosphate buffer, pH 7.2, for 3 hours followed by 1.0% osmium tetroxide in the same buffer for 3 hours. After dehydration through an acetone series, the samples were embedded in Spurr's resin and then polymerised overnight at 70℃ (Anonymous 1986). Ultrathin sections of 100 nm thick were made with a diamond knife in an ultramicrotome and double-stained with a saturated solution of uranyl acetate in 50% ethyl alcohol (Weakley 1972) and lead solution (Sato 1968), and then examined in a JEOL JEM-1200EX transmission electron microscope at 80 kV.

For quantitative analyses, the lengths of 100 randomly selected tracheids were measured from macerations obtained with Franklin's method (Berlyn & Miksche 1976) and the tangential diameters and radial wall thicknesses of 25 randomly selected tracheids were measured from transverse surfaces of permanent slides. The numbers of uniseriate rays per mm^2 in tangential surfaces and ray densities, *i.e.* the numbers of rays per mm in tangential direction of transverse surfaces, were counted in 10 randomly selected parts in the permanent slides. In tangential surfaces of permanent slides, the heights of 100 rays and numbers of biseriate rays within the circle of 3 mm diameter were also measured by random selection. These quantitative features were measured in a profile projector or a video monitor attached to a video camera on a compound microscope or a stereomicroscope. Statistical analyses for these quantitative measurements were obtained from Tukey's studentized range test of SAS system.

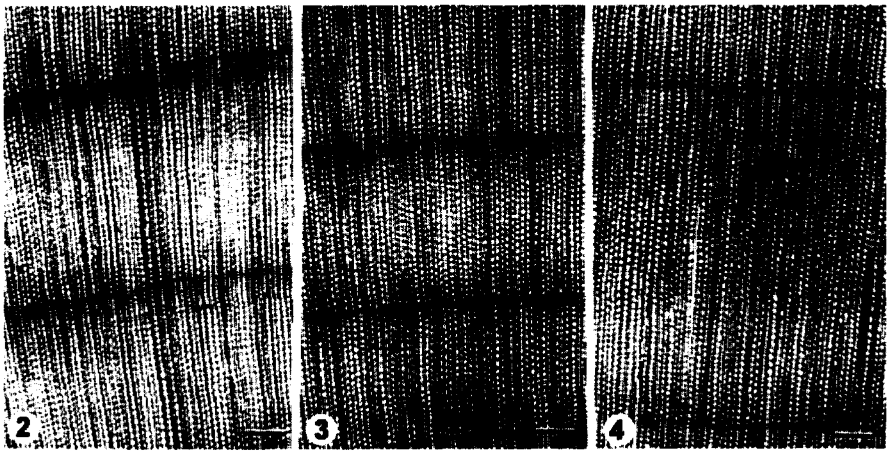
3. RESULTS

The growth rings were wide in the compression wood, intermediate in the lateral wood, and narrow in the opposite wood, although the ring widths in all the zones varied (Table 1). Tracheid transition from early wood to late wood in the compression wood was very gradual. In both lateral and opposite woods, however, the transition was more abrupt and the width of late wood was a little larger than in the compression wood. Thus, the demarcation between early wood and late wood was relatively more difficult to determine in the compression wood than in the lateral and opposite woods. There were also many instances where the complete width of a ring in the compression wood was made up of wide tracheids, giving the impression that the ring was made up entirely of early wood (Figures 2～4).

