Quantitative Anatomical Characteristics of Compression Wood, Lateral Wood, and Opposite Wood in the Stem Wood of *Ginkgo biloba* L.

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Quantitative aspects were investigated and compared for anatomical characteristics among compression wood (CW), lateral wood (LW), and opposite wood (OW) in the stem wood of *Ginkgo biloba*. Characteristics of each part were observed in the 5th, 10th, and 15th to 20th growth rings *via* optical and scanning electron microscopy. The crystalline characteristics were measured using an X-ray diffractometer. The microfibril angles (MFAs) were measured using the iodine method applied to the tangential section, as well as from the slopes of the pit apertures. The CW and OW showed similar tracheid lengths in the 5th and 10th growth rings; however, the CW was the shortest in the 15th to 20th growth rings. The CW showed the highest ray height and lowest ray number in each growth ring. The MFAs of the CW were greater than those in the LW and OW from both measurement methods. The MFAs obtained from the iodine method were smaller than that of the MFAs obtained from the pit aperture measurements. The CW had the lowest relative crystallinity in each growth ring, whereas the crystal width of the CW was the smallest in the 5th and 15th to 20th growth rings.

Keywords: Ginkgo biloba L.; Compression wood; Lateral wood; Opposite wood; Quantitative analysis; MFA

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INTRODUCTION

Reaction wood on the lower sides of branches and leaning stems of conifers, also known as compression wood (CW), restores the vertical growth of stems or branches and is recognized by a darkened color on its transverse surface (Barnett *et al.* 2014). Lateral wood (LW) and opposite wood (OW) occur in the leaning stems or branches alongside CW (Timell 1986; Eom and Butterfield 1997). LW is the intermediate between OW and CW (Timell 1986). The occurrence of CW has been shown to cause several abnormalities in the anatomical characteristics of both qualitative and quantitative aspects (Timell 1986; Eom 1991; Eom and Butterfield 1997, 2001). There are tracheid characteristics in qualitative aspects that appear as helical cavities, excessive lignification in the middle (S_2) layer, a thicker cell wall, differently shaped pit borders, an absence of the inner (S_3) layer, intercellular spaces, and distorted and bifurcated tracheid tips (Fujita *et al*. 1979; Yumoto *et al*. 1983; Timell 1986; Yoshizawa *et al.* 1987). In comparison, in the quantitative aspects, the CW shows higher microfibril angles (MFAs) in the S_2 layer, shorter tracheid lengths, higher ray heights, and lower ray numbers (Onaka 1949; Timell 1986; Eom and Butterfield 1997, 2001).

Ginkgo biloba is an ancient gymnosperm species; therefore, many researchers are interested in studying its anatomical characteristics. Several studies have reported that *G. biloba* shows characteristics similar to conifers, and yet this species also shows some different characteristics such as varied size of tracheid lumen and a number of idioblasts with druse (Scott *et al.* 1962; Srivastava 1963; Timell 1986).

The quantitative aspects of anatomical characteristics in the CW of *G. biloba* have been reported in a few studies (Onaka 1949; Eom 1991; Shirai *et al.* 2016). Onaka (1949) reported that the number of rays in CW was lower than that in normal wood, whereas the ray heights in CW were higher than that in normal wood. Eom (1991) reported that the anatomical characteristics between CW and OW in *G. biloba* were distinctively different for both qualitative and quantitative aspects. Eom also reported that the CW showed a thicker cell wall, lower number of rays, and higher ray heights than that of the OW, whereas the tracheid length was nearly identical. Shirai *et al.* (2016) reported that the MFA, air dry density, and lignin content in CW-like reaction wood of *G. biloba* were higher than that in the OW and LW, whereas the cellulose content was lower than that in the OW and LW. These authors concluded that the negative gravitropism in the stem wood of *G. biloba* was similar to that of other conifer species.

In the previous study (Purusatama *et al.* 2018), the authors investigated and compared the qualitative aspects of anatomical characteristics in CW, LW, and OW in the stem wood of *G. biloba*. It was reported that CW showed characteristics differing from LW and OW, such as a circular tracheid shape, intercellular spaces, spiral checks on the cell wall, a piceoid pit in the crossfield, slit-like bordered pits, and distorted tracheid tips. Until now, the anatomical characteristics of *G. biloba* have been mostly investigated using branch wood. Furthermore, there has been a lack of information regarding the quantitative aspects of the anatomical characteristics in CW, LW, and OW. Therefore, the objectives of the present study are to investigate and compare the quantitative aspects of the anatomical characteristics for CW, LW, and OW in the stem wood of *G. biloba*.

EXPERIMENTAL

Materials

In the present study, 24-year-old *Ginkgo biloba* wood was obtained from Hongcheon-gun, Gangwon-do, Republic of Korea (37.6970°N, 127.8887°E). Hongcheon-gun had average high temperature from 1.6°C (January) to 30.2°C (August), average humidity from 57.8% (April) to 77.4 % (July), and average rainfall from 397mm (July) to 19.1mm (December). The fundamental information of the experimental wood is shown in Table 1 (Purusatama *et al.* 2018).

Methods

Microscopy

The CW, LW, and OW samples were defibrillated in Schültz's solution (Han *et al*. 1999) for 3 days. The tracheid length was measured randomly in 50 tracheids from the CW in the 5^{th}, 10^{th}, and 15^{th} to 20^{th} growth rings, and then compared with those in the LW and OW from the same growth rings. The number of uniseriate rays was counted in 20 areas of a 0.5×0.5 mm^2 microscopic screen in tangential sections. The ray height and ray number were randomly measured from 50 uniseriate rays in the 5th, 10th, and 15th to 20th growth rings of CW, LW, and OW.

