A Comparative Study on Quantitative Anatomical Characteristics of Compression, Lateral, and Opposite Woods in *Agathis loranthifolia* and *Pinus merkusii*

Byantara Darsan Purusatama,[a] Suk Woo Kim,[b] and Nam Hun Kim [c,]*

Quantitative anatomical characteristics and their radial variation in compression (COW), lateral (LAW), and opposite (OPW) woods of *Agathis loranthifolia* and *Pinus merkusii* stem woods growing in Indonesia were observed and compared to understand wood quality. The length, diameter, wall thickness, and lumen diameter of tracheids and ray height and numbers were observed using optical microscopy. In both species, COW had the shortest tracheid length, smallest tracheid and lumen diameter, thickest cell wall, and highest ray numbers among the parts, while LAW and OPW showed comparable or variable values in quantitative characteristics. In *A. loranthifolia*, COW had the highest ray height, whereas, in *P. merkusii,* it had the lowest uniseriate and fusiform ray heights. No significant difference was observed in ray numbers and heights between LAW and OPW. In both species, the tracheid length and lumen-to-diameter ratio in COW, LAW, and OPW tended to increase from near the pith to near the bark while the wall-to-diameter ratio decreased. The ray heights of all parts increased with increasing distance from the pith, whereas the ray number decreased.

DOI: 10.15376/biores.19.1.925-943

Keywords: Agathis loranthifolia; Compression wood; Lateral wood; Opposite wood; Pinus merkusii; Quantitative anatomical characteristics

Contact information: a: Institute of Forest Science, Kangwon National University. Chuncheon 24341, Republic of Korea; b: Division of Forest Science, Kangwon National University, Chuncheon 24341, Republic of Korea; c: Department of Forest Biomaterials Engineering, College of Forest and Environmental Sciences, Kangwon National University, Chuncheon 24341, Republic of Korea;
** Corresponding author: kimnh@kangwon.ac.kr*

INTRODUCTION

Compression wood (COW) is classified as an abnormal wood tissue in conifers resulting from a response to mechanical stress experienced by a tree. In the stem wood, COW tends to push back, leaning the stem back to the vertical position, whereas in the branch wood, COW maintains the position of the branch against gravity. COW occurs on the lower side of a leaning stem and branches of conifers. Lateral woods (LAW) and opposite woods (OPW) also occur. The transverse surface of COW in the stem or branch commonly shows a darker brown or reddish color compared to the lateral and opposite sides (Timell 1973; Park 1979 and 1980; Purusatama and Kim 2018). In qualitative characteristics, the tracheid of COW typically shows a circular shape with a highly lignified S_2 layer and helical cavities in the cell wall, frequently surrounded by intercellular spaces (Timell 1986; Purusatama *et al.* 2018; 2021). In quantitative analysis, COW comprises a shorter tracheid length, smaller radial diameter, lower relative crystallinity, and smaller crystallite width compared to LAW and OPW. In addition, no significant differences exist in pit number and diameter in the cross-field of *Pinus densiflora* and *Ginkgo biloba* between COW, LAW, and OPW (Purusatama *et al.* 2020; Purusatama and Kim 2020). LAW and OPW of *G. biloba* tended to show comparable tracheid length, ray height, and ray number (Purusatama *et al.* 2018). Besides, in temperate conifers, LAW and OPW showed a difference in tracheid diameter and cell wall thickness (Kienholz 1930; Park *et al.* 1979; Eom and Butterfield 1997; Eom and Butterfield 2001; Yong *et al.* 2022)

A. loranthifolia and *P. merkusii*, which are commonly distributed in mountain areas of Indonesia, are fast-growing wood species widely planted in Indonesian plantation forests. Both wood species are generally utilized for paneling, molding, packaging, furniture, musical instruments, and the raw materials for pulp and paper (Martawijaya *et al.* 2005; Darmawan *et al.* 2018; Trisatya *et al.* 2021). The wood of both species shows comparable mechanical properties with commercial temperate softwoods such as Korean red pine and Sitka spruce (Nugroho and Surjokusumo 2002; Darmawan *et al.* 2018). However, compression wood frequently occurs in both species, which is a challenge for the Indonesian wood industry.

Understanding the characteristics of a woody stem is essential in evaluating wood quality and technical application. Specifically, the qualitative and quantitative anatomical characteristics of wood are valuable information for wood quality evaluation. To date, studies on the qualitative and quantitative anatomical characteristics of reaction wood in tropical softwood are limited.

Qualitative studies of reaction wood in tropical softwoods revealed that the helical cavity was absent in COW from *Agathis spp.*, *Araucaria spp.*, and *Agathis robusta* (Westing 1965; Timell 1986). A mild COW rich in lignin in the S_2 layer, helical cavity, and round shape of tracheid was found in *Araucaria brasiliana* (Yoshizawa and Idei 1986). Pandit and Rahayu (2007) reported that the COW of *A. loranthifolia* showed a circular shape tracheid in the transverse surface and helical cavities in the radial section, and S_3 was absent in the COW. Kim *et al.* (2015) revealed that mild COW of *Agathis borneensis* consistently showed intercellular spaces and high lignification in the outer part of the S_2 layer, while the rounded-shaped tracheid and helical cavities were absent. Purusatama *et al.* (2021) indicated that COW of *P. merkusii* and *A. loranthifolia* showed distinctive qualitative anatomical characteristics compared to LOW and OPW as helical cavities, slit-like bordered pit, and irregular arrangement of tracheid. They also found that helical ribs occurred in the COW of *P. merkusii* but were absent in the COW of *A. loranthifolia*.

For quantitative analysis of reaction wood in tropical softwoods, Purusatama *et al.* (2022) examined the COW, LAW, and OPW in *P. merkusii* and *A. loranthifolia* and revealed that COW and OPW in *P. merkusii* showed comparable tangential tracheid diameters. In contrast, COW had a significantly smaller tangential lumen diameter and tangential wall thickness than that for LAW and OPW. In *A. loranthifolia*, COW showed the smallest tangential tracheid and lumen diameters and the thickest tangential wall thickness among the parts, whereas LAW and OPW showed comparable tracheid characteristics. Safitri *et al.* (2023) reported that COW and OPW in *P. merkusii* seedlings showed comparable tracheid length, diameter, wall thickness, and ray frequency, whereas COW showed a significantly higher ray height and smaller tracheid proportion compared to OPW.

Studies on the radial variation of quantitative anatomical characteristics of COW, LAW, and OPW are few. Kienholz (1930) revealed that the tracheid length and diameter in COW, OPW, and side wood of *Tsuga mertensiana* increased with increasing growth ring number. Park *et al.* (1979; 1980) reported that the tracheid diameter and the cell wall thickness in COW, OPW, and side wood of *Pinus densiflora* branch wood increased from pith to bark, and the microfibril angles of all parts decreased. Purusatama and Kim (2018) revealed that the tracheid length and ray height of COW, LAW, and OPW in *Gingko biloba* stem wood increased from the 5^{th} to 20^{th} growth ring, whereas the ray number decreased. Purusatama and Kim (2020) showed that the radial tracheid diameter of COW in *Gingko biloba* increased with the increasing distance from the pith, whereas that in *Pinus densiflora* decreased. The radial tracheid diameter of LAW and OPW in *Gingko biloba* and *Pinus densiflora* was constant from the pith toward the bark.

To date, studies on the qualitative and quantitative anatomical characteristics of COW, LAW, and OPW in the stem of tropical softwood, including the radial variation, are lacking. A previous study revealed the difference in qualitative anatomical characteristics between COW, LAW, and OPW and between *A. loranthifolia* and *P. merkusii* (Purusatama *et al.* 2021). In this study, the quantitative anatomical characteristics of COW, LAW, and OPW in *A. loranthifolia* and *P. merkusii* were observed and compared in the radial direction to provide valuable information for effectively utilizing both species.

EXPERIMENTAL

Materials

The information on the sample trees used in the present study is similar to that of previous studies (Purusatama *et al.* 2020; 2021; 2022). A 65-year-old *Agathis loranthifolia* tree and a 49-year-old *Pinus merkusii* tree, each having a tilt of the stem axis close to 45° were obtained from Gunung Walat University Forest, Sukabumi, West Java, Indonesia (6.882937° N, 106.818511° E) (Fig. 1). The wood discs with a diameter of approximately 400 mm were taken from a height of 4 m above the ground. The wood disc was divided into three parts: COW, LOW, and OPW (Fig. 1).