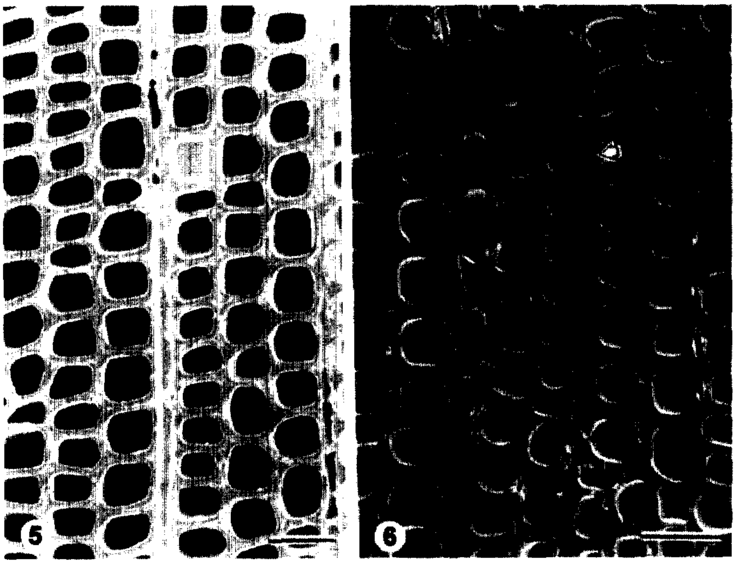
When viewed transversely, compression wood tracheids showed a roundish outline except at the growth ring boundary, but lateral and opposite wood tracheids were angular to rectangular in outline (Figure 5 & 6). Intercellular spaces were occasionally detected in the compression wood except in the late wood at the growth ring boundary but were absent from both the lateral and opposite woods (Figure 5 & 6). This phenomenon is related to the shape of the tracheids in transverse section.

Slit-like extensions of the bordered pit openings caused by the location of pit apertures within short and narrow helical grooves were observed in the compression wood tracheids but not in the tracheids of opposite or lateral wood (Figures 7～10).

Distorted tracheid tips (Figure 11) and irregularly shaped tracheids resembling the vasicentric tracheids of some hardwood species (Figure 12) occurred more frequently in the compression wood than in the lateral or



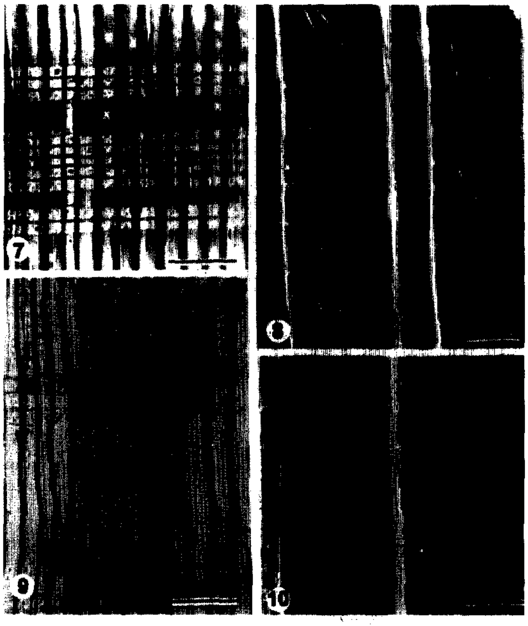
Figs. 2-4. Transverse surfaces showing the tracheid transition from early to late wood. -2: Stem lateral wood with abrupt transition and distinct late wood, -3: Branch opposite wood with somewhat abrupt transition and intermediate late wood, -4: Branch compression wood with gradual transition and indistinct late wood. Scale bars = 200 ㎛.



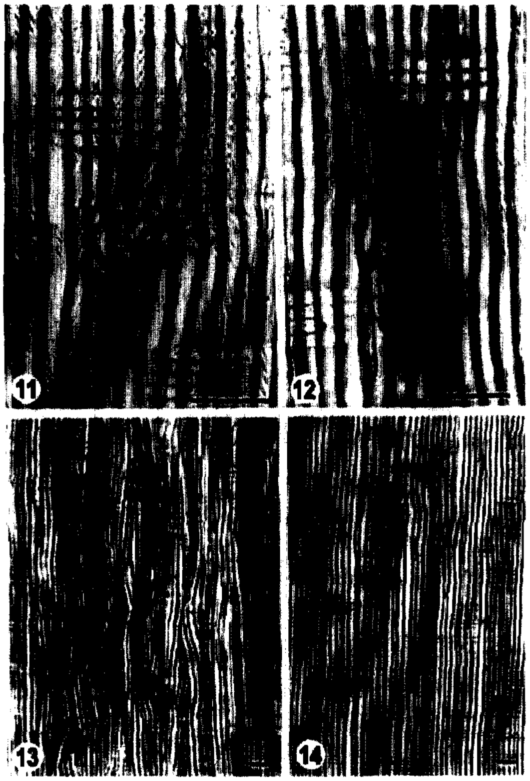
Figs. 5-6. Tracheid outlines and intercellular spaces (arrow) in transverse surfaces. -5: Branch opposite wood with angular tracheids and no intercellular spaces, -6: Stem compression wood with rounded tracheids and intercellular spaces. Scale bars = 20 ㎛.

opposite wood. The interlocked cell arrangement in the radial surface of compression wood (Figures 13 & 14) is the result of frequently occurring distorted tracheid tips and irregularly shaped tracheids.