Table 1. Fundamental Information of Sample Tree

Samples	Age	DBH (cm)	Type	Examined Growth Ring	Density (g/cm^3)
Ginkgo biloba	24	15	CW	5th, 10th, and 15th to 20th	0.50
			LW	5th, 10th, and 15th to 20th	0.47
			OW	5th, 10th, and 15th to 20th	0.51

To measure MFAs in the S_2 layer of the tracheid wall, tangential sections were prepared from the CW, LW, and OW with a microtome cutting thin slices (20 to 30 µm), and the slices were soaked in Schültz's solution for 3 days. The thin slices were stained using the iodine staining method (Senft and Bendtsen 1985). The MFAs in the S_2 layer were also measured from the slope of the pit apertures and spiral checks in the radial sections of the CW, LW, and OW (Donaldson 1991). To observe all the quantitative characteristics, an optical microscope (Eclipse E600; Nikon, Tokyo, Japan) connected to an image analysis system (IMT i-Solution Lite, Vancouver, Canada) and a scanning electron microscope (JSM-5510; Jeol Ltd., Tokyo, Japan, 15kV) were used.

Crystalline characteristics

An X-ray diffractometer (DMAX2100V; Rigaku, Tokyo, Japan) equipped with a Cu target (λ = 0.1542 nm) was used for measuring the crystalline properties. The relative crystallinity and crystallite width were calculated using Segal's equation (Segal *et al.* 1959) and the Scherrer's equation (Burton *et al.* 2009), respectively.

Statistical analysis

Differences in the quantitative features among the CW, LW, and OW were statistically analyzed with one-way analysis of variance and post-hoc Duncan's multiple range tests (SPSS ver. 21, IBM Corp., New York, USA).

RESULTS AND DISCUSSION

Tracheid Length

The tracheid lengths of CW, LW, and OW in the 5th, 10th, and 15th to 20th growth rings of *G. biloba* are shown in Table 2. The tracheid lengths of CW, LW, and OW were increased significantly with increasing growth rings. The CW and OW had similar tracheid lengths in the 5th and 10th growth rings; however, CW had the shortest tracheid lengths in the 15th to 20th growth rings. The LW showed the longest tracheid length in the 5th and 10th growth rings, whereas there was no significant difference between LW and OW in the 15th to 20th growth rings. As reported by Timell (1986) and Tsoumis (1991), tracheid lengths become longer from pith to bark in conifers. Several studies (Onaka

1949; Wardrop and Dadswell 1950; Yozhizawa *et al.* 1987) have reported that tracheid lengths in CW were considerably shorter than that in normal wood in many conifers. The average tracheid lengths in CW are shorter than that in normal wood because the formation of CW is accompanied by cambial activity with an increase in pseudo-transverse divisions (Yoshizawa *et al.* 1987).

Table 2. Tracheid Lengths in CW, LW, and OW of *Ginkgo biloba*

Type	Tracheid Lengths (μm)		
	5th	10th	15th to 20th
CW	1638^{A} (125)	1852^{A} (114)	2016^{A} (98)
LW	1918^{B} (123)	1960^{B} (123)	2228^{B} (138)
OW	1635^{A} (123)	1863^{A} (135)	2239^{B} (158)

Note: The numbers in parenthesis are the standard deviations. The same capital letters beside the mean value are insignificant at the 5% significance level between the CW, LW, and OW using Duncan's multiple range tests.

In a previous study, tracheid lengths were similar between the CW and OW in the branch wood of *G. biloba* (Eom 1991). Tracheid lengths between the CW and OW are similar in the stem wood of radiata pine, whereas LW had the longest tracheid length in the stem wood and branch wood of the radiata pine (Eom and Butterfield 1997). In addition, the OW was the longest tracheid lengths in the stem wood of New Zealand rimu (*Dacrydium cupressinum*), whereas CW, LW, and OW did not show significant differences in the branch wood (Eom and Butterfield 2001).

Ray Height and Ray Number

The ray height (expressed as number of cells) and ray number of CW, LW, and OW in the 5th, 10th, and 15th to 20th growth rings of *G. biloba* are shown in Table 3.

Table 3. Ray Height and Ray Number in CW, LW, and OW of *Ginkgo biloba*

Type	Growth Rings					
	5th		10th		15th to 20th	
	Ray Heights (cells)	Ray Number /mm^2	Ray Heights (cells)	Ray Number /mm^2	Ray Heights (cells)	Ray Number /mm^2
CW	2.57^{B} (0.69)	14.90^{A} (1.48)	4.39^{B} (0.92)	12.65^{A} (1.11)	5.15^{B} (0.82)	8.80^{A} (1.12)
LW	1.88^{A} (0.64)	17.90^{B} (2.55)	3.45^{A} (0.88)	13.10^{AB} (1.30)	4.29^{A} (0.93)	11.30^{B} (0.46)
OW	2.06^{A} (0.59)	17.30^{B} (1.87)	3.53^{A} (0.92)	13.50^{B} (0.87)	4.04^{A} (0.86)	11.90^{B} (1.14)

Note: The numbers in parenthesis are the standard deviations. The same capital letters beside the mean value are insignificant at the 5% significance level between the CW, LW, and OW using Duncan's multiple range tests.