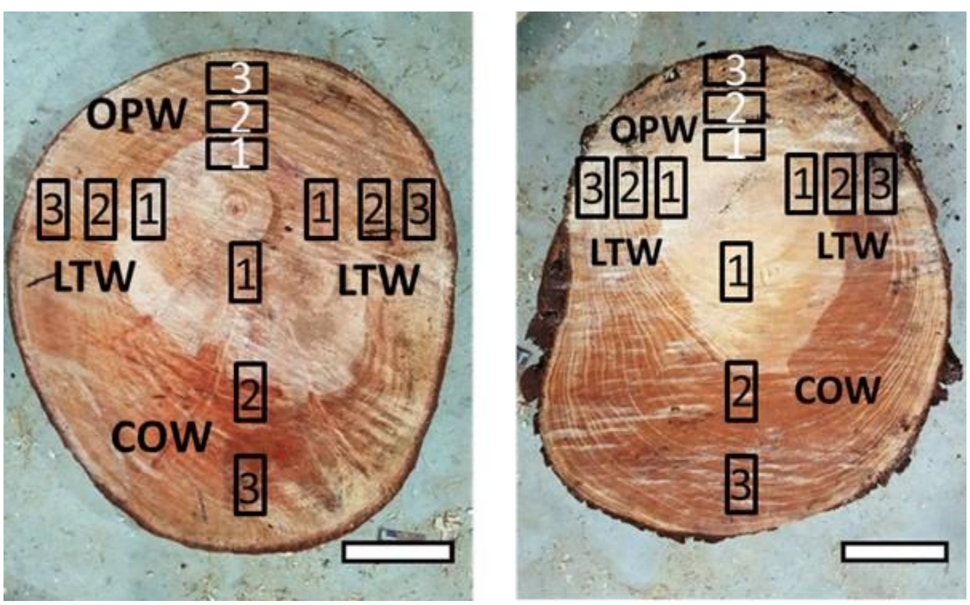


Fig. 1. Fresh-cut wood discs of *Agathis loranthifolia* (left) and *Pinus merkusii* (right). NP, middle zone, and NB are represented with 1, 2, and 3, respectively. Scale bars = 100 mm

The quantitative anatomical characteristics of each part were observed in three zones according to the distance from the pith, such as near the pith (NP), middle zone, and near the bark (NB). The NP, middle zone, and NB in COW were 50, 200, and 350 mm from the pith (Fig. 1).

Microscopy

Measurement of tracheid length

For the tracheid length measurement, matchstick-sized specimens of approximately 1 mm wide and 20 mm to 30 mm in length were prepared from each zone of COW, LAW, and OPW. The samples from each part were soaked in Schultze reagent (100 mL of 35% nitric acid [HNO3] and 0.6 g of 99.5% potassium chlorate [KClO3]) for three days and heated at 60 to 70 °C for 1 h (Park *et al.* 1993; Savero *et al.* 2022). The samples were stirred several times until they were unraveled during the heating process. Tracheid length was measured randomly with 50 tracheids using a measuring microscope (MM-40; Nikon, Tokyo, Japan) connected to an image analysis software (IMT i-solution lite, version 9.1; Burnaby, British Columbia, Canada).

Measurement of tracheid and ray properties

Wood discs were converted to small blocks (10 mm^3) and soaked in a mixture of glycerin and water (50:50). Then, the samples were heated with a heating plate for 30 to 45 min. Cross and tangential sections with a 15 to 20 µm thickness were prepared using a sliding microtome (Nippon Optical Works Co, Ltd., Tokyo, Japan). All slices were stained with 1% safranin solution and dehydrated by a graded series of alcohol (50%, 70%, 90%, 95%, and 99%) and xylene. Canada balsam was used as a mounting medium for permanent slides.

The tracheid diameter, lumen diameter, and tracheid wall thickness on the cross-section were measured from 50 earlywood tracheids according to Cuny *et al.* (2014), as shown in Fig. 2. The double wall thickness was determined by calculating the difference between the diameter of the tracheid and that of the lumen. The ratios of the lumen-to-diameter and wall-to-diameter in the radial and tangential directions were measured from 50 earlywood tracheids.

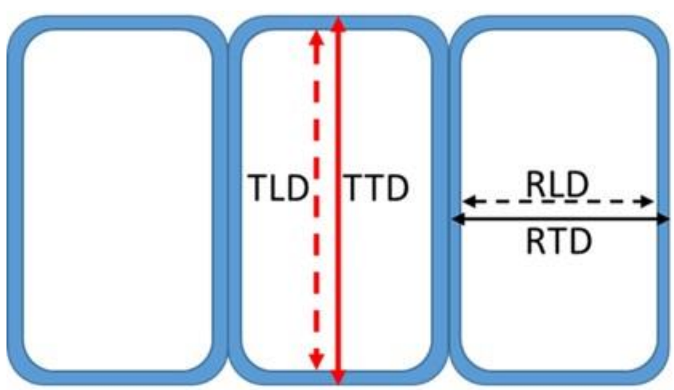


Fig. 2. Illustration of tracheid dimension measurement on the cross-section. TLD and TTD represent tangential lumen and tracheid diameters, while RLD and RTD are radial lumen and tracheid diameters, respectively

Ray number was measured in 20 areas of 1 × 1 mm^2 microscopic screen in tangential sections. The ray height of uniseriate and fusiform rays was randomly measured from 50 rays in each zone of COW, LAW, and OPW. The tracheid and ray properties were observed with an optical microscope (Eclipse E600; Nikon, Tokyo, Japan) with image analysis software (IMT i-solution lite, version 9.1; Burnaby, British Columbia, Canada).

Statistical Analysis

One-way analysis of variance and post-hoc Duncan's multiple range tests were used to analyze the significant differences in the quantitative anatomical characteristics between COW, LAW, and OPW and between NP, middle zone, and NB using SPSS software (SPSS ver. 26, IBM Corp., New York, USA).

RESULTS AND DISCUSSION

Tracheid Lengths

The tracheid lengths in COW, LAW, and OPW of *A. loranthifolia* and *P. merkusii* are shown in Table 1. Near the pith of *A. loranthifolia*, COW had a comparable tracheid length to LAW, and OPW had the longest tracheid length. Compression wood had the shortest tracheid length in the middle zone and near the bark, whereas LAW and OPW showed no significant differences. Regarding the average tracheid length, the COW of both species had the shortest tracheid length, whereas LAW and OPW were similar in length. In *P. merkusii*, no significant difference in the tracheid length was observed in COW, LAW, and OPW near the pith. Compression wood had the shortest tracheid length in the middle zone and near the bark. Lateral wood had the longest tracheid length in the middle zone, whereas OPW had the longest tracheid length near the bark. The tracheid lengths of COW, LAW, and OPW from both species increased from near the pith to near the bark.

In the present study, the tracheid length of all parts near the pith of both species showed a comparable length, whereas significant differences were observed in the middle zone and near the bark. In addition, the tracheid length of COW, LAW, and OPW in both species increased from pith to bark. Kienholz (1930) revealed that the compression and opposite side of *Tsuga mertensiana* had a comparable tracheid length at the 11^{th} to 21^{st} growth rings (near the pith). In contrast, the tracheid length of the compression side was distinctively shorter than the opposite side at the 31^{st} to 81^{st} growth rings. Wardrop and Dadswell (1950) reported that the tracheid length of the compression side near the pith (3^{rd} to 9^{th} growth rings) of *Pinus radiata* stem wood was comparable with the opposite side. The compression side had a shorter tracheid than the opposite side from the 10^{th} to 20^{th} growth rings. Purusatama and Kim (2018) reported that in the stem wood of *Ginkgo biloba*, COW and OPW had similar tracheid lengths at the 5^{th} and 10^{th} growth rings, and LAW had the longest. Furthermore, COW had the shortest tracheid length at the 15^{th} to 20^{th} growth rings, whereas LAW and OPW had similar tracheid lengths. Regarding the radial variation, the tracheid lengths of reaction wood in *Tsuga mertensiana*, *Pinus radiata*, and *Gingko biloba* increased with increasing growth ring numbers (Kienholz 1930; Wardrop and Dadswell 1950; Purusatama and Kim 2018).

The average tracheid length of COW, LAW, and OPW in *A. loranthifolia* and *P. merkusii* was categorized as medium length according to the IAWA list for softwood identification (IAWA Committee 2004). The average tracheid length of reaction wood in both species was noticeably longer than those of temperate reaction wood, such as *Tsuga* *mertensiana* (Kienholz 1930), *Pinus radiata* (Wardrop and Dadswell 1950), and *Gingko biloba* (Purusatama and Kim 2018), which is categorized as short according to the IAWA list for softwood identification (IAWA Committee 2004).

Table 1. Tracheid Length: COW, LAW, and OPW; *A. loranthifolia* and P. *merkusii*

Tracheid Length (µm)					
		NP	Middle	NB	Average
A. loranthifolia	COW	3024 (586)^{aA}	3055 (484)^{aA}	3894 (549)^{aB}	3325 (493)^{a}
	LAW	3177 (315) ^{aA}	4061(367) ^{cB}	4773 (422) ^{bC}	4004 (799)^{b}
	OPW	3408 (498)^{bA}	4172 (486)^{bB}	4651 (608)^{bB}	4144 (522)^{b}
P. merkusii	COW	2858 (399)^{aA}	3406 (576)^{aB}	4139 (320)^{aC}	3468 (642)^{a}
	LAW	2994 (605) ^{aA}	4129(465)^{cB}	4516 (317)^{bC}	3880 (791) ^{b}
	OPW	3006 (328) ^{aA}	3811 (267)^{bB}	4749 (434)^{cC}	3855 (872) ^{b}

* COW, LAW, OPW indicate compression, lateral, and opposite wood, respectively, and NP and NB represent near the pith and near the bark. Numbers in parentheses are standard deviations. The results of Duncan's multiple range tests at the 5% significance level between parts and between zones are represented with superscript letters beside the mean values. The same lowercase letters in the row represent insignificant differences between parts, and the same capital letters in the line indicate insignificant differences between zones.

