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Anatomical Comparisons of Compression, Opposite, and Lateral Woods in New Zealand Radiata Pine (*Pinus radiata* D. Don)*1

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뉴질랜드産 라디아타소나무의 壓縮異常材, 對應材 및 側面材의 解剖學的 特性 比較*1

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요 약

뉴질랜드産 라디아타소나무의 樹幹 및 枝材에 發達되어 있는 壓縮異常材, 對應材 및 側面材의 解剖學的 特性을 光學顯微鏡, 走射電子顯微鏡 그리고 透過電子顯微鏡을 이용하여 組織學的 및 構成要素의 數量的 側面에서 比較, 檢討하였다.

組織學的인 面에서 볼 때 春材로부터 秋材로의 假導管 移行은 對應材나 側面材보다 壓縮異常材가 훨씬 더 漸進的이었다. 偏心生長으로 인해 年輪幅은 壓縮異常材가 가장 컸고 그 다음이 側面材 및 對應材의 순이었으며 秋材率 역시 壓縮異常材가 對應材 및 側面材보다 컸다. 橫斷面上 假導管 形狀面에서 壓縮異常材가 圓形을 나타내는 반면 對應材와 側面材는 角形을 띠고 있었다. 또한 壓縮異常材에서만 假導管의 細胞壁에 螺旋腔과 螺旋裂 (helical cavity and check), 슬릿(slit)形 壁孔口가 存在하였으나 S_3層이 缺如되어 있었으며 屈曲된 先端과 不規則한 形狀의 假導管 및 細胞間隙이 자주 觀察되었다. 直交分野 壁孔은 壓縮異常材가 가문비나무型 그리고 對應材 및 側面材는 소나무型 壁孔을 나타냈다.

數量的 特性 면에서 볼 때 假導管의 길이는 壓縮異常材가 가장 짧고 側面材가 가장 길었으며 假導管의 壁 두께는 壓縮異常材가 對應材나 側面材보다 두꺼웠다. 垂直樹脂溝는 對應材가 그리고 水平樹脂溝(紡錐形 放射組織)는 壓縮異常材의 쪽이 많았다.

結論的으로 보면 라디아타소나무의 壓縮異常材는 근본적으로 對應材나 側面材와는 相異한 特性을 지녔으나 對應材와 側面材는 거의 類似한 特性을 共有하는 것으로 밝혀졌다.

Keywords : Radiata pine(*Pinus radiata*), stem, branch, compression wood, opposite wood, lateral wood, anatomy

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1. INTRODUCTION

The inclined stems and branches in gymnosperms commonly display eccentric growth with well-developed compression wood to the lower side and suppressed opposite wood to the upper side. 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).

When viewed macroscopically in transverse surface, compression wood can be easily distinguished from surrounding tissues by its darker colour. Most of its anatomical features have been thoroughly investigated by numerous researchers since long. 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). Lateral wood (side wood) was considered as normal wood or as an intermediate between opposite and compression wood(Timell, 1973).

Worldwide radiata pine plantations cover 3.69 million hectares with Chile having 35%, New Zealand 34%, and Spain 7% of this total. In New Zealand, forests cover about 27% or 7.4 million hectares of the land area and comprise indigenous forests of 6.1 million hectares and non-native plantations of 1.3 million hectares (Anonymous, 1995). Of the total area planted, 89% is radiata pine and the remaining 5% is Douglas-fir, 4% other conifers, and 2% hardwoods(New Zealand Ministry of Forestry, 1988).

This paper details anatomical comparisons of compression, opposite, and lateral wood in the stem and branch of New Zealand radiata pine (*Pinus radiata* D. Don), an important species as a raw material.

2. MATERIALS & METHODS

A 41-year-old stem and a 21-year-old branch of radiata pine(*Pinus radiata*) containing well-developed compression, lateral, and opposite wood(Fig. 1) were obtained from Whitecliffs and Bottle Lake Forest Park, South Island, New Zealand. Small cubes of about 1~2 cm per side were softened in water for 90 minutes. Transverse, radial, and tangential sections of 20~30μm thickness were cut with a sliding microtome, and permanent slides prepared following general laboratory techniques(Japan Wood Research Society, 1985) were used in the light microscopic studies.