In the compression wood tracheids, fine striations in the form of fine checks or grooves were observed on the lumen surfaces (Figures



Figs. 7-10. Bordered pits in tracheid radial walls. -7 & 8: Branch compression wood showing slit-like bordered pit openings caused by the location of pit apertures within short and narrow helical grooves, -9 & 10: Branch opposite wood and stem lateral wood showing normal circular bordered pit openings. Scale bars = 100 μm (7 & 9), 6 μm (8 & 10).



Figs. 11-14. Tracheid shapes and arrangement seen in radial surfaces. -11 & 12: Branch and stem compression wood tracheids with distorted tips and irregular shapes, -13: Branch compression wood showing interlocked tracheid arrangement, -14: Stem lateral wood showing regular tracheid arrangement. Scale bars = 100 μm.

15~18) and the innermost S_3 layer of secondary wall was absent (Figure 19). In the tracheids of lateral and opposite woods, the S_3 layer was sometimes absent but occasionally highly developed (Figures 20~24).

Cross-field pits in the compression wood appeared to be piceoid due to slit-like pit apertures, which caused by the location of pit apertures within short and narrow helical grooves in the tracheid wall, beyond the outline of the pit border (Figures 15 & 16) but those in the lateral or opposite wood tracheids showed cupressoid to taxodioid types (Figures 17 & 18).

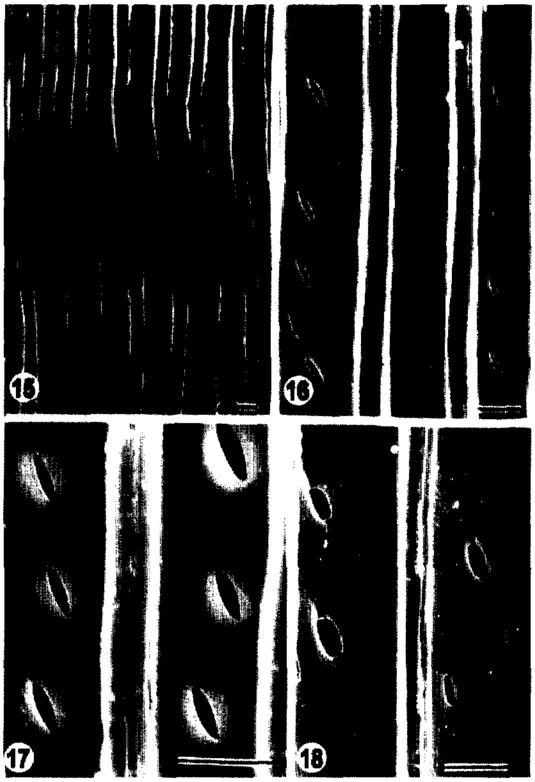
Trabeculae traversing the lumina of single cells were found in the compression, lateral, and opposite woods and were more common than those traversing several tracheids in a radial file (Figures 25~28).

Quantitative features of each tissue type are listed in Table 1. Compression wood tracheids were somewhat shorter than those of opposite or lateral wood in stem but not different from opposite or lateral wood tracheids in branch. The walls were thicker in the compression wood than in the lateral or opposite wood. No difference, however, was noticed in their tangential diameters between compression, lateral, and opposite woods.

Ray densities, *i.e.* the numbers of rays per mm in a tangential direction of transverse surface, did not differ between compression, lateral, and opposite woods. Uniseriate rays in the compression wood were fewer than in the lateral or opposite wood, but the numbers of biseriate rays (Figures 29 & 30) in tangential surfaces were almost the same between compression, lateral, and opposite woods. Uniseriate and biseriate rays did not differ in height between compression, lateral, and opposite woods.