Tracheid Diameter, Lumen Diameter, and Wall Thickness

The cross-sections of COW, LAW, and OPW in *A. loranthifolia* and *P. Merkusii* are shown in Figs. 3 and 4, respectively.

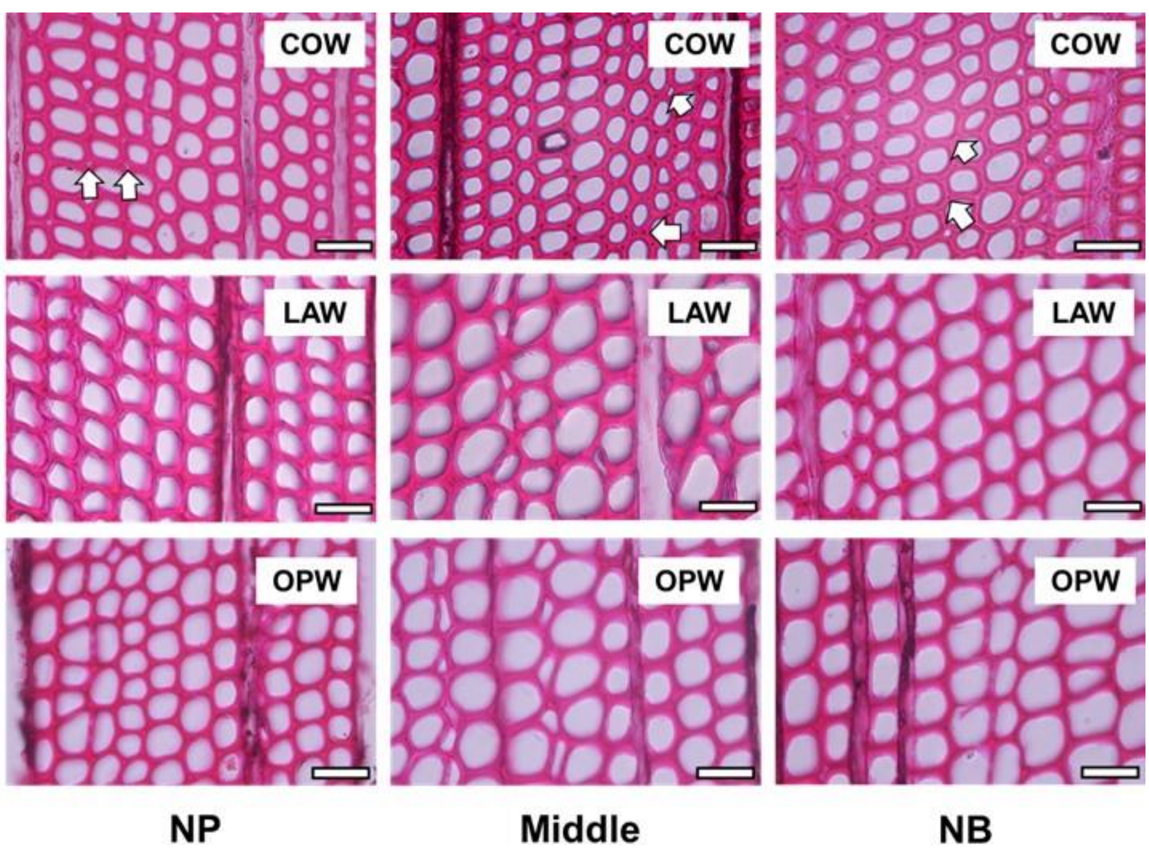


Fig. 3. The cross-section of COW, LAW, and OPW near the pith (NP), middle zone, and near the bark (NB) of *A. loranthifolia.* Intercellular spaces in COW (white arrows). Scale bars: 50 µm

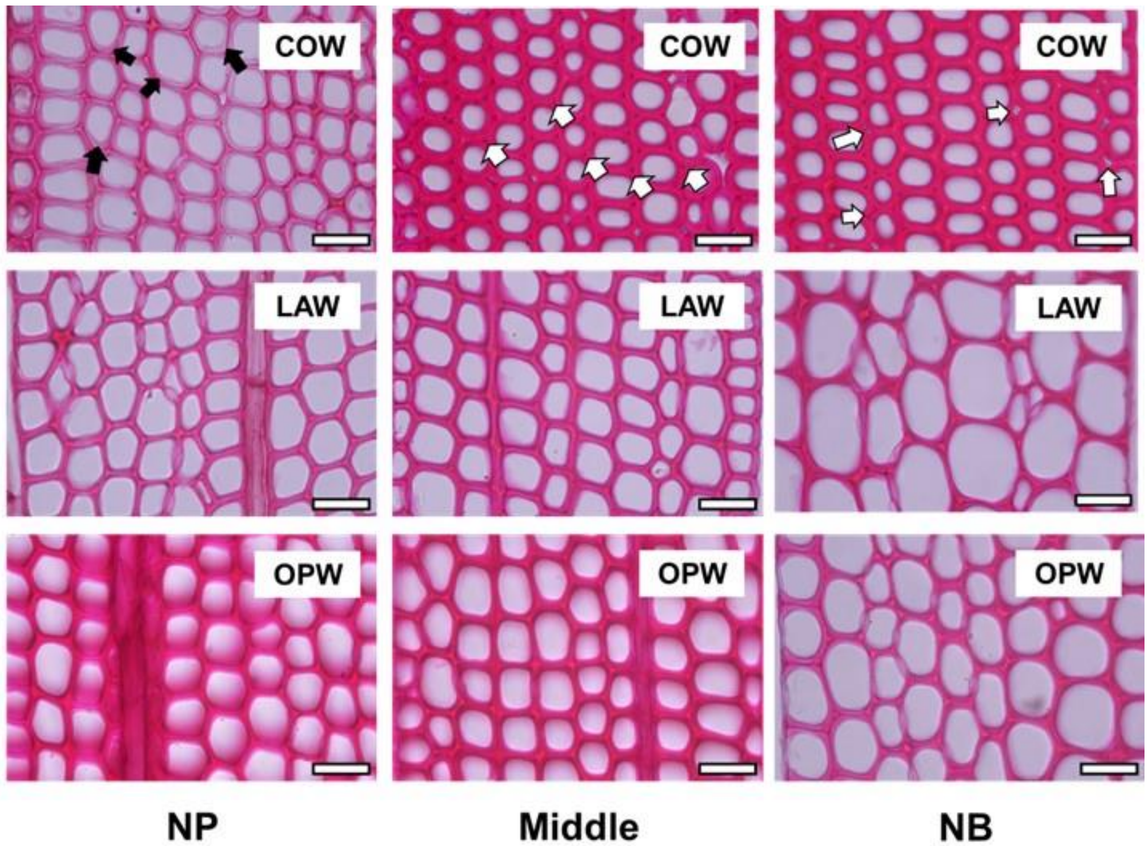


Fig. 4. The cross-section of COW, LAW, and OPW near the pith (NP), middle zone, and near the bark (NB) of *A. loranthifolia.* Intercellular spaces in COW (white arrows); Round lumen near the pith of COW (black arrows). Scale bars: 50 µm

In *A. loranthifolia*, the COW in each zone showed typical anatomical features with circular tracheid shapes and several intercellular spaces. In contrast, LAW and OPW showed oval lumens with angular outlines and no intercellular spaces. Near the pith of *P. merkusii*, the tracheid of COW showed a round lumen with an angular outline with no intercellular space. In the middle zone and near the bark, COW displayed circular tracheid shapes and numbers of intercellular spaces. Lateral wood and OPW near the pith and in the middle zone exhibited angular lumens and tracheid outlines, whereas near the bark of both parts showed oval tracheid lumens with angular outlines.

Table 2 shows the tracheid diameters in the radial and tangential directions of COW, LAW, and OPW in *A. loranthifolia* and *P. Merkusii*. In *A. loranthifolia*, COW near the pith had the greatest radial tracheid diameter, whereas LAW and OPW showed comparable values. The tangential tracheid diameters of COW and LAW were comparable, and OPW had a greater tangential tracheid diameter than that of COW and LAW. In the middle zone and near the bark, COW had the smallest radial and tangential tracheid diameter among all parts. Lateral wood in the middle zone had a significantly smaller radial tracheid diameter than that of OPW, whereas the tangential tracheid diameter of LAW was significantly greater than that of OPW. Furthermore, OPW near the bark had a significantly greater radial tracheid diameter than that of LAW, whereas LAW and OPW had comparable tangential tracheid diameters. COW had the smallest average value of radial and tangential tracheid diameter. Lateral wood had a significantly smaller radial tracheid diameter than that of OPW, whereas the tangential tracheid diameter was comparable between LAW and OPW. The tracheid diameter of COW decreased from near the pith to near the bark, whereas that of LAW and OPW increased.

