BIODIVERSITAS
Volume 24, Number 7, July 2023
Pages: 3796-3803

ISSN: 1412-033X
E-ISSN: 2085-4722
DOI: 10.13057/biodiv/d240717

Anatomical characteristics of the leaning stem in *Pinus merkusii* seedling

NEVLYA MIA SAFITRI, FANANY WURI PRASTIWI, SYIFA SALSABILA, YOGI FERIAWAN, ALIF BRILIANTO, WIDYANTO DWI NUGROHO♥

Departement of Forest Product Technology, Faculty of Forestry, Universitas Gadjah Mada, Jl. Agro No. 1 Bulaksumur, Sleman 55281, Yogyakarta, Indonesia. Tel./fax.: +62-8-222-3000-776, ♥email: wdnugroho@ugm.ac.id

Manuscript received: 30 November 2022. Revision accepted: 11 July 2023.

Abstract. *Safitri NM, Prastiwi FW, Salsabila S, Feriawan Y, Brilianto A, Nugroho WD. 2023. Anatomical characteristics of the leaning stem in* Pinus merkusii *seedling. Biodiversitas 24: 3796-3803. Pinus merkusii* Jungh. & de Vriese is one of the tropical conifer species. The species formed reaction wood called compression wood (CW) when the stem grows in an abnormal position. CW in stem wood is frequently found to cause several problems for utilization in the use of its products. However, there are few studies on the anatomical characteristics of reaction wood in tropical conifer. This study aimed to observe the differences in anatomical characteristics between compression (CW) and opposite (OW) woods in leaning the stem of *P. merkusii* seedlings and their anatomical differences compared to normal wood (NW). Approx. 1-year-old *P. merkusii* seedlings from a nursery in Trenggalek, East Java, Indonesia, that were naturally bent or tilted were used in the study. Anatomical characteristics of wood, namely the dimension of tracheids, rays, resin canals, and the proportion of cells were observed in the study. The results showed that CW of *P. merkusii* seedlings formed a rounded tracheid shape and intercellular space. The differences between CW and OW in *P. merkusii* seedlings were significant in terms of height of ray cells, tracheid proportion, and resin canal proportion. However, tracheid length, tracheid diameter, tracheid wall thickness, resin canal diameter and frequency, rays frequency, and ray proportion were not significantly different compared to OW and NW.

Keywords: Anatomical characteristics, compression wood, leaning stem, *Pinus merkusii*, reaction wood

INTRODUCTION

Abnormal growth or changes in the position of stems or branches due to mechanical stimuli, e.g. rain, wind, gravity, landslides, wounding, and bending in woody plants induce the formation of a specific tissue called reaction wood (RW) (Nugroho et al. 2012, 2013; Wistuba et al. 2013; Gardiner et al. 2014; Groover 2016). Compression wood (CW) is reaction wood in gymnosperm trees, one of which is a conifer and formed on the lower side of the stem or branch wood and accompanied by opposite wood (OW) which is used to describe wood formed on the stem across from RW, whereas the term normal wood (NW) refers to wood formed in upright trees (Gardiner et al. 2014; Groover 2016). CW has distinctive anatomical characteristics compared to NW and OW. The majority of the references stated that CW tracheids are typically shorter and rounded in appearance with thicker cell walls and many intercellular spaces can be seen between individual cells when compared to OW and NW. However, the appearance of tracheids in non-reaction wood which are more rectangular to hexagonal and the complete lack of intercellular spaces. These features can be used for CW classification because they are more or less pronounced in mild, moderate, and severe CW, which is certainly influenced by several factors, such as the degree of inclination of the stem or branches (Gardiner et al. 2014; Groover 2016; Gril et al. 2017).

Conifers such as *Picea mariana*, *Pinus banksiana*, and *P. merkusii* are woody species widely utilized for industrial forest plantations (Cunningham 2012; Krause et al. 2013). *Pinus merkusii* Jungh. & de Vriese is a conifer species native to Indonesia and is the only variety of pine with a natural distribution in the southern equator (Edy et al. 2012; Farjon 2013). This species is widely cultivated in Indonesian plantations and has become commercial raw materials for the wood industry, such as lumber, wood panels, musical instruments, pulp and paper, and non-wood forest product industries (Cunningham 2012; Edy et al. 2012; Sukarno et al. 2015; Purusatama et al. 2021). In the timber industry, information about the characteristics and properties of wood is important to optimize its utilization.

There are some studies concerning the reaction of wood in tropical softwood. Purusatama et al. (2021) reported that CW of *P. merkusii* and *Agathis loranthifolia* trees showed different anatomical characteristics compared to OW in both species. In addition, CW has 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. Furthermore, Purusatama et al. (2022) reported that CW of *P. merkusii* and *A. loranthifolia* showed different wood properties, such as hardness and fracture morphology. However, information about the quantitative anatomical characteristics of compression wood in *P. merkusii* is still poorly reported.

Reaction wood frequently occurs in fast-growing conifers from the plantation forest and causes many problems in the wood industry because it produces wood quality that tends to be lower or different from NW and is considered a wood defect (Liu et al. 2012; Li et al. 2014; Purusatama et al. 2021). Therefore, this study aimed to observe the differences in anatomical characteristics between compression (CW) and opposite (OW) woods in leaning stem of *P. merkusii* seedlings and their anatomical differences compared to normal wood (NW). This study can help in understanding the relationship between tree growth and wood properties, responding to silvicultural treatments on wood properties due to mechanical stress on the tree, and making decisions about the rational and effective use of this wood for future utilization.