For the scanning electron microscopic studies, 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-

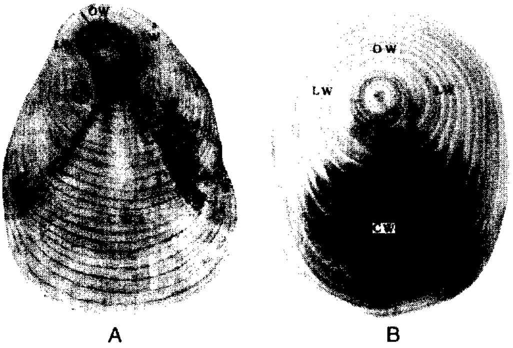


Fig. 1. Compression (CW), opposite (OW), and lateral wood (LW) in the stem (A) and branch (B) of radiata pine (*Pinus radiata* D. Don). Scale bars = 2 cm.

dried, glued on to specimen stubs with double-sided carbon tabs, sputter-coated with gold to a thickness of 50nm(Exley *et al.*, 1974 · 1977), and observed in a Leica S440 scanning electron microscope at 10kV.

For the transmission electron microscopic studies, small wood blocks of about $1.5 \times 1.5 \times 1mm^3$ 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 polymerized overnight at 70℃(Anonymous, 1986). Ultrathin sections of 100nm thickness 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 80kV.

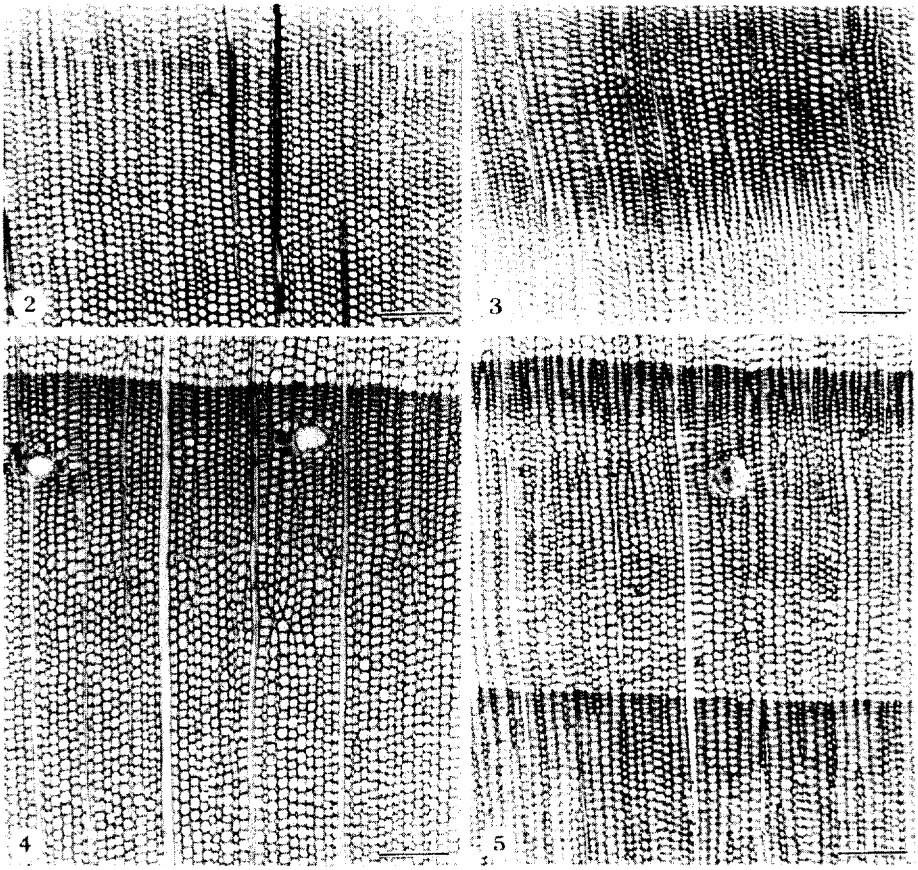
For the quantitative analyses of each tissue, the lengths of 100 randomly selected tracheids were measured from macerations obtained with Schultze's solution(Berlyn & Miksche, 1976) and the tangential diameters and wall thicknesses of 25 randomly selected tracheids were measured from transverse surfaces of permanent slides. The numbers of vertical and horizontal resin canals(fusiform rays) in the respective transverse and tangential surfaces of 4π mm^2, the numbers of uniseriate rays per mm in tangential surfaces, and ray densities, *i.e.* the numbers of rays per mm^2 in tangential direction of transverse surfaces, were counted in 10 randomly selected parts in the permanent slides. The heights and widths of 20 fusiform rays and the respective heights and widths of 100 and 20 uniseriate rays were also measured by random selection in tangential surfaces of permanent slides. 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.