The relationship between ray height and ray number is shown in Fig. 1. The ray heights of CW, LW, and OW were increased significantly with increased growth rings.

The ray height was different among the CW, LW, and OW in each growth ring. The CW had the highest ray height in each growth ring, whereas there was no significant difference between the LW and OW. As reported by Kim *et al.* (2009), the ray height increased from near the pith to approximately the 10th to 20th growth ring and was almost constant from the following rings in *Pinus koraiensis* and *Larix kaempferi*. Onaka (1949) reported that CW of *G. biloba* showed slightly higher ray height compared to normal wood. In addition, Lee and Eom (1988) and Eom (1991) reported that CW had higher ray heights than that of OW in the branch wood of *P. koraiensis* and *G. biloba*. Furthermore, the CW in five conifers had higher ray height compared to normal wood as reported by Verrall (as cited in Timell 1986). The CW had higher ray height than that of LW and OW in the stem of radiata pine (Eom and Butterfield 2001).

The ray number significantly decreased with increasing growth rings in the stem wood of *G. biloba*. The ray number was significantly different among CW, LW, and OW in each growth ring. The CW had the lowest ray number, whereas there was no significant difference between the LW and OW. The ray numbers in *P. koraiensis* and *L. kaempferi* were decreased from the pith to the 10th to 20th growth rings and were almost constant for the following rings toward the bark (Kim *et al.* 2009). The ray number of CW was lower than that of the normal wood in *G. biloba* and other conifer species (Onaka 1949; Timell 1986). Eom (1991) reported that the ray numbers of CW were fewer than that of OW in the branch wood of the Ginkgo tree. As reported by Ollinma (as cited in Timell 1986), the CW of *P.abies* had 34 rays /mm^2, while the normal wood of *P.abies* showed 40 rays/mm^2. Eom and Butterfield (2001) reported that the ray number of CW was lower than that of LW and OW in the stem wood and branch wood of New Zealand rimu. In several conifers CW showed greater ray number than normal wood. As reported by Verrall (as cited in Timell 1986), CW in *Larix laricina, Picea mariana Pinus palustris, Thuja occidentalis,* and *Thuja plicata* showed greater ray number compared to normal wood.

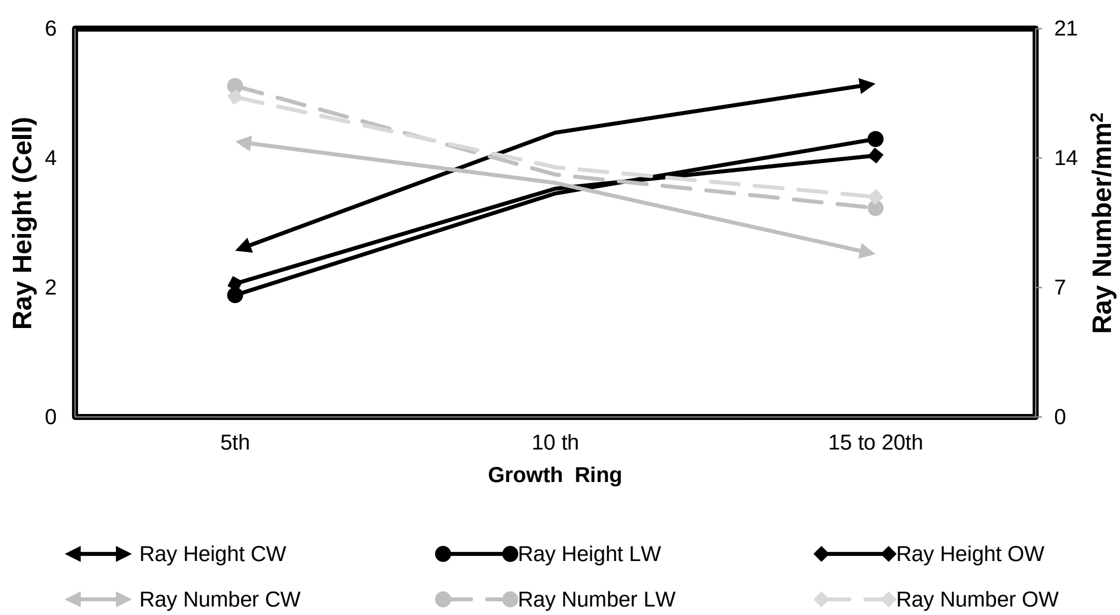

Fig. 1. Relationship between ray height and ray number of CW, LW, and OW in the stem wood of *Ginkgo biloba*

Microfibril Angle

The MFA was measured from the microfibril orientation revealed by the iodine staining method in the tangential section and from the slopes of the pit aperture and spiral check in the radial section. The light micrographs of the tracheid walls in the tangential sections are shown in Fig. 2. The iodine solution formed a dark crystal between microfibrils and revealed the orientation of the microfibril. As reported in a study by Senft and Bendtsen (1985), iodine solution and nitric acid produce crystals in the cell wall that align with the MFA. The CW showed distinct microfibril orientation and a greater slope of MFA than that of the LW and OW in each growth ring measured.

The scanning electron micrographs of the pit apertures and spiral checks in the radial section of CW, LW, and OW of *G. biloba* are shown in Fig. 3. The spiral checks in the tangential wall of CW are shown in Fig. 4. The MFA was also measured from the slope of the pit apertures and spiral checks in the tracheid wall in the radial section. As reported in a study by Cockrell (1974), the inner aperture of the pits and striations or splits of latewood tracheids had almost similar slope orientation with the S_2 microfibril. Donaldson (1991) measured the MFA by observing single cell walls from bordered or crossfield pit apertures of chemical pulp fibers.