MATERIALS AND METHODS

Study area

Pinus merkusii seedlings grown from a private nursery located in Trenggalek, East Java, Indonesia (8° 05’43.2” S and 111° 33’46.1” E, 720 m asl.) were used in the study. The study area was situated with an average temperature range from 19º to 32º, average humidity ranges from 60% to 95%, and average annual rainfall from 18 mm (February) to 35 mm (December) (BMKG 2022). The samples were obtained from the nursery and observed at the Laboratory of Wood Formation and Quality Improvement, Department of Forest Products Technology, Faculty of Forestry, Universitas Gadjah Mada, Yogyakarta, Indonesia.

Plant materials

This study used 10 seedlings of *P. merkusii* as representative specimens and planted as 1-year-old seedlings in 2022. The average height and diameter of these seedlings were about approx. 70 cm and 20 mm (Liu et al. 2012; Oliet et al. 2019). Five seedlings were naturally leaned (Figure 1) and five other seedlings were upright (normal stem) (Figure 2).

Procedures

Specimen preparation

Samples measuring 2 cm in length were taken from the seedlings (10 cm above the ground) and fixed in 4% glutaraldehyde in 0.1 M phosphate buffer (pH 7.3) for sample fixation. Furthermore, transverse and tangential wood sections (15 μm in thickness) were cut from the segments on a sliding microtome (Yamatokohki, Saitama, Japan). Sections were stained with a 0.1 % solution of safranin (WAKO Pure Chemical Industries) for 3 min, dehydrated with a graded ethanol series, cleared with xylol solution, and mounted on glass slides, fixed in resin (Entellan new; Merck, Darmstadt, Germany) and covered with coverslips. Meanwhile, maceration of wood was conducted by boiling the wood in Franklin solution of CH_3COOH 100% and H_2O_2 50% (1:10) until disintegrated into fibers (Nugroho et al. 2012).

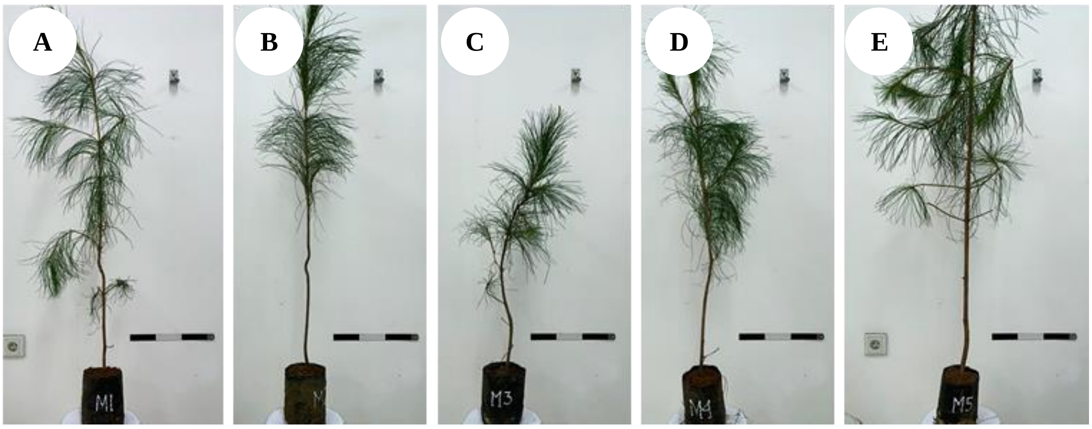

Figure 1. Five seedlings of *Pinus merkusii* are affected by the leaned stem position. Scale bars: 30 cm

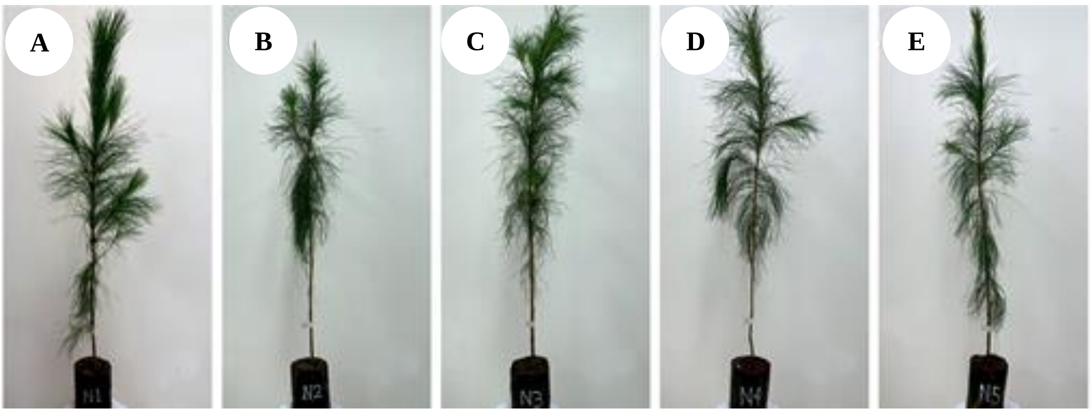

Figure 2. Five seedlings of *Pinus merkusii* with upright stems. Scale bar: 30 cm