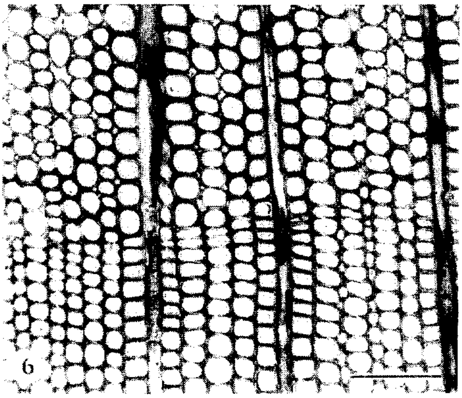
3. RESULTS & DISCUSSION

Transition from earlywood to latewood in compression wood is gradual to very gradual with the exception of a few growth rings which show a somewhat abrupt transition (Figs. 2 and 3).

Both in lateral and opposite wood, however, the transition is somewhat abrupt to abrupt, though wide rings generally show a more gradual transition than narrow ones (Figs. 4 and 5). Thus demarcation between earlywood and latewood is more difficult in compression wood than in lateral and opposite wood(Figs. 2 and 5). Lee and Eom(1984 · 1988) and Eom and Lee(1985) observed a gradual transition in compression wood and an abrupt transition in opposite wood. The transition in opposite wood was reported to be abrupt in narrow increments but to become more gradual in wider rings by Timell(1973 · 1986).

Growth ring width is wider in compression wood, intermediate in lateral wood, and narrower in opposite wood, though the ring width in all three zones is variable (Table 1). Proportion of latewood in lateral wood appears to be a little larger than in opposite wood (Figs. 4 and 5). Both lateral and opposite wood, however, have a much smaller proportion of latewood than compression wood and furthermore show a great variation in the proportion of latewood, in which some growth rings consist mostly of earlywood with very small latewood and the proportion of latewood also varies within a ring(Figs. 2~5). Compression wood shows a more or less constant and large latewood proportion, and there are many instances where the complete width of the ring in compression wood is made up of thick-walled, rounded tracheids causing the ring to appear to be made up entirely of latewood(Fig. 2), similarly to the observations of Core *et al.*(1961) and Lee and Eom(1988). Timell(1986) concluded that the growth ring tended to be wide in compression





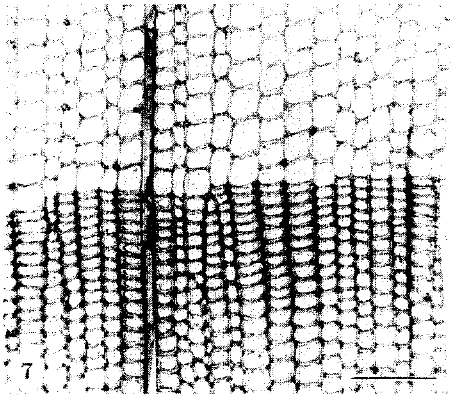


Fig. 2~5. Transverse sections showing tracheid transition from earlywood to latewood.

Fig. 2. Very gradual transition in branch compression wood.