Compression wood in each zone of *P. merkusii* had the smallest radial tracheid diameter. Near the pith and bark of *P. merkusii*, LAW and OPW had comparable radial tracheid diameters. In the middle zone, LAW had a significantly greater radial tracheid diameter than that of OPW. Near the pith of *P. merkusii*, the tangential tracheid diameter of COW was greater than that of OPW, whereas LAW had the greatest tangential tracheid diameter. In the middle zone, the tangential tracheid diameter of COW was the smallest, and that of LAW was the greatest. Near the bark, COW, LAW, and OPW had comparable tangential tracheid diameters. Compression wood had the smallest average value of radial and tangential tracheid diameters, whereas LAW had a significantly greater tracheid diameter than that of OPW. Significant differences were observed in the average tracheid diameter in radial and tangential directions between the parts. The tracheid diameter of COW, LAW, and OPW in *P. merkusii* increased from near the pith to near the bark.

Table 2. Tracheid Diameter in COW, LAW, and OPW of *A. loranthifolia* and P. *merkusii*

		Radial Tracheid Diameter (µm)				Tangential Tracheid Diameter (µm)			
		NP	Middle	NB	Mean	NP	Middle	NB	Mean
A. loranthifolia	COW	33.9 $(4.3)^{bB}$	26.3 $(4.7)^{aA}$	27.6 $(3.8)^{aA}$	29.3 $(5.4)^{a}$	32.4 $(5.1)^{aB}$	28.2 $(6.4)^{aA}$	29.6 $(4.7)^{aA}$	30.1 $(2.2)^{a}$
	LAW	31.8 $(5.0)^{aA}$	41.6 $(5.6)^{bB}$	43.6 $(7.3)^{bB}$	39.0 $(7.9)^{b}$	33.3 $(5.3)^{aA}$	48.9 $(7.0)^{cC}$	41.8 $(5.3)^{bB}$	41.3 $(8.1)^{b}$
	OPW	31.9 $(4.4)^{aA}$	45.2 $(6.4)^{cB}$	52.4 $(10.4)^{cC}$	43.8 $(11.4)^{c}$	37.0 $(5.2)^{bA}$	44.7 $(8.0)^{bB}$	45.1 $(7.4)^{bB}$	42.2 $(4.6)^{b}$
P. merkusii	COW	33.2 $(4.6)^{aB}$	27.6 $(3.8)^{aA}$	40.7 $(6.5)^{aC}$	33.8 $(6.6)^{a}$	41.7 $(7.8)^{abB}$	32.8 $(3.7)^{aA}$	46.4 $(6.8)^{aC}$	40.3 $(6.9)^{a}$
	LAW	39.6 $(6.9)^{bA}$	63.6 $(8.3)^{cB}$	61.9 $(8.8)^{bB}$	55.0 $(13.6)^{c}$	43.5 $(7.9)^{bA}$	50.3 $(9.4)^{cB}$	47.4 $(10.4)^{aB}$	47.1 $(9.7)^{c}$
	OPW	40.6 $(6.5)^{bA}$	41.6 $(6.3)^{bA}$	60.2 $(8.5)^{bB}$	47.5 $(11.3)^{b}$	40.1 $(8.6)^{aA}$	41.7 $(6.2)^{bA}$	46.8 $(8.9)^{aB}$	42.8 $(8.4)^{b}$

* Numbers in parentheses are standard deviations. The results of Duncan's multiple range tests at the 5% significance level between parts and between zones are represented with superscript letters beside the mean values. The same lowercase letters in the row represent insignificant differences between parts, and the same capital letters in the line indicate insignificant differences between zones.

Table 3 shows the lumen diameters in the radial and tangential directions of COW, LAW, and OPW in both species. In *A. loranthifolia*, COW, LAW, and OPW near the pith showed no significant difference in the radial lumen diameter. Compression wood had the smallest lumen diameter in the middle zone and near the bark. The radial lumen diameter of LAW was significantly smaller than that of OPW in the middle zone and near the bark. The tangential lumen diameter of LAW and OPW was comparable in the middle zone, whereas LAW near the bark showed a significantly smaller tangential lumen diameter compared to OPW. The lumen diameter of COW decreased from near the pith to near the bark, whereas that of LAW and OPW increased.

The lumen diameter of COW in each zone of *P. merkusii* had the smallest value among all parts. Near the pith of *P. merkusii*, LAW had a significantly smaller radial tracheid lumen diameter than that of COW, whereas LAW and OPW had comparable tangential tracheid lumen diameters. In the middle zone, the tracheid lumen diameter of LAW was significantly greater than that of COW and OPW, whereas no significant difference was observed in the tracheid lumen diameter of LAW and OPW near the bark. The lumen diameter of COW, LAW, and OPW in *P. merkusii* increased from near the pith to near the bark.

Table 3. Lumen Diameter in COW, LAW, and OPW of *A. loranthifolia* and P. *merkusii*

		Radial Lumen Diameter (μm)				Tangential Lumen Diameter (μm)			
		NP	Middle	NB	Mean	NP	Middle	NB	Mean
A. loranthifolia	COW	22.3 (3.4)^{aA}	17.0 (3.9)^{aB}	18.0 (3.2)^{aB}	19.1 (4.2)^{a}	21.0 (4.4)^{aB}	18.5 (5.7)^{aA}	19.3 (4.4)^{aAB}	23.2 (8.1)^{a}
	LAW	22.5 (4.4)^{aA}	32.2 (5.8)^{bB}	34.8 (6.2)^{bC}	29.9 (7.6)^{b}	24.2 (5.1)^{bA}	37.9 (6.1)^{bC}	32.2 (6.2)^{bB}	37.3 (10.3)^{b}
	OPW	23.9 (3.8)^{aA}	36.5 (5.6)^{cB}	43.7 (9.5)^{cC}	34.7 (10.6)^{c}	28.1 (4.8)^{cA}	35.6 (7.4)^{bB}	36.5 (7.5)^{cB}	33.6 (8.9)^{b}
P. merkusii	COW	16.1 (3.7)^{aB}	12.9 (2.9)^{aA}	27.1 (7.1)^{aC}	18.7 (7.8)^{a}	22.3 (5.4)^{aB}	15.9 (3.0)^{aA}	31.3 (6.3)^{aC}	23.2 (8.1)^{a}
	LAW	28.1 (6.5)^{bA}	54.0 (8.9)^{cB}	52.1 (9.0)^{bB}	44.7 (14.4)^{c}	30.4 (7.3)^{bA}	42.2 (9.0)^{cB}	39.2 (10.4)^{bB}	37.3 (10.3)^{b}
	OPW	30.6 (4.6)^{cA}	32.3 (6.0)^{bA}	52.6 (7.9)^{bB}	38.5 (11.8)^{b}	29.5 (7.7)^{bA}	31.6 (6.4)^{bA}	39.8 (8.8)^{bB}	33.6 (8.9)^{b}

* Numbers in parentheses are standard deviations. The results of Duncan's multiple range tests at the 5% significance level between parts and between zones are represented with superscript letters beside the mean values. The same lowercase letters in the row represent insignificant differences between parts, and the same capital letters in the line indicate insignificant differences between zones.

Table 4 shows the tracheid wall thicknesses of COW, LAW, and OPW in *A. loranthifolia* and *P. merkusii*. In *A. loranthifolia*, COW near the pith had the thickest cell wall among all parts. Lateral wood had a thicker radial wall thickness than that of OPW, whereas LAW and OPW had comparable tangential wall thicknesses. In the middle zone, COW, LAW, and OPW had comparable radial wall thicknesses. Lateral wood had the thickest tangential wall among the parts, whereas COW and OPW had comparable tangential wall thicknesses. Near the bark, the radial wall thickness of COW and OPW was comparable, whereas LAW showed a thicker radial wall thickness than that of COW and OPW. The tangential wall thickness of COW near the bark was the thickest among all parts, and that of LAW and OPW was comparable.

In *P. merkusii*, COW had the thickest tracheid wall in each zone. The tracheid wall of LAW near the pith and bark was significantly thicker than that of OPW. Lateral wood and OPW had comparable radial wall thicknesses in the middle zone, whereas OPW had a thicker tangential wall thickness than that of LAW. The tracheid wall thickness of COW decreased from near the pith to near the bark, whereas LAW had similar values in each zone. The radial cell wall thickness of OPW increased with increasing distance, but the tangential wall was stable.