Sample photography and parameters observed

Images of all samples were recorded under a light microscope (Olympus BX51 series) with a digital camera (DP70 Olympus Corporation) connected to a computer for anatomical observation. Compression wood formation, growth eccentricity, wood anatomical characteristics among compression, opposite and normal woods were observed and measured. The anatomical characteristics of wood, such as the dimension of tracheids (length, cell diameter, and cell wall thickness), rays (ray height and ray frequency), resin canals (cell diameter and frequency) and proportion of cells (tracheids, rays, and resin canals) were documented and analyzed. For the measurement of tracheid dimensions, 30 randomly selected tracheids were measured as well as the measurement for rays height. Rays frequency (number of rays) was determined by counting their presence in a 1 mm field of 10-15 randomly selected areas. The 15 randomly selected resin canals were measured to determine the resin canal diameter. Resin canal frequency (the number of resin canals) was determined by counting their presence in a 1 mm^2 field of 5 randomly selected areas. The proportion of tracheids, rays, and resin canals was determined by the sum of average tracheids, rays, or resin canal area/total analyzed area in % of 5 randomly selected areas. In addition, images of tracheids obtained from maceration of samples were recorded under Dino-Lite digital microscope (AM4115ZTL series) to measure the length of tracheids (Nugroho et al. 2012).

Data analysis

Parameter measurements were performed using FIJI Image-J software according to the IAWA list and all results were statistically analyzed using the SPSS software (SPSS ver. 25, IBM Corp., Armonk, NY, USA) at 95% confidence level. The effect of wood parts (compression wood and opposite wood) on the anatomical characteristics in naturally inclined stems was analyzed by one-way analysis of variance (ANOVA) and the significance of differences was calculated at $p<0.05$. From these results, data on the influence and differences in wood anatomical characteristics between compression wood and opposite wood in *P. merkusii* seedlings will be obtained.

RESULTS AND DISCUSSION

Compression wood formation and growth eccentricity

The results showed that CW was developed on the lower part of leaning stem of *P. merkusii* seedlings, while it was not found in the normal position of stems. The differences in anatomical characteristics on the transverse section between NW and CW are presented in Figure 3. The transverse section of the stem of *P. merkusii* seedling formed an eccentricity where the position of the pith was not in the center but shifted towards the upper side of the stem when compared to the NW. Kojima et al. (2012) reported that growth eccentricity and the presence of excessive compressive growth stresses on the lower side of inclined stems or branches are well-known characteristics of CW in gymnosperm trees and several angiosperm trees belonging to the genera *Pseudowintera*, *Buxus*, and *Hebe*. Janecka et al. (2016, 2020) have also pointed out that the formation of CW and eccentric growth occur together in the vast majority of cases.

In gymnosperms including *P. merkusii,* reaction wood forms on the lower side of the leaning stem or branches and is termed 'compression wood', whereas the term 'opposite wood' refers to wood formed on the stem across from reaction wood (typically on the top of the stem) and the term 'normal wood' refers to wood formed in upright trees (Gardiner et al. 2014; Groover 2016). CW has been shown to cause several anatomical abnormalities in both qualitative and quantitative aspects (Joffre et al. 2014; Ruelle 2014). These features can be used for CW classification as mild, moderate, and severe based on its anatomy (Gardiner et al. 2014; Groover 2016; Gril et al. 2017; Purusatama et al. 2021). The woody stems and branches of trees can respond to gravitropic stimulation by generating asymmetric mechanical stress via the development of specialized secondary xylem, known as 'reaction wood. Most trees are capable of producing reaction wood, which is fundamentally important to tree growth, development, survival and evolution of trees including reorienting displaced stem, reinforcing stress points, maintaining leaning or posture control stem or branches angles as a tree grows, and can be used to date disturbances, e.g. landslides, wind, bank erosion, snow or avalanche in forest ecosystems using dendrochronology. Thus, the mechanisms responsible for bending woody stems are fundamentally different from those in herbaceous stems (Nugroho et al. 2012, 2013; Wistuba et al. 2013; Gardiner et al. 2014; Alméras and Clair 2016; Groover 2016).

Differences in wood anatomical characteristics among compression, opposite and normal woods

Cell shape

The cell shape of CW, OW, and NW on the stems of *P. merkusii* seedlings are shown in Figures 3B, 3D, and 3E. The shape of the cells in the CW tends to be more rounded or shortened with thicker cell walls than OW and NW. The cells are rectangular but nearly rounded or shortened (slightly rounded cells) with increasing cell wall thickness in OW, whereas in NW, the cell shape tends to be rectangular, larger in size, and thinner cell wall compared to CW and OW. This study is in line with other studies in *Podocarpus*, *Ginkgo biloba*, *P. densiflora*, *P. merkusii* and *A. loranthifolia* that showed CW tracheids are shorter and rounded in appearance with thicker cell walls, and reduced cell diameter than characteristics of tracheid in NW. However, the appearance of tracheids in non-reaction wood which are more rectangular to hexagonal (Groover 2016; Purusatama and Kim 2020; Purusatama et al. 2021). Based on research findings, *P. merkusii* in this study can be classified as relatively severe CW and can influence wood's physical properties. It has been reported that the thick tracheids with rounded appearances of compression wood induce increased density and reduced permeability, which influence the effectiveness of pretreatment and provide unsuitable properties for some products made from this wood, such as pulp and paper and biochemicals (Ji et al. 2013; Hiraide et al. 2021). In addition, the OW which is located on the upper side of CW, has almost similar anatomical characteristics to the NW (Donaldson and Radotic 2013; Gardiner et al. 2014; Groover 2016).

