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# Comparative wood anatomy of *Rubroshorea leprosula* across multiple populations in Sumatra Island, Indonesia

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**Abstract.** *Fadilah A, Dwiyanti FG, Triadiati, Hikmat A, Karlinasari L, Siregar IZ. 2026. Comparative wood anatomy of* Rubroshorea leprosula *across multiple populations in Sumatra Island, Indonesia. Biodiversitas 27 (2): d270204. https://doi.org/10.13057/biodiv/d270204.* Red meranti wood (*Rubroshorea leprosula*) is classified in strength classes II-IV and durability classes III-IV, making it suitable for light and heavy construction due to its high wood quality. This has led to widespread exploitation, illegal logging, and illicit trade, particularly from natural forests. Current conservation strategies lack adequate scientific support, particularly in species and origin identification, which are crucial for wood tracking. Wood anatomy is a simple, rapid, and reliable method for identifying wood species. Therefore, this study aimed to evaluate the wood anatomy of *R. leprosula* by examining visual, macroscopic, and microscopic structures to identify key characteristics that differentiate between populations. Visual characteristics were assessed based on wood color, pattern, texture, gloss, and grain orientation. Macroscopic observations were made of growth rings, vessels, intercellular canals, axial parenchyma, and ray parenchyma. Microscopic analysis was performed using a light microscope to observe cellular structures qualitatively and quantitatively. Samples were collected from five populations in Sumatra, Indonesia. Fifty wood samples (ten per population) were analyzed. Data were statistically analyzed using One-Way ANOVA and post-hoc tests to identify significant differences between populations. The results showed that evaluation of the microscopic structure successfully identified key characteristics, particularly variations in vessel diameter, that consistently differentiated among populations, with significant differences (p-value = 0.00000545) ranging from 105.2-158.7μm, most notably between samples from Bukit Tigapuluh National Park and Harapan Rainforest (p-value<0.025). This anatomical variation, potentially related to hydraulic conductivity and ecological adaptation, indicates population differentiation. This study contributes to forest biology by linking anatomical traits to adaptive functions and traceability, which are essential for the sustainable management of tropical timber resources.

**Keywords:** Commercial wood, red meranti, *Rubroshorea*, timber tracking, wood anatomy

## INTRODUCTION

Red meranti is considered a primary commercial product in the timber trade, the leading roundwood commodity with a total volume of 653.49 thousand m3 in 2020 (BPS 2021). Red meranti has a straight and cylindrical trunk, mainly sourced from natural forests. However, there are plantation efforts to produce wood from sustainably managed forests (Wistara et al. 2016). Previous reports have shown that the survival rate of the wood exceeds 67%, with a Mean Annual Diameter Increment (MADI) above 1.7 cm/year (Widiyatno et al. 2020).

As part of Dipterocarpaceae, red meranti consists of about 75 species distributed in the lowland rainforests of Malaya, Sumatra, Borneo, the Philippines, and the Moluccas (van Steenis 1983). As part of the Sundaland hotspot, in Indonesia, Sumatra's biogeographic history has significantly influenced the distribution and differentiation of its species. This contributes to wood anatomical variation in species and populations, which is relevant for conservation. *Rubroshorea leprosula*, known *as meranti tembaga*, is a red meranti wood species. The harvested wood has good prospects as it is classified into strength classes II-IV and durability classes III-IV. It is traded regionally and internationally for light and heavy construction including furniture, flooring, and plywood (Alex et al. 2023). However, its high value has driven unsustainable harvesting and illegal logging. *Rubroshorea leprosula* usually occurs in late successional stages and is a climax species in lowland dipterocarp forests with low regeneration rates (Nurfatma et al. 2017). It exhibits low regeneration in degraded habitats such as Tesso Nilo National Park (Kusumo et al. 2016). It therefore has low dominance in protected forests like Bukit Barisan Selatan National Park (Prayoga et al. 2019). These ecological traits make the species vulnerable to habitat disturbance and overexploitation, such as that concentrated around the now-abandoned PT. Patriadi concession. This logging activity remains active in Gunung Leuser National Park, where loggers target *R. leprosula*, which is easier to locate, cut down, and process than other species (Harnelly et al. 2016).

Indonesia exported illegal wood to partner countries such as China and Japan from 2001 to 2010, with volumes estimated at 11,000 $m^3$ and 12,000 $m^3$ of Roundwood Equivalent (RWE), respectively (Ji et al. 2018). In 2013, about 50% of the 80 million $m^3$ of RWE was illegally produced, originating from Indonesia (Hoare 2015). However, only 3,829 $m^3$ of illegal wood was seized in 2017 (Ministry of Environment and Forestry 2019). This situation highlights the urgent need for conservation efforts to protect the existing populations of *R. leprosula*. The United Nations Office on Drugs and Crime (UNODC) (2016) published a wood identification guide to combat illegal wood, noting that wood identification relies on visual, chemical, and genetic methods (Dormontt et al. 2015). The most established method in wood identification is the visual method, which provides a study of wood anatomy for taxonomic characterization based on the internal structure of wood. Wood anatomy provides a scientifically grounded, cost-effective method that can be undertaken at the genus level, occasionally at the species and provenance levels, but requires abundant identification and has gained traction in timber tracking applications (Dormontt et al. 2015; Cetera et al. 2021), including prominent members of Dipterocarpaceae.

In a study by Adi et al. (2020), wood anatomy was used to distinguish variations in red meranti wood from the *Shorea* genus according to trade groups. Intraspecific variation in wood anatomical structures, such as vessel diameter and fiber wall thickness, is taxonomically relevant and ecologically meaningful for plant adaptation to local environmental conditions, including precipitation, drought, and temperature (Taia 2020; Pandey 2021). Wood anatomy has identified variations in fiber wall thickness in red meranti to assess wood quality, such as wood density and specific gravity, which correlate with natural durability (Bosman 1996; Praptoyo and Sudaryono 2012; Dadzie and Amoah 2015; Sulistyo et al. 2018). The effects of geographical provenance on wood density have been studied for the valued hardwoods due to their practical implications for tree breeding and conservation programs (Nazari et al. 2020; Sousa et al. 2021). Furthermore, decreasing fiber wall thickness reduces wood strength as indicated by the mechanical properties of wood (Wistara et al. 2016). A clear research gap remains on anatomical variation in *R. leprosula* in Indonesia, as it is scarce. Current work has focused on broader taxonomic or commercial groupings rather than local differentiation, which could inform conservation strategies and timber tracking systems. Given the increasing demand for wood traceability and the ecological vulnerability of *R. leprosula*, research that integrates wood anatomical, ecological, and geographic data is urgently needed to increase the reliability of origin identification. Therefore, this study aims to evaluate the wood anatomy of *R. leprosula* across five natural populations on Sumatra Island by identifying key characteristics that distinguish populations through comparative analysis of visual, macroscopic, and microscopic structures. By establishing the extent of wood anatomical variation among populations, the findings will contribute to the development of a robust timber tracking database and provide ecological insights to support the conservation and sustainable use of this important tropical timber species.

## MATERIALS AND METHODS

### Study location and plant material

Wood core samples of *R. leprosula* were collected from five populations across Sumatra Island, Indonesia. These populations were selected based on their natural occurrence across different ecological and geographical areas that vary in forest type, elevation, rainfall, and disturbance history. The selection aimed to capture the environmental conditions of *R. leprosula*, allowing comparison of wood anatomical variation across habitats. Samples were collected from a site at an elevation of 25-197 meters above sea level. Sampling locations included Soraya Research Station in Aceh Province (-2.919717 S, 97.918573 E) and Tesso Nilo National Park in Riau Province (-0.199247 S, 101.976471 E), characterized by lowland tropical rainforest and high annual rainfall, Bukit Tigapuluh National Park in Riau Province (-0.835869 S, 102.518547 E), a mixed dipterocarp forest with undulating terrain, Hutan Harapan of PT. Restorasi Ekosistem Indonesia (PT. REKI) in Jambi Province (-2.175743 S, 103.368698 E), an area of secondary forest undergoing ecological restoration with varied topography, and Bukit Barisan Selatan National Park in Lampung Province (-5.563085 S, 104.42086 E) encompassing montane forest ecosystems (Figure 1).

Field sampling was conducted under research permit No. B-7775/IV/KS.00.00/8/2022 and No. B-1636/IV/KS.00/2/2024, issued by the National Research and Innovation Agency, No. SK. 192/KSDAE/SET.3/KSA.2/10/2022 and No. SK. 73/KSDAE/SET.3/KSA.2/4/2024, issued by Direktur Jenderal Konservasi Sumber Daya Alam Dan Ekosistem. All procedures complied with national and institutional guidelines for biodiversity research and specimen collection. Representative voucher specimens were deposited in the Laboratory of Forest Genetics and Molecular Forestry, Department of Silviculture, Institut Pertanian Bogor, Bogor, Indonesia. Wood cores were collected from the trunks of ten selected healthy mature trees, each with a diameter of 30 cm or more, from each of the five populations. Sampling was conducted by drilling a horizontal hole 130 cm above ground level in the tree trunk using a 5 mm diameter and 24-cm long increment borer (Haglöf, Sweden). Samples were collected from the outer bark down to the inner pith. The purpose of this tree sampling was to ensure homogeneity. Fifty specimens from five populations were collected, stored in plastic straws, and packed in ziplock bags with silica gel for laboratory analysis. The sample position distribution was determined for each wood core: heartwood (near the pith) and sapwood (near the bark). The sample was cut into approximately 1 cm long segments to facilitate observation. Wood anatomical examinations were conducted at the Laboratory of Plant Physiology and Genetics in the Department of Biology, Institut Pertanian Bogor.