Table 4. Cell Wall Thickness: COW, LAW, OPW: *A. loranthifolia* and P. *merkusii*

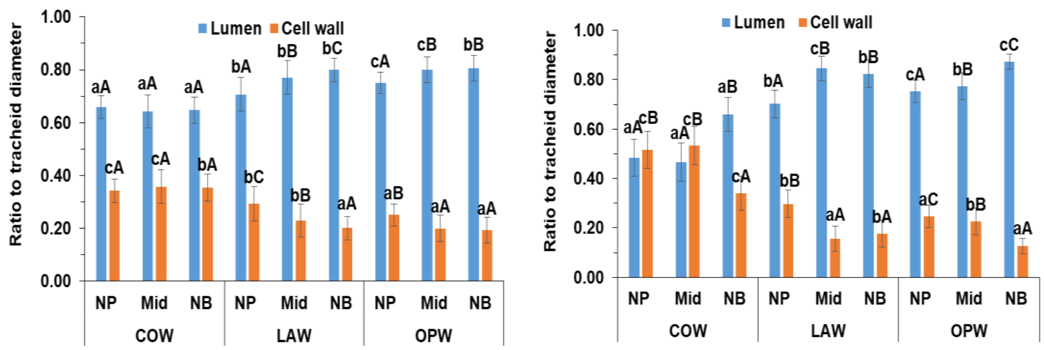
		Radial Wall Thickness (µm)				Tangential Wall Thickness (µm)			
		NP	Middle	NB	Mean	NP	Middle	NB	Mean
A. loranthifolia	COW	5.8 (1.0)^{cB}	4.7 (1.0)^{aA}	4.8 (0.8)^{bA}	5.1 (1.0)^{b}	5.7 (0.9)^{bB}	4.8 (0.9)^{aA}	5.1 (0.9)^{bA}	5.2 (1.0)^{c}
	LAW	4.6 (1.2)^{bA}	4.7 (1.2)^{aA}	4.4 (1.2)^{aA}	4.6 (1.2)^{a}	4.6 (1.0)^{aA}	5.5 (1.4)^{bB}	4.3 (1.1)^{aA}	4.8 (0.6)^{b}
	OPW	4.0 (0.8) ^{aA}	4.5 (1.1)^{aB}	5.1 (1.2)^{bC}	4.5 (1.1)^{a}	4.4 (1.0)^{aA}	4.6 (0.9)^{aA}	4.3 (1.2)^{aA}	4.4 (0.2)^{a}
P. merkusii	COW	8.5 (1.5)^{cC}	7.3 (1.4)^{bB}	6.7 (0.8)^{cA}	7.5 (1.0)^{c}	9.7 (2.1)^{cC}	8.5 (1.3)^{cB}	7.6 (1.0)^{cA}	8.6 (1.8)^{c}
	LAW	5.8 (0.9)^{bB}	4.8 (1.4)^{aA}	4.9 (1.2)^{bA}	5.2 (0.5)^{b}	6.6 (1.1)^{bB}	4.1 (1.1)^{aA}	4.1 (1.2)^{bA}	4.9 (1.7)^{b}
	OPW	5.1 (1.1)^{aB}	4.7 (1.2)^{aB}	3.8 (1.0)^{aA}	4.5 (0.7)^{a}	5.3 (1.2)^{aB}	5.0 (1.3)^{bB}	3.4 (1.2)^{aA}	4.6 (1.5)^{a}

*Numbers in parentheses are standard deviations. The results of Duncan's multiple range tests at the 5% significance level between parts and between zones are represented with superscript letters beside the mean values. The same lowercase letters in the row represent insignificant differences between parts, and the same capital letters in the line indicate insignificant differences between zones.

The COW of both species had a smaller tracheid and lumen diameter and a thicker tracheid wall than that of LAW and OPW. Lateral wood and OPW of *A. loranthifolia* had comparable tracheid diameter, lumen diameter, and cell wall thickness. However, in *P. merkusii*, LAW had a greater tracheid diameter, lumen diameter, and cell wall thickness than OPW. Several studies have reported a significant difference in tracheid diameter and wall thickness between COW, LAW, and OPW. Kienholz (1930) outlined that in the earlywood of *Tsuga mertensiana*, the tracheid radial diameter of COW was smaller than those of opposite and side wood. Furthermore, side wood had the largest radial tracheid diameter, and OPW was intermediate. Besides, in the latewood, the tangential diameters of COW, LAW, and OPW were comparable. Park *et al.* (1979) revealed that COW in the branch wood of *Pinus densiflora* had a smaller tracheid diameter and thicker cell wall than OPW and side wood. In the stem wood of *Pinus radiata*, COW had a smaller tangential diameter and thicker radial wall than LAW and OPW, whereas LAW showed a slightly greater tangential diameter and thicker radial wall than OPW (Eom and Butterfield 1997). Eom and Butterfield (2001) reported that COW, LAW, and OPW in the stem of *Dacrydium cupressinum* had similar tangential tracheid diameters. Moreover, COW had the thickest radial wall, and OPW had a thicker radial wall than LAW. Purusatama and Kim (2020) reported that the COW of *Ginkgo biloba* had the smallest radial tracheid diameter, whereas the OPW had a slightly larger radial tracheid diameter than LAW. They also demonstrated that the COW of *Pinus densiflora* had the smallest radial tracheid diameters, and LAW had the largest diameter among the parts. Yong *et al.* (2022) reported that COW of *Taxodium* hybrid had a smaller tracheid diameter and thicker double wall thickness than that of LAW and OPW, whereas LAW had a significantly smaller tracheid diameter and thicker double wall thickness than that of OPW. Several studies exist on the tracheid properties of normal wood (Sarén *et al.* 2001; Lindström 2007; Lee *et al.* 2014; Kim *et al.* 2022). However, studies on the radial variation in tracheid diameter and tracheid wall thickness of reaction wood are limited. Kienholz (1930) outlined that the tangential diameter of the latewood and radial tracheid diameter of earlywood in COW, OPW, and side wood of *Tsuga mertensiana* increased with increasing growth ring number. Onaka (1949) described that the tracheid radial diameter of COW decreased with increasing age, whereas that of OPW showed an opposite tendency. Park *et al.* (1979) reported that the tracheid diameter and cell wall thickness in the branch and stem wood of *Pinus densiflora* increased from pith to bark. Purusatama and Kim (2020) revealed that the radial tracheid diameter of COW, LAW, and OPW in *Ginkgo biloba* slightly increased with increasing growth ring number. In addition, the radial tracheid diameters were significantly decreased in COW of *Pinus densiflora*, and that in OPW was significantly increased with increasing growth ring number. The LAW showed no specific trend with increasing growth ring number.

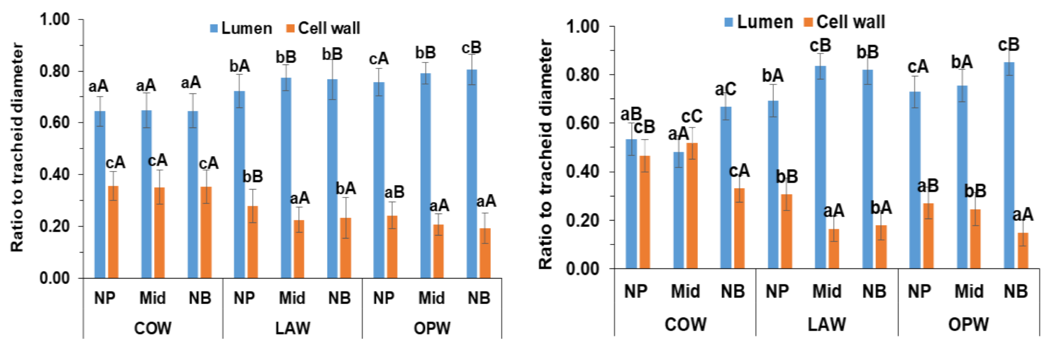
Lumen- and Wall-to-diameter Ratios

Figures 5 and 6 show the ratios of the lumen-to-diameter and wall-to-diameter in the radial and tangential directions of *A. loranthifolia* and *P. merkusii*, respectively. In both species, COW had a higher ratio of wall-to-diameter than that of LAW and OPW, whereas the lumen-to-diameter ratio in LAW and OPW was higher than in COW.



(A) (B)

Fig. 5. Radial lumen- and wall- to diameter ratio in *A. loranthifolia* (A) and *P. merkusii* (B). The same lowercase letters on the histograms represent insignificant differences between parts, and the same capital letters on the histograms indicate insignificant differences between zones.



(A) (B)

Fig. 6. Tangential lumen- and wall-to-diameter ratio in *A. loranthifolia* (A) and *P. merkusii* (B). The same lowercase letters on the histograms represent insignificant differences between parts, and the same capital letters on the histograms indicate insignificant differences between zones.

In *A. loranthifolia*, LAW near the pith and in the middle zone showed a higher tangential wall-to-diameter and lower lumen-to-diameter. In contrast, LAW and OPW near the bark showed a comparable value. LAW near the pith and the bark had higher tangential wall-to-diameter and lower lumen-to-diameter than OPW, whereas, in the middle zone, LAW and OPW showed a comparable value. In addition, the lumen-to-diameter ratio was greater than the wall-to-diameter ratio of COW, LAW, and OPW. The ratios of the lumen-to-diameter and wall-to-diameter of COW were constant from near the pith to the bark. The ratio of lumen-to-diameter in LAW and OPW increased with increasing distance from the pith, whereas the wall-to-diameter ratio decreased.

Near the pith and the bark of *P. merkusii*, LAW had higher radial and tangential wall-to-diameter and lower lumen-to-diameter ratios than OPW, whereas, in the middle zone, OPW showed a higher wall-to-diameter and smaller lumen-to-diameter ratios.

COW near the pith and in the middle zone showed a comparable portion of tracheid lumen and cell wall, whereas, near the bark, the lumen-to-diameter ratio was noticeably greater than the wall-to-diameter ratio. LAW and OPW had a higher portion of lumen than cell walls in all zones. The ratio of tracheid lumen-to-diameter in COW, LAW, and OPW increased from near the pith to the bark, whereas the tracheid wall-to-diameter decreased.

Yong *et al.* (2022) reported that the wall-to-cavity ratio of COW tracheid in a young stem of *Taxodium* hybrid was significantly higher than LAW and OPW, and that of LAW was higher than that of OPW. Additionally, they showed that the cavity-to-diameter ratio of COW tracheid was the smallest, whereas LAW and OPW had comparable values.