Fig. 3 & 4. Somewhat abrupt transition in stem compression wood and stem opposite wood, respectively.

Fig. 5. Abrupt transition and a more gradual transition in wide ring than in narrow one in branch lateral wood(Scale bars = 200 μm).

Fig. 6. Transverse section of branch compression wood showing rounded tracheids and intercellular spaces with the exception of growth ring boundary(Scale bar =100μm).

Fig. 7. Transverse section of stem lateral wood showing square to rectangular or angular tracheids(Scale bar = 100 μm).

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

Feature	Stem			Branch		
	CW	LW	OW	CW	LW	OW
Ring width (mm)						
Range	0.4~11.8	0.3~4.8	0.2~3.6	0.2~7.2	0.2~4.6	0.4~3.0
Average	6.58	1.28	0.85	3.76	1.81	1.43
Tracheid						
Length (μm)						
Range	811~3676	1081~3757	1135~3702	865~3243	919~3460	1000~3081
Average	2209.5	2373.2	2271.9	1904.6	2136.0	2027.0
Tangential diameter (μm)						
Range	10.0~35.0	12.5~45.0	10.0~43.3	14.2~37.5	11.7~43.3	8.3~41.7
Average	23.27	28.37	27.33	25.77	25.83	26.80
Radial wall thickness (μm)						
Range	3.8~6.3	1.7~5.8	2.1~5.0	3.3~6.7	2.1~5.0	2.1~4.6
Average	5.05	3.58	3.08	5.28	3.12	3.35
Resin canal (no./4π mm^2)						
Vertical						
Range	4~10	4~9	6~11	2~12	5~8	5~13
Average	6.8	6.1	8.2	6.5	6.3	7.7
Horizontal (fusiform ray)						
Range	8~20	4~12	8~20	4~20	4~12	4~16
Average	13.2	7.2	11.2	11.6	7.6	9.2
Ray						
Density (no./mm)						
Range	4~6	2~7	3~7	2~6	3~6	3~7
Average	4.8	4.2	4.7	4.1	4.5	4.7
Number (no./mm^2)						
Uniseriate						
Range	25~33	32~41	29~39	24~31	28~39	32~41
Average	29.7	35.2	34.1	28.4	32.6	35.3
Height (μm)						
Fusiform						
Range	143~407	207~450	123~333	133~330	190~350	200~387
Average	266.3	277.8	244.7	237.2	250.3	287.7
Uniseriate						
Range	23~403	31~427	47~396	39~396	47~403	39~442
Average	159.6	149.3	153.4	144.5	145.4	147.2
Width (μm)						
Fusiform						
Range	33.3~60.0	33.3~53.3	30.0~53.3	30.0~53.3	40.0~66.7	43.3~66.7
Average	43.67	43.67	42.67	45.17	49.83	53.33
Uniseriate						
Range	10.0~23.3	6.7~23.3	10.0~23.3	10.0~23.3	6.7~30.0	10.0~26.7
Average	16.33	16.33	16.67	16.67	17.67	18.83

wood, intermediate in lateral wood, and narrow in opposite wood, and that the latewood proportion to be very large in compression wood.

intermediate in lateral wood, and small in opposite wood. Jaccard(1919) and Lee and Eom(1988) indicated considerable variation in growth ring widths in opposite and compression wood. Timell(1973) noted that the ring widths in opposite wood varied greatly with wide rings containing a much higher proportion of latewood than the narrow ones. This was contrary to Mork 's observation(1928) that the narrow increments had a higher latewood proportion than the wider ones. Park(1983) also suggested that growth ring width and proportion of latewood decreased continuously at a relatively steep rate from compression side to opposite side.

Compression wood tracheids, when viewed transversely, are usually round in outline except at the growth ring boundary(Figs. 6 and 14) as reported by Cote *et al.* (1967) and Yoshizawa *et al.* (1982). Lateral and opposite wood tracheids, however, are square to rectangular or angular in outline(Fig. 7). Timell(1973 · 1986) described the outline of tracheids as square, rectangular, or angular in opposite wood, angular in normal wood, and round in compression wood.