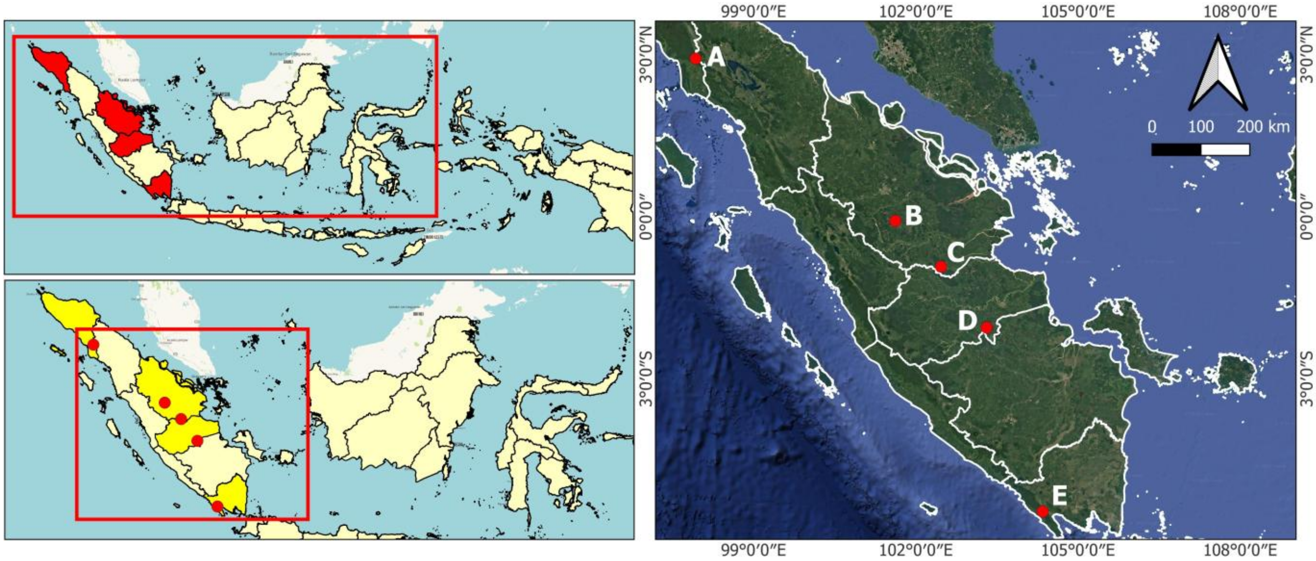

**Figure 1.** Map of *Rubroshorea leprosula* wood core sample collection locations in five populations in Sumatra, Indonesia. A. Sumatra Island at Soraya Research Station, B. Tesso Nilo National Park, C. Bukit Tigapuluh National Park, D. Harapan Forest, and E. Bukit Barisan Selatan National Park

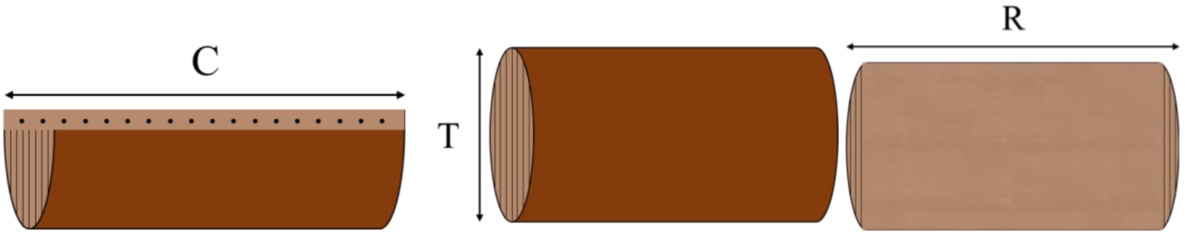

**Figure 2.** Determination of three wood planes based on tree axes from incremental borer (Haglöf, Sweden) samples. C: Cross-section, T: Tangential, and R: Radial

## Wood anatomy analysis

### *Visual characteristics*

Visual characteristics of the wood samples were assessed based on five variables: color, pattern, texture, gloss, and grain orientation. Visual characteristics are qualitative and are observed based on following the Indonesian National Standard (SNI) 8491:2018 for Macroscopic Wood Identification. This standard, widely used in Indonesia, provides a systematic framework for evaluating wood features visible to the naked eye. Specific protocols were applied consistently for each variable to ensure standardization and comparability across parameters. Visual characteristics were observed on fifty heartwood segments, 1 cm in length. Before analysis, the wood surface was uniformly polished with a cutter to improve the clarity of anatomical features. Heartwood color was assessed using the Munsell Soil Color Chart by Macbeth Color and Photometer Division (2002), a tool recommended in SNI 8491:2018 that ensures accurate and repeatable color classification relevant to wood properties. The wood color observations were conducted for approximately 10 minutes per sample to ensure consistency. The evaluation of wood pattern is examined in three predetermined planes (cross-section, tangential, and radial) as illustrated in Figure 2 using the naked eye or a magnifying glass. Wood texture was assessed on the cross-section and classified as coarse, medium, or fine, with adjustments made based on vessel size observed microscopically. Grain orientation was evaluated in the tangential plane and categorized into straight or oblique grain arrangements. Lastly, wood gloss was assessed on three wood planes (cross-section, tangential, and radial) and classified as either shiny or dull based on the reflectance to light.

### *Macroscopic Structure*

Macroscopic observations of wood structure were conducted based on eleven standardized variables: growth rings, vessel porosity, vessel grouping, vessel arrangement, presence of tyloses, presence of deposits, type of axial parenchyma, type of ray parenchyma, size of ray parenchyma, and presence of axial and radial intercellular canals. Macroscopic structures are qualitative, and all observations followed the guidelines outlined in the SNI 8491:2018 for Macroscopic Wood Identification. Macroscopic structures were observed on fifty segments of heartwood, 1 cm in length. The wood surfaces were polished uniformly before observation with a cutter to ensure the clarity of anatomical features. All variables were examined consistently on the cross-section plane of the wood, as illustrated in Figure 2, using a magnifying glass. Digital images were captured using a Dino-Lite

AF7915MZT microscope connected to the DinoCapture 3.0 software to support detailed documentation and verification of the observed features.

*Microscopic structure*

The specimens used for microscopic structure analysis were the same wood samples previously examined for visual characteristics and macroscopic structure, ensuring continuity and consistency across observational levels. Thin sections were prepared from each sample of heartwood to ensure homogeneity. The preparation of thin sections followed the method described by Sass (1958). Wood samples were softened by immersing them in distilled water for 7 to 14 days, depending on the wood density. Softened wood samples were sliced into thin sections with a thickness of 5-10 µm, prepared from the cross-section (1 x 0.5 cm), tangential (ø = 0.5 cm), and radial (1 x 0.5 cm) planes as shown in Figure 2 using a GLS1 sliding microtome. Two replicate thin sections in each plane (n = 2) were obtained per tree to ensure representative observations. Each section was stained with a 1% safranin solution for 5 to 6 hours and then rinsed with distilled water. Dehydration was carried out in a graded ethanol series (10%, 30%, 50%, 70%, and 96%) followed by xylene treatment. To prevent tissue overlap, the sections were carefully mounted on glass slides before being permanently preserved using Entellan mounting medium. Observations were carefully carried out using an optical microscope (Trinocular Olympus CX33 LED with Indomicro Digital Camera) at magnifications of 40×, 100×, and 400×, and analyzed through image analysis software (IndoMicro and ImageJ). Microscopic structure features were evaluated qualitatively and quantitatively based on the International Association of Wood Anatomists (IAWA) List of Microscopic Features for Hardwood Identification (Alfonso et al. 1989), ensuring consistency in terminology and interpretation.

### Data analysis

This study employed an integrated approach by combining the analysis of visual characteristics, macroscopic, and microscopic structures. This multi-level approach was selected to ensure a comprehensive and reliable identification in line with best practices in wood anatomy research. Visual characteristics, macroscopic, and microscopic structures observed qualitatively were presented descriptively and indexed to assign weights to each variable. For quantitative assessment, tangential vessel diameters were measured on cross-sections from 25 representative vessels per tree. The height of each ray parenchyma was measured on tangential sections from 25 ray parenchyma per tree. Radial and tangential fiber diameters, lumen diameters, and fiber wall thicknesses were measured from 50 fibers per tree on cross-sections. These sample sizes were selected to balance accuracy and efficiency while capturing representative anatomical variation. All measurements were conducted using an optical microscope with the same protocol and under consistent lighting at magnifications of 100× and 400× to ensure comparability across parameters. Qualitative and quantitative data are presented in structured tables and figures designed to clarify and support meaningful interpretation of the anatomical data. The data were then analyzed using the One-Way ANOVA and post-hoc tests to determine the data significant differences in wood anatomical features across populations. Analysis was performed using R Studio software.

## RESULTS AND DISCUSSION

### Visual Characteristics

The visual characteristics of the wood core samples were assessed based on SNI 8491:2018 and presented as qualitative data. These data were subsequently analyzed using an indexing method to assign weight to each variable. Testing for normality in visual characteristics data found that the wood color variable was not normally distributed, but could still be further analyzed. Erwin et al. (2023) found that the wood color of nearly all red meranti species was reddish-brown. More precise details on wood color were obtained using the brightness (L), red-green (a), and yellow-blue color level (b) parameters. Red-green color level (a) demonstrated a strong tendency toward red coloration. Ogata et al. (2008) found that the wood color of the *R. leprosula* species was pale red. However, red meranti wood exposed to outdoor weather conditions for 150 days will gradually change color and aesthetic appearance (discoloration) to gray (Erwin et al. 2023). As summarized in Table 1, wood color varied across locations, with the Bukit Tigapuluh National Park population showing light reddish-brown as the dominant color. This aligns with the visual observations depicted in Figure 3, where Tesso Nilo National Park wood samples appear notably paler than others. In contrast, samples from Hutan Harapan and Bukit Barisan Selatan National Park displayed relatively similar coloration, generally falling into two comparable color groups.