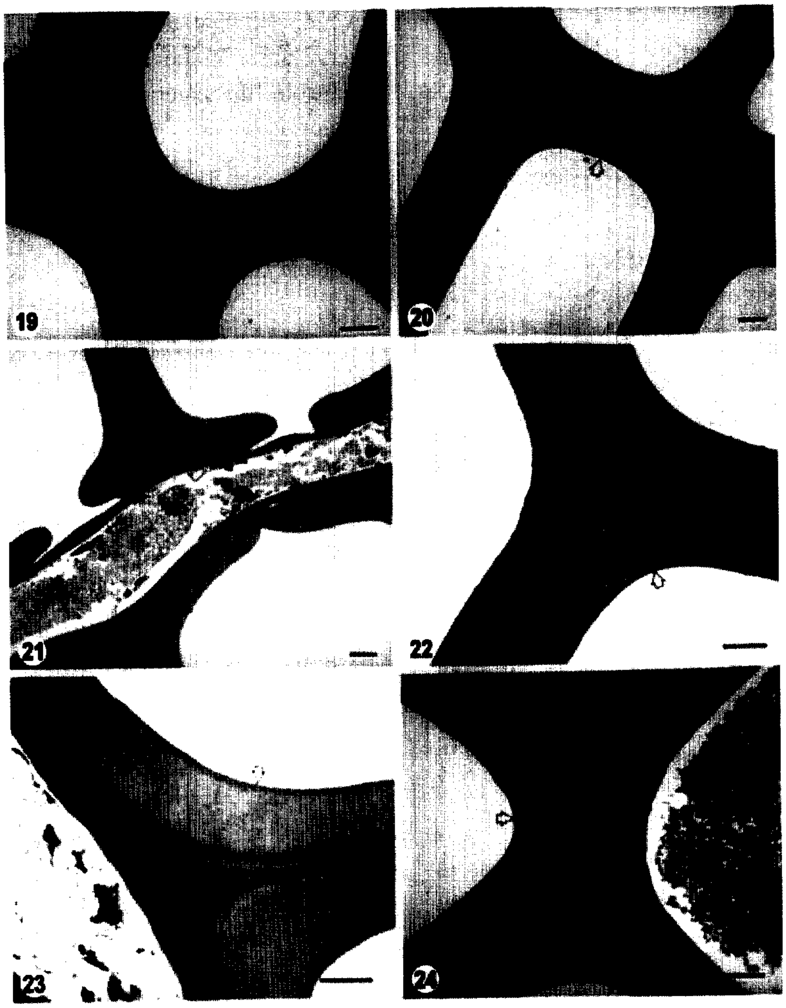
4. DISCUSSION

In this study, compression, lateral, and opposite woods formed in the stems and branches of rimu (*Dacrydium cupressinum* Lamb.) are compared.



Figs. 15-18. The innermost wall layer structure of tracheids in radial surfaces. -15 & 16: Stem and branch compression wood tracheids with fine striations and piceoid cross-field pits, -17 & 18: Branch lateral wood and stem opposite wood tracheids with smooth surfaces and normal cupressoid to taxodioid cross-field pits. Scale bars = 6 μm.