Helical cavities and checks within the S2 layer of tracheid(Figs. 8 and 9) and seemingly slit-like pit openings which are caused by the location of pit apertures at the bottom of long and narrow helical grooves in the radial wall of tracheid(Figs. 9~10) are observed only in compression wood and occurred both in the earlywood and latewood. Many of the helical cavities are branched(Figs. 8 and 15~16) and some of the helical checks appear to be associated with pit openings(Figs. 10 and 11). Boyd(1973) indicated that helical fissures occurred only beyond the lignin-dense layer inside S1 or the outer proportion of the S2 layer and many were branched. Timell(1978 · 1986) suggested that the slit-like pit openings could be used as an identification criterion because of their common occurrence in compression wood. He also noted that the helical cavities developed into checks of schizogenous origin which were probably formed on drying and sometimes associated with pit openings. Wardrop and Davies(1964), Cote *et al.* (1968), and Timell(1979 · 1986) all gave some attention to the origin of these helical cavities, perhaps the most conspicuous feature of compression wood, but this problem has not been resolved as yet.

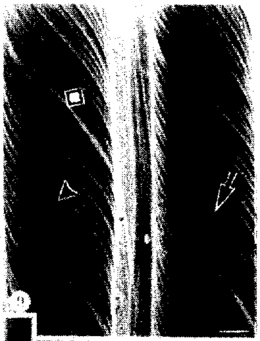


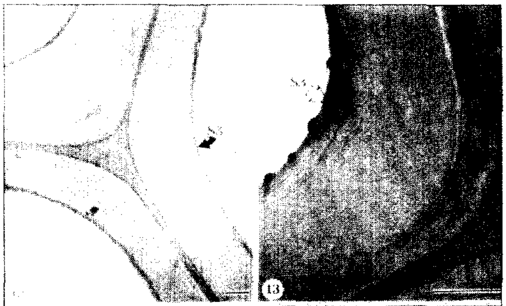
Fig. 8. Transverse section of tracheid showing helical cavities (arrowhead) and checks (arrow) within the S2 layer in stem compression wood(Scale bar = 1 μm).

Fig. 9. Radial section of tracheids showing helical cavities (arrowhead) and check (arrow) and slit-like pit openings (diamond) caused by the location of pit apertures at the bottom of helical grooves in branch compression wood (Scale bar = 3 μm).

Fig. 10. Helical check (arrow) associated with the intertracheid pit opening in radial wall of tracheid in branch compression wood(Scale bar = 1 μm).

Fig. 11. Helical checks (arrow) associated with tracheid pit opening in the cross-field pits of stem compression wood(Scale bar = 3 μm).

Compression wood tracheids lack the inner or S3 layer of secondary wall as reported by Boyd (1973) and Panshin and de Zeeuw(1980), but the S3 wall layers are observed in the tracheids of lateral and opposite wood(Figs. 8 and 12



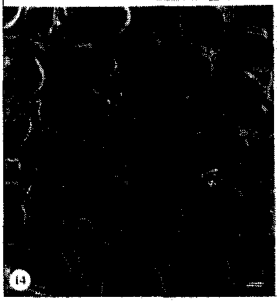
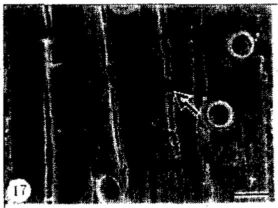
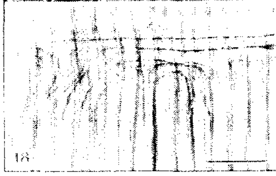


Fig. 12~13. Transverse sections of tracheids with S3 wall layer in stem lateral wood and branch opposite wood, respectively (Scale bars = 1 μm).

Fig. 14~15. Bands of lignin (arrow) traversing intercellular spaces in transverse sections of stem and branch compression wood, respectively(Scale bars = 4 μm).

Fig. 16. Parental primary wall (arrow) traversing intercellular space in transverse section of branch compression wood(Scale bar = 4 μm).