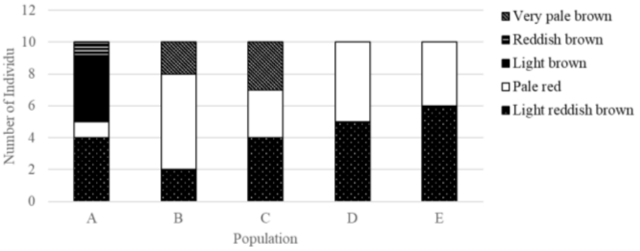

**Figure 3.** Distribution of wood color of *R. leprosula* based on the Munsell Soil Color Chart by Macbeth Color and Photometer Division (2002) in Sumatra, Indonesia. A. Soraya Research Station, B. Tesso Nilo National Park, C. Bukit Tigapuluh National Park, D. Harapan Forest, and E. Bukit Barisan Selatan National Park

**Table 1.** Visual characteristics of *R. leprosula* wood from five natural populations in Sumatra, Indonesia, assessed based on the SNI 8491:2018 for Macroscopic Wood Identification, including wood color, pattern, texture, gloss, and grain orientation

<table>
<tr><th rowspan="2">Variables</th><th colspan="5">Population</th></tr>
<tr><th>A</th><th>B</th><th>C</th><th>D</th><th>E</th></tr>
<tr><td>Color</td><td><b>Light brown</b>, <b>light reddish-brown</b>, pale red, reddish brown</td><td>Light reddish-brown, <b>pale red</b>, very pale brown</td><td><b>Light reddish-brown</b>, pale red, very pale brown</td><td colspan="2"><b>Light reddish-brown, pale red</b></td></tr>
<tr><td>Pattern</td><td colspan="5">Plain</td></tr>
<tr><td>Texture</td><td colspan="5">Medium</td></tr>
<tr><td>Grain orientation</td><td>Wavy, <b>straight</b></td><td colspan="4">Straight</td></tr>
<tr><td>Gloss</td><td colspan="5">Shiny</td></tr>
</table>

Note: Bold letters indicate the most common characteristics. A. Soraya Research Station, B. Tesso Nilo National Park, C. Bukit Tigapuluh National Park, D. Harapan Forest, and E. Bukit Barisan Selatan National Park

The visual characteristics observed in this study are consistent with those reported by Praptoyo and Sudaryono (2012), who documented similar visual characteristics among the *R. leprosula* sample across different sites. In the present study, wood samples from all five Sumatra populations exhibited a comparable pattern, texture, and gloss. Grain orientation was generally straight across populations; however, one specimen from Soraya Research Station showed a wavy grain orientation, indicating minor intraspecific variation. Despite this slight deviation, the variables of wood pattern, texture, gloss, and grain orientation displayed uniformity, producing identical x-values across samples. Consequently, these variables were not suitable for inferential statistical analysis.

## Macroscopic structure

The macroscopic structure observations were conducted following the guidelines of SNI 8491:2018 and presented as qualitative data. In the *R. leprosula*, the boundaries of growth rings are indistinct. Due to seasonal changes, the clarity of growth rings in wood is affected by abrupt structural changes at the boundary between earlywood and latewood. Furthermore, hardwood species' indistinct growth rings result from the distribution of their vessel. *Rubroshorea leprosula* wood exhibits a diffuse-porous distribution, which means there are minimal or only slight differences in vessel size between growth rings and in the proportions of earlywood and latewood. Data normality testing on macroscopic structures indicated that the variables of presence of deposits, axial parenchyma type, and the presence of intercellular canals were generally not normally distributed but were suitable for further analysis. In contrast, the variables of growth rings, wood porosity, vessel groupings, vessel arrangement, presence of tyloses, ray parenchyma type, and ray parenchyma size all showed identical x values, rendering them unsuitable for further analysis. Referring to Crivellaro et al. (2015), the presence of deposits in *R. leprosula* was classified as yellow. This is consistent with the results of Dewi et al. (2020), who stated that the deposits in vessels of *R. leprosula* used as wooden ship materials on Riau Island were brownish-yellow. The macroscopic structures are summarized in Table 2.

A previous study by Dewi et al. (2020) reported that the axial parenchyma of *R. leprosula* used as boatbuilding material in the Riau Islands appeared in narrow bands up to three cells wide. Similarly, Praptoyo and Sudaryono (2012) described axial parenchyma in *R. leprosula* from natural forests and intensively managed stands as forming concentric bands, vasicentric patterns, and scanty paratracheal types. In contrast, macroscopic observations from the present study showed that apotracheal axial parenchyma arranged in continuous tangential bands was the most consistently observed feature across all populations (Table 2). Paratracheal axial parenchyma types varied among populations: Soraya Research Station and Bukit Barisan Selatan National Park exhibited thin-winged aliform and confluent forms; Tesso Nilo National Park showed thin-winged aliform parenchyma; Bukit Tigapuluh National Park displayed unilateral and vasicentric types; and Hutan Harapan exhibited sparse and unilateral paratracheal parenchyma. These macroscopic structures were visually confirmed using Dino-Lite imaging, as shown in Figure 4, which also captures the presence of axial intercellular canals. Such macroscopic structures observable using a hand lens or even the naked eye represent diagnostic traits that can be readily utilized for rapid field identification of *R. leprosula*.

## Microscopic structure

In all studied populations of *R. leprosula*, the vessel elements exhibited consistent anatomical patterns as shown in Table 3 and illustrated in Figure 9. Growth ring boundaries were indistinct across all samples, and the wood consistently displayed diffuse porosity, indicating a lack of seasonal variation in vessel size. Vessels were primarily solitary or in short radial multiples, and all populations exhibited simple perforation plates. Notably, tyloses were frequently observed occluding the vessel lumens, which may relate to physiological processes such as heartwood formation or environmental adaptation mechanisms. The indistinct growth ring boundaries observed align with the typical characteristics of diffuse porous species, where transitions between earlywood and latewood vessels are subtle or absent (Ruffinatto et al. 2023). However, in *R. leprosula*, the absence of abrupt changes in vessel distribution, axial parenchyma, or fiber wall thickness across growth increments makes the growth rings nearly undetectable. This anatomical profile aligns with previous descriptions by Bosman (1996), Praptoyo and Sudaryono (2012), Sulistyo et al. (2018), and Joni et al. (2024), who also reported diffuse porosity with vessels occurring solitarily or in radial and diagonal multiples. The consistency of these traits across geographically distinct populations suggests strong species-level anatomical stability.

In the tangential sections of *R. leprosula* wood from all five populations, ray parenchyma and fiber characteristics showed both similarities and variations. Uniseriate, biseriate, and multiseriate ray parenchyma were observed in samples from Soraya Research Station, Tesso Nilo National Park, Bukit Tigapuluh National Park, and Hutan Harapan. In contrast, the Bukit Barisan Selatan National Park population displayed only biseriate and multiseriate ray parenchyma. About fiber structure, both septate and non-septate fibers were present in the Soraya Research Station and Tesso Nilo National Park populations. In contrast, the remaining three populations displayed only non-septate fibers. These differences may reflect intraspecific anatomical variation influenced by local environmental conditions or genetic diversity.

**Table 2.** Macroscopic structure of *R. leprosula* wood from five natural populations in Sumatra, Indonesia, assessed based on the SNI 8491:2018 for Macroscopic Wood Identification, including growth rings, vessel features, axial and ray parenchyma, and intercellular canals

| Variables | Population | | | | |
|---|---|---|---|---|---|
| | A | B | C | D | E |
| Growth ring | Indistinct or absent | | | | |
| Porosity | Wood diffuse-porous | | | | |
| Vessel grouping | Solitary and radial/diagonal multiples | | | | |
| Vessel arrangement | Diagonal/radial | | | | |
| Tyloses | Present | | | | |
| Deposits | **Absent**, Present | | | | |
| Axial parenchyma | Paratracheal axial parenchyma (thin-winged aliform, confluent)<br>**Apotracheal axial parenchyma (continuous tangential bands)** | Paratracheal axial parenchyma (thin-winged aliform)<br>**Apotracheal axial parenchyma (continuous tangential bands)** | Paratracheal axial parenchyma (unilateral, vasicentric)<br>**Apotracheal axial parenchyma (continuous tangential bands)** | Paratracheal axial parenchyma (sparse, unilateral)<br>**Apotracheal axial parenchyma (continuous tangential bands)** | Paratracheal axial parenchyma (thin-winged aliform, confluent)<br>**Apotracheal axial parenchyma (continuous tangential bands)** |
| Ray parenchyma type | Rough | | | | |
| Ray parenchyma size | Uniseriate | | | | |
| Intercellular canals | **Axial**, radial | | | Axial | |

Note: Bold letters indicate the most common characteristics. A. Soraya Research Station, B. Tesso Nilo National Park, C. Bukit Tigapuluh National Park, D. Harapan Forest, and E. Bukit Barisan Selatan National Park

**Table 3.** Microscopic structure of *R. leprosula* from five natural populations in Sumatra, Indonesia, assessed based on Alfonso et al. (1989), including growth ring, vessel, axial and ray parenchyma, and fiber cell

| Variables | Population | | | | |
|---|---|---|---|---|---|
| | A | B | C | D | E |
| Growth rings | Indistinct or absent | | | | |
| Porosity | Wood diffuse-porous | | | | |
| Vessel groupings | Solitary and radial/diagonal multiples | | | | |
| Vessel arrangement | Diagonal/radial | | | | |
| Tyloses | Present | | | | |
| Perforation plates | Simple | | | | |
| Septate fibers | Fiber-septate and non-septate | | | | |
| Axial Parenchyma | Paratracheal axial parenchyma (lozenge-aliform, confluent) | Paratracheal axial parenchyma (lozenge-aliform) | Paratracheal axial parenchyma (scanty, vasicentric, lozenge-aliform) | Paratracheal axial parenchyma (scanty) | Paratracheal axial parenchyma (lozenge-aliform, confluent) |
| | **banded parenchyma (bands more than three cells wide)** | | | | |
| Ray parenchyma width | Uniseriate, biseriate, **multiseriate** | | | | |