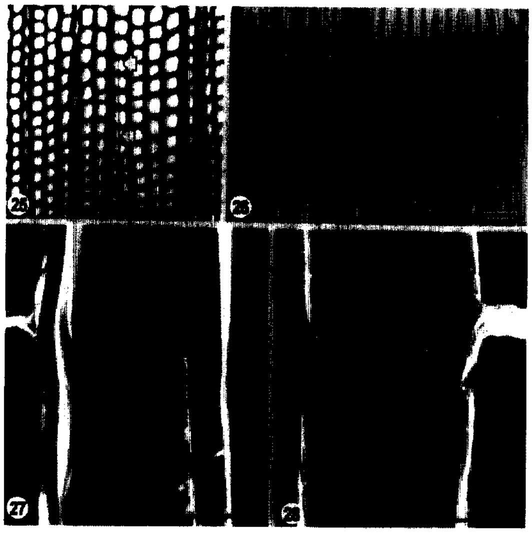
Qualitatively, the growth rings are wide in the compression wood, intermediate in the lateral wood, and narrow in the opposite wood because of the growth eccentricity, although considerable variation in ring width is observed in all three zones (Table 1), as reported by Lee and Eom (1988) and Eom and Butterfield (1997). Jaccard (1919) and Lee and Eom (1988) indicated considerable variation in growth ring widths in the opposite and compression woods. The tracheid transition from early wood to late wood in the compression wood is more gradual than in the opposite and lateral woods, which makes demarcation between the early and late woods in the compression wood more difficult to observe than in the opposite and lateral woods (Figures 2～4). A gradual transition in the compression wood and an abrupt transition in the opposite or lateral wood, and easier demarcation between early and late woods in the opposite or lateral wood than in the compression wood were noted by Lee and Eom (1984, 1988), Eom and Lee (1985), and Eom and Butterfield (1997). Timell (1973) noted that the ring widths in the opposite wood varied greatly with wide rings containing a much higher proportion of late wood than the narrow ones, but Mork (1928) observed that the narrow increments had a higher late wood proportion than the wider ones. Park (1983) also suggested that growth ring width and proportion of late wood decreased continuously at a relatively



Figs. 19-24. Tracheid wall structures in transverse surfaces. -19: Branch compression wood tracheids without S_3 layer, -20 & 21: Branch and stem opposite wood tracheids with highly developed S_3 layer (arrow) or without S_3 layer, -22: Stem lateral wood tracheids with slight to highly developed S_3 layer (arrow), -23 & 24: Branch lateral wood tracheids with slight to highly developed S_3 layer (arrow) or without S_3 layer. Scale bars = 2 ㎛.

steep rate from the compression to opposite side.

Both the lateral and opposite woods reveal a slightly higher proportion of late wood than the compression wood. In the compression wood, however, a more or less constant and very large early wood proportion occurs and there are many instances where the complete width of the ring seems to consist entirely of early wood (Figures 2～4). This is in disagreement with the observations of Core *et al.* (1961) and Lee and Eom (1988) who reported instances where the complete width of the ring in the compression wood was made up of thick-walled, rounded tracheids causing the ring to appear to be made up of entirely of late wood. Timell (1986)



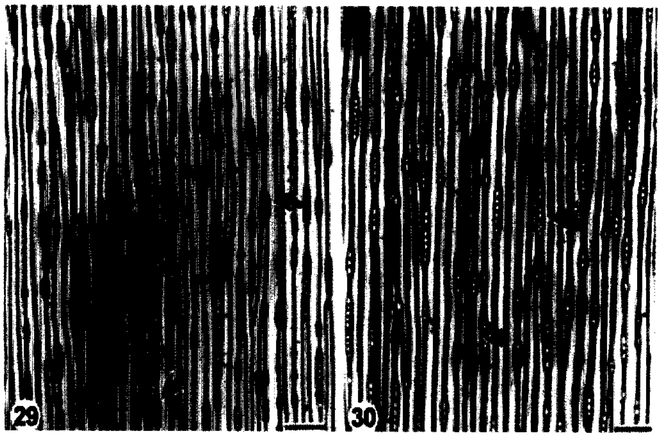
Figs. 25-28. Trabeculae (arrow). -25 & 26: Stem lateral wood and branch opposite wood with trabeculae traversing several tracheids in a radial file, -27 & 28: Branch lateral wood and stem compression wood with a trabecula traversing the lumina of single tracheid. Scale bars = 50 ㎛ (25 & 26), 6 ㎛ (27 & 28).

concluded that the growth ring tended to be wide in the compression wood, intermediate in the lateral wood, and narrow in the opposite wood, and that the late wood proportion to be very large in the compression wood, intermediate in the lateral wood, and small in the opposite wood.

The shape of tracheids in the transverse surface is more or less round in the compression wood except at the growth ring boundary (Figures 4 & 6), as reported by Côté *et al.* (1967) and Yoshizawa *et al.* (1982). This contrasts with square to angular cell outline in the lateral and opposite woods (Figures 2, 3 & 5). Timell (1973, 1986) described that the cross-sectional outline of tracheids as square, rectangular, or angular in the opposite wood, angular in the normal wood, and round in the compression wood.