The MFAs of the CW, LW, and OW in the 5th, 10th, and 15th to 20th growth rings of *G. biloba* are shown in Table 4. Variations in the measured MFA obtained from the iodine staining method and the pit aperture measurements are shown in Fig. 5. The MFA decreased with increasing growth rings in the CW, LW, and OW in the stem wood of *G. biloba*. The MFAs in the CW, LW, and OW in the 5th growth ring had narrow ranges, whereas the MFAs in the 10th and 15th to 20th growth rings had wide ranges. From the results of the iodine staining method, the MFA of the CW showed a higher value than that of the LW and OW in each growth ring. The MFA from the pit aperture and spiral check of the CW was higher than that from the LW and OW in the 5th and 10th growth rings, whereas the CW showed a higher MFA but no significant difference in the LW and OW in the 15th to 20th growth rings. The MFA from the pit aperture measurement in the radial sections showed mostly higher values than that of the iodine method in the tangential sections.

Table 4. Microfibril Angle in CW, LW, and OW of *Ginkgo biloba*

Type	5th		10th		15th to 20th	
	Iodine	Pit Aperture	Iodine	Pit Aperture	Iodine	Pit Aperture
CW	43.5°^{B} (2.60)	43.1°^{B} (3.18)	40.5°^{B} (1.3)	43.0°^{B} (2.45)	39.7°^{B} (1.10)	39.3°^{A} (3.03)
LW	40.1°^{A} (1.1)	41.2°^{AB} (1.47)	27.7°^{A} (4.1)	34.0°^{A} (4.36)	27.0°^{A} (3.8)	36.0°^{A} (4.36)
OW	40.1°^{A} (0.7)	40.4°^{A} (1.02)	26.0°^{A} (4.9)	37.3°^{A} (3.26)	26.1°^{A} (2.51)	37.4°^{A} (3.56)

Note: The numbers in parenthesis are the standard deviations. The same capital letters beside the mean value are insignificant at the 5% significance level between the CW, LW, and OW using Duncan's multiple range tests.

Previous studies regarding MFA in CW include Eun and Kim (2008a), who reported that the MFAs of *P. densiflora*, *P. koraiensis*, and *P. rigida* were 16.4°, 14.4°, and 26.2°, respectively. Shirai *et al.* (2016) reported that the MFA was higher in the lower side (CW-like) of the inclined stem of *G. biloba* than in the upper side and lateral side. Sahlberg *et al.* (1997) reported that the CW had a higher fibril angle than that of normal wood in Norway spruce *via* an X-ray diffraction analysis. The CW showed a higher MFA than that of adult normal wood, whereas the CW had the same MFA as that of juvenile normal wood in *Picea abies* and *Abies alba* (Gorisek *et al.* 1999). Donaldson *et al*. (2004) reported that the CW had mostly higher MFA than that of OW in *P. radiata*, except in a few early juvenile rings and the mild CW. Harris (1977) reported that CW was similar to the OW in the stem wood of radiata pine. The MFA in the tangential walls was considerably smaller than that in the radial walls (Preston 1934; Gorisek *et al.* 1999).