Ray Numbers and Height

The tangential sections of COW, LAW, and OPW in *A. loranthifolia* and *P. merkusii* are shown in Figs. 7 and 8, respectively.

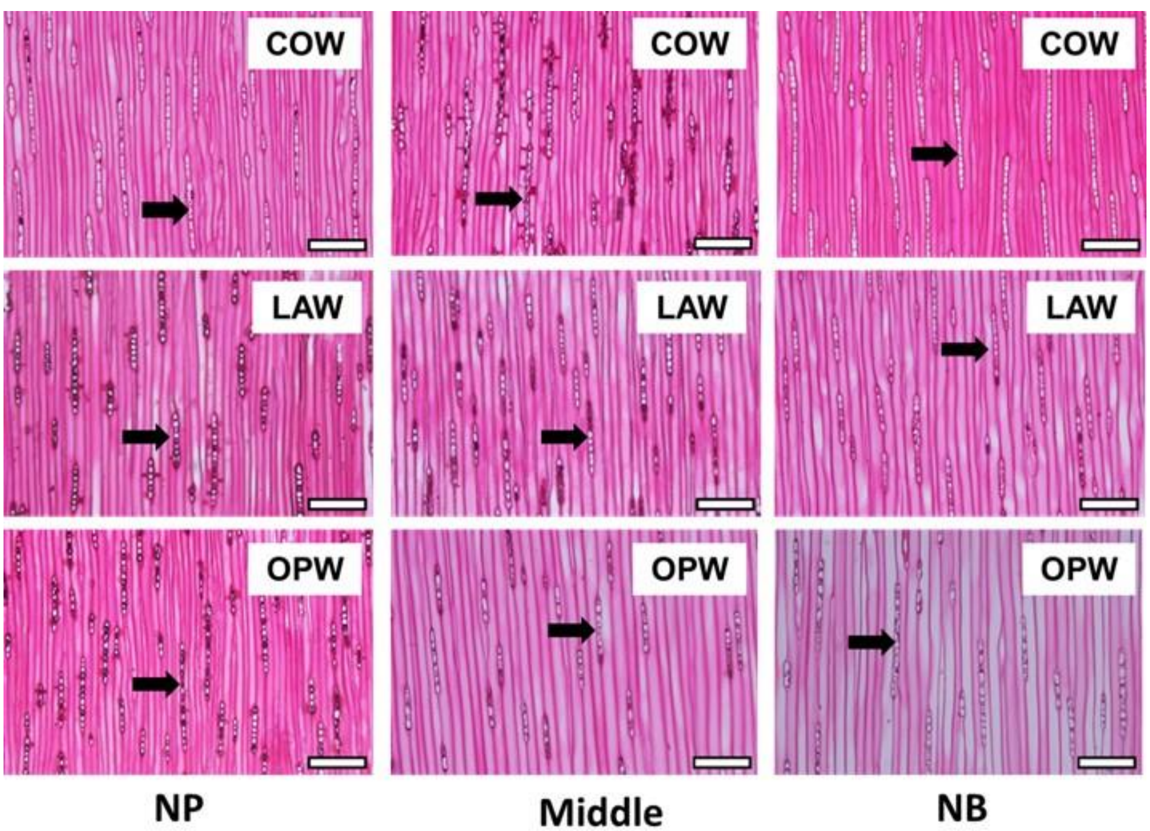


Fig. 7. The tangential sections of COW, LAW, and OPW near the pith (NP), middle zone, and near the bark (NB) of *A. loranthifolia.* Uniseriate rays in each zone of COW, LAW, and OPW (black arrows). Scale bars: 200 µm

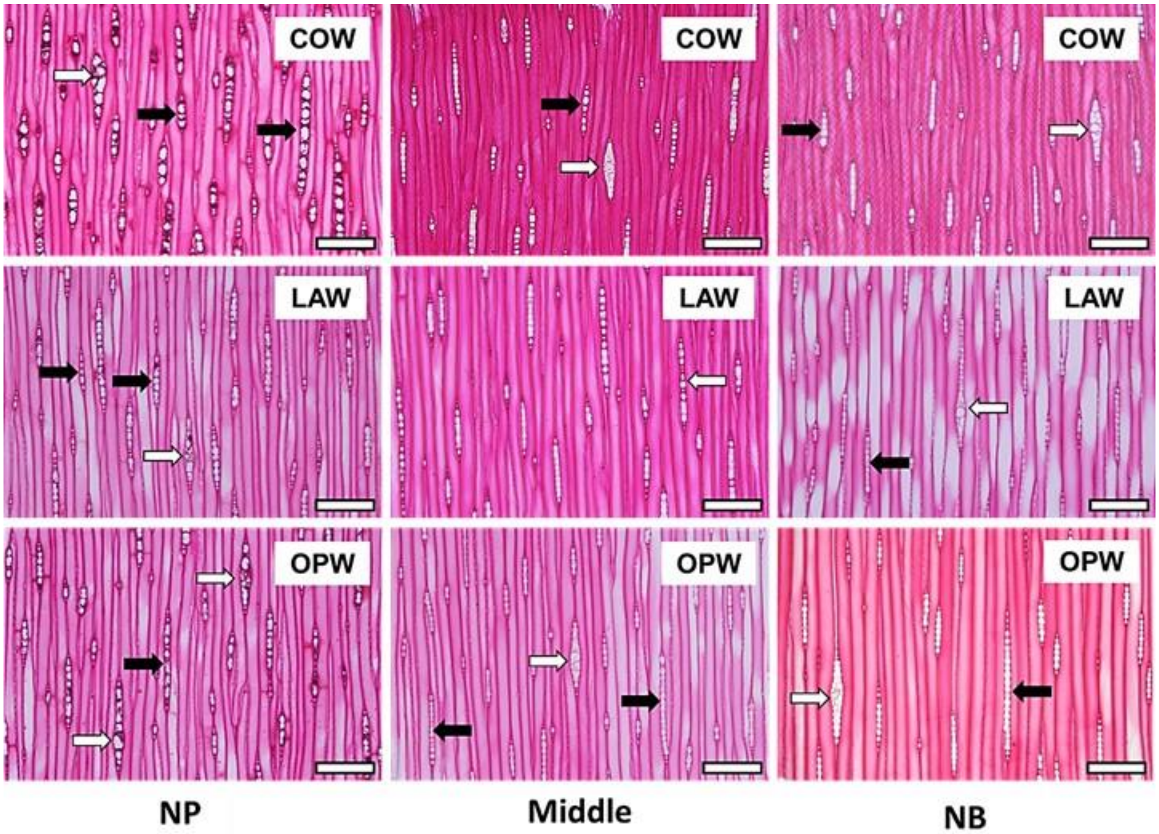


Fig. 8. The tangential sections of COW, LAW, and OPW near the pith (NP), middle zone, and near the bark (NB) of *P. merkusii.* Uniseriate rays (black arrows) and fusiform rays (white arrows) in each zone of COW, LAW, and OPW. Scale bars: 200 µm

In *A. loranthifolia*, uniseriate rays were dominant in each zone of all parts, and there were no fusiform rays. In *P. merkusii*, uniseriate and fusiform rays were generally observed in all parts.

The ray numbers per mm^2 of COW, LAW, and OPW in *A. loranthifolia* and *P. merkusii* are presented in Table 6. In *A. loranthifolia*, COW and LAW near the pith had the smallest ray numbers, whereas OPW had the highest numbers. Compression wood had the highest ray numbers among parts in the middle zone and near the bark, whereas no significant difference was observed for LAW and OPW. In *P. merkusii*, COW had the highest ray numbers in each zone. Lateral wood and OPW of *P. merkusii* had similar ray numbers near the pith and bark, whereas OPW had significantly higher ray numbers than that of LAW in the middle zone. In both species, COW had the highest average ray numbers, whereas LAW and OPW were similar. The ray numbers of COW, LAW, and OPW in both species decreased from near the pith to near the bark.

Several studies on ray numbers in COW of several temperate conifers have been conducted. Onaka (1949) reported that the number of rays in COW of *Abies firma*, *Abies mayriana*, *Gingko biloba*, *Larix gmelinii*, and *Pinus densiflora* were lower than those in normal wood. Timell (1986) revealed that the ray numbers of COW in *Larix laricina*, *Picea mariana*, and *Pinus palustris* were higher than that of normal wood. Chung and Lee (1989) described that COW had higher ray numbers than OPW and side wood in the stem wood of *Pinus densiflora*, and the ray numbers of OPW were slightly higher than that of side wood. In addition, Eom and Butterfield (1997; 2001) reported that COW ray numbers in the stem and branch wood of *Pinus radiata* and *Dacrydium cupressinum* were the smallest between COW, LAW, and OPW; however, LAW and OPW were comparable. Purusatama and Kim (2018) described that COW had lower ray numbers than that of LAW and OPW in the stem wood of *Ginkgo biloba*, while there was no significant difference between LAW and OPW.

Regarding the radial variation of ray numbers in softwood, some studies identified the boundary between juvenile and mature wood using normal wood. Kim *et al*. (2009) reported that the ray numbers in *Pinus koraiensis* and *Larix kaempferi* decreased from the pith to the 10^{th} to 20^{th} growth rings and were almost constant from the 20^{th} growth ring toward the bark. Kim *et al.* (2020) showed that the ray numbers in normal wood of *Larix gmelinii* and *Larix kaempferi* decreased gradually from the pith to the 20^{th} and 30^{th} growth rings, respectively, and the ray numbers of both species were stable.