Intercellular spaces formed by round tracheids are detected only in the compression wood (Figure 6). These intercellular spaces were known to be present frequently in the compression wood of *Larix*, *Picea*, *Pinus*, and *Pseudotsuga* (Timell 1981, 1986). Harris (1991) reported, however, that intercellular spaces might be absent from all grades of compression wood in radiata pine.

Fine striations (Figures 15 & 16) on the tracheid lumen surfaces are observed only in the



Figs. 29-30. Biseriate rays (arrow) in tangential surfaces. -29: Branch opposite wood, -30: Stem compression wood. Scale bars = 100 ㎛.

Table 1. Quantitative features of compression (CW), lateral (LW), and opposite (OW) woods.

Feature	Stem			Branch		
	CW	LW	OW	CW	LW	OW
Ring width (mm)						
Range	0.8~2.3	0.4~0.2	0.05~1.9	0.4~2.4	0.3~2.1	0.1~1.8
Average	1.19	1.00	0.84	1.36	1.04	0.75
Tracheid						
Length (μm)						
Range	700~3750	750~4250	950~3950	850~3900	950~3600	950~3650
Average	2177.5A	2300.0A,B	2493.5B	2391.0A	2413.0A	2217.5A
Tangential diameter (μm)						
Range	8.8~37.5	10.0~38.8	11.3~33.8	12.5~36.3	12.5~37.5	10.0~32.5
Average	25.30A	24.00A	25.20A	25.30A	24.00A	25.20A
Radial wall thickness (μm)						
Range	2.5~8.8	1.3~5.6	1.3~4.4	3.1~6.9	1.9~4.4	1.3~4.5
Average	5.08A	3.68B	2.73C	4.98A	2.94B	2.88B
Ray						
Density (no./mm)						
Range	5~8	3~8	4~9	4~9	5~9	3~8
Average	6.5A	6.8A	6.3A	6.0A	5.9A	6.1A
Number						
Uniseriate (no./mm^2)						
Range	92~115	99~122	102~132	92~120	108~147	120~143
Average	100.3A	110.9B	116.5B	102.7A	126.3B	129.5B
Biseriate (no./circle of 3 mm diameter)						
Range	1~7	1~5	2~6	2~5	2~7	3~6
Average	3.6A	4.0A	3.8A	3.5A	3.0A	3.4A
Height (cell no.)						
Range	1~16	1~14	1~12	1~15	1~12	1~13
Average	4.3A	4.4A	4.1A	4.1A	4.1A	3.9A

* Means with the same letter within the stem or branch are not significantly different at a 0.05 level.

compression wood. Butterfield *et al.* (2000) described that these fine striations appeared as fine checks or grooves and considered these faint striations as a form of very weakly developed helical thickenings. Helical cavities and checks are not observed but slit-like bordered pit openings are observed in the compression wood tracheids (Figures 7 & 8). Thus, the occurrence of slit-like pit openings appears to be the most important character in separation of compression wood from lateral (normal) and opposite woods. Timell (1978, 1986) suggested that the pits in tracheids of compression wood appeared to be crossed diagonally by a slit which extended the pit annulus when viewed in longitudinal sections in the light microscope and these slit-like pit openings could be one of the most important features in separating compression wood from normal wood because of their common occurrence in compression wood.

The S_3 layer of secondary wall are not observed in the compression wood tracheids (Figure 19), following the general description by Boyd (1973), Panshin and de Zeeuw (1980), and Eom and Butterfield (1997). In the tracheids of lateral and opposite woods, however, the S_3 layer occasionally absent but can also be slightly to highly developed (Figures 20 ~24). The lack of S_3 layer in some opposite or lateral wood tracheids is unusual and probably not the result of compression wood. Wardrop (1964) and Côté and Day (1965), on the other hand, believed that the absence of S_3 layer in normal wood tracheids was probably due to very mild compression wood. Timell (1973, 1986) concluded the S_3 layer to be thickest in the opposite wood, thin in the normal (lateral) wood, and absent in the compression wood, but Harris (1991) noted that traces of S_3 wall layer could occasionally be identified in all grades of compression wood in radiata pine.