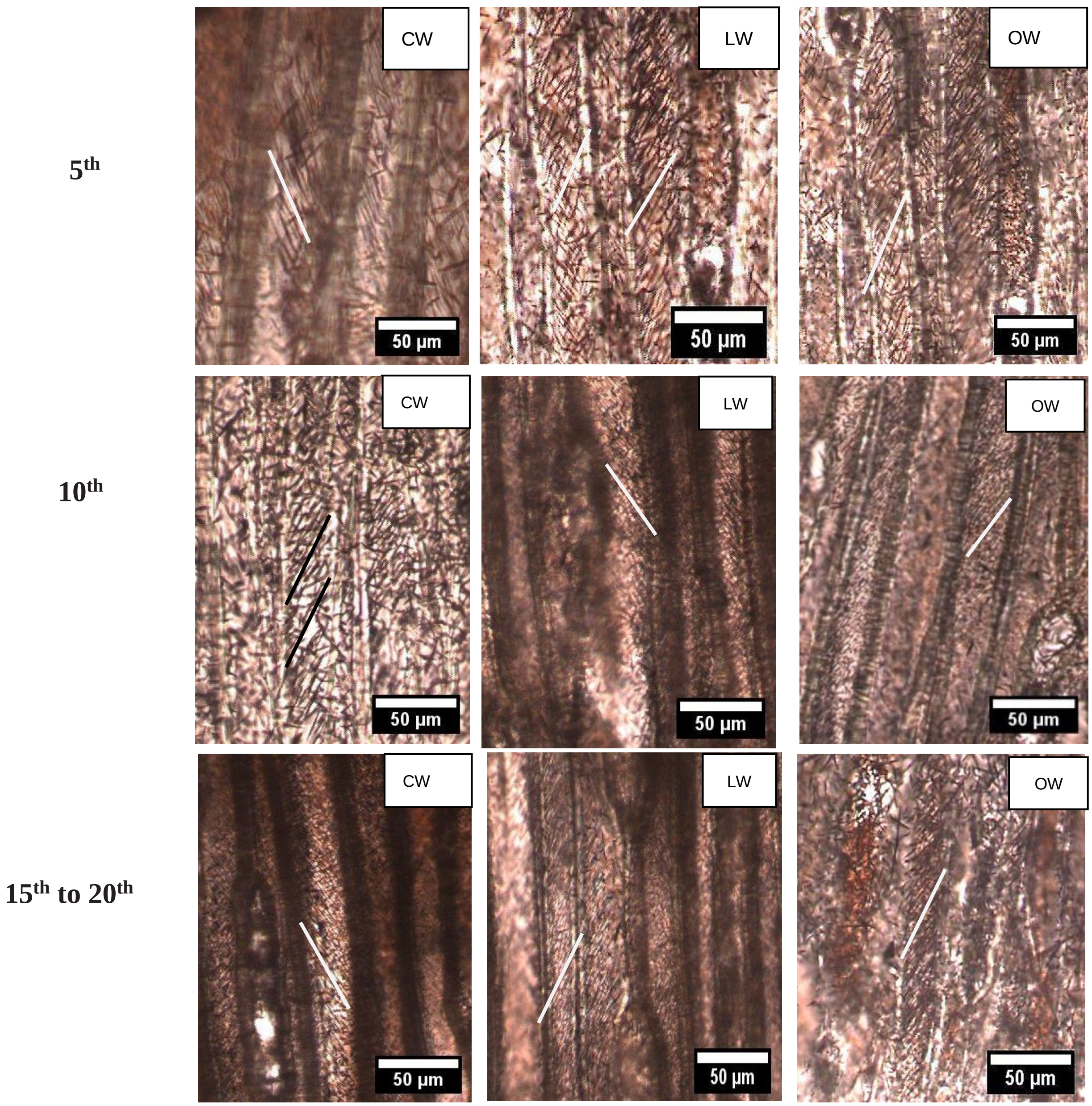

Fig. 2. Iodine crystals deposited in the tracheid wall of the tangential section in the stem wood of *Ginkgo biloba*

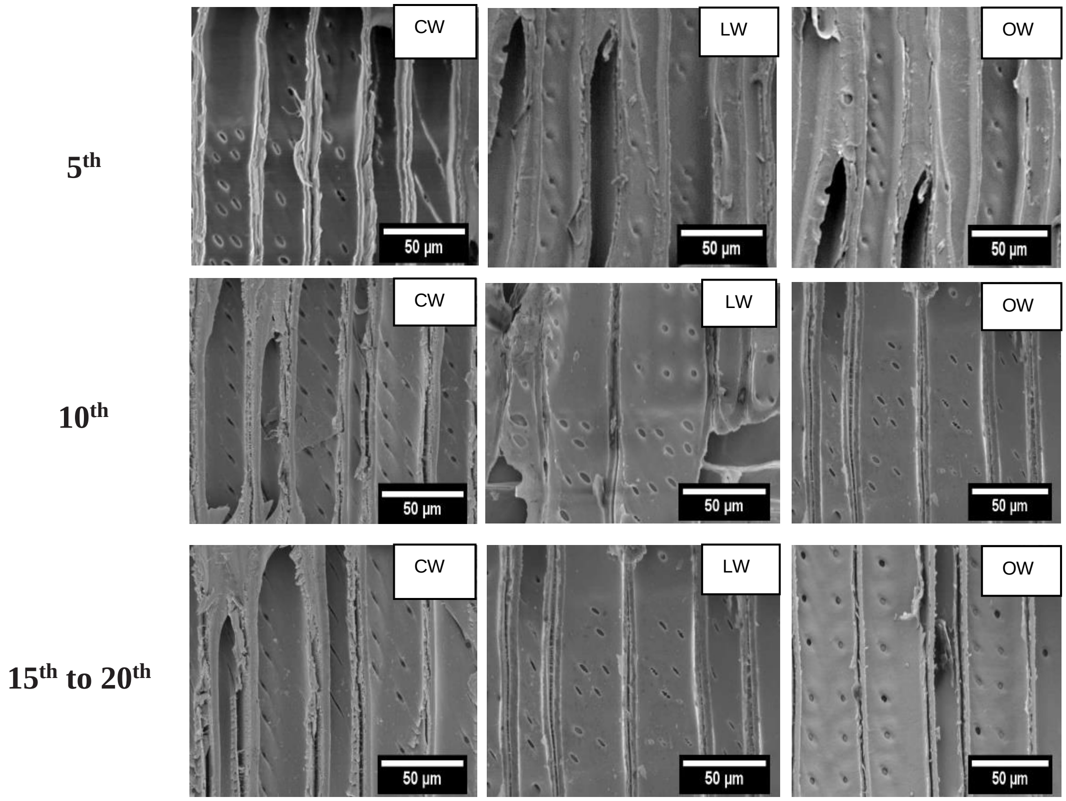

Fig. 3. Scanning electron micrographs of the pit aperture and spiral check on radial sections of CW, LW, and OW in the stem wood of *Ginkgo biloba*