Note: Bold letters indicate the most common characteristics. A. Soraya Research Station, B. Tesso Nilo National Park, C. Bukit Tigapuluh National Park, D. Harapan Forest, and E. Bukit Barisan Selatan National Park

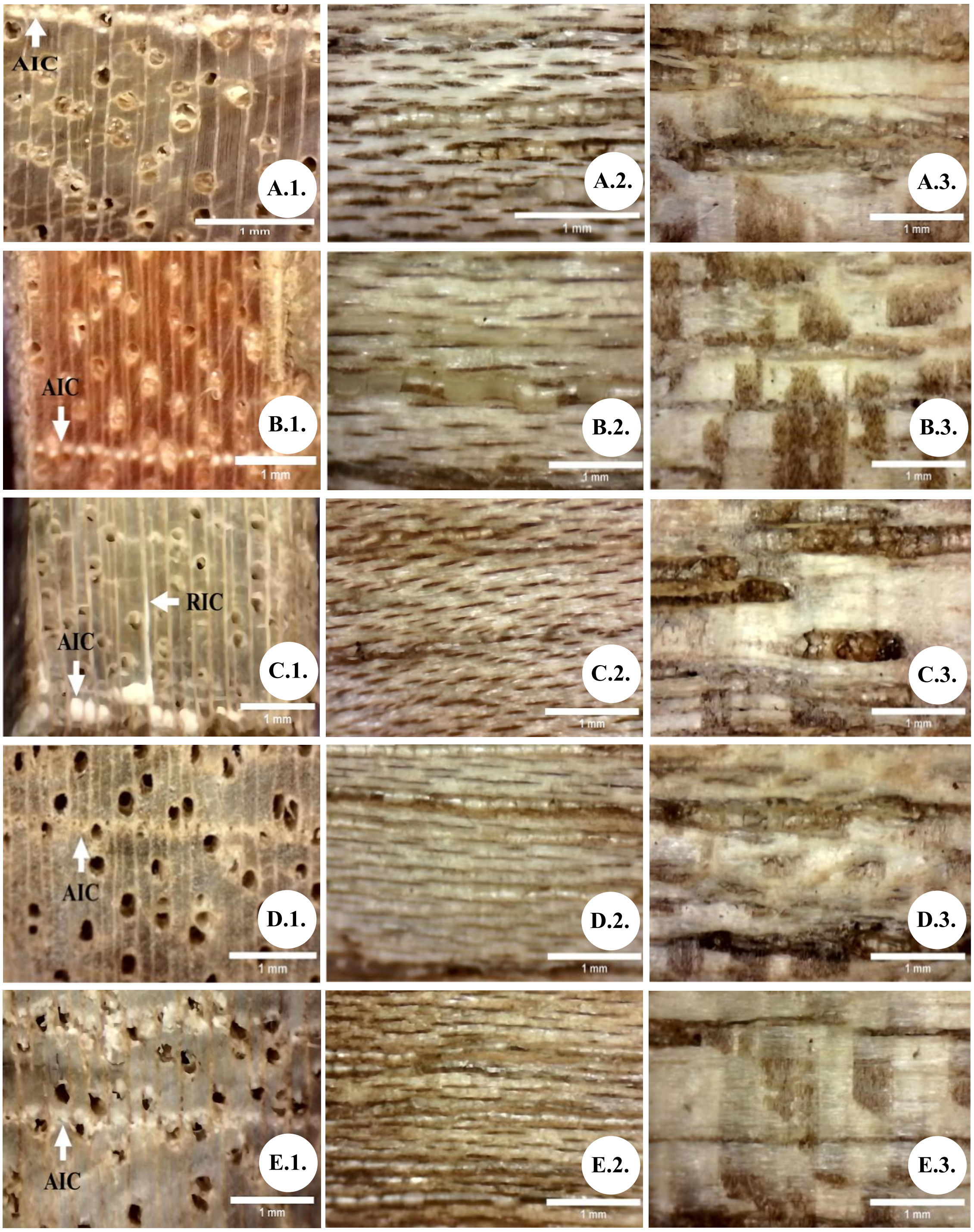

**Figure 4.** Dino-Lite captures (20X magnification) of cross-section (1), tangential (2), and radial (3) views of *R. leprosula* form in Sumatra, Indonesia. A. Soraya Research Station, B. Tesso Nilo National Park, C. Bukit Tigapuluh National Park, D. Harapan Forest, and E. Bukit Barisan Selatan National Park. AIC: Axial Intercellular Canal, RIC: Radial Intercellular Canal

In the radial section of *R. leprosula* wood from Soraya Research Station, Tesso Nilo National Park, Bukit Tigapuluh National Park, and Bukit Barisan Selatan National Park consistently exhibited body ray parenchyma dominated by procumbent cells, accompanied by a single row of upright or square marginal cells. In contrast, the Hutan Harapan population displayed a more heterogeneous ray parenchyma structure, with a mixture of procumbent, square, and upright cells within the same rays. Such variation may indicate subtle anatomical differentiation among populations, potentially reflecting environmental or genetic influences. Additionally, radial intercellular canals were consistently observed in samples from Soraya Research Station, Tesso Nilo National Park, and Bukit Tigapuluh National Park. These canals formed tubular structures oriented parallel to the wood rays and represent a typical anatomical feature of *R. leprosula*, distinguishing it from other red meranti species.

**Table 4.** The quantitative anatomical features of *R. leprosula* from five natural populations in Sumatra, Indonesia, assessed based on Alfonso et al. (1989), including vessel diameter, fiber diameter, fiber lumen diameter, fiber wall thickness, and ray parenchyma height

| ***Rubroshorea leprosula*** | **Characters** | | | | |
|---|---|---|---|---|---|
| | **VD ($\bar{X}$, range) µm** | **FD ($\bar{X}$, range) µm** | **LD ($\bar{X}$, range) µm** | **FWT ($\bar{X}$, range) µm** | **RH ($\bar{X}$, range) µm** |
| Soraya Research Station | 111.88<br>(93.51-125.26) | 24.45<br>(20.03-29.63) | 13.10<br>(10.92-18.41) | 5.68<br>(2.33-6.54) | 460.36<br>(314.19-662.12) |
| Tesso Nilo National Park | 133.33<br>(105.85-199.32) | 22.74<br>(20.27-28.11) | 15.17<br>(11.65-19.97) | 3.79<br>(2.43-6.67) | 473.20<br>(311.51-788.33) |
| Bukit Tigapuluh National Park | 135.43<br>(110.84-162.84) | 24.05<br>(20.06-29.46) | 14.98<br>(10.01-19.91) | 4.53<br>(2.09-6.49) | 547.00<br>(304.13-883.05) |
| Hutan Harapan | 95.09<br>(85.00-113.00) | 23.54<br>(21.04-25.33) | 15.23<br>(10.35-19.87) | 4.15<br>(2.01-6.49) | 515.60<br>(328.00-652.79) |
| Bukit Barisan Selatan National Park | 112.79<br>(98.39-127) | 24.80<br>(21.17-29.69) | 15.50<br>(10.11-19.04) | 4.65<br>(2.10-6.99) | 675.49<br>(362.02-980.82) |
| Ogata et al. (2008) (Malaya, Sumatra, Kalimantan) | 250-330 | 15-30 | - | 2-6 | 750-3500 |
| Praptoyo and Sudaryono (2012); Sulistyo et al. (2018) (Kalimantan) | 160.36 | 22.88 | 18.84 | 2.02 | - |
| Wistara et al. (2016) (Kalimantan) | - | 24.70<br>(20.30-29.10) | 14.80<br>(10.90-18.70) | 5.00<br>(3.90-6.10) | - |
| Helmling et al. (2018) (Malaya, Sumatra, Kalimantan) | 312.00<br>(139.00-421.00) | 21.00 | - | 4.30 | - |
| Adi et al. (2020) (Sumatra, Kalimantan) | 162.00<br>(100.00-200.00) | - | - | - | - |
| Joni et al. (2024) (Kalimantan) | - | 23.69<br>(20.13-26.10) | 20.20<br>(16.23-22.75) | 1.75<br>(1.63-1.95) | - |
| Aiso et al. (2025) (Kalimantan) | 166.00<br>(151.00-181.00) | 21.60<br>(20.10-23.10) | 19.56<br>(18.14-20.98) | 1.02<br>(0.98-1.06) | - |

Note: $\bar{X}$: Mean, VD: Vessel Diameter, FD: Fiber Diameter, LD: Fiber Lumen Diameter, FWT: Fiber Wall Thickness, RH: Ray Parenchyma Height

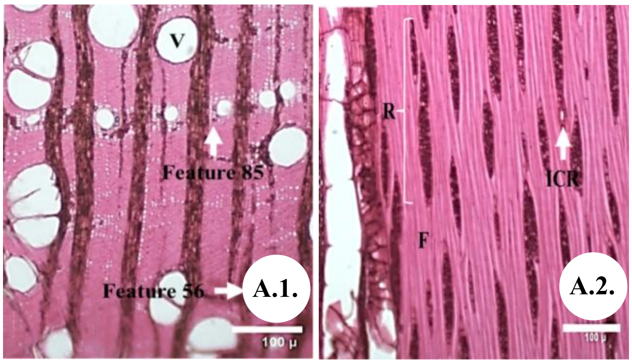

**Figure 5.** Optical microscope captures (4X10 magnification) showing tylosis (feature 56) and axial parenchyma bands more than three cells wide (feature 85) (A.1.), and Radial Intercellular Canal (RIC) (feature 130) (A.2.) in *R. leprosula* from Soraya Research Station population in Sumatra, Indonesia. V: Vessel, R: Ray parenchyma, F: Fiber

