



Full Length Research Article

Qualitative Anatomical Characteristics of Compression, Lateral, and Opposite Woods in *Pinus merkusii* and *Agathis loranthifolia*

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ABSTRACT

This study aimed to observe and compare the qualitative anatomical characteristics of compression (CW), lateral (LW), and opposite (OW) woods in the stem wood of Sumatran pine (*Pinus merkusii*) and *Agathis loranthifolia*. The anatomical characteristics were observed using optical microscopy and scanning electron microscopy. CW showed a gradual transition from earlywood to latewood in both species, circular tracheid shape, many intercellular spaces, irregular tracheid tips, helical cavities, and slit-like bordered pits. CW of Sumatran pine showed an indistinct growth ring, while CW of *Agathis* showed a distinct growth ring. Helical ribs occurred only in CW of Sumatran pine. LW and OW showed an oval tracheid with an angular outline, regular tracheid arrangement, and tapered tracheid tips in both species. LW and OW showed mainly uniseriate bordered pits in Sumatran pine, while LW and OW of *Agathis* frequently showed multiseriate bordered pits. CW, LW, and OW showed fusiform and uniseriate rays in Sumatran pine, while those of *Agathis* showed uniseriate rays. In conclusion, CW showed distinctive qualitative anatomical characteristics to LW and OW in both species, while LW and OW mainly showed similar characteristics. In particular, there were considerably distinctive characteristics between CW from both species.

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1. Introduction

Compression wood (CW) is a reaction wood formed due to the mechanical stress of trees and restores the vertical growth (gravitropism) in the main stems or branch woods of conifers. Moreover, CW occurs on the lower side of the stem or branch wood (Barnett et al. 2014). Besides, Lateral (LW) and opposite wood (OW) also occur in a leaning stem and branch wood of reaction wood (Ruelle 2014). CW has distinctive anatomical characteristics compared to normal wood, LW, and OW. Qualitatively, CW showed helical cavities, helical ribs, round tracheid shape, thicker cell wall than normal wood, highly lignified S₂ layer, numbers of intercellular spaces, distorted bordered pits, and cross-field pits (Donaldson and Singh 2013). Quantitatively, CW had a shorter tracheid length, smaller radial diameter, lower relative crystallinity, and smaller

crystallite width than LW and OW (Purusatama and Kim 2018; Purusatama and Kim 2020; Purusatama et al. 2020). Moreover, Wimmer and Johansson (2014) reported that CW had distinctive physical and mechanical properties to normal wood, and CW is an undesirable raw material for commercial lumber, wood-based panels, and pulp and paper manufacture.

Sumatran pine (*Pinus merkusii*) and Agathis (*Agathis loranthifolia*) woods are widely planted in Indonesian plantation forests. In addition, both species are common raw materials for lumber, wood panels, musical instruments, and pulp and paper industries (Martawijaya et al. 2005). For the anatomical characteristics, Sumatran pine wood shows window-like and pinoid pits in the cross-field, resin canals, bordered pit, and uniseriate and fusiform rays, while Agathis wood shows tracheids with resinous materials, cupressoid and taxodioid pits in the cross-field, uniseriate rays, and hexagonal bordered pit (Jang et al. 2014; Ogata et al. 2008).

There are a few studies on the anatomical characteristics of reaction wood in tropical softwood. Westing (1965) reported that the helical cavity was absent in the CW of *Agathis* spp. and *Araucaria* spp. Timell (1986) also mentioned that helical cavities were absent in CW of *Agathis robusta*. As reported by Pandit and Rahayu (2007), the CW of *Agathis loranthifolia* showed a circular shape tracheid in the transverse surface and helical cavities in the radial section. Moreover, the S_3 was absent in the CW, and the MFA in the S_2 layer was distinctively greater than normal wood. Kim et al. (2015) revealed that in *Agathis borneensis*, mild CW showed intercellular spaces, while the rounded-shaped tracheid and helical cavities were absent. In addition, greater lignification of the outer part of the S_2 layer occurred in mild CW of *Agathis borneensis*.

As mentioned above, Sumatran pine and Agathis are common species in the plantation forest and commercial raw materials for the wood industry in Indonesia. However, reaction wood frequently occurs in fast-growing conifers from the plantation forest, such as *Agathis*, *Pinus*, and *Podocarpus*, and caused many problems in the wood industry (Pandit and Rahayu 2007). However, there is still lack on the intrinsic characteristics of reaction wood in conifers from tropical wood species. Furthermore, there is still no comparative study on the anatomical characteristics of CW, LW, and OW from tropical wood conifers. Therefore, this study aimed to investigate and compare the qualitative anatomical characteristics of CW, LW, and OW in Sumatran pine and Agathis woods.

2. Materials and Methods

2.1. Materials

A tree for each Sumatran pine and Agathis was obtained from Gunung Walat IPB University Forest, Sukabumi, West Java, Indonesia (6.882937°N, 106.818511°E). The basic information of the sample trees is presented in **Table 1**. In this study, the qualitative anatomical characteristics were investigated in the wood disc of Sumatran pine at diameter breast height (DBH) and Agathis at 3 m above the DBH, which has the same diameter.

2.2. Microscopy

The qualitative anatomical characteristics, such as the tracheid shape and arrangement, helical cavities, helical ribs, intercellular spaces, and ray properties, were observed with optical microscopy and scanning electron microscopy. For optical microscopy, wood discs were converted to small blocks (1 cm³) and softened in a boiling mixture of glycerin and water (50:50).

Thin slices with a 15-20 μm thickness were prepared using a sliding microtome (Nippon optical works Co, LTD., Tokyo, Japan). All thin slices were stained with 1% safranin solution and dehydrated by grade series of alcohol (50%, 70%, 90%, 95%, and 99%) and xylene. Permanent slides were prepared with Canada balsam. For the tracheid tip observation, the CW, LW, and OW samples were soaked in Schultze reagent for three days and delignified using Franklin's method (Franklin 1945). The anatomical observation was performed with an optical microscope (Eclipse E600; Nikon, Tokyo, Japan) is connected to an image analysis system (IMT i-Solution Lite, Vancouver, Canada). For the scanning electron microscopy, the small wood blocks (1 cm^3) of CW, LW, and OW from both species were air-dried, and the samples were coated with gold using a Cressington sputter coater (ULVAC G-50DA, Japan). The coated samples were observed under a scanning electron microscope (SEM) (JSM-5510, Japan, 15 kV).

Table 1. Basic information of the sample trees

No.	Species	Age	DBH	Location
1	Sumatran pine (<i>Pinus merkusii</i>)	49 (since 1970)	40 cm	Gunung Walat IPB University Forest, Sukabumi, West Java, Indonesia (6.882937°N, 106.818511°E)
2	Agathis (<i>Agathis lorantifolia</i>)	65 (since 1954)	89 cm	

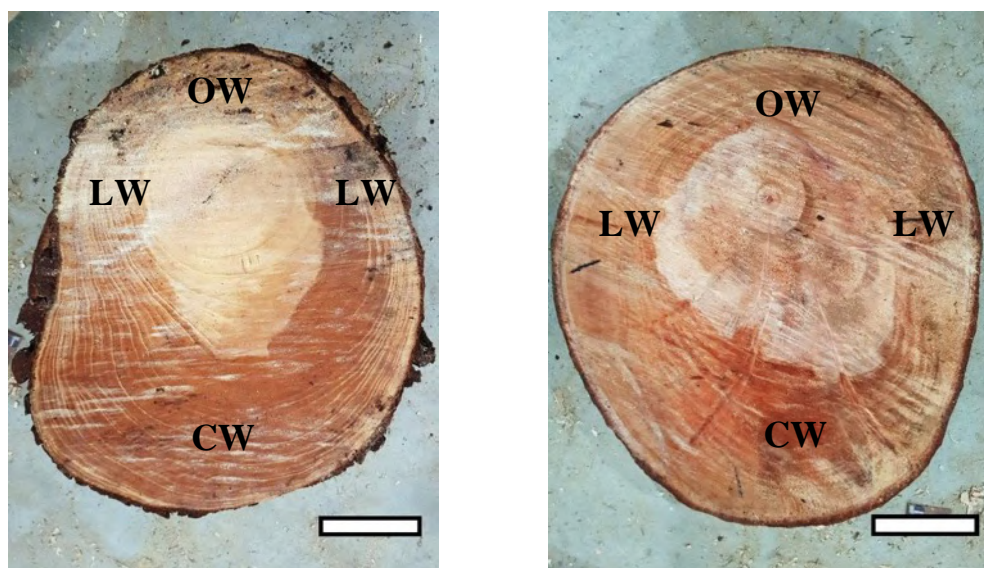


Fig. 1. A fresh cut wood discs of *Pinus merkusii* (left) and *Agathis lorantifolia* (right).
- Scale bars = 10 cm.

3. Results and Discussion

3.1. Anatomical Characteristics of Compression, Lateral, and Opposite Woods in the Three Sections

3.1.1. Cross-section

The optical micrographs of the cross-section in CW, LW, and OW of Sumatran pine and Agathis are presented in **Fig. 2**. CW of Sumatran pine displayed a gradual transition from earlywood to latewood, while LW and OW showed an abrupt transition. In addition, the growth

ring boundary was indistinct in CW, and it was distinct in LW and OW. In *Agathis*, CW exhibited a gradual transition from earlywood to latewood, while LW and OW showed no transition from earlywood to latewood. Furthermore, the growth ring boundary was distinct in CW, LW, and OW of *Agathis*. Kim et al. (2015) mentioned that mild CW exhibited indistinct growth ring boundary in *A. borneensis*, while normal wood displayed recognizable growth rings. Additionally, Jang et al. (2014) mentioned that *A. loranthifolia* showed a distinct growth ring boundary and no transition from earlywood to latewood. As Chung and Lee (1989) reported, CW exhibited a gradual transition from earlywood to latewood in *Pinus densiflora*. Eom and Butterfield (1997) described that CW presented a gradual transition from earlywood to latewood of *Pinus radiata*, while LW and OW had an abrupt transition. In addition, CW and OW showed an abrupt transition from earlywood to latewood in the stem wood of *Ginkgo biloba*, while LW showed gradual transition (Purusatama et al. 2018).

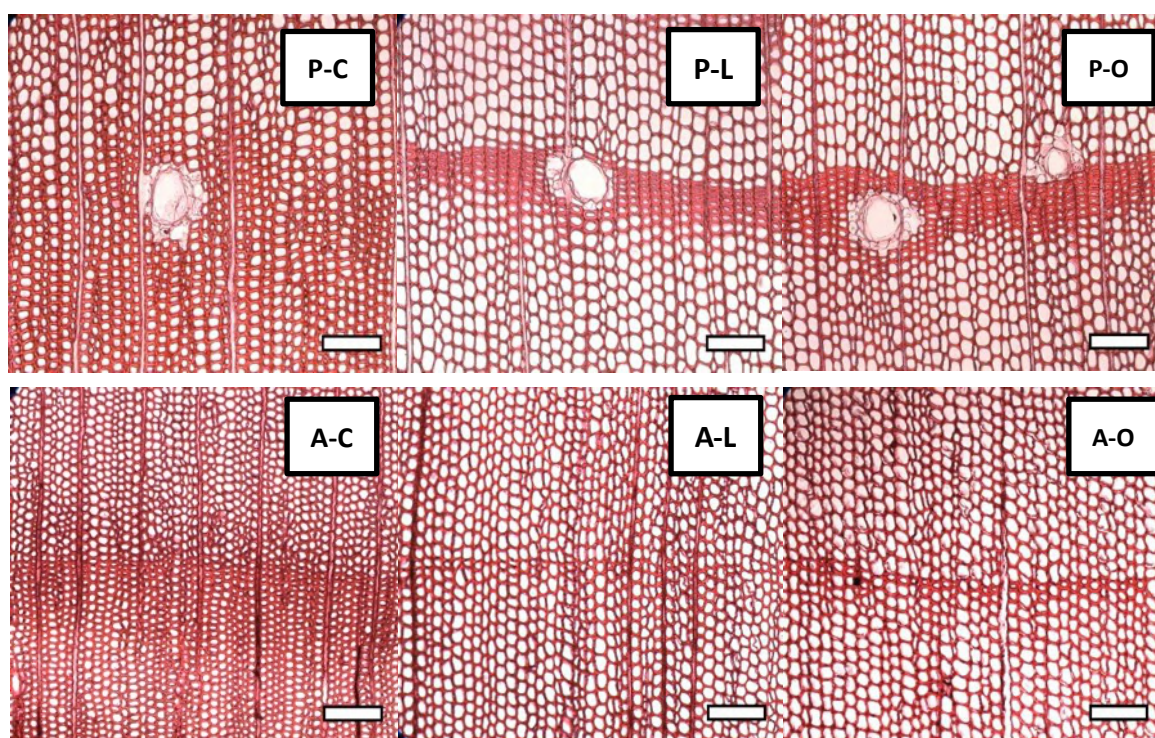


Fig. 2. Optical micrographs of the cross-section in CW, LW, and OW of Sumatran pine (P-C, P-L, and P-O) and *Agathis* (A-C, A-L, and A-O), respectively. – Scale bars= 200 µm.

The scanning electron micrographs of the cross-section in CW, LW, and OW of Sumatran pine and *Agathis* are presented in **Fig. 3**. In both species, CW showed a circular shape tracheid, helical cavities and intercellular spaces. Furthermore, LW and OW displayed oval lumen with angular outlines and no intercellular spaces in both species. As summarized by Yoshizawa et al. (1985), a round tracheid shape, intercellular spaces, and helical cavities occurred in the CW from *Pinaceae* and *Araucariaceae*. Pandit and Rahayu (2007) reported that CW showed a circular shape tracheid in the transverse surface of *A. loranthifolia*, while the normal wood exhibited a rectangular form. Kim et al. (2015) revealed that mild CW of *A. borneensis* showed a similar tracheid shape with the normal wood, and helical cavities were absent on the cross-section of mild CW. Eom and Butterfield (2001) mentioned that CW showed round outline, helical cavities, and intercellular spaces, while LW and OW showed angular to rectangular in outline in the stem wood and branch wood of New Zealand rimu. Additionally, Purusatama et al. (2018) reported that CW presented

circular tracheids with angular outlines and many intercellular spaces in the stem wood of *Ginkgo biloba*, while LW and OW showed rectangular tracheids and fewer intercellular spaces.

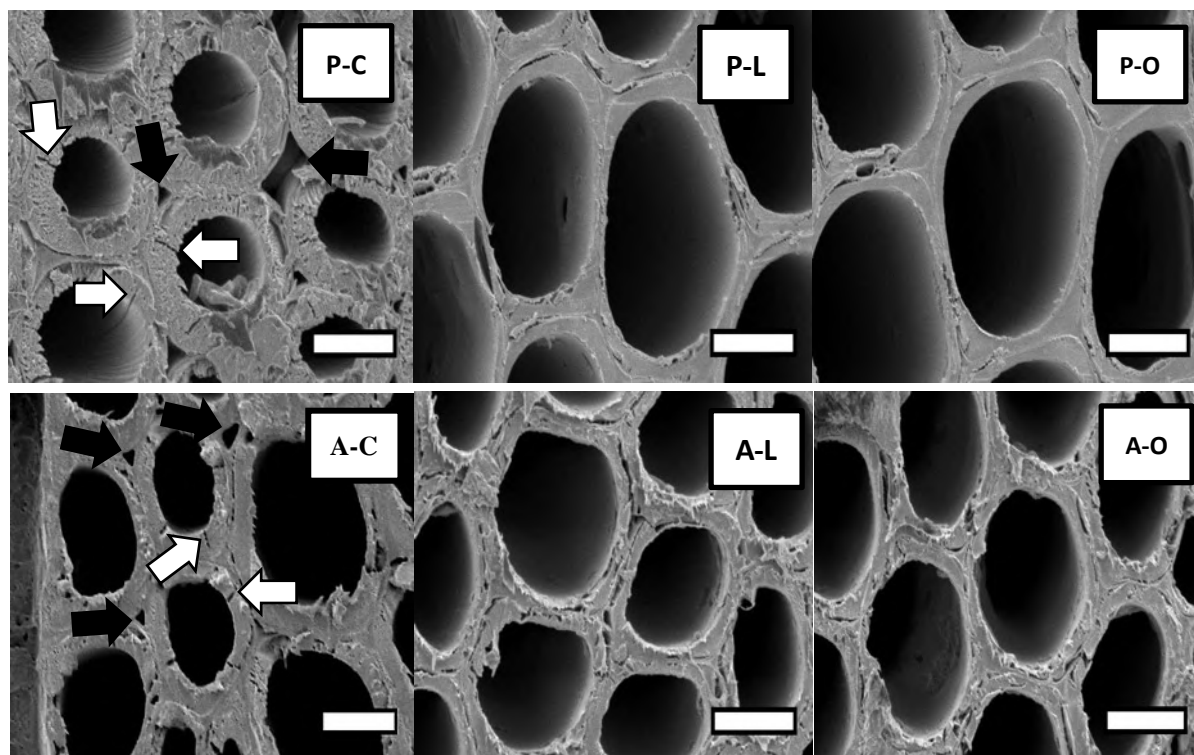


Fig. 3. Scanning electron micrographs of the cross-section in CW, LW, and OW of Sumatran pine (P-C, P-L, and P-O) and Agathis (A-C, A-L, and A-O), respectively. Helical cavities (white arrow) and intercellular spaces (black arrow) occurred in CW of both species.

– Scale bars = 15 μ m.

3.1.2. Radial section

The optical micrographs and scanning electron micrographs of the radial section in CW, LW, and OW of Sumatran pine and Agathis are presented in **Fig. 4** and **Fig. 5**, respectively. CW of both species showed slit-like bordered pits and irregular tracheid arrangement. Additionally, as shown in **Fig. 6**, CW of Sumatran pine clearly displayed helical cavities and helical ribs. In Agathis, CW showed only a few helical cavities without helical ribs. In both species, LW and OW showed a regular arrangement of tracheids in the radial section. In Sumatran pine, LW and OW showed bordered pits with mostly uniseriate and few biseriate, while LW and OW of Agathis showed commonly multiseriate (2-3 rows) bordered pits.

Yoshizawa and Idei (1987) summarized that the slit-like bordered pit, helical cavities, and helical ribs were found in CW of *Pinacea*, such as *Abies firma*, *Abies sachalinensis*, *Cedrus deodara*, *Larix leptolepis*, *Picea abies*, *Picea glehnii*, *Picea jezoensis*, *Pinus pentaphylla*, and *Pinus densiflora*. Additionally, the authors also mentioned that those characteristics also appeared in mild CW of *Araucaria brasiliana*. Pandit and Rahayu (2007) mentioned that CW showed helical cavities in the radial section of *A. loranthifolia*. As Westing (1965) reported, the helical cavity was absent in CW of *Agathis* spp. and *Araucaria* spp. Moreover, Timell (1986) also described that helical cavity was absent in CW of *Agathis robusta*. In *A. borneensis*, the tracheid of mild CW had intercellular spaces, while the rounded-shaped tracheid and helical cavities were absent (Kim et al. 2015). In our previous study, the radial section of CW showed an irregular

arrangement of tracheids in earlywood, helical cavities, and slit-like bordered pit (Purusatama et al. 2018; Purusatama and Kim 2018).

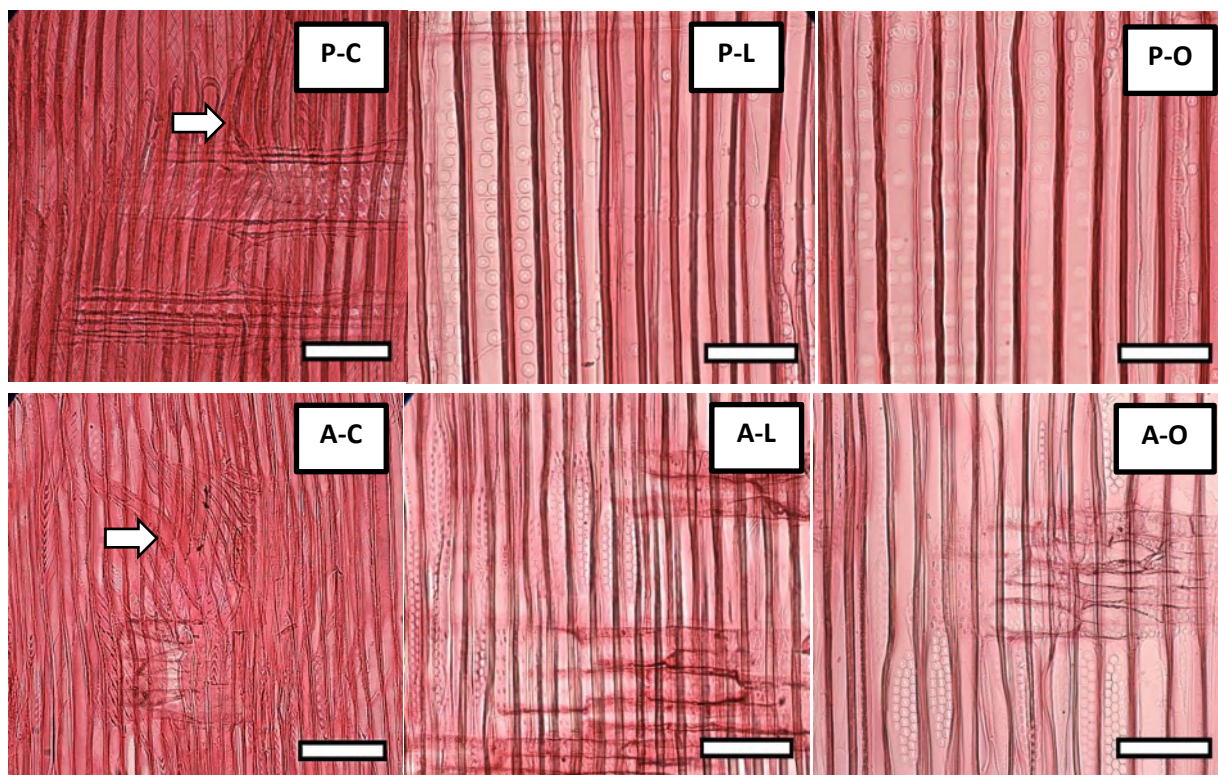


Fig. 4. Optical micrographs of the radial section in CW, LW, and OW of Sumatran pine (P-C, P-L, and P-O) and Agathis (A-C, A-L, and A-O), respectively. The irregular arrangement of tracheid in CW (white arrow). –Scale bars = 125 μ m.

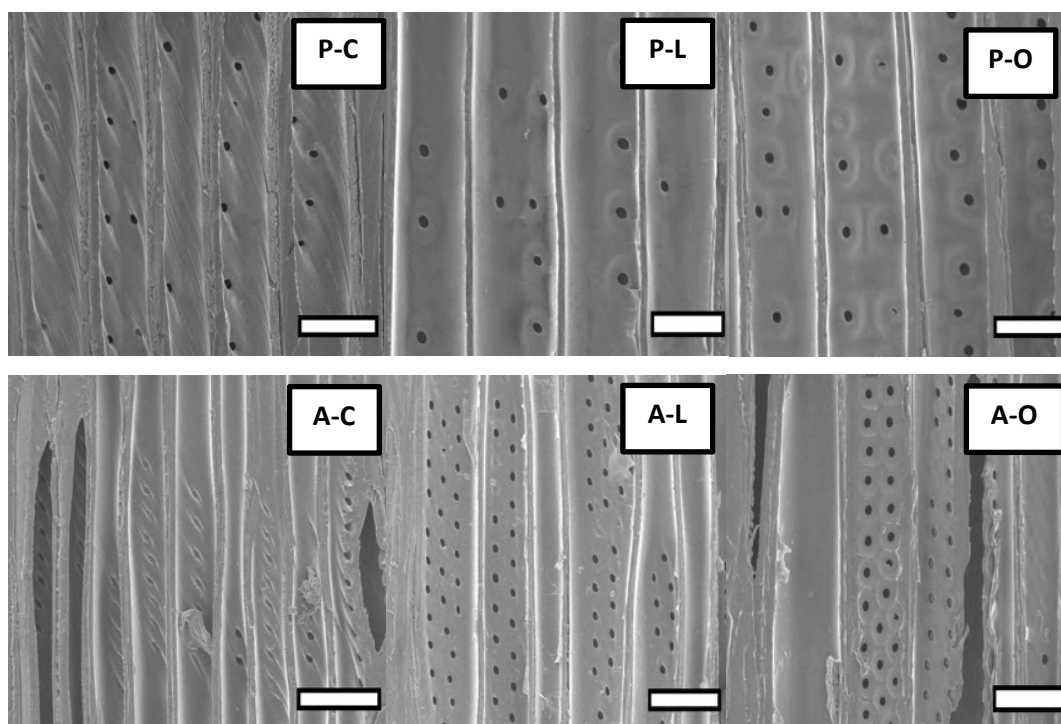


Fig. 5. Scanning electron micrographs of the radial section in CW, LW, and OW of Sumatran pine (P-C, P-L, and P-O) and Agathis (A-C, A-L, and A-O). –Scale bars = 50 μ m.

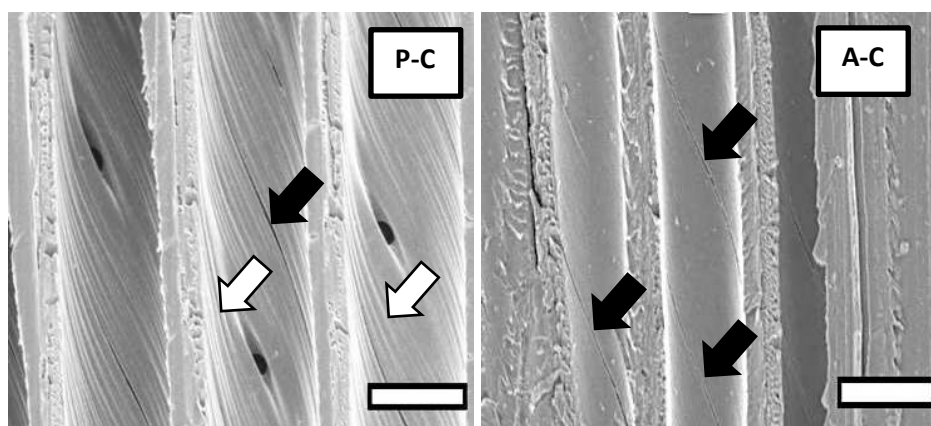


Fig. 6. Scanning electron micrographs of the radial section in CW of Sumatran pine (P-C) and Agathis (A-C). Helical ribs (white arrow) only occurred in CW of Sumatran pine and helical cavities (black arrow) in CW of both species. –Scale bars = 25 μ m.

3.1.3. Tangential section

The optical micrographs of the tangential section in CW, LW, and OW of Sumatran pine and Agathis are presented in **Fig. 7**. In Sumatran pine, CW, LW, and OW showed uniseriate and fusiform rays. In Agathis, CW, LW, and OW showed uniseriate rays in the tangential section. Additionally, a few biseriate rays were discovered in the LW of Agathis. As shown in **Fig. 8**, helical cavities occurred in the tracheid wall of CW from both species, but the helical ribs only occurred in the CW of Sumatran pine. As [Timell \(1986\)](#) reported, the helical cavities occurred in the tangential wall of CW of *Pinus resinosa*, *Larix laricina*, and *Pseudotsuga menziesii*. [Purusatama and Kim \(2018\)](#) revealed that the CW of *Ginkgo biloba* showed helical cavities in the tangential section.

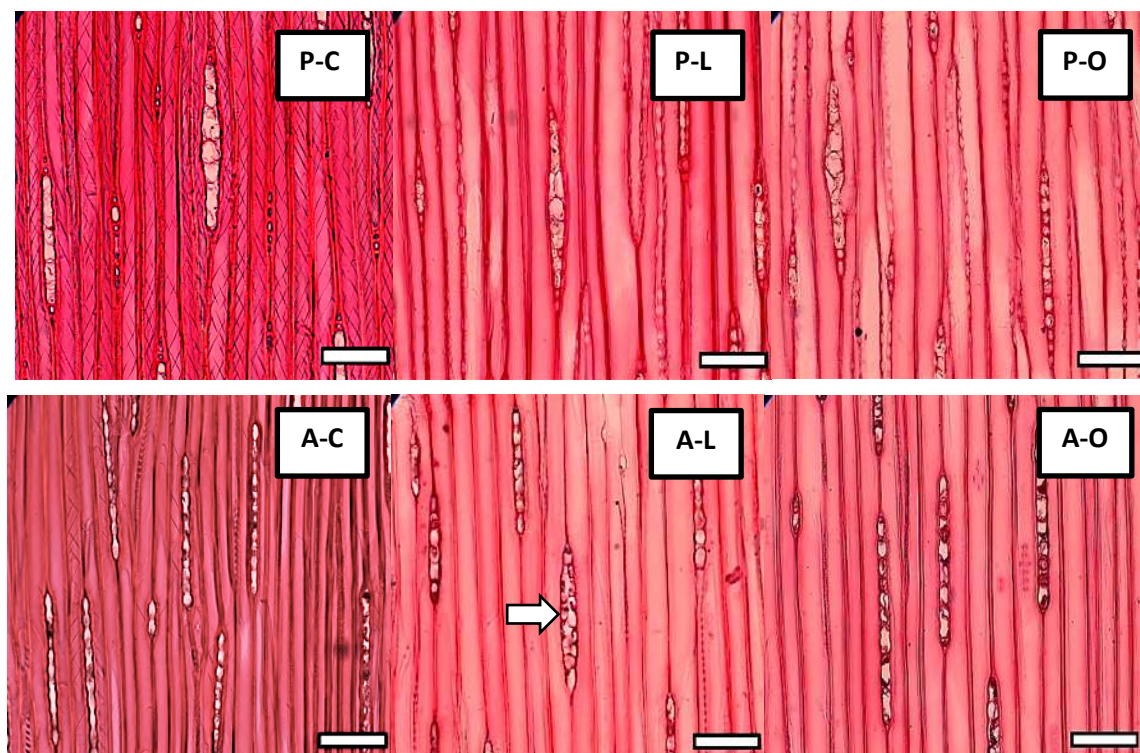


Fig. 7. Optical micrographs of the tangential section in CW, LW, and OW of Sumatran pine (P-C, P-L, and P-O) and Agathis (A-C, A-L, and A-O). Biseriate ray in LW of Agathis (white arrow). –Scale bars = 125 μ m.

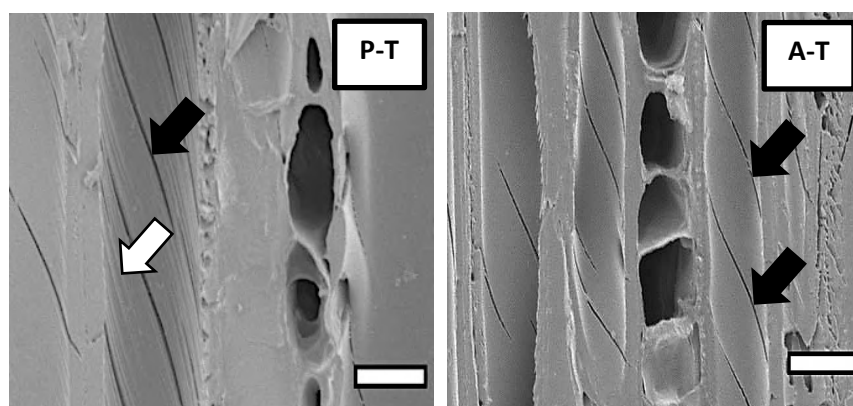


Fig. 8. Scanning electron micrographs of the tangential section in CW of Sumatran pine (P-T) and Agathis (A-T). Helical ribs (white arrow) only occurred in CW of Sumatran pine and helical cavities (black arrow) in CW of both species. –Scale bars = 25 μ m.