Liu et al. (2012) reported that the characteristics of compression wood tracheid in 3-years-old loblolly pine seedlings artificially tilted at angles of 0°, 15°, 30°, 45°, and 60° from the vertical showed that as the increase of the inclined angle, the wall thickness of tracheid increased and the outline of the tracheid became round, the inter tracheidular spaces were obvious and increased gradually in all sections derived from the inclined seedlings. However, the critical angle of inclination in the seedlings studied was about 30° or 45° from the vertical. Meanwhile, Kim et al. (2015) reported that CW can occur in a range of severity types from mild to severe. Severe CW is characterized by rounded cell shape, the presence of intercellular spaces, high lignification in the outer part of the S2 layer, and darker color wood in transversely cut greenwood discs. On the other hand, mild CW is difficult to detect because the cell forms and wood color are frequently similar to those of normal wood, however, tracheids are slightly rounded to normal in appearance, and the presence of intercellular spaces is not a consistent feature. In addition, Donaldson and Radotic (2013) and Ruelle (2014) showed that tracheids in severe CW usually change structure or size when compared to NW. The tracheid in CW has a more rounded shape while the NW shows a more rectangular shape.

Intercellular space

The result showed that there was space among cells, namely intercellular space, in the CW zone of *P. merkusii* seedling (Figures 3B, 3D, and 3E). In contrast, there were no intercellular spaces in OW and NW. This study is in line with previous studies on *Podocarpus*, *G. biloba*, *P. densiflora*, *P. merkusii* and *A. loranthifolia*, which reported that CW was characterized by differences in the number of intercellular spaces located between individual cells of CW when compared to NW. It is known that the most characteristic feature of severe CW is the rounded shape of the tracheids with intercellular spaces at the corners (Donaldson and Radotic 2013; Joffre et al. 2014; Ruelle 2014). This intercellular space is formed due to changes in the shape of the tracheid cells, which are more rounded or shortened due to edges that are cut or bent during CW formation (Groover 2016; Purusatama and Kim 2020; Purusatama et al. 2021).

Quantitative wood anatomical characteristics on compression, opposite and normal woods

The results of measurements and statistical analysis by one-way ANOVA test (P-value ≤ 0.05) on several wood anatomical variables in CW, OW, and NW from the stems of *P. merkusii* seedlings are presented in Table 1.

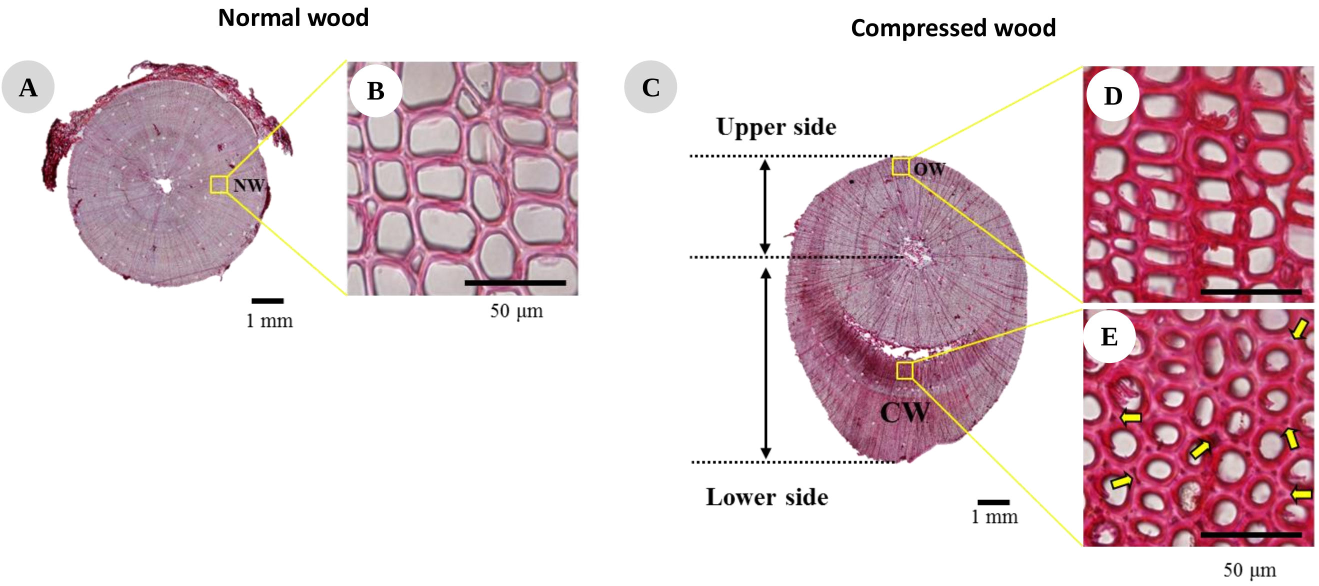

Figure 3. Normal and compression wood of *Pinus merkusii* seedling stems viewed in transverse section by safranin staining: (A) growth of normal wood (straight stem) with concentric shape, (B) normal wood has rectangular cells and thinner walls, (C) growth eccentricity of compression wood (inclined stem), (D) opposite wood has slightly rounded cells and relatively thick cell walls, (E) compression wood has rounded but not fully circular cell with intercellular spaces and thick cell walls. Yellow arrows indicate intercellular spaces at the corners of rounded tracheids

Tracheid

The length and cell wall thickness of tracheids were not significantly different between CW and OW in naturally leaned *P. merkusii* seedling stems (Table 1). The results showed that tracheids in CW tended to have shorter tracheids and thicker cell walls than OW and NW. This study is in line with several previous studies that reported reduced or shorter CW tracheid length and thicker cell walls compared to NW in *P. yunnanensis* (Ji et al. 2013) and *Picea abies* (Janecka et al. 2016, 2020). CW tracheids may be of importance in the generation of stresses contributing to growth towards a vertical direction of the stem or branch. This causes intrusive growth of the cell tips to be limited and CW tracheid develops truncated ends (Joffre et al. 2014). Furthermore, according to TAPPI (1998), the measured *P. merkusii* tracheid fiber length (Table 1) is classified as long fiber. The length of tracheid among CW, OW, and NW were shown in Table 1 and their micrograph of the tracheid was presented in Figure 4.