### *Soraya Research Station*

At Soraya Research Station, microscopic structure observations revealed distinct anatomical features of *R. leprosula.* As shown in Figure 5, apotracheal axial parenchyma appeared as continuous tangential bands more than three cells wide surrounding the axial intercellular canals. Additional types of axial parenchyma, including paratracheal parenchyma of the lozenge-aliform and confluent forms, were also identified through microscopic examination. However, these features are not clearly visible in the image provided. Quantitative anatomical features for this population are presented in Table 4. The mean tangential vessel diameter measured 111.88 µm (range: 93.51-125.26 µm). The fiber diameter, fiber lumen diameter, and fiber wall thickness were 24.45 µm (range: 20.03-29.63 µm), 13.10 µm (range: 10.92-18.41 µm), and 5.68 µm (range: 2.33-6.54 µm), respectively. Based on the ratio between the fiber lumen diameter and double wall thickness, the lumen diameter was less than three times the double wall thickness, classifying the fibers as thin-to thick-walled, consistent with the criteria outlined in Alfonso et al. (1989). The mean ray parenchyma height for this population measured 460.36 µm (range: 314.19-662.12 µm), indicating relatively tall multiseriate rays. These qualitative and quantitative anatomical features correspond with the descriptions summarized in Table 3 and the anatomical variation illustrated in Figure 9.

### *Tesso Nilo National Park*

At Tesso Nilo National Park, microscopic structure observations revealed distinct anatomical features of *R. leprosula.* As shown in Figure 6, apotracheal axial parenchyma appeared as continuous tangential bands more than three cells wide surrounding the axial intercellular canals. Additional types of axial parenchyma, including paratracheal parenchyma of the lozenge-aliform forms, were also identified through microscopic examination. However, these features are not clearly visible in the image provided. Quantitative anatomical features for this population are presented in Table 4. The mean tangential vessel diameter measured 133.33 µm (range: 105.85-199.32 µm). The fiber diameter, fiber lumen diameter, and fiber wall thickness were 22.74 µm (range: 20.27-28.11 µm), 15.17 µm (range: 11.65-19.97 µm), and 3.79 µm (range: 2.43-6.67 µm), respectively. Based on the ratio between the fiber lumen diameter and double wall thickness, the lumen diameter was more than three times the double wall thickness of the fiber, which is categorized as a very thin-walled, consistent with the criteria outlined in Alfonso et al. (1989). Additionally, the mean ray parenchyma height for this population measured 473.20 µm (range: 311.51-788.33 µm). These qualitative and quantitative anatomical features correspond with the descriptions summarized in Table 3 and the anatomical variation illustrated in Figure 9.

*Bukit Tigapuluh National Park*

At Bukit Tigapuluh National Park, microscopic structure observations revealed distinct anatomical features of *R. leprosula*. As shown in Figure 9, apotracheal axial parenchyma appeared as continuous tangential bands more than three cells wide surrounding the axial intercellular canals. Additional types of axial parenchyma, including paratracheal parenchyma of the scanty, vasicentric, lozenge-aliform forms, were also identified through microscopic examination. However, these features are not clearly visible in the image provided. Quantitative anatomical features for this population are presented in Table 4. The mean tangential vessel diameter measured 135.43 µm (110.84-162.84 µm). The fiber diameter, fiber lumen diameter, and fiber wall thickness were 24.05 µm (range: 20.06-29.46 µm), 14.98 µm (range: 10.01-19.91 µm), and 4.53 µm (range: 2.09-6.49 µm), respectively. Based on the ratio between the fiber lumen diameter and double wall thickness, the lumen diameter was three times wider than the double wall thickness of the fiber; it can be categorized as a very thin-walled, consistent with the criteria outlined in Alfonso et al. (1989). The mean ray parenchyma height for this population measured 547.00 µm (range: 304.13-883.05 µm). These qualitative and quantitative anatomical features correspond with the descriptions summarized in Table 3 and the anatomical variation illustrated in Figure 7.

*Hutan Harapan*

At Hutan Harapan, microscopic structure observations revealed distinct anatomical features of *R. leprosula*. As shown in Figure 9, apotracheal axial parenchyma appeared as continuous tangential bands more than three cells wide surrounding the axial intercellular canals. Additional types of axial parenchyma, including paratracheal parenchyma of the scanty forms, were also identified through microscopic examination. However, these features are not clearly visible in the image provided. Quantitative anatomical features for this population are presented in Table 4. The mean tangential vessel diameter measured 95.09 µm (range: 85.00-113.00 µm). However, the fiber diameter, fiber lumen diameter, and fiber wall thickness were 23.54 µm (range: 21.04-25.33 µm), 15.23 µm (range: 10.35-19.87 µm), and 4.15 µm (range: 2.01-6.49 µm), respectively. Based on the ratio between the fiber lumen diameter and double wall thickness, the lumen diameter was less than three times the double wall thickness; it can be categorized as a thin to thick-walled according to Alfonso et al. (1989). The mean ray parenchyma height for this population measured 515.60 µm (range: 328-652.79 µm). These qualitative and quantitative anatomical features correspond with the descriptions summarized in Table 3 and the anatomical variation illustrated in Figure 8.

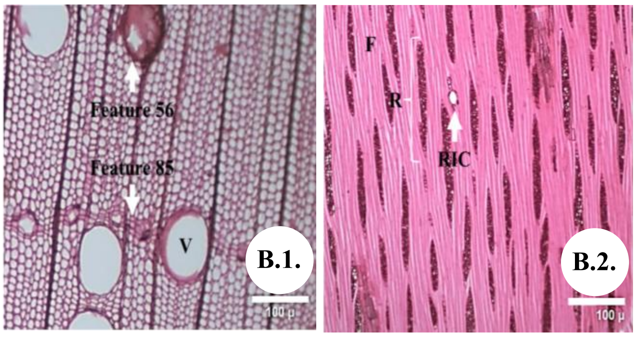

**Figure 6.** Optical microscope captures (4X10 magnification) showing tylosis (feature 56) and axial parenchyma bands more than three cells wide (feature 85) (B.1.), and Radial Intercellular Canal (RIC) (feature 130) (B.2.) in *Rubroshorea leprosula* from Tesso Nilo National Park population, in Sumatra, Indonesia. V: Vessel, R: Ray Parenchyma, F: Fiber

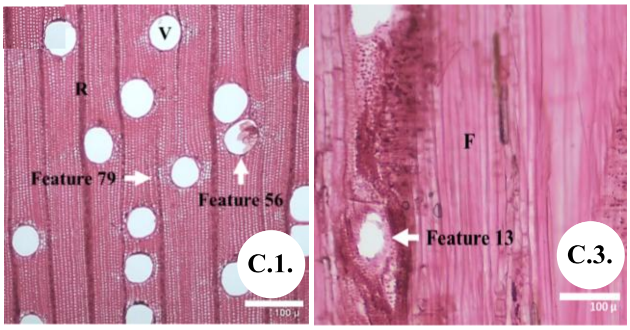

**Figure 7.** Optical microscope captures (4X10 magnification) showing tylosis (feature 56) and axial parenchyma vasicentric (feature 79) (C.1.), and captures (10x10 magnification) a simple perforation plate (feature 13) (C.3.) in *Rubroshorea leprosula* from Bukit Tigapuluh National Park population in Sumatra, Indonesia. V: Vessel, R: Ray Parenchyma, F: Fiber

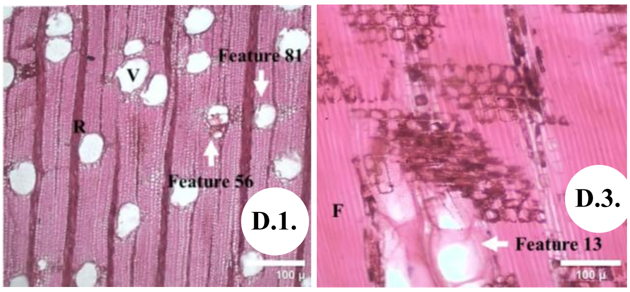

**Figure 8.** Optical microscope captures (4X10 magnification) showing tylosis (feature 56) and axial parenchyma lozenge-aliform (feature 81) (D.1.), and captures (10X10 magnification) a simple perforation plate (feature 13) (D.3.) in *Rubroshorea leprosula* from Hutan Harapan population in Sumatra, Indonesia. V: Vessel, R: Ray Parenchyma, F: Fiber

**Table 5.** Summary of mean tangential vessel diameters classification of *R. leprosula* from five natural populations in Sumatra, Indonesia, assessed based on Alfonso et al. (1989)

| **Populations** | **Range tangential diameter of the vessel** | **Mean tangential diameter of vessel** | **Classification of the tangential diameter of vessel** |
|---|---|---|---|
| Soraya Research Station | 93.51-125.26 µm | 111.88 µm | 100-200 µm |
| Tesso Nilo National Park | 105.85-199.32 µm | 133.33 µm | 100-200 µm |
| Bukit Tigapuluh National Park | 110.84-162.84 µm | 135.43 µm | 100-200 µm |
| Hutan Harapan | 85.00-113.00 µm | 95.09 µm | 50-100 µm |
| Bukit Barisan Selatan National Park | 98.39-127 µm | 112.79 µm | 100-200 µm |