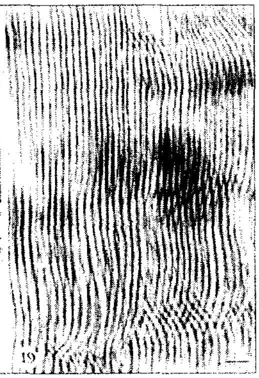


Fig. 17. Parental primary wall (arrow) traversing intercellular space in radial section of stem compression wood(Scale bar = 10 μm).

Fig. 18~19. Radial sections of stem compression wood showing distorted tracheid tips and irregularly shaped tracheids, respectively(Scale bars = 100 μm).

~13). Timell(1973 · 1986) concluded these S3 layers to be thick in opposite wood, thin in normal wood, and absent in compression wood, but Harris(1991) noted that traces of S3 wall layer could be occasionally identified in all grades of compression wood in radiata pine.

Intercellular spaces are frequently detected in compression wood except at the growth ring boundary(Figs. 6 and 14~16) but are absent both from lateral and opposite wood(Fig. 7). This phenomenon is related to the shape of tracheids in transverse section. Intercellular spaces were known to be present frequently in 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.

Band of lignin(Figs. 14~15) and parental primary wall(Figs. 16~17) traversing intercellular spaces are occasionally observed in compression wood as reported by Resch and Blaschke(1968) and Mio and Matsumoto(1982).

Distorted tracheid tips(Fig. 18) and irregularly shaped tracheids resembling the vasicentric tracheids of some hardwood species through deviation from the normal straight shape(Fig. 19) frequently occur in compression wood but not in lateral and opposite wood. The tracheid distortion was indicated as a feature of compression wood by Onaka(1949) and Wardrop and Dadswell(1952) and believed to be caused by the 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.

Normal resin canals(Figs. 4~5) occur but traumatic resin canals are absent both in the earlywood and latewood of compression, lateral, and opposite wood. Tylosoids(Fig. 20) which arise through the proliferation of thin-walled epithelial cells are commonly detected in the

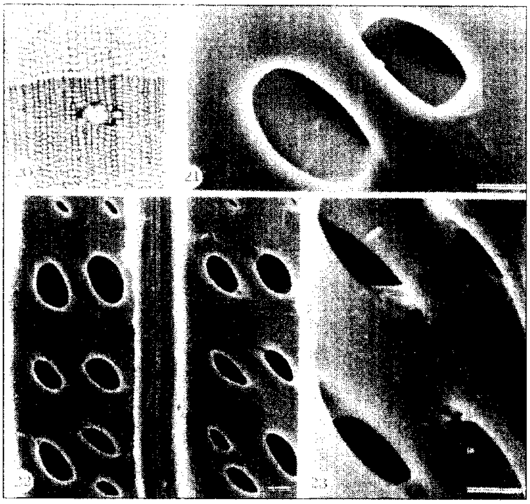


Fig. 20. Normal resin canal with tylosoid in transverse section of stem opposite wood (Scale bar = 200 ㎛).
Fig. 21~23. Cross-field pits in earlywood as seen from tracheid lumen.
Fig. 21. Pinoid type in branch opposite wood.
Fig. 22. Pinoid type in branch lateral wood.
Fig. 23. Piceoid type in branch compression wood(Scale bars = 2 ㎛).

resin canals of each wood. Timell(1973) and Lee and Eom(1988) observed normal resin canals both in the earlywood and latewood of compression and opposite wood. Traumatic resin canals were identified in some species by Core *et al.*(1961) and Lee and Eom(1988), and these authors concluded these resin canals of wound origin not to be a constant feature of compression wood. Sato and Ishida(1983) in comparing vertical resin canals noted a smaller number of vertical resin canals, more frequent occurrence of narrow vertical canals, more frequent absence of axial parenchyma cell, a lower proportion of thin-walled axial epithelial cells, and a higher proportion of irregularly shaped axial epithelial cells in compression wood than in normal wood.