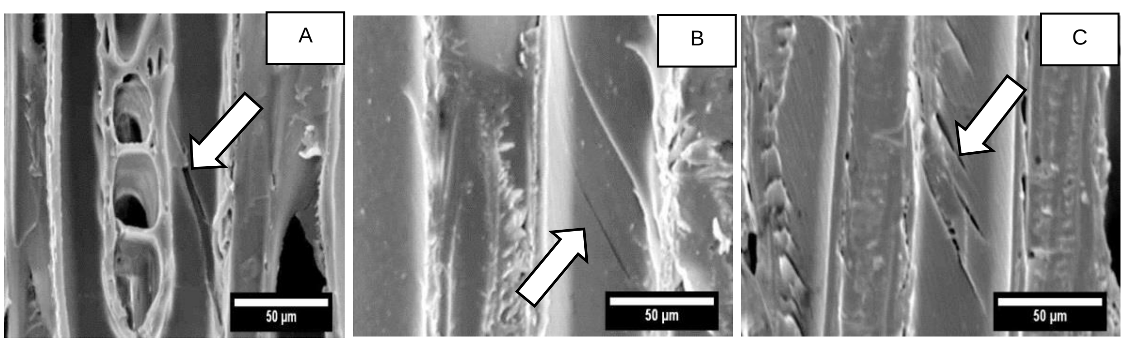

Fig. 4. Scanning electron micrographs of spiral checks (white arrow) on the tangential section of the CW in *G. biloba* in the 5th (A), 10th (B), and 15th to 20th (C) growth ring

Crystalline Characteristics

Crystalline characteristics of CW, LW, and OW in the 5th, 10th, and 15th to 20th growth rings of *G. biloba* are shown in Table 5. The relative crystallinity of CW, LW, and OW was slightly increased with increasing growth rings. Andersson *et al.* (2003, 2004) reported that the relative crystallinity increased from the pith to the bark in *Picea abies* and *P. sylvestris*. Uprichard and Lloyd (1980) reported that the lignin content had opposite correlation with the cellulose content with the increasing growth rings.

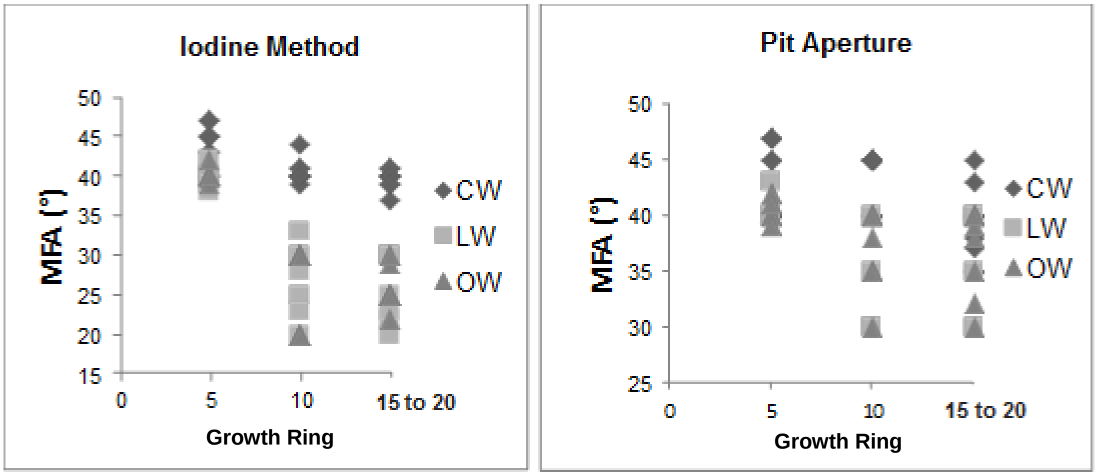

Fig. 5. Variation of measured MFA obtained from the iodine method and the pit aperture of CW, LW, and OW in the stem wood of *G. biloba*

The CW had the lowest relative crystallinity in each growth ring, whereas the LW had the highest. The CW had lower relative crystallinity than that of normal wood and OW (Parham 1971; Timell 1982, 1986). Tanaka *et al.* (1981) reported that the relative crystallinity in *P. densiflora* was 50% to 60% in OW, approximately 50% in normal wood, and 45% to 50% in CW. Eun *et al*. (2008b) reported that the relative crystallinity in *P. koraiensis*, *P. densiflora*, and *P. rigida* were 61.7%, 60.6%, and 49.4%, respectively. Compared to *P. densiflora* (Tanaka *et al.* 1981), the CW of *G. biloba* had a higher relative crystallinity. This could be caused by higher cellulose content and lower lignin content in *G. biloba* than that in other conifer species. Timell (1982, 1986) reported that the CW and normal wood of *G. biloba* contained less galactan and lignin but more celullose and galactomanannan than that of other conifer species.

Table 5. Crystalline Characteristics in CW, LW, and OW in the Stem Wood of *Ginkgo biloba*

Growth Rings	Type	Crystallinity (%)	Crystal Width (nm)
5th	CW	53.5 (1.58)	2.55 (0.14)
	LW	57.2 (2.95)	2.80 (0.17)
	OW	56.2 (2.42)	2.82 (0.23)
10th	CW	53.5 (1.18)	2.64 (0.11)
	LW	61.8 (2.03)	2.64 (0.44)
	OW	58.0 (1.67)	2.73 (0.02)
15th to 20th	CW	56.8 (1.93)	2.58 (0.37)
	LW	65.5 (0.60)	2.89 (0.14)
	OW	62.0 (0.84)	2.68 (0.21)

Note: Numbers in parenthesis are standard deviations

The average crystal widths of CW, LW, and OW in the stem wood of *G. biloba* were 2.55 to 2.89 nm. The crystal width of the CW was the smallest among the CW, LW, and OW in the 5th and 15th to 20th growth rings, whereas the CW and LW were similar in the 10th growth rings. The crystal width of *G. biloba* in the present study was smaller than that of other conifer species. In *P. densiflora* (Tanaka *et al*. 1981), Norway spruce, Scots pine (Andersson *et al.* 2003), and *G. biloba* (Andersson *et al*. 2015), the crystal widths were approximately 3.1 to 3.2 nm. Eun *et al*. (2008b) reported that the crystal widths in the stem wood of *P. densiflora*, *P. koraiensis*, and *P. rigida* were 2.8 to 3.1 nm. The CW had smaller crystal size than that of the normal wood and OW of *P. densiflora* (Tanaka *et al*. 1981).