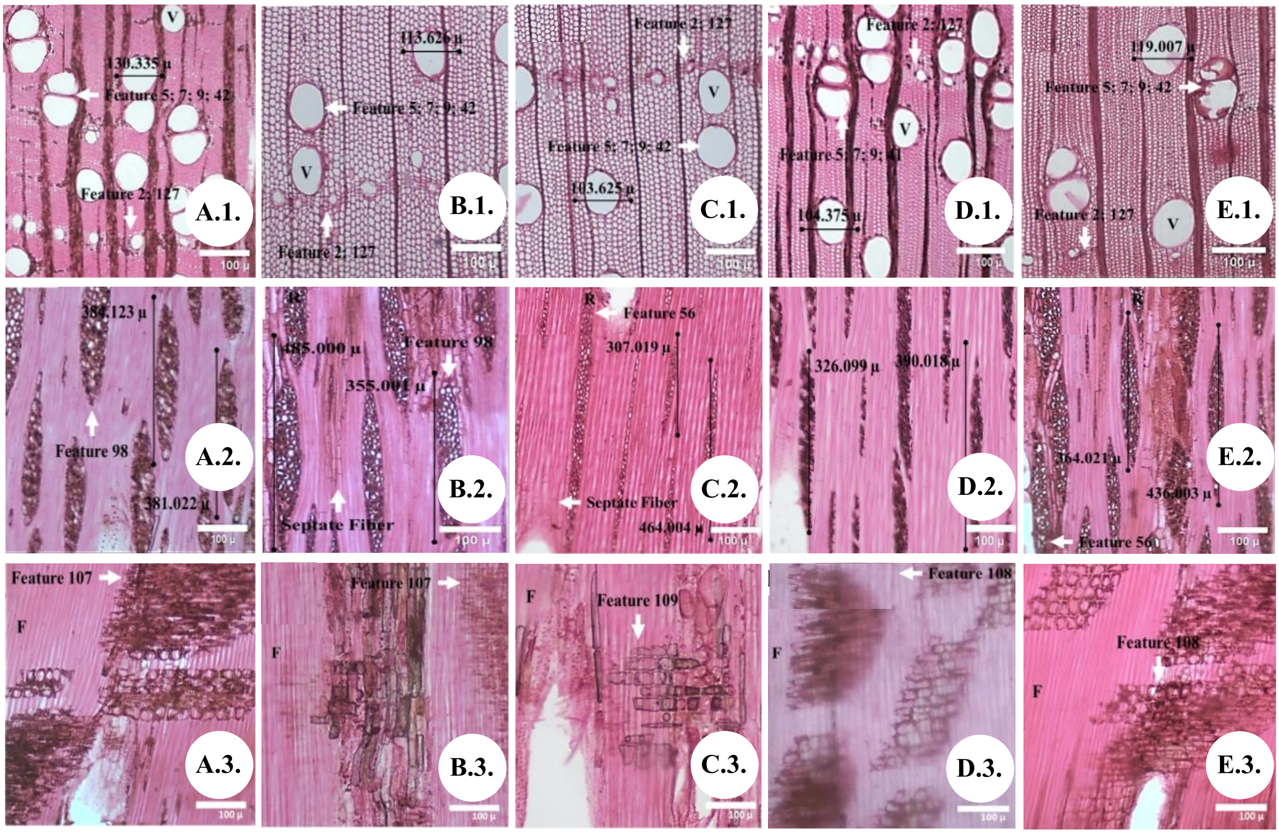

**Figure 9.** Optical microscope captures (4X10 and 10X10 magnification) of cross-sections (1), tangential (2), and radial (3) views of *R. leprosula* from Sumatra, Indonesia. A. Soraya Research Station, B. Tesso Nilo National Park, C. Bukit Tigapuluh National Park, D. Harapan Forest, and E. Bukit Barisan Selatan National Park. V: Vessel, R: Ray parenchyma, F: Fiber

The quantitative anatomical features of *R. leprosula* from Tesso Nilo National Park were generally consistent with findings reported in earlier studies. Praptoyo and Sudaryono (2012), Helmling et al. (2018), and Sulistyo et al. (2018) documented vessel diameters for *R. leprosula* ranged 139-421 µm. In contrast, all Sumatra populations examined in this study showed smaller vessel diameters than those reported by Ogata et al. (2008) which ranged 207 to 330 µm. In terms of fiber dimensions, including fiber diameter, lumen diameter, and fiber wall thicknesses, the values found in Sumatra populations were consistent with those reported in previous studies. The ray parenchyma height from the Bukit Tigapuluh National Park population was found to be relatively lower compared to the other populations.

The quantitative anatomical features of *R. leprosula*, namely vessel diameter and more precise quantitative descriptors such as mean, range, and standard deviation are a general applicability category for easy use when identifying unknown features and distinguishing difficult qualitative features. When compiling the database, the number of samples and the number of measurements performed per sample should be recorded. Different computer programs allow storing different amounts of information and use different algorithms to match quantitative features. This publication shows the variation of vessel diameter and its classification in each population based on Alfonso et al. (1989), as shown in Table 5.

As illustrated in Table 4, the *R. leprosula* population from Hutan Harapan exhibited the smallest mean vessel diameter among all observed populations. This finding aligns with the observations of Adi et al. (2020). Since vessel diameter directly influences wood texture, the relatively small vessel size in Hutan Harapan wood supports its classification as having a medium texture based on Alfonso et al. (1989) definitions. In terms of fiber anatomical features, all populations displayed fiber wall thicknesses greater than those reported by Joni et al. (2024), suggesting possible environmental or genetic influences affecting fiber development. These thicker walls may contribute to higher mechanical strength or resistance to degradation. Furthermore, the ray parenchyma height reached its maximum in this study at 980.82 µm. However, this value remains below the upper limit of 3,500 µm reported by Ogata et al. (2008). The overall variation in quantitative anatomical features is visualized in Figure 10, which presents boxplots of vessel diameter, fiber dimensions, and ray parenchyma height across all populations. This graphical representation complements the tabular data by illustrating interquartile ranges, medians, and outliers.

As shown in Table 6, the One-Way ANOVA test revealed a statistically significant difference in vessel diameter among the five *R. leprosula* populations (p-value = 0.00000545). To further explore these differences, Dunn's post hoc test was performed and presented in Table 7. The pairwise comparisons clearly indicate that Tesso Nilo National Park and Bukit Tigapuluh National Park had significantly larger vessel diameters compared to Hutan Harapan. These findings suggest that environmental conditions or genetic factors may play a crucial role in determining vessel diameter within *R. leprosula*. As summarized in Table 8, no significant differences were found for other measured features, including fiber diameter, fiber lumen diameter, fiber wall thickness, and ray parenchyma height (p-value>0.05 across all anatomical features). This consistency across populations implies a relatively stable anatomical structure for these features, regardless of site or environmental variation, and suggests that vessel diameter may be a more sensitive indicator of ecological or genetic divergence among populations.

## Discussion

Research on tropical hardwoods shows that trees in natural forests have different wood properties than those in plantations of the same species. Based on Table 1, our analysis across five natural populations revealed limited variations in visual characteristics. The reddish-brown heartwood color indicated potential genetic conservation or stabilizing selection on wood color traits. This finding aligns with Erwin et al. (2023), supports the hypothesis of genetic influence on wood color, and provides ecological signaling within the *Rubroshorea* group (Ogata et al. 2008). Chemical composition, organic extractives, and inorganic deposits are related to wood color formation, which were not assessed in the wood samples in this study. While extractives primarily affect wood color, the wood structure (i.e., cell wall mass related to wood density), defined by wood anatomy, can be considered. Dark-colored tropical wood ($L_{*} < 50$) showed high density and fiber proportion, indicating that wood structure may better explain color variation (Bessa et al. 2023). In this high-density tropical wood, fiber types ranged from thin to thick-walled, indicating significant anatomical diversity as classified by Alfonso et al. (1989). The ratio of fiber wall thickness to fiber diameter affects wood color; darker tropical woods usually have more thick-walled fibers. Due to its consistent influence across species, the effect of wood density on color is more pronounced in tropical species than in other anatomical and physical properties. In Bessa et al. (2023), *Diospyros* spp. are recognized for their black colored wood, which results from organic matter in the vessel during the heartwood formation. In *Quercus* spp., the ring-porous structure is linked to brown wood color. Vessel features may slightly affect wood color, but their ecological significance is key in tropical environments where vessel diameter is more relevant than fiber wall thickness in determining species distribution. The consistent wood density might explain the similar wood color across different locations. While it cannot be quantified, it can be illustrated by the pale red wood color found in Tesso Nilo National Park. This population has a mean fiber wall thickness of 3.79 µm, classified as very thin-walled, indicating a lower wood density. The wood color from Soraya Research Station (5.68 µm), Bukit Tigapuluh National Park (4.53 µm), Hutan Harapan (4.15 µm), and Bukit Barisan Selatan National Park (4.65 µm) is light reddish brown and thin to thick-walled fibers, indicating higher density. Physiological performance traits such as hydraulic conductivity, drought resistance, and mechanical strength are closely linked to microscopic anatomical features.