Cross-field pits in the earlywood of compression wood appear to be piceoid due to slit-like pit apertures, which are sometimes extended by checks, beyond the outline of the pit border (Figs. 11 and 23) but those in the earlywood of lateral or opposite wood are pinoid(Figs. 21 and 22). Lee and Eom(1988) noted that the cross-field pits in compression wood seemed to be unsuitable for diagnostic purpose due to their severe morphological alteration, but the pits in opposite wood appeared to be useful as an identification criterion because of only a very slight deviation from the normal shape.

Quantitative features of each tissue are listed in Table 1. Tracheids appear relatively short in compression wood, intermediate in opposite wood, and long in lateral wood like the report by Petric(1962). The result in present study, however, differs with Wardrop and Dadswell (1950) who indicated in radiata pine that the tracheids in opposite wood were longer than those both in normal and compression wood. Verrall(1928) reported that tracheids in compression wood were considerably shorter than those either in opposite or lateral wood but opposite and lateral wood were very similar in tracheid length. Park(1984) found that the length of latewood tracheids increased slightly from compression side to lateral side but decreased thereafter to opposite side in peripheral positions. Also, 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 opposite wood, short in compression wood, and intermediate in normal wood.

Tracheid walls appear to be thicker in compression wood than in lateral and opposite wood. No consistent pattern, however, is noticed in their tangential diameters between compression, lateral, and opposite wood. The normal wood tracheids in the stem of radiata pine were reported by Patel(1971) to have average dimensions of 38.35 ㎛(range 21.8~56.6 ㎛) in tangential diameter, 3.45 ㎛(range 1.20~6.60 ㎛)

in wall thickness, and 2720μm(range 730~4780 μm) in length. Panshin and de Zeeuw(1980) reported the wall thickness of compression wood tracheids to be approximately twice that of comparable normal tracheids, and Lee and Eom (1988) also found the tracheid walls in compression wood to be thicker than those in opposite wood. Park(1986) reported that wall thickness of latewood tracheids decreased towards opposite side from compression side but such a decrease could not be demonstrated in earlywood. In the tracheid diameters, Park *et al.*(1979) recorded that there was no significant difference between compression, opposite, and lateral wood. Kienholz(1930), however, indicated that the tracheids in normal wood had slightly larger diameters than those in compression wood but opposite and compression wood were very similar in this respect.

Vertical resin canals are slightly more numerous in opposite wood than either in compression or lateral wood. Horizontal resin canals(fusiform rays), however, are the least common in lateral wood and are somewhat more numerous in compression wood than in opposite wood. The vertical resin canals were found to be fewer in compression wood than in opposite wood(Onaka, 1949; Lee & Eom, 1988), whereas the horizontal resin canals (fusiform rays) were detected to be more numerous in compression wood than in opposite wood (Lee & Eom, 1988).

Ray densities, *i.e.* the numbers of rays per mm in tangential direction of transverse surfaces, appear to show no difference and uniseriate and fusiform rays exhibit no consistent trend in height and width between compression, lateral, and opposite wood. Uniseriate rays in compression wood, however, are somewhat fewer than in lateral and opposite wood. This is in disagreement with Lee and Eom(1988) who found the fusiform rays in compression wood to be wider and lower than in opposite wood and uniseriate rays to be more numerous and higher in compression wood than in opposite wood. Verrall(1928) reported that the rays were slightly but consistently more frequent in compression wood than in normal wood, and Kennedy(1970) indicated that compression wood had a much greater proportion of narrow rays, in part biseriate, than normal wood. Timell(1972 · 1986) suggested that the larger number and size of the rays occasionally observed in compression wood might be associated with rapid growth characteristics of this wood. Also, Kramer and Kozlowski(1979) noted that the anatomy of ray cells was essentially the same in normal and compression wood though sometimes a higher frequency and larger size of ray cells occurred in compression wood, reflecting a higher overall rate of growth. Normal wood rays in stem of radiata pine, on the other hand, were found to have average numbers of 4.6(range 2~8) per mm in transverse surface and 22.4(range 12.0 ~36.5) per mm^2 in tangential surface by Patel (1971).

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