Distorted tracheid tips and irregularly shaped tracheids occur more frequently in the compression wood, resulting in an interlocked appearance in the radial surface (Figures 11~14). This tracheid distortion was noted as a feature of compression wood by Onaka (1949) and Wardrop and Dadswell (1952), and believed to be the result of sliding or intrusive growth by Timell (1981). Yoshizawa *et al.* (1985) suggested that flattened and L-shaped tips of tracheids increased in frequency with the development of compression wood due to disturbed intrusive growth between adjacent cells.

Cross-field pits in the compression wood appear to be unsuitable for diagnostic purpose due to their anomalous shapes (Figures 7, 15 & 16) but those in the opposite and lateral woods are useful for identification because they deviate only slightly from normal (Figures 9, 17 & 18). The cross-field pits in normal rimu wood have been reported to be cupressoid to taxodioid by Patel (1967) and Pocknall (1977). Lee and Eom (1988) and Eom and Butterfield (1997) noted that the cross-field pits in the compression wood could not be used for diagnostic purpose due to their severe morphological alteration but those in the opposite wood appeared to be useful for identification because of only a very slight deviation form the normal shape.

Irrespective of compression, lateral, and opposite woods, a single trabecula traversing the lumina of single cells is more common than trabeculae traversing several tracheids in a radial file (Figures 25~28). Yumoto and Ohtani (1981) indicated that trabeculae were composed of the same wall layers as those of host cells.

Compression wood tracheids are significantly shorter than those of opposite wood only in stem materials (Table 1). This differs from the report by Petric (1962) that tracheids were short in the compression wood, intermediate in the opposite wood, and long in the lateral (normal) wood. But our result for stem woods agrees with Wardrop and Dadswell (1950) who indicated in radiata pine that the tracheids in the opposite wood were longer than those in the normal and compression woods. Verrall (1928) reported that tracheids in the compression wood were considerably shorter than those in the opposite or lateral wood but opposite and lateral wood were very similar in tracheid length. Park (1984) found that the length of late wood tracheids increased slightly from the compression side to the lateral side but decreased thereafter to the opposite side in peripheral positions. Shelbourne and Ritchie (1968) suggested that tracheid length of normal wood was greater than that of compression wood with an inverse relationship with the intensity of compression wood, and Timell (1973) concluded the tracheids to be relatively long in the opposite wood, short in the compression wood, and intermediate in the normal wood.

Tracheid walls appear to be thicker in the compression wood but the cell diameters show no differences between compression, lateral, and opposite woods (Table 1). Panshin and de Zeeuw (1980) reported the wall thickness of compression wood tracheids to be approximately twice that of comparable normal tracheids. Lee and Eom (1988) also found the tracheid walls in the compression wood to be thicker than those in the opposite wood. Park (1986) reported that wall thickness of late wood tracheids decreased towards the opposite side from the compression side but such a decrease could not be demonstrated in early wood. For tracheid diameters, Park *et al.* (1979) recorded that there was no significant difference between compression, opposite, and lateral woods. Kienholz (1930), however, indicated that the tracheids in the normal wood had slightly larger diameters than those in the compression wood but those in the opposite and compression woods had similar diameters.

Ray densities appear to show no difference between compression, lateral, and opposite woods but uniseriate rays are significantly fewer in the compression wood (Table 1), like the report by Eom and Butterfield (1997). However, this is in disagreement with the observations of Lee and Eom (1988) who found uniseriate rays were more numerous and higher in the compression wood than in the opposite wood, and Verrall (1928) and Kennedy (1970) who reported that the rays were slightly but consistently more frequent in the compression wood than in the normal wood. The heights of uniseriate and biseriate rays are similar in the compression, lateral, and opposite woods and the numbers of biseriate rays in tangential surfaces are almost the same (Table 1). Eom and Butterfield (1997) reported that uniseriate ray heights exhibited no consistent trend between compression, lateral, and opposite woods, but Lee and Eom (1988) noted that biseriate rays were common in the compression wood but their detection was very difficult in the opposite wood.

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