**Table 6.** Statistical analysis on the quantitative anatomical features of *Rubroshorea leprosula* from five natural populations on Sumatra Island, Indonesia, using One-Way ANOVA Test

| Variables | n | Chi-square test | df | p-value |
|---|---|---|---|---|
| Vessel diameter | 10 | 27.213 | 4 | 0.00000545* |
| Fiber diameter | 10 | 3.3741 | 4 | 0.473 |
| Lumen diameter | 10 | 2.5704 | 4 | 0.498 |
| Fiber wall thicknesses | 10 | 5.8503 | 4 | 0.195 |
| Ray parenchyma height | 10 | 6.6918 | 4 | 0.053 |

Note: *: Statistically significant at p-value < 0.05, n: Number of sample trees, df: Degree of freedom

**Table 7.** Pairwise multiple comparisons of vessel diameter of *Rubroshorea leprosula* from five natural populations in Sumatra, Indonesia, using the Bonferroni adjust method

| | A | B | C | D |
|---|---|---|---|---|
| **B** | 0.41427 | - | - | - |
| **C** | 0.02673 | 1.00000 | - | - |
| **D** | 0.00946** | 0.01632** | 0.00022** | - |
| **E** | 1.00000 | 0.49871 | 0.03699 | 0.00756** |

Note: Pairwise adjust method: Bonferroni, Chi-squared: 27.213; df: 4, **: Statistically significant at p-value < 0.025. A. Soraya Research Station, B. Tesso Nilo National Park, C. Bukit Tigapuluh National Park, D. Harapan Forest, and E. Bukit Barisan Selatan National Park

**Table 8.** Summary of quantitative anatomical characteristics of *R. leprosula* from five natural populations in Sumatra, Indonesia, including statistical analysis using the One-Way ANOVA and post-hoc tests with the Bonferroni pairwise adjustment method

| | **A** | **B** | **C** | **D** | **E** | **p-value (One-Way ANOVA)** | **p-value (Post-hoc)** |
|---|---|---|---|---|---|---|---|
| VD (X̄, SD) µm | 111.88±10.00 | 133.33±26.21 | 135.43±16.84 | 95.09±10.38 | 112.79±7.66 | 0.00001* | A ~ D (0.00946)**<br>B ~ D (0.01632)**<br>C ~ D (0.00022)**<br>E ~ D (0.00756)** |
| FD (X̄, SD) µm | 24.45±2.68 | 22.74±2.38 | 24.05±3.42 | 23.54±2.69 | 24.80±1.03 | 0.4973 | |
| LD (X̄, SD) µm | 13.10±2.36 | 15.17±2.56 | 14.98±3.53 | 15.23±3.18 | 15.50±3.78 | 0.6321 | |
| FWT (X̄, SD) µm | 5.68±1.19 | 3.79±1.42 | 4.53±1.51 | 4.15±2.11 | 4.65±2.03 | 0.2106 | |
| RH (X̄, SD) µm | 460.36±123.90 | 473.20±155.93 | 547.00±183.53 | 515.60±220.71 | 675.49±98.57 | 0.1531 | |

Note: *: Significance at p-value < 0.05, **: Significance at p-value < 0.025, X̄ : Mean, SD: Standard Deviation; VD: Vessel Diameter, FD: Fiber Diameter, LD: Lumen Diameter, FWT: Fiber Wall Thickness, RH: Ray parenchyma height. A. Soraya Research Station, B. Tesso Nilo National Park, C. Bukit Tigapuluh National Park, D. Harapan Forest, and E. Bukit Barisan Selatan National Park

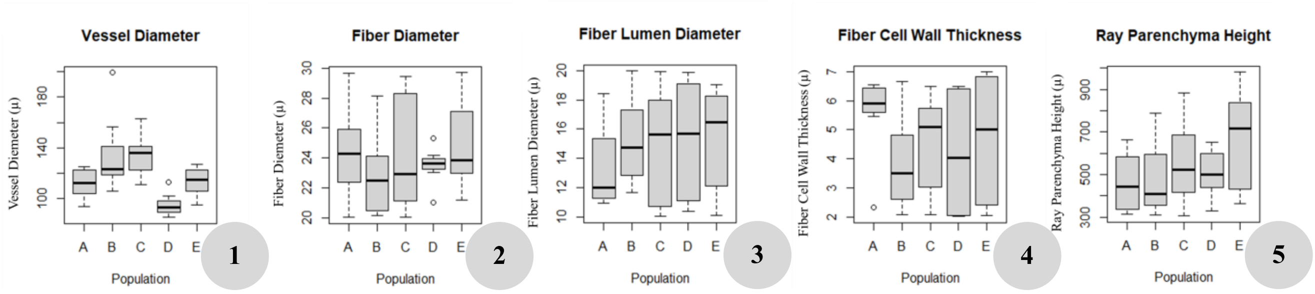

**Figure 10.** The boxplot illustrates of quantitative anatomical characteristics data of *R. leprosula*. 1. Diameter of vessel cells, 2. Diameter of fiber cells, 3. Diameter of fiber lumens, 4. Thickness of fiber walls, 5. Height of ray parenchyma cells in Sumatra, Indonesia. A. Soraya Research Station, B. Tesso Nilo National Park, C. Bukit Tigapuluh National Park, D. Harapan Forest, and E. Bukit Barisan Selatan National Park

Color variations in hardwoods may result from complex anatomical patterns and species-specific changes in brightness (Sahin et al. 2020). Adi et al. (2020) demonstrated that specific extractives influencing color in *Shorea* species are detectable within the NIR spectral region of 6,200-5,600 cm-1, underscoring the chemical basis of wood coloration. While Nelson et al. (1969) emphasized that environmental factors such as soil composition can also affect variations in heartwood color, as seen in studies on black walnut and Japanese walnut (Makoto et al. 2021). Soil properties can influence heartwood color characteristics through tree growth. The importance of these data for future research lies in their potential to predict which wood extracts influence the heartwood color of *R. leprosula* due to the uniformity of color across populations. Furthermore, the content of minor elements such as Fe, Mg, Cu, and others in the soil is a primary determinant that influences heartwood color variation. The wood species *R. leprosula* predominantly grew on reddish-brown latosol soils in Gunung Dahu Research Forest (GDRF) (Attarik et al. 2024). In the current study, *R. leprosula* grew naturally on yellow-red podzolic soil types (Andita and Kahfi 2019; Sari et al. 2019). However, the similarity of soil types across the study sites cannot fully explain the observed resemblance in wood color among all populations. Table 1 shows that stability in heartwood color may reflect an adaptive strategy to ensure consistent signaling for ecological interactions. This suggests that factors beyond general soil classification, such as specific variations in soil chemical composition, mineral content, or microenvironmental conditions, may influence wood color expression. A detailed analysis of soil composition is necessary to understand the interaction between soil conditions and wood color expression in dipterocarps.

To summarize and systematically analyze the macroscopic structure of *R. leprosula* wood, we present anatomical features in Table 2. This allows for limited variations, such as growth rings, porosity, vessel grouping, vessel arrangement, tylosis presence, ray parenchyma type, and ray parenchyma size, which are largely uniform across populations and unsuitable for further statistical analysis. Variations were observed in the presence of deposits, axial parenchyma type, and intercellular canals, which appear to form two distinct groups, although neither could be quantified. In the populations of Soraya Research Station, Tesso Nilo National Park, and Bukit Tigapuluh National Park, radial intercellular canals were visibly abundant in cross-sections. In contrast, in the Bukit Barisan Selatan National Park and Hutan Harapan populations, radial intercellular canals were rarely observed in cross-section.

Table 2 presents the results of macroscopic observations of wood structure regarding axial and radial intercellular canals based on populations of the wood species *R. leprosula* from natural forests. The width of the axial intercellular canals varied between samples within a single tangential row (6 to 8 cells). Axial intercellular canals in a concentric line were observed in this study, aligning with earlier descriptions by Sass et al. (1995) and supporting the notion of integrated defensive and transport systems in dipterocarps. Axial intercellular canals were frequently observed forming tangential bands alongside axial parenchyma, which can give a false impression of growth ring boundaries. Axial intercellular canals never form in outer annual rings that are three years old or older. This suggests that the numerous tangential lines of resin canals observed in trees do not form overnight, but may be the cumulative result of responses to various stimuli at varying intervals over many years. Radial intercellular canals are found within the ray parenchyma, forming a fusiform appearance based on macroscopic structural observations. These canals create a continuous network within the xylem and phloem. Radial intercellular canals are abundant secretory structures that extend across the wood grain in a radial direction. Cvetković et al. (2022) stated that radial intercellular canals were consistently present in all species of yellow meranti. Interestingly, radial intercellular canals are not universally present in the red meranti group. Abe and Fujii (2008) reported the occurrence of radial intercellular canals in the *Rubroshorea* group primarily in *Shorea leprosula*, *S. ovata*, and *S. teysmaniana*. Radial intercellular canals are a defining anatomical feature of *R. leprosula* (Tsumura et al. 2011). Their presence likely reflects an adaptive trait driven by localized biotic pressures. For instance, populations exhibiting frequent radial canals were found in areas potentially subject to higher herbivore or pathogen activity, such as Tesso Nilo National Park. The differentiation in radial canal abundance across populations could signal an early stage of ecological or even genetic divergence, possibly reflecting local adaptation mechanisms of *R. leprosula*.

Macroscopic structural variables (presence of deposits, type of axial parenchyma, presence of intercellular canals) recorded for 50 individual trees from five populations showed variation (see Table 2 for details). This study's absence of radial intercellular canals may be attributed to multiple factors. One possible explanation is the variation in land pressure caused by pathogens and pests. Ong et al. (2020) and Ng et al. (2023) reported biotic damage in tropical hardwoods from wood borers like *Euryphagus lundii* and *Glenea* sp., as well as sap-sucking insects like *Pedroniopsis* sp. These biological pressures may trigger the formation of radial intercellular canals as part of the tree's defensive response. *Rubroshorea leprosula* from the Dipterocarpaceae produces oleoresin through radial intercellular canals. The oleoresin in the radial intercellular canals of *R. leprosula* functions as an adaptive structure formed due to environmental stress. *Rubroshorea leprosula* experiencing higher pest pressure, mechanical damage, or drought invests more in defense traits through canal formation, resin production, or secondary metabolites. Therefore, the presence or absence of radial intercellular canals may vary depending on exposure to wounding agents in different populations. However, radial intercellular canal development variation cannot fully explain the functional differentiation. This supports the hypothesis proposed by Esteban et al. (2024), suggesting that traumatic intercellular canals may form in response to wounding or pest attacks. Traumatic intercellular canals also produce metabolic products that help repel pathogens and pests, seal wounds with a hydrophobic and mechanical barrier, and prevent infection (Martín and López 2023). Additionally, this study relied on increment core samples, which may have limited the detection of radial intercellular canals, as these features are often infrequent, unevenly distributed, and may occur in concentric formations resulting from stress, wounding, or disease conditions that increment core methods may not adequately capture (Zarnudin et al. 2015). As such, narrow cores might not capture them, even if they are in the tree. Further research, including complete cross-section sampling and assessment of local biotic stressors, is needed to confirm the relationship between environmental pressures and the development of radial intercellular canals in *R. leprosula*. The anatomical features of the radial intercellular canals are associated with the physical properties of the wood. According to Bosman (1996), the high percentage area occupied by vessels and intercellular canals in *R. leprosula* has been linked to a reduced proportion of fiber cells, lower wood density, and relatively low specific gravity. These features suggest that populations with developed intercellular canal systems may resist pests and diseases better, but consider the wood quality.