Rays

The ray cells of CW, OW, and NW on tangential cross-sections of the *P. merkusii* seedling with 0.1% safranin stain and images were recorded under a light microscope (Figure 5). The results showed that the height of ray cells of CW was significantly higher compared to OW in naturally leaned *P. merkusii* seedling stems (P = 0.00). Although the frequency of ray cells was not significantly different (Table 1), the CW of the *P. merkusii* seedling stems tended to produce a greater number of rays compared to the OW and NW. This probably resulted from the necessity of ray parenchyma cells for transferring statistics and dynamic loads, and transporting water and nutrients, especially for juvenile wood (Tomczak 2014). However, this result still requires further understanding and research into the possible relationship between cambial age and other differences in wood ray traits. Eom and Butterfield (2001) reported that the rays of CW were found to have higher ray heights and lower ray numbers than those of OW and NW in *Dacrydium cupressinum*. The greater availability of photosynthate on the CW side was attributed to higher ray frequency in CW. However, other studies revealed no difference in ray size for CW and NW (Gardiner et al. 2014). Furthermore, CW, OW, and NW rays in *P. merkusii* seedlings showed uniseriate and fusiform rays (Figure 5).

Resin canals

The diameter and frequency of resin canals were not significantly different between CW and OW in naturally leaned *P. merkusii* seedling stems (Table 1). The results showed that resin canals in CW tended to have a larger vertical resin canal diameter compared to OW and NW. In addition, the anatomical features of resin canals in the transverse section of CW, OW, and NW of *P. merkusii* seedlings were presented in Figure 6.

The resin canals are reservoirs for secretions resulting from the mechanism of the tree being disturbed (stress), and the resin is formed due to the separation of parenchyma cells, creating empty spaces between these cells. This canal is also influenced by environmental and physiological factors of the tree. The production of sap is determined by the thickness of the epithelial cells surrounding the resin canal (Susilowati et al. 2013; Westbrook et al. 2015). It is known that the larger the diameter and frequency of the resin canals, then it can produce and be able to accommodate more resin. Even so, the size, frequency and proportion of resin canals are still largely influenced by the genetics of trees which naturally have the ability to form different resin canal, and are then influenced by the environmental and physiological factors of the tree. In addition, it can also be influenced by species, tree age and other maintenance activities resulting in different resin canal conditions. Lee and Eom (1988) observed that the number of vertical resin canals in the CW of *P. koraiensis* was fewer than in OW and that traumatic vertical resin canals were only observed in compression wood, but this feature does not seem to be consistent in CW because in this study, vertical resin canals were found in CW, OW, and NW of *P. merkusii*.

Table 1. Analysis of variance (ANOVA) test of reaction wood properties in *Pinus merkusii* seedlings

Properties	Normal wood (NW)	Sig.	Part of the reaction wood	
			Compression Wood (CW)	Opposite Wood (OW)
Tracheid				
Length (mm)	2.67 ± 0.17	0.26 (ns)	2.30 ± 0.41	2.53 ± 0.12
Diameter (μm)	23.34 ± 0.23	0.88 (ns)	22.75 ± 0.15	22.38 ± 0.27
Wall thickness (μm)	2.82 ± 0.14	0.88 (ns)	3.02 ± 0.12	2.99 ± 0.08
Rays				
Height (μm)	122.74 ± 5.81	0.00*	119.27 ± 5.82	100.70 ± 6.75
Frequency	4.04 ± 0.34	1.00 (ns)	4.32 ± 0.25	4.18 ± 0.24
Resin canal				
Diameter (μm)	116.36 ± 0.05	0.81 (ns)	127.64 ± 0.02	123.27 ± 0.04
Frequency	2.00 ± 0.06	1.00 (ns)	2.00 ± 0.06	1.70 ± 0.09
Proportion (%)				
Tracheid	94.58 ± 0.02	0.01*	91.20 ± 2.04	94.87 ± 0.90
Rays	3.82 ± 1.11	0.54 (ns)	3.95 ± 2.56	3.19 ± 0.76
Resin canal	1.60 ± 0.01	0.00*	4.85 ± 0.91	1.94 ± 0.40

Note: * = significance at 5% level of one-way ANOVA test; ns = no significance; values are means ± standard errors. Significance was estimated for the effect of wood parts (compression wood and opposite wood) on wood anatomical characteristics in naturally inclined stems