CONCLUSIONS

1. Both the tracheid length and ray height of CW, LW, and OW (in terms of the number of cells) were significantly increased with increasing growth rings, whereas the ray number and MFA were significantly decreased with the increasing growth rings in the stem wood of *G. biloba*.
2. Tracheid length of the CW and OW did not show any significant difference in the 5th and 10th growth rings, whereas LW had the longest tracheid among the CW, LW, and OW. The CW had the shortest tracheid in the 15th to 20th growth rings, whereas the LW and OW had no significant differences.
3. The ray height of the CW was the highest among the CW, LW, and OW in each growth ring, whereas the CW had the lowest ray number.
4. The MFAs of the CW obtained from the iodine method and pit aperture measurements were higher than that of the LW and OW in each growth ring, whereas the MFAs from the pit aperture measurement showed no significant difference among the CW, LW, and OW in the 15th to 20th growth rings.
5. The MFAs obtained from the iodine method were smaller than that of the MFAs obtained from the pit aperture measurements.
6. The relative crystallinity and crystal width of the CW were mainly smaller than that of the LW and OW in the stem wood of *G. biloba*.
7. The quantitative aspects of the anatomical characteristics in the CW were distinctively different from that in the LW and OW, whereas the LW and OW showed mostly similar characteristics.

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REFERENCES CITED

Andersson, S., Serimaa, R., Paakkari, T., Saranpää, P., and Pesonen, E. (2003). "Crystallinity of wood and the size of cellulose crystallites in Norway spruce (*Picea abies*)," *J. Wood Sci.* 49(6), 531-537. DOI: 10.1007/s10086-003-0518-x

Andersson, S., Wang, Y., Pönni, R., Hänninen, T., Mononen, M., Ren, H., Serimaa, R., and Saranpää, P. (2015). "Cellulose structure and lignin distribution in normal and compression wood of the Maidenhair tree (*Ginkgo biloba* L.)," *J. Integr. Plant Biol.* 57(4), 388-395. DOI: 10.1111/jipb.12349

Andersson, S., Wikberg, H., Pesonen, E., Maunu, S. L., and Serimaa, R. (2004). "Studies of crystallinity of Scots pine and Norway spruce cellulose," *Trees* 18(3), 346-353. DOI: 10.1007/s00468-003-0312-9

Barnett, J. R., Gril, J., and Saranpää, P. (2014). "Introduction," in: *The Biology of Reaction Wood*, B. Gardiner, J. Barnett, P. Saranpää, and J. Gril (eds.), Springer Science & Business Media, New York, USA, pp. 1-11. DOI: 10.1007/978-3-642-10814-3

Burton, A. W., Ong, K., Rea, T., and Chan, I. Y. (2009). "On the estimation of average crystallite size of zeolites from the Scherrer equation: A critical evaluation of its application to zeolites with one-dimensional pore systems," *Micropor. Mesopor. Mat.* 117(1), 75-90. DOI: 10.1016/j.micromeso.2008.06.010

Cockrell, R. A. (1974). "A comparison of latewood pits, fibril orientation, and shrinkage of normal and compression wood of giant sequoia," *Wood Sci. Technol.* 8(3), 197-206. DOI: 10.1007/BF00352023

Donaldson, L. A. (1991). "The use of pit apertures as windows to measure microfibril angle in chemical pulp fibres," *Wood Fiber Sci.* 23(2), 290-295.

Eom, Y. G. (1991). "Anatomical comparison between compression and opposite wood in a branch of *Ginkgo biloba L*," *Journal of the Korean Wood Science and Technology* 19(3), 77-85.

Eom, Y. G., and Butterfield, B. G. (1997). "Anatomical comparisons of compression, opposite, and lateral woods in New Zealand radiata pine (*Pinus radiata* D. Don)," *Journal of the Korean Wood Science and Technology* 25(2), 88-99.

Eom, Y. G., and Butterfield, B. G. (2001). "Anatomical comparison of compression, opposite, and lateral woods in New Zealand rimu (*Dacrydium cupressinum* Lamb.)," *Journal of the Korean Wood Science and Technology* 29(3), 1-13.

Eun, D. J., and Kim, N. H. (2008a). "Variation of microfibril angle within stems of three commercial softwoods grown in Korea," *Journal of the Korean Wood Science and Technology* 36(4), 77-83.

Eun, D. J., Kwon, S. M., and Kim, N. H. (2008b). "Variation of fine structure of wood cellulose within stems of 3 commercial softwood species grown in Korea," *Journal of the Korean Wood Science and Technology* 36(1), 12-20.

Fujita, M., Saiki, H., Sakamoto, J., Araki, N., and Harada, H. (1979). "The secondary wall formation of compression wood tracheid. IV: Cell wall structure of transitional tracheids between normal wood and compression wood," *Bulletin of the Kyoto University Forests* 51, 247-256.