The qualitative microscopic structure of the *R. leprosula* wood sample trees from five natural populations in the study area is presented in Table 3, which was generally conserved across populations, and could not be further analyzed. However, the quantitative microscopic structure exhibited population variations (Figure 10). The mean values of the anatomical characteristics across all five Sumatra populations were: vessel diameter 117.70 µm, fiber diameter 23.92 µm, fiber lumen diameter 14.80 µm, fiber wall thickness 4.56 µm, and ray parenchyma height 534.33 µm (Table 4). Statistical analysis using the One-Way ANOVA test confirmed a significant difference in vessel diameter, reinforcing this trait's potential ecological and physiological implications. The five *R. leprosula* populations analyzed in this study differed in wood vessel diameter in the following order: Bukit Tigapuluh National Park > Tesso Nilo National Park > Bukit Barisan Selatan National Park > Soraya Research Station > Hutan Harapan (Table 4). The boxplot analysis also supported these significant variations (Figure 10). Significant anatomical variability among *R. leprosula* populations, particularly in vessel diameter, suggests potential adaptive responses to differing environmental conditions. The smaller mean vessel diameter observed in the Hutan Harapan population may reflect adaptive plasticity to environments with lower water availability or intermittent moisture supply. Narrower vessels reduce water transport efficiency and enhance resistance to embolism under drought stress (Hajek et al. 2016; Kotowska et al. 2021). Larger vessel diameters observed in Bukit Tigapuluh National Park populations suggest an ecological strategy suited to wetter habitats, where maximizing hydraulic conductivity is advantageous and the risk of embolism is lower. This indicates that individuals from the Bukit Tigapuluh population have greater water uptake potential but may also be more susceptible to embolism during drought.

A summary of the mean vessel diameter classification of *R. leprosula* from five natural populations in Sumatra is shown in Table 5. The mean vessel diameter observed in the Harapan Forest can be classified in the 50-100 µm range. This may reflect an adaptation to reduce the risk of embolism in dry environments. In *S. robusta*, vessels with diameters around 50 µm are reported to be large and are an adaptation to increase water conduction. Vessel diameter determines potential hydraulic conductivity (Baral et al. 2019). Larger vessels are associated with greater hydraulic efficiency and potentially support faster growth rates in mesic locations (Mercy et al. 2023), consistent with *Shorea* and *Hopea* observations showing similar vessel plasticity across rainfall gradients. These large vessels are considered an adaptive trait that enhances water conduction efficiency. King et al. (2005) noted that species with larger vessels and lower wood density tended to be more competitive in mixed dipterocarp forests with light interception. These wood anatomical features collectively influence growth performance under various environmental conditions. This anatomical variation reflects phenotypic plasticity in response to microecological pressures. However, while larger vessels increase water transport efficiency and support growth in humid conditions, their presence may also increase susceptibility to cavitation during drought stress. This trade-off between vessel size and susceptibility to cavitation reflects a fundamental ecological strategy within dipterocarp genera, many of which have adapted to seasonal tropical forest conditions, where soil water availability fluctuates throughout the year. Our findings on vessel diameter in *R. leprosula* from Soraya Research Station, Tesso Nilo National Park, Bukit Tigapuluh National Park, and Bukit Barisan Selatan National Park are consistent with reports by Ogata et al. (2008), Helmling et al. (2018), Sulistyo et al. (2018), and Adi et al. (2020), which indicates potential adaptation to high-humidity environments. Furthermore, vessel diameter is crucial in adapting hydraulic systems to different climates. Similarly, vessel diameter varied independently of climatic conditions in the area of origin for resistance to embolism. Still, it differed significantly between populations of origin, which may reflect differences or adaptation of local factors to the environment other than climate, such as soil texture and drainage. Therefore, *R. leprosula* may adapt to local climatic conditions by modifying the hydraulic properties primarily through adjustments in the diameter of vessels. Rana et al. (2009) demonstrated that wider vessels increase water conductance. These differences are particularly evident in natural forest stands, differing from previous studies comparing planted and natural populations (Praptoyo and Sudaryono 2012; Sulistyo et al. 2018). Populations with narrower vessels may be better suited for restoration in areas affected by drought or degradation. Populations with larger vessels could be prioritized for productive plantations in potentially humid zones. These findings demonstrate a genetically programmed response to environmental conditions. Recent genetic differentiation across populations due to the fragmented distribution of lowland dipterocarp forests in Sumatra and historical demographic events such as geographic isolation, genetic drift, and bottleneck or founding effects may contribute to wood structural variability. Understanding the relationship between wood anatomy and ecological function is crucial.

The statistical analysis on the quantitative anatomical features of *R. leprosula* using the One-Way ANOVA Test is listed in Table 6. Significant differences in vessel diameter across populations highlight potential local adaptation to distinct microenvironmental conditions in Sumatra. The variation in vessel diameter is illustrated using a box plot (Figure 10). Vessel diameter exhibited the most pronounced variation compared to other anatomical features and correlates with several biological and environmental factors. Larger vessels typically enhance water transport efficiency, suggesting trees in humid areas generally develop wider leaves. Conversely, trees in dry or cold environments tend to form narrower stems to reduce the risk of embolism (air bubbles that block water flow and disrupt the hydraulic system). The Hutan Harapan, with smaller vessel diameters, may have anatomical configurations that optimize resistance to embolism. This adaptation enhances survival in areas with slow water uptake or shallow soils, where air bubbles can disrupt water flow. In contrast, the Bukit Tigapuluh National Park population with larger vessels better adapts to moist environments. These observations align with broader ecological trends. Chambers-Ostler et al. (2023) found that the mean vessel diameter in tropical trees of the genus *Cedrela* increased with site wetness. The increase in vessel diameter aligns with findings by Sulistyo et al. (2018), who examined *R. leprosula* trees planted through silvicultural treatments that exhibited rapid tree growth performance and produced larger vessel diameters, reinforcing the link between vessel size and growth performance. Kotowska et al. (2021) demonstrated the positive correlation between vessel diameter and growth rate. Seasonal growth dynamics illustrate this pattern: rapidly growing trees, such as those in early growing seasons, form wide vessels to meet water and nutrient demands, while late-season growth tends to produce smaller, thick-walled vessels for structural support. Vessels function as the main pathways for water transport in angiosperms; their diameter directly affects water uptake rate, hydraulic efficiency, and vulnerability to cavitation in dry conditions (Pandey 2021; Mercy et al. 2023). These functional implications align with general ecological theory that tropical tree species adjust xylem traits such as vessel diameter in response to site water availability, elevation, and disturbance regime.

This study provides a comprehensive wood anatomical characterization of *R. leprosula* from five natural populations across Sumatra, highlighting consistent features and ecologically meaningful variation. Key diagnostic anatomical features included vessel diameter, fiber diameter, fiber lumen diameter, fiber wall thickness, and ray parenchyma height. Among these, vessel diameter emerged as the most ecologically informative, exhibiting statistically significant differences across populations and likely reflecting local adaptation to variation in water availability and drought stress. Significant differences in vessel diameter were observed, potentially influencing tree growth and hydraulic conductivity. In particular, smaller vessel diameters may have greater hydraulic capacity under drought-prone conditions, supporting the hypothesis of a xylem structure-function trade-off in dipterocarps. The smaller vessel diameters in the Hutan Harapan population may reflect adaptation to drier environmental conditions. Narrow vessels help reduce the risk of embolism (the interruption of water flow due to air bubbles) and allow for more efficient water transport under low ground pressure. Smaller vessels have a lower flow capacity, limiting water and nutrient transport. This can inhibit *R. leprosula* growth, especially when water is abundant. Small vessels have a lower flow rate, so they cannot distribute water and nutrients quickly to all parts of the plant. This condition causes reduced energy production, ultimately reducing plant growth. Despite the slower growth rate due to small vessels, the quality of the wood produced can be higher because small vessels are usually distributed more evenly and densely in the wood tissue, resulting in a smoother and denser wood structure. Consistent features and differences across populations suggest that genetic divergence may occur due to limited gene flow, geographic isolation, and habitat fragmentation. This study supports ongoing efforts to combat illegal logging by providing a scientific basis for timber tracking and accurate species identification, where diagnostic features such as vessel diameter offer reliable wood anatomical benchmarks for determining timber origin. Ultimately, this research enhances our understanding of the variation in wood anatomy of *R. leprosula* and highlights its importance not only for taxonomic classification, but also for informing adaptive forest restoration, provenance selection, and developing climate-resilient species conservation strategies. Future research should integrate genomic tools with comprehensive environmental monitoring, such as water availability, soil composition, and biotic interactions. This is essential for understanding how genetics and local adaptation influence wood anatomical variation and functional resilience in *R. leprosula*, other *Rubroshorea* and *Dipterocarpus* species.

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