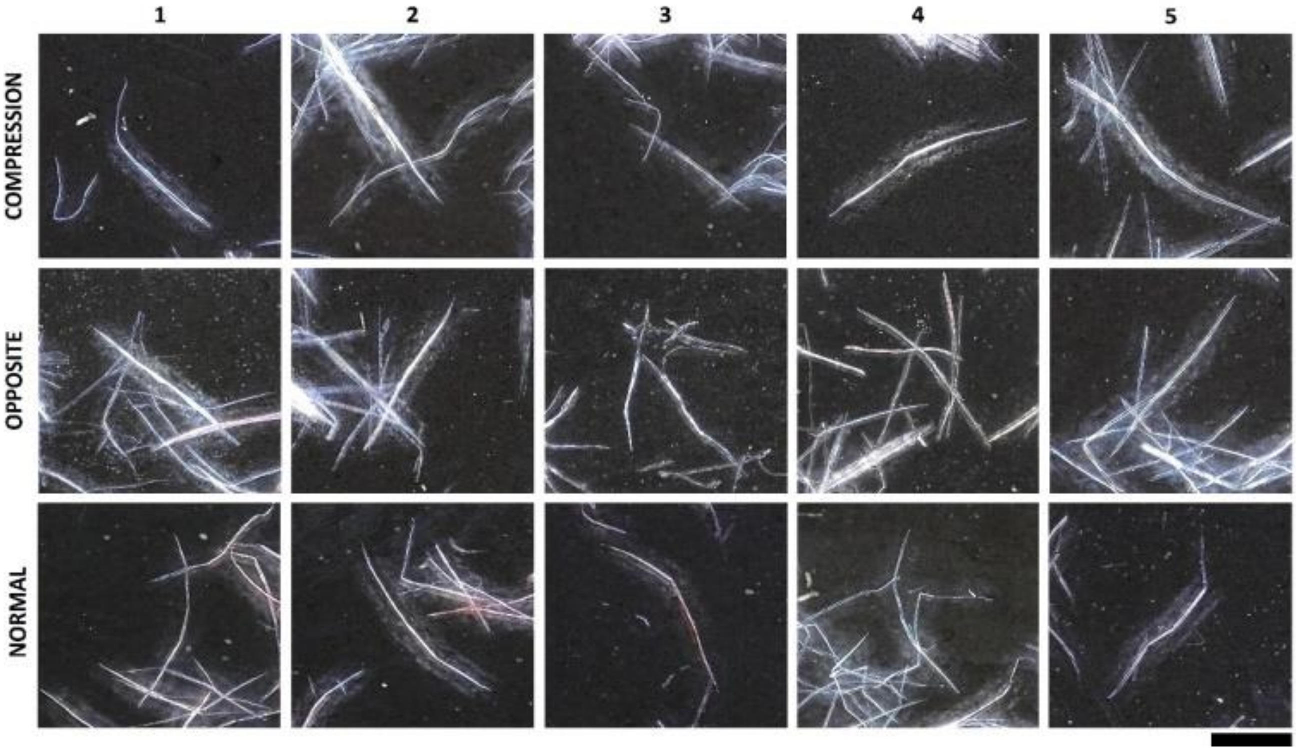

Figure 4. Tracheid length between compression, opposite, and normal woods on a *Pinus merkusii* seedling stem. Scale bar: 1 mm

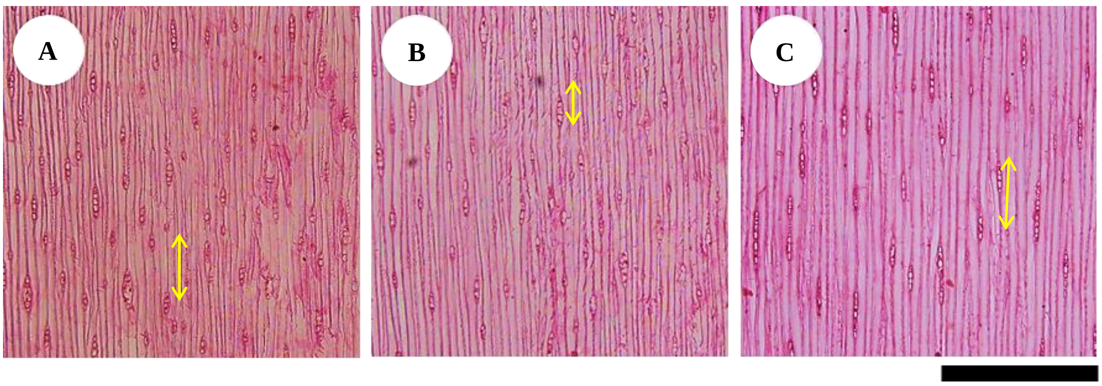

Figure 5. Rays on the tangential cross-sections of *Pinus merkusii* seedlings in zones: (A) compression wood, (B) opposite wood, and (C) normal wood. The yellow arrows indicate rays. Scale bar: 500 μm

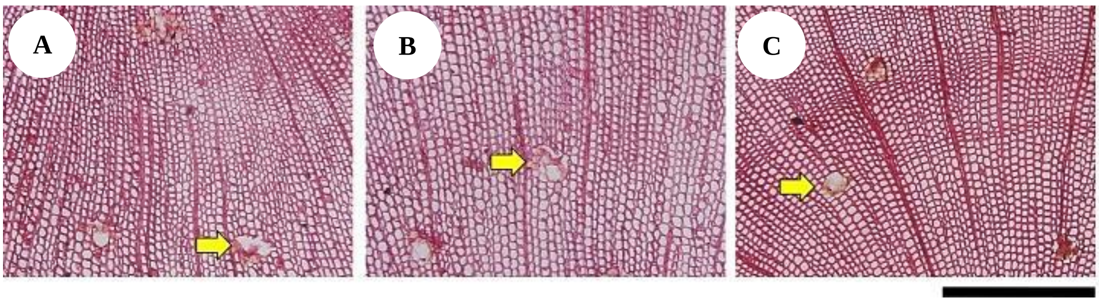

Figure 6. Presence of resin canals in transverse sections of *Pinus merkusii* seedlings in zones: (A) compression wood, (B) opposite wood, and (C) normal wood. The yellow arrows indicate resin canals. Scale bar: 500 μm