However, the radial variation of ray numbers in the reaction wood of softwood has rarely been examined. Purusatama and Kim (2018) reported that the ray numbers of COW, LAW, and OPW in stem wood *Ginkgo biloba* decreased with increasing growth numbers.

Table 6. Ray Numbers of COW, LAW, and OPW in *A. loranthifolia* and P. *merkusii*

Ray number (Rays/mm^2)					
		NP	Middle	NB	Average
A. loranthifolia	COW	20.4 (1.9)^{aB}	19.5 (1.4)^{bB}	17.2 (1.0)^{bA}	19.0 (1.6)^{b}
	LAW	21.0 (2.6)^{aC}	16.2 (1.7)^{aB}	13.2 (1.0)^{aA}	16.8 (3.9)^{a}
	OPW	22.4 (1.5)^{bC}	16.6 (2.9)^{aB}	14.2 (2.2)^{aA}	17.7 (4.1)^{a}
P. merkusii	COW	22.1(1.6)^{bC}	20.0 (1.6)^{cB}	16.9 (1.4)^{bA}	19.6 (2.6)^{b}
	LAW	20.5 (1.2)^{aC}	16.4 (2.2)^{aB}	14.9 (2.7)^{aA}	17.3 (2.9)^{a}
	OPW	20.5 (2.0)^{aC}	17.9 (1.8)^{bB}	13.7 (1.6)^{aA}	17.4 (3.5)^{a}

* Numbers in parentheses are standard deviations. The results of Duncan's multiple range tests at the 5% significance level between parts and between zones are represented with superscript letters beside the mean values. The same lowercase letters in the row represent insignificant differences between parts, and the same capital letters in the line indicate insignificant differences between zones.

The ray heights of uniseriate rays in *A. loranthifolia* and *P. merkusii* are shown in Table 7. Near the pith of *A. loranthifolia*, there was no significant difference in ray height between parts. In the middle zone and near the bark, COW had the highest ray height, whereas LAW and OPW were not significantly different. Moreover, COW had the highest average ray height, whereas LAW and OPW were similar. In *P. merkusii*, COW had the smallest uniseriate ray height in each zone, whereas LAW and OPW were not significantly different. In addition, the uniseriate ray heights of COW, LAW, and OPW in both species increased from near the pith to near the bark. Timell (1986) reported that the ray heights of COW in *L. laricina*, *P. mariana*, and *P. palustris* were higher than that of normal wood. Chung and Lee (1989) indicated that COW had a smaller ray height than that of OPW and side wood in the stem of *Pinus densiflora*, whereas side wood and OPW had similar ray heights. Eom and Butterfield (1997) reported that COW in radiata pine had higher uniseriate ray heights than that of LAW and OPW, whereas OPW had slightly higher uniseriate ray heights than LP. Furthermore, in *Dacrydium cupressinum*, COW, LAW, and OPW had comparable uniseriate ray heights. Purusatama and Kim (2018) showed that COW had higher ray heights than LAW and OPW in stem wood *G. biloba*, whereas there was no significant difference between LAW and OPW. It can be suggested that the ray height of COW was distinctively different from those of LAW and OPW, and variations existed in the ray height of the reaction wood between species.

The radial variation in ray height of the present study is consistent with a few previous studies on the radial variation of ray height in temperate compression wood and normal wood. Purusatama and Kim (2018) reported that the ray height in COW, LAW, and OPW of *G. biloba* increased with increasing growth numbers. Furthermore, the ray heights in normal wood of *P. koraiensis*, *L. kaempferi*, and *L. gmelinii* increased with increasing growth ring and were constant after approximately the 20th and 25th growth number (Kim *et al.* 2009; Kim *et al.* 2020).

Table 7. Uniseriate Ray Heights of COW, LAW, and OPW in *A. loranthifolia* and P. *merkusii*

Ray Height (cell number)					
		NP	Middle	NB	Average
A. loranthifolia	COW	7.1 (2.1)^{aA}	9.6 (2.7)^{bB}	10.7 (3.2)^{bB}	9.1 (1.8)^{a}
	LAW	6.7 (2.0)^{aA}	7.9 (1.5)^{aB}	9.1 (2.6)^{aC}	7.9 (1.2)^{b}
	OPW	6.5 (2.3)^{aA}	7.7 (2.1)^{aB}	8.4 (2.6)^{aB}	7.5 (0.9)^{b}
P. merkusii	COW	5.7 (1.5)^{aA}	8.2 (1.7)^{aB}	9.8 (1.5)^{aC}	7.9 (2.0)^{a}
	LAW	8.8 (2.0)^{bA}	10.3 (2.2)^{bB}	10.9 (2.5)^{bB}	10.0 (1.1)^{b}
	OPW	8.7 (2.9)^{bA}	10.7 (3.2)^{bB}	10.8 (2.9)^{bB}	10.0 (1.2)^{b}

* Numbers in parentheses are standard deviations. The results of Duncan's multiple range tests at the 5% significance level between parts and between zones are represented with superscript letters beside the mean values. The same lowercase letters in the row represent insignificant differences between parts, and the same capital letters in the line indicate insignificant differences between zones.

The fusiform ray heights of COW, LAW, and OPW in *P. merkusii* are presented in Table 8. There was no significant difference in the fusiform ray height among COW, LAW, and OPW near the pith, whereas, in the middle zone, Lateral wood had a higher fusiform ray height than COW and OPW. Additionally, fusiform ray heights were not significantly different between COW and OPW. Near the bark, the fusiform ray height of COW was the smallest, whereas those of LAW and OPW were not significantly different. Moreover, COW had the smallest average fusiform ray height, and that of LAW and OPW were comparable. The fusiform ray heights of COW, LAW, and OPW increased from near the pith to near the bark. Studies on fusiform ray height in the reaction wood of temperate conifers are limited. Lee and Eom (1988) reported that COW in the branch wood of *Pinus koraiensis* had a smaller fusiform ray height than OPW. In *Pinus densiflora*, the COW of stem wood had the smallest fusiform ray height, whereas the side wood was the highest among the parts (Chung and Lee 1989). Furthermore, the fusiform ray height of COW in *P. radiata* was intermediate between those of LAW and OPW, which were the highest and the lowest, respectively (Eom and Butterfield 1997).

The results of the present study are consistent with previous studies on the radial variation in fusiform ray height of normal wood. Lev-Yadun (1998) found a gradual increase with age in the ray heights of *Pinus halepensis* and *Pinus pinea*. In addition, Kim *et al.* (2009) revealed that the fusiform ray height increased from the pith toward the bark and stabilized after the 15 to 20th growth ring. Furthermore, the fusiform ray heights in normal wood of *L. kaempferi* and *L. gmelinii* increased with increasing growth ring number and became constant after approximately the 25th annual growth number (Kim *et al.* 2020).

Table 8. Fusiform Ray Heights of COW, LAW, and OPW in *Pinus merkusii*

Fusiform Ray Height (μm)				
	NP	Middle	NB	Average
COW	224.0^{aA} (42.9)	225.6^{aA} (46.0)	268.8^{aB} (50.1)	239.4^{a} (25.4)
LAW	239.9^{aA} (43.0)	253.5^{bA} (44.1)	309.0^{bB} (42.5)	267.5^{b} (36.6)
OPW	223.9^{aA} (57.0)	231.6^{aA} (56.3)	316.5^{bB} (79.4)	257.3^{b} (51.4)

* Numbers in parentheses are standard deviations. The results of Duncan's multiple range tests at the 5% significance level between parts and between zones are represented with superscript letters beside the mean values. The same lowercase letters in the row represent insignificant differences between parts, and the same capital letters in the line indicate insignificant differences between zones.

CONCLUSIONS

1. In both species, the tracheid of compression wood (COW) had the shortest length, and lateral wood (LAW) and opposite wood (OPW) were similar. The tracheid lengths of all parts increased from near the pith to the bark.
2. Compression wood of both species had the smallest tracheid and lumen diameter and lumen-to-diameter ratio, whereas the tracheid wall thickness and the wall-to-diameter ratio of COW were high.
3. In *Agathis loranthifolia*, OPW had a greater radial tracheid and lumen diameter than that of LAW, whereas LAW and OPW had similar radial cell wall thicknesses. The tangential and lumen diameters of LAW and OPW were comparable, and the tangential wall of LAW was significantly thicker than that of OPW. In *Pinus merkusii*, LAW had a greater tracheid and lumen diameter and a thicker cell wall than that of OPW.
4. In *A. loranthifolia*, the tracheid diameter of COW decreased from near the pith to near the bark, whereas that of LAW and OPW increased. In *P. merkusii*, the tracheid diameters of COW, LAW, and OPW increased as the distance from the pith increased.
5. In *A. loranthifolia*, the lumen-to-diameter and wall-to-diameter ratios of each zone in COW were constant. The lumen-to-diameter ratios in LAW and OPW of both species and COW of *P. merkusii* increased as the distance from the pith increased, and vice versa for the wall-to-diameter ratio.
6. In both species, COW had the highest average ray numbers among parts. Moreover, in *A. loranthifolia*, COW had the highest average ray height, whereas, in *P. merkusii*, COW had the smallest uniseriate ray height in each zone. Lateral wood and OWP of both species showed comparable ray properties. The ray height of all parts increased with increasing distance from the pith, whereas the ray numbers decreased.
7. In conclusion, the COW of both species showed significantly different tracheid and ray properties to LAW and OPW. Lateral wood and OPW of both species showed distinctive tracheid properties, whereas the ray properties were comparable. The reaction woods of *A. loranthifolia* and *P. merkusii* had distinctive tracheid and ray properties. The results of the present study can be used to identify and evaluate the reaction woods of both species for effective utilization. Further studies on the chemical

and mechanical properties, such as chemical component ratio, bending, tensile, and abrasion properties, should be considered.