Gorisek, Z., Torelli, N., Vilhar, B., Grill, D., and Guttenberger, H. (1999). "Microfibril angle in juvenile, adult and compression wood of spruce and silver fir," *Phyton-Horn.* 39(3), 129-132.

Han, J. S., Mianowski, T., and Lin, Y. (1999). "Validity of plant fiber length measurement – A review of fiber length measurement based on kenaf as a model," in: *Kenaf Properties, Processing and Products*, T. Sellers, T., N. A. Reihert (eds.), Mississippi State University, Mississippi State, 149-167.

Harris, J. M. (1977). "Shrinkage and density of radiata pine compression wood in relation to its anatomy and mode of formation," *New Zeal. J. For. Sci.* 7(1), 91-106.

Kim, N. H., Kwon, S. M., and Chun, K. W. (2009). "Radial variation of rays in two commercial softwoods grown in Korea," *Wood Fiber Sci.* 41(2), 138-144.

Lee, P. W., and Eom, Y. G. (1988). "Anatomical comparison between compression wood and opposite wood in a branch of Korean pine (*Pinus koraiensis*)," *IAWA J.* 9(3), 275-284. DOI: 10.1163/22941932-90001077

Onaka, F. (1949). "Studies on compression and tension wood," *Wood Res-Slovakia* 24(3), 1-88.

Parham, R. A. (1971). "Crystallinity and ultrastructure of ammoniated wood: Part I. X-ray crystallinity," *Wood Fiber Sci.* 2(4), 311-320.

Preston, R. D. (1934). "The organization of the cell wall of the conifer tracheid," *Philos. T. Roy. Soc. B.* 224(511), 131-174. DOI: 10.1098/rstb.1934.0017

Purusatama, B. D., Kim, Y. K., Jeon, W. S., Lee, J. A., Kim, A. R., and Kim, N. H. (2018). "Qualitative anatomical characteristics of compression wood, lateral wood, and opposite wood in a stem of *Ginkgo biloba* L.," *Journal of the Korean Wood Science and Technology* 46(2), 125-131. DOI: 10.5658/WOOD.2018.46.2.125

Sahlberg, U., Salmén, L., and Oscarsson, A. (1997). "The fibrillar orientation in the S2-layer of wood fibres as determined by X-ray diffraction analysis," *Wood Sci. Technol.* 31(2), 77-86. DOI: 10.1007/BF00705923

Scott, R. A., Barghoorn, E. S., and Prakash, U. (1962). "Wood of Ginkgo in the tertiary of western North America," *Am. J. Bot.* 49(10), 1095-1101. DOI: 10.2307/2439157

Segal, L., Creely, J. J., Martin, A. E., and Conrad, C. M. (1959). "An empirical method for estimating the degree of crystallinity of native cellulose using the X-ray diffractometer," *Text. Res. J.* 29(10), 786-794. DOI: 10.1177/004051755902901003

Senft, J. F., and Bendtsen, B. A. (1985). "Measuring microfibrillar angles using light microscopy," *Wood Fiber Sci.* 17(4), 564-567.

Shirai, T., Yamamoto, H., Matsuo, M., Inatsugu, M., Yoshida, M., Sato, S., Sujan, K. C., Suzuki, Y., Toyoshima, I., and Yamashita, N. (2016). "Negative gravitropism of *Ginkgo biloba*: Growth stress and reaction wood formation," *Holzforschung* 70(3), 267-274. DOI: 10.1515/hf-2015-0005

Srivastava, L. M. (1963). "Cambium and vascular derivatives of *Ginkgo biloba*," *J. Arnold Arboretum* 44(2), 165-192.

Tanaka, F., Koshijima, T., and Okamura, K. (1981). "Characterization of cellulose in compression and opposite woods of a *Pinus densiflora* tree grown under the influence of strong wind," *Wood Sci. Technol.* 15(4), 265-273. DOI: 10.1007/BF00350944

Timell, T. E. (1982). "Recent progress in the chemistry and topochemistry of compression wood," *Wood Sci. Technol.* 16(2), 83-122. DOI: 10.1007/BF00351097

Timell, T. E. (1986). *Compression Wood in Gymnosperms* (Vol. 1-3), Springer-Verlag, Berlin, Germany. DOI: 10.1163/22941932-90001077

Tsoumis, G. (1991). *Science and Technology of Wood: Structure, Properties, Utilization* (Vol. 115), Van Nostrand Reinhold, New York, USA.

Uprichard, J. M., and Lloyd, J. A. (1980). "Influence of tree age on the chemical composition of radiata pine," *New Zeal. J. For. Sci.* 10(3), 551-557.

Wardrop, A. B., and Dadswell, H. E. (1950). "The nature of reaction wood II. The cell wall organization of compression wood tracheids," *Aust. J. Biol. Sci.* 3(1), 1-13. DOI: 10.1071/BI9500001

Yoshizawa, N., Kiyomiya, M., and Idei, T. (1987). "Variations in tracheid length and morphological changes in tracheid tips associated with the development of compression wood," *Wood Sci. Technol.* 21(1), 1-10. DOI: 10.1007/BF00349713

Yumoto, M., Ishida, S., and Fukazawa, K. (1983). "Studies on the formation and structure of the compression wood cells induced by artificial inclination in young trees of *Picea glauca*: IV. Gradation of the severity of compression wood tracheids," *Research Bulletins of the College Experiment Forests Hokkaido University* 40(2), 409-454.

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