Cell proportion

The results showed that the tracheid proportion and resin canal proportions between CW and OW in naturally leaned *P. merkusii* seedling stems were significantly different (Table 1). In addition, the results also showed that CW on the stems of *P. merkusii* seedlings produced a lower tracheid proportion and higher resin canal proportion than OW and NW. Although the rays proportion was not significantly different, the ray cells tended to produce a higher rays proportion compared to the OW and NW. The modification of anatomical characteristics such as cell proportion in response to mechanical stimuli might be related to gravitropism of plants (Nugroho et al. 2012, 2013). In addition, the modification of anatomical characteristics is regulated by plant hormones. Several types of plant hormones play a major role in the regulation of various key physiological processes in plants. Certain plant hormones can physiologically stimulate the formation of resin canal which is beneficial to pine resin production or important for forestry industry sustainability. In previous studies, it has been shown that these plant hormones such as auxin, GAs, and ethylene all play important, interacting roles in the induction and regulation of reaction wood formation including gravitropism and wood anatomical characteristics (Nugroho et al. 2012, 2013; Susilowati et al. 2013; Groover 2016; De zio et al. 2020; Aloni 2021).

In conclusion, CW, OW, and NW in *P. merkusii* at the seedling showed different anatomical characteristics. The naturally leaning stem of *P. merkusii* seedlings formed compression wood in the lower part of the leaned stem and had an eccentric growth on the stem. CW of leaning stem of *P. merkusii* seedlings formed a rounded tracheid shape and intercellular space. The differences between CW and OW in leaning stem of *P. merkusii* seedlings were significant in terms of the height of ray cells, tracheid proportion, and resin canal proportion. However, tracheid length, tracheid diameter, tracheid wall thickness, resin canal diameter and frequency, rays frequency, and ray proportion were not significantly different between CW and OW.

ACKNOWLEDGEMENTS

The authors would like to thank the Ministry of Research, Technology and Higher Education (RISTEKDIKTI) and Universitas Gadjah Mada, Yogyakarta, Indonesia, for the research funding by Grant *Penelitian Tesis Magister* (PTM) No. 1955/UN1/DITLIT/Dit-Lit/PT.01.03/2022 in 2022.

REFERENCES

Alméras T, Clair B. 2016. Critical review on the mechanisms of maturation stress generation in trees. J R Soc Interface 13: 20160550. DOI: 10.1098/rsif.2016.0550.

Aloni R. 2021. Vascular Differentiation and Plant Hormones. Springer Nature Switzerland, Cham. DOI: 10.1007/978-3-030-53202-4

BMKG. 2022. Retrieved from Data Online Pusat Database-BMKG. https://dataonline.bmkg.go.id/webfaq.

Cunningham A. 2012. Pine resin tapping techniques used around the world. In: Fett-Neto AG, Rodrigues-Corrêa KCS (eds). Pine Resin: Biol, Chemist and Appl Research Signpost, T.C., Kerala.

De Zio E, Montagnoli A, Karady M, Terzaghi M, Sferra G, Antoniadi I, Scippa GS, Ljung K, Chiatante D, Trupiano D. 2020. Reaction wood anatomical traits and hormonal profiles in poplar bent stem and root. Front Plant Sci 11: 590985. DOI: 10.3389/fpls.2020.590985.

Donaldson LA, Radotic K. 2013. Fluorescence lifetime imaging of lignin autofluorescence in normal and compression wood. J Microsc 251: 178-187. DOI: 10.1111/jmi.12059.

Edy D, Saputra MH, Suhada DA. 2012. Natural distribution and potential of *Pinus merkusii* Kerinci strain in the Kerinci Seblat National Park and its surroundings. Procceding Seminar on Research Results of BPK Aek Nauli. Aek Nauli Forestry Research Institute, Medan. Januari 2012. [Indonesian]

Eom YG, Butterfield BG. 2001. Anatomical comparisons of compression opposite and lateral wood in New Zealand rimu (*Dacrydium cupressinum* Lamb.). J Korean Wood Sci Technol 29 (3): 1-13.

Farjon A. 2013. *Pinus merkusii*. The IUCN Red List of Threatened Species 2013: T32624A2822050. https://www.iucnredlist.org/species/32624/2822050.

Gardiner B, Barnett J, Saranpaa P, Grill J. 2014. The Biology of Reaction Wood. Springer, Berlin. DOI: 10.1007/978-3-642-10814-3.

Gril J, Jullien D, Bardet S, Yamamoto H. 2017. Tree growth stress and related problems. J Wood Sci 63: 411-432. DOI: 10.1007/s10086-017-1639-y.

Groover A. 2016. Gravitropisms and reaction woods of forest trees - evolution, functions and mechanisms. New Phytol 211: 790-802. DOI: 10.1111/nph.13968.

Hiraide H, Tobimatsu Y, Yoshinaga A, Lam PY, Kobayashi M, Matsushita Y, Fukushima K, Takabe K. 2021. Localised laccase activity modulates distribution of lignin polymers in gymnosperm compression wood. New Phytol 230: 2186-219. DOI: 10.1111/nph.17264.

Janecka K, Kaczka RJ, Gärtner H, Harvey JE, Treydte K. 2016. The influence of compression wood on the strength of the climatic signal in tree rings of Norway spruce. Proceedings of the Dendrosymposium. Potsdam. 20-23 May 2015. DOI: 10.2312/GFZ.b103-16042. [Spain]

Janecka K, Kaczka RJ, Gärtner H, Harvey JE, Treydte K. 2020. Compression wood has a minor effect on the climate signal in tree-ring stable isotope records of montane Norway spruce. Tree Physiol 40: 1014-1028. DOI: 10.1093/treephys/tpaa038.