ACKNOWLEDGMENTS

This research was supported by the Science and Technology Support Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Science and ICT (MSIT) (NRF-2019K1A3A9A01000018; NRF-2022R1A2C1006470), Basic Science Research Program through the NRF funded by the Ministry of Education (No. 2018R1A6A1A03025582), and R&D Program for Forest Science Technology (Project No. 2021350C10-2323-AC03) provided by the Korea Forest Service (Korea Forestry Promotion Institute). We also would like to express our deepest gratitude to the late Prof. Fauzi Febrianto for his invaluable contributions to this research.

REFERENCES CITED

Chung, Y. J., and Lee, P. W. (1989). "Anatomical studies on the features of rays in compression wood of Korean red pine (*Pinus densiflora* S. Et Z.)," *Journal of Korean Society of Forest Science* 78(2), 119-131.

Cuny, H. E., Rathgeber, C. B. K., Frank, D., Fonti, P., and Fournier, M. (2014). "Kinetics of tracheid development explain conifer tree-ring structure," *New Phytologist* 203, 43-44. DOI: 10.1111/nph.12871

Darmawan, W., Nandika, D., Afaf, B. D. H., Rahayu, I., and Lumonjja, D. (2018). "Radial variation in selected wood properties of Indonesian Merkusii Pine," *Journal of the Korean Wood Science and Technology* 46(4), 323-337. DOI: 10.5658/WOOD.2018.46.4.323

Denne, P., and Gasson, P. (2008). "Ray structure in root-and stem-wood of *Larix decidua*: Implications for root identification and function," *IAWA Journal* 29(1), 17-23. DOI: 10.1163/22941932-90000166

Eom, Y. G., and Butterfield, B. G. (1997). "Anatomical comparisons of compression, opposite, and lateral woods in New Zealand radiata pine (*Pinus radiat*a 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.

IAWA Committee. (2004). "IAWA list of microscopic features for softwood identification," *IAWA Journal* 25, 1-70.

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

Kim, D. H., Kim, S. H., Jo, J. I., Kim, J. H., Purusatama, B. D., Lee, S. H., and Kim, N. H. (2020). "Ray properties in the stems of Dahurian larch (*Larix gmelinii*) and Japanese larch (*Larix kaempferi*)," *IAWA Journal* 42(2), 134-142. DOI: 10.1163/22941932-bja10031

Kim, D. H., Kim, J. H., Purusatama, B. D., Suri, I. F., Yang, G. U., Febrianto, F., and Kim, N. H. (2022). "A comparative study of the tracheid and crystalline properties of Dahurian larch (*Larix gmelinii*) and Japanese larch (*Larix kaempferi*) wood," *BioResources* 17(2), 2768-2779. DOI: 10.15376/biores.17.2.2768-2779

Kienholz, R. (1930). "The wood structure of a "pistol-butted" mountain hemlock," *American Journal of Botany* 17(8), 739-764. DOI: 10.1002/j.1537-2197.1930.tb04919.x

Lee, A.-H., Jang, J.-H., Kim, N.-H., and Park, B.-H. (2014). "Anatomical characteristics of Yellow-hearted pine (*Pinus densiflora* for. erecta Uyeki)," *Journal of Forest and Environmental Science* 30(1), 56-61. DOI: 10.7747/JFS.2014.30.1.56

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 Journal* 9(3), 275-284. DOI: 10.1163/22941932-90001077

Lindström, H. (2007). "Fiber length, tracheid diameter, and latewood percentage in Norway spruce: Development from pith outward," *Wood and Fiber Science* 29(1), 21-34.

Martawijaya, A., Kartasujana, I., Kadir, K., and Prawira, S.A. (2005). *Atlas Kayu Indonesia Jilid I*. Pusat Penelitian dan Pengambangan Hasil Hutan, Bogor.

Nugroho, N., and Surjokusumo, S. (2002) "*Agathis loranthifolia* an excellent structure material for wooden aircraft," *7th World Conference on Timber Engineering* 2, 370-376.

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

Pandit, I. K. N., and Rahayu, I. S. (2007). "Ultra-structure of compression wood of Agathis (*Agathis loranthifolia* Salisb.) and its relation to physical properties," *Jurnal Ilmu dan Teknologi Kayu Tropis* 5(1), 1-6.

Park, S.-J., Lee, J.-Y., Cho, N.-S., and Cho, B.-M. (1993). *Wood Science Experiment Book*, Gwangil Munhwasa, Seoul, Korea.

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

Purusatama, B. D., and Kim, N. H., (2018). "Quantitative anatomical characteristics of compression wood, lateral wood, and opposite wood in the stem wood of *Ginkgo biloba* L.," *BioResources* 13(4), 8076-8088. DOI: 10.15376/biores.13.4.8076-8088

Purusatama, B. D., and Kim, N. H., (2020). "Cross-field pitting characteristics of compression, lateral, and opposite wood in the stem wood of *Ginkgo biloba* and *Pinus densiflora*," *IAWA Journal* 41(1), 48-60. DOI: 10.1163/22941932-00002107

Purusatama, B. D., Choi, J. K., Lee, S. H., and Kim, N. H. (2020). "Microfibril angle, crystalline characteristics, and chemical compounds of reaction wood in stem wood of *Pinus densiflora*," *Wood Science and Technology* 54, 123-137. DOI: 10.1007/s00226-019-01140-w

Purusatama, B. D., Kim, J. H., Yang, G. U., Febrianto, F., Hidayat, W., Lee, S. H., and Kim, N. H. (2021). "Qualitative anatomical characteristics of compression, lateral, and opposite woods in *Pinus merkusii* and *Agathis loranthifolia,*" *Jurnal Sylva Lestari* 9(2), 213-222. DOI: 10.23960/jsl29213-222

Purusatama, B. D., Febrianto, F., Lee, S. H., and Kim, N. H. (2022). "Hardness and fracture morphology of reaction wood from *Pinus merkusii* and *Agathis loranthifolia*," *Wood Science and Technology* 56, 1331-1351. DOI:10.1007/s00226-022-01413-x

Safitri, N. M., Prastiwim, F. W., Salsabila, S., Feriawan, Y., Brilianto, A., Nugroho, W. D.

(2023). "Anatomical characteristics of the leaning stem in *Pinus merkusii* seedling," *Biodiversitas* 24(7), 3796-3803. DOI: 10.13057/biodiv/d240717

Sarén, M.-P., Serimaa, R., Andersson, S., Paakkari, T., Saranpää, P., and Pesonen, E. (2001). "Structural variation of tracheids in Norway spruce (*Picea abies* [L.] Karst.)," *Journal of Structural Biology* 136(2), 101-109. DOI: 10.1006/jsbi.2001.4434

Savero, A. M., Kim, J.-H., Purusatama, B. D., Prasetia, D., Park, S.-H., and Kim, N.-H. (2022). "A comparative study on the anatomical characteristics of *Acacia mangium* and *Acacia hybrid* grown in Vietnam," *Forests* 13(10), 1700. DOI: 10.3390/f13101700

Trisatya, D. R., Iqbal, M., and Sulastiningsih, I. M. (2021). "Enhancing the properties of damar (*Agathis loranthifolia* Salisb.) wood by making hybrid bamboo-wood composite," *IOP Conference Series: Earth and Environmental Science* 914(1), article 012066. DOI:10.1088/1755-1315/914/1/012066

Timell, T. E. (1973). "Studies on opposite wood in conifers. Part I: Chemical composition," *Wood Science and Technology* 7(1), 1-5. DOI: 10.1007/BF00353373

Timell, T. E. (1986) *Compression Wood in Gymnosperms*, Springer-Verlag, Berlin, Germany.

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

Westing, A. H. (1965). "Formation and function of compression wood in gymnosperms," *The Botanical Review* 31, 381-480. DOI: 10.1007/BF02859131

Yong, L., Bi, Y., Shi, J., Wang, X., and Pan, B. (2022). "Response of tracheid structure characteristics and lignin distribution of taxodium hybrid Zhongshanshan to external stress," *Forests* 13(11), article 1792. DOI: 10.3390/f13111792

Yoshizawa, N. and Idei, T. (1987). "Some structural and evolutionary aspects of compression wood tracheids," *Wood and Fiber Science* 19(4), 343-352.

Article submitted: October 28, 2023; Peer review completed: November 27, 2023; Revised version received and accepted: December 5, 2023; Published: December 13, 2023.

DOI: 10.15376/biores.19.1.925-943