3.2. Tracheid tip characteristics

The light micrographs of the tracheid tips of CW, LW, and OW in Sumatran pine and Agathis are presented in **Fig. 9**. CW of Sumatran pine showed a bifurcate and tapered tracheid tip with helical cavities, while LW and OW showed tapered tracheid tips. In Agathis, CW showed bifurcated tracheid tips and helical cavities, while LW and OW showed tapered tracheid tips. In our previous study, CW of *Ginkgo biloba* showed branched (bifurcated) tracheid tips, while LW and OW showed normal (tapered) tracheid tip (Purusatama et al. 2018). Yoshizawa et al. (1985) reported that CW is identical with abnormal tracheid tip types, such as flattened, bifurcated, abnormally expanded, transversely elongated, L-shaped, and locally elongated. In addition, the tapered tracheid tip commonly occurred in normal wood. Moreover, Yoshizawa et al. (1987) revealed that about 20% of the tip observed in the normal wood of *Larix* were abnormal, which flattened, L-shaped, and locally elongated tips were dominant.

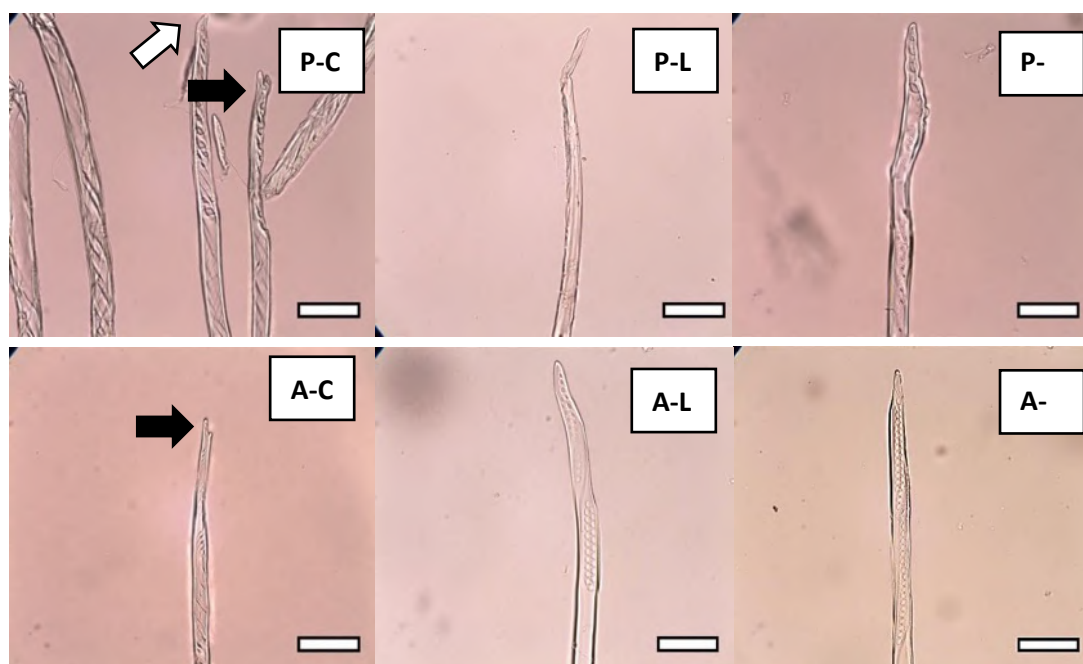


Fig. 9. Optical micrographs of the tracheid tips in CW, LW, and OW of Sumatran pine (P-C, P-L, and P-O) and Agathis (A-C, A-L, and A-O). Tapered (white arrow) and bifurcated (black arrow) tracheid tips in CW. –Scale bar: 50 μ m.

4. Conclusions

Compression wood of both species showed distinctive qualitative anatomical characteristics to LW and OW, while LW and OW mainly showed similar characteristics. Furthermore, there were distinctive differences in the CW of both species. In the cross-section, CW of Sumatran pine showed an indistinct growth ring boundary, while LW and OW showed a distinct growth ring boundary. CW, LW, and OW of *Agathis* showed distinct growth ring boundaries. In the radial section, the CW in both species showed an irregular arrangement of tracheid and a slit-like bordered pit with helical cavities, while LW and OW comparatively regular arrangements. Additionally, the helical ribs occurred only in the CW of Sumatran pine. LW and OW of Sumatran pine displayed uniseriate and biseriate bordered pits, while LW and OW of *Agathis* showed multiseriate bordered pits (2-3 rows). CW, LW, and OW of Sumatran pine showed fusiform rays and uniseriate rays in the tangential section, while those of *Agathis* showed mainly uniseriate rays. CW of Sumatran pine showed bifurcated and tapered tracheid tips, while CW of *Agathis* showed only bifurcated tracheid tips. LW and OW in both species showed tapered tracheid tips.

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