Ji Z, Ma JF, Zhang ZH, Xu F, Sun RC. 2013. Distribution of lignin and cellulose in compression wood tracheids of *Pinus yunnanensis* determined by fluorescence microscopy and confocal raman microscopy. Ind Crops Prod 47: 212-217. DOI: 10.1016/j.indcrop.2013.03.006.

Joffre T, Neagu RC, Bardage SL, Gamstedt EK. 2014. Modelling of the hygroelastic behaviour of normal and compression wood tracheids. J Struct Biol 185 (1): 89-98. DOI: 10.1016/j.jsb.2013.10.014.

Kim YS, Lee KH, Wong AH. 2015. Occurrences of mild compression wood in *Agathis borneensis* and *Dacrydium elatum*. IAWA J 36 (4): 378-386. DOI: 10.1163/22941932-20150108.

Kojima M, Becker VK, Altaner CM. 2012. An unusual form of reaction wood in Koromiko [*Hebe salicifolia* G. Forst. (Pennell)], a southern hemisphere angiosperm. Planta 235: 289-297. DOI: 10.1007/s00425-011-1503-z.

Krause C, Déry Bouchard CA, Plourde PY, Mailly D. 2013. Compression wood and stem horizontal displacement in black spruce and Jack pine plantations in the boreal forest. For Ecol Manag 302: 154-162. DOI: 10.1016/j.foreco.2013.03.048.

Lee PW, Eom YG. 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.

Li X, Evans R, Gapare W, Yang X, Wu HX. 2014. Characterizing compression wood formed in radiata pine branches. IAWA J 35 (4): 385-394. DOI: 10.1163/22941932-00000073.

Liu YM, Liu SQ, Zhou L, Qian LC. 2012. Characteristics of compression wood tracheid of loblolly pine induced by artificial inclination. Adv Mater Res 528: 113-116. DOI: 10.4028/www.scientific.net/AMR.528.113.

Nugroho WD, Nakaba S, Yamagishi Y, Begum S, Marsoem SN, Ko JH, Jin HO, Funada R. 2013. Gibberellin mediates the development of gelatinous fibres in the tension wood of inclined *Acacia mangium* seedlings. Ann Bot 112: 1321-1329. DOI: 10.1093/aob/mct198.

Nugroho WD, Yamagishi Y, Nakaba S, Fukuhara S, Begum S, Marsoem SN, Ko JH, Jin HO, Funada R. 2012. Gibberellin is required for the formation of tension wood and stem gravitropism in *Acacia mangium* seedlings. Ann Bot 110: 887-895. DOI: 10.1093/aob/mcs148.

Oliet JA, Ortiz de Urbina E, Sánchez-Pinillos M, Tardío-Cerrillo G. 2019. Matching seedling size to planting conditions: Interactive response with soil moisture. iForest 12: 220-225. DOI: 10.3832/ifor2801-012.

Purusatama BD, Febrianto F, Lee SH, Kim NH. 2022. Hardness and fracture morphology of reaction wood from *Pinus merkusii* and *Agathis loranthifolia*. Wood Sci Technol 56: 1331-1351. DOI: 10.1007/s00226-022-01413-x.

Purusatama BD, Kim JH, Yang GU, Febrianto F, Hidayat W, Lee SH, Kim NH. 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 BD, Kim NH. 2020. Cross-field pitting characteristics of compression, lateral, and opposite wood in the stem wood of *Ginkgo biloba* and *Pinus densiflora*. IAWA J 41 (1): 48-60. DOI: 10.1163/22941932-00002107.

Ruelle J. 2014. Morphology, anatomy and ultrastructure of reaction wood. In: Gardiner B, Barnett, Saranpaa P, Gril J (eds). The Biology of Reaction Wood. Springer, Berlin. DOI: 10.1007/978-3-642-10814-3_2.

Sukarno A, Hardiyanto EB, Marsoem SN, Na'iem M. 2015. Oleoresin production, turpentine yield and components of *Pinus merkusii* from various indonesian provenances. J Trop For Sci 27: 136-141.

Susilowati A, Wahyudi I, Supriyanto, Siregar IZ, Corryanti, Iswanto AH. 2013. Resin duct anatomical structure of high resin yielder *Pinus merkusii*. J Ilmu Teknol Kayu Tropis 11 (2): 120-130. [Indonesian]

TAPPI. 1998. Fiber length of pulp by classification: Test Method T 233 cm-95. TAPPI PRESS, Atlanta.

Tomczak A. 2014. Relationships between selected tree characteristics and the properties of juvenile wood in Scots pine (*Pinus sylvestris* L.). For Res Pap 75: 237-244. DOI: 10.2478/frp-2014-0023.

Westbrook JW, Walker AR, Neves LG, Munoz P, Resende MFR, Neale DB, Peter GF. 2015. Discovering candidate genes that regulate resin canal number in *Pinus taeda* stems by integrating genetic analysis across environments, ages, and populations. New Phytol 205: 627-641. DOI: 10.1111/nph.13074.

Wistuba M, Malik I, Gärtner H, Kojs P, Owczarek P. 2013. Application of eccentric growth of trees as a tool for landslide analyses: The example of *Picea abies* Karst. in the Carpathian and Sudeten Mountains (Central Europe). Catena 111: 41-55. DOI: 10.1016/j.catena.2